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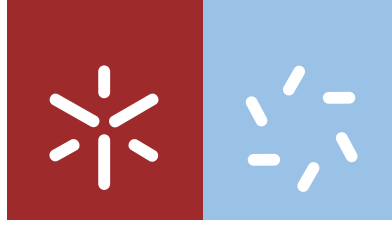
Study of seasonal changes in behaviour to understand the social functions of the animal personality

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Dissertação de Mestrado
Mestrado em Ecologia

Trabalho realizado sob orientação do
Doutor Gonçalo Canelas Cardoso
e da
Professora Doutora Fernanda Maria Fraga Mimoso Gouveia Cássio

outubro de 2018

DECLARAÇÃO

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Study of seasonal changes in behaviour to understand the social functions of the animal personality

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É AUTORIZADA A REPRODUÇÃO INTEGRAL DESTA TESE/TRABALHO APENAS PARA EFEITOS DE INVESTIGAÇÃO, MEDIANTE DECLARAÇÃO ESCRITA DO INTERESSADO, QUE A TAL SE COMPROMETE.

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Assinatura: _____

Se às vezes digo que as flores sorriem
E se eu disser que os rios cantam,
Não é porque eu julgue que há sorrisos nas flores
E cantos no correr dos rios…
É porque assim faço mais sentir aos homens falsos
A existência verdadeiramente real das flores e dos rios.
Porque escrevo para eles me lerem sacrifico-me às vezes
À sua estupidez de sentidos…
Não concordo comigo mas absolvo-me,
Porque só sou essa cousa séria, um intérprete da Natureza,
Porque há homens que não percebem a sua linguagem,
Por ela não ser linguagem nenhuma.

Alberto Caeiro, in "O Guardador de Rebanhos - Poema XXXI"

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ABSTRACT

Study of seasonal changes in behaviour to understand the social functions of the animal personality

Animals can plastically change behaviour according to the environment while maintaining differences in personality (i.e., consistent behavioural differences between individuals). An important environmental change for animal behaviour is seasonality, including the transition from the non-breeding to the breeding season. There is little research on whether differences in animal personality change between seasons, yet this can give important cues on the functions of animal personality. If differences in personality are important for breeding, I expect that those differences accentuate in the breeding season. Otherwise, I expect that personality differences remain identical or attenuate during breeding.

I used the common waxbill (*Estrilda astrild*) to study how behavioural differences are affected by seasonality. I used two behavioural assays: a mirror test, to assess response to a social stimulus, and a tonic immobility test, to evaluate fear. The mirror test was shown before to reflect personality type in this species, while the tonic immobility test is not related to the waxbill reactive-proactive personality axis. I found that, from one Autumn to the next, behavioural differences among individuals remained stable and mean behaviour and behavioural variation of the population did not change in either of the two behavioural assays. Thus, behaviour did not change appreciably after one year, in the same season.

From Autumn to Spring, behavioural differences also remained stable in both behavioural tests, although in the mirror test the population shifted to more proactive behaviour. Importantly, in the mirror test, behavioural differences among individuals were accentuated in the breeding season. This accentuation of individual differences was unique to the personality assay (mirror test), since differences in tonic immobility were attenuated instead. Additionally, in the mirror test, the behavioural type of individuals predicted their behavioural changes from Autumn to Spring, with proactive individuals becoming more proactive. These results confirm that common waxbills have stable personality differences, and the accentuation of those differences in Spring suggests a function of personality in the context of breeding.

Keywords: animal personality, seasonal changes, personality differences, breeding, *Estrilda astrild*

RESUMO

Estudo das alterações sazonais no comportamento para entender as funções sociais da personalidade animal

Os animais podem alterar o seu comportamento de acordo com o ambiente, mantendo as suas diferenças de personalidade (isto é, diferenças consistentes de comportamento entre indivíduos). Uma importante alteração ambiental que afeta o comportamento animal é a sazonalidade, a qual inclui a transição da época não reprodutora para a reprodutora. São poucos os estudos sobre a alteração das diferenças na personalidade entre épocas, no entanto estas podem fornecer pistas importantes sobre as funções da personalidade animal. Se as diferenças de personalidade forem importantes na reprodução, espero que essas diferenças se acentuem na época reprodutora. Ou, no caso contrário, espero que as diferenças de personalidade se mantenham idênticas ou atenuem durante a reprodução.

Usei o bico-de-lacre (*Estrilda astrild*) para estudar diferenças comportamentais nas épocas reprodutora e não reprodutora, recorrendo a dois testes comportamentais: o teste do espelho, para avaliar resposta a estímulos sociais, e o teste de imobilidade tónica, para avaliar medo. Já foi mostrado que, nesta ave, o teste do espelho reflete o eixo de personalidade reativo-proativo, enquanto que o teste de imobilidade tónica não. De um Outono para o outro, encontrei diferenças estáveis entre os indivíduos, e o comportamento médio da população e sua variação mantiveram-se inalterados em ambos os testes. Assim, não há alteração significativa do comportamento após um ano, na mesma época.

Do Outono para a Primavera, as diferenças entre os indivíduos também se mantiveram consistentes em ambos os testes. Mas no teste do espelho a população tornou-se mais proativa e, mais importante, as diferenças entre os indivíduos acentuaram-se na época reprodutora. Esta acentuação foi única do teste do espelho, porque, em vez de aumentar, as diferenças comportamentais na imobilidade tónica atenuaram. Ainda, no teste do espelho, o tipo de personalidade dos indivíduos previu as suas alterações comportamentais do Outono para a Primavera, com os indivíduos proativos tornarem-se mais proactivos. Estes resultados confirmam diferenças de personalidade no bico-de-lacre e a acentuação destas diferenças na Primavera sugere funções de personalidade no contexto reprodutor.

Palavras-chave: personalidade animal, alterações sazonais, diferenças de personalidade, reprodução, *Estrilda astrild*

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LIST OF ABREVIATIONS

ICC – INTRA-CLASS CORRELATION

PC1 – FIRST PRINCIPAL COMPONENT

PCA – PRINCIPAL COMPONENT ANALYSIS

RFID – RADIO-FREQUENCY IDENTIFICATION

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1 | INTRODUCTION

Behavioural ecology emerged by incorporating several fields, such as ethology, evolutionary biology, game theory and economic decision-making. In behavioural ecology, the term "personality" refers to individual differences in one or more behaviours that are consistent (i.e., repeatable) across different contexts or situations, and across time (Dall et al., 2004; Sih et al., 2004b; Réale et al., 2007). Differences of these individually-repeatable behaviours may be correlated with each other, constituting a 'behavioural syndrome' (Sih et al., 2004b). A behavioural syndrome refers to the pattern of correlations between these repeatable behavioural differences of individuals within a species or population. When referring to the particular arrangement of behaviours expressed by a certain individual, then one uses the expression "behavioural type" of that individual (Bell, 2007). Individual repeatability of behaviour refers to the proportion of variation in behaviour across a population that is attributed to differences between individuals, as opposed to variation within-individuals. A behaviour is considered highly repeatable when the same individual is measured multiple times, and its behavioural differences are small (low within-individual variation) compared to the differences among different individuals (high between-individual variation; Wuerz & Krüger, 2015).

The study of animal personality has been growing remarkably in the last two decades (von Merten et al., 2017), seeking to understand how and why individuals differ consistently in their behaviour, and the ecological and evolutionary implications of those differences (Beckmann & Biro, 2013; Dall & Griffith, 2014). Work on animal personality has allowed the assessment of the role of hormones, physiology and metabolism in an individual's behaviour (Réale et al., 2010a), and led to improvements in the tools to assess among-individual variation and repeatability of behavioural traits (Dingemanse et al., 2010a; Mathot et al., 2012; Roche et al., 2016).

Depending on the species, animal personality has often been described using some of five broad traits, which may be correlated among themselves: (1) *shyness-boldness*, an individual's reaction to any risky situation, such as predators and humans; (2) *exploration-avoidance*, an individual's reaction to a new situation, such as new habitat, new food or novel objects; (3) *activity,* the general level of activity of an individual, such as locomotion and space use; (4) *aggressiveness*, an individual's agonistic reaction towards conspecifics; (5) *sociability*, an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour) (Réale et al., 2007; McEvoy et al., 2015).

Although personality traits may consistently differ between individuals, and give rise to diverse personality types, frequently personality types can be organized along one main axis: from proactive/risk-taking individuals at one extreme to reactive/cautious individuals at the other (Gracceva et al., 2014). This reactive-proactive axis is a common behavioural axis across many animal species (e.g., Koolhaas et al., 1999; Réale et al., 2010b; Favati et al., 2014; Hall et al., 2015). Proactive individuals are often both more aggressive and bolder, less neophobic, explore their environment or novel environments faster and readily create persistent routines, while, at the other extreme of the continuum, reactive individuals are the opposite (Sih et al., 2004a; Groothuis & Carere, 2005; Aplin et al., 2014).

As part of reactive-proactive behavioural syndromes, several studies showed that exploratory behaviour, one of the most studied traits in animal personality, is often related to boldness, activity and aggression (Aplin et al., 2014) in many different species (e.g., great tits, *Parus major*: Dingemanse et al., 2002; European starlings, *Sturnus vulgaris*: Minderman et al., 2009; zebra finches, *Taeniopygia gutatta*: Schuett & Dall, 2009; house sparrows, *Passer domesticus*: Mutzel et al., 2011; fairy-wrens, *Malurus cyaneus*: Hall et al., 2015). For example, slow-exploring great tits that respond to changes in their environment in a more versatile way (Both et al., 2005), are relatively unaggressive and respond fearfully to novel objects (Verbeek et al., 1994). While proactive individuals engage in more risk-prone behaviour with potentially high rewards, reactive individuals prioritize risk-averse behaviour that enhances survival in detriment of high productivity (e.g., great tits: Aplin et al., 2014), indicating that the reactive-proactive axis may reflect a trade-off between risk-aversion and productivity (Wolf et al., 2007).

1.1 | ECOLOGICAL SIGNIFICANCE OF ANIMAL PERSONALITY

Variation in personality traits can affect the way individuals interact with their environment, whether predators, food sources, habitat, or in social or sexual interactions with conspecifics (Réale et al., 2007). Animal personality can, therefore, influence a range of essential ecological and evolutionary processes (Sih et al., 2012; Wolf & Weissing, 2012), such as species distributions (e.g., Duckworth, 2006), species responses to environmental changes (e.g., Schindler et al., 2010) and speciation rates (e.g., Sih et al., 2004a). Also, personality can influence population dynamics and selection through its effects on interspecific interactions (e.g., Moya-Laraño, 2011; Belgrad & Griffen, 2016), dispersal (e.g., Cote et al., 2010a), parental care (e.g., Both et al., 2005; Sinn et al., 2008), exploration strategies (e.g., Arvidsson et al., 2017), disease spread (e.g., Krause et al., 2010) and even offspring phenotype (e.g., Boon et al., 2007). There are a few ecological factors that have been correlated with certain personality

traits namely resource availability (e.g., Dingemanse et al., 2004), habitat quality (e.g., Belgrad et al., 2017), habitat stability (Carvalho et al., 2013), social context (e.g., Nicolaus et al., 2016), temperature (e.g., Biro et al., 2010) and predation (e.g., Bell & Sih, 2007).

Animal personality can also contribute to consistent individual differences in life-history traits such as productivity (e.g., Sih et al., 2012; Aplin et al., 2014), reproductive success (e.g., Dingemanse et al., 2004), growth (e.g., Boon et al., 2007), fecundity and survival (e.g., Smith & Blumstein, 2008; Réale et al., 2010b). Different personality traits can also influence various aspects of fitness (e.g., Both et al., 2005; Dingemanse & Réale, 2005; Smith & Blumstein, 2008). For example, in great tits, variation in exploratory behaviour affects both adult survival and reproductive success (Dingemanse et al., 2004) or, in yellow-bellied marmot (*Marmota flaviventris*), reproductive success is affected by variation in aggressive behaviour (Armitage & Van Vuren, 2003). Several other studies found that proactive individuals have higher fitness compared to reactive ones, at least in some ecological circumstances. For example, in years with high resource availability, fast-exploring territorial males of great tits may favour from their aggressive behaviour, competing successfully with non-territorial males for territorial space (Dingemanse et al., 2004), and more aggressive males of western bluebirds (*Sialia mexicana*) have an advantage over less aggressive males in colonizing new habitat patches and competition for territories (Duckworth & Badyaev, 2007; Duckworth, 2008). However, in situations such as high population density, with consequent facilitation of kin interactions, non-aggressive western bluebirds' males may be allowed to acquire territories, favouring a higher fitness (Duckworth, 2008). A similar study showed that slow-exploring and non-aggressive great tits performed relatively better in a population with high levels of density (Nicolaus et al., 2016).

Frequency-dependent selection also contributes to the maintenance of high levels of personality variation in the population (Sloan Wilson et al., 1994) and, therefore, of several behavioural tactics (Wolf & McNamara, 2012). In this type of selection, the relative fitness of a genotype depends on the relative frequencies of other genotypes in the population, where rare types could be favoured (Gromko, 1977). In social species, it is possible that the fitness of a given behaviour depends negatively on its frequency (e.g., Lichtenstein & Pruitt, 2015), giving rise to a stable coexistence of different behavioural types (Dall et al., 2004). For example, in three species of a social spider (*Anelosimus*), both docile and aggressive individuals enjoy their greatest reproductive success when the aggressive phenotype is rare within the colony and the success of the rare-type decreases when their frequency increases (Lichtenstein & Pruitt, 2015).

Individual variation in personality traits can also influence species invasions and may contribute to their success (Chapple et al., 2012). Previous studies suggested that personality-dependent dispersal plays an important role in invasions (Cote et al., 2010b), where the personality type of the disperser may improve its colonization success (Cote & Clobert, 2007; Duckworth & Badyaev, 2007; Duckworth & Kruuk, 2009). Individuals with high dispersal rates are often the ones who are bolder, more exploratory and more aggressive compared to less dispersive individuals (Fraser et al., 2001; Dingemanse et al., 2003; Cote & Clobert, 2007; Duckworth & Badyaev, 2007; Pintor et al., 2008; Duckworth & Kruuk, 2009; Cote et al., 2010b). Social behaviour may also influence dispersion (Cote & Clobert, 2007; Blumstein et al., 2009) and, consequently, be an important behavioural mechanism in invasion processes (Cote et al., 2010b). Sociability may also be related to high chances of acquiring and transmitting parasites and diseases (Barber & Dingemanse, 2010). Studies suggest that, at high population density, less social individuals disperse more to colonize empty patches (Cote et al., 2010b), and are the ones most common at the invasion front (Chapple et al., 2012).

1.2 | PLASTICITY IN ANIMAL PERSONALITY

It is not only personality types that can be important for fitness and be under selection, but also whether and how those personality types express some behavioural plasticity in response to environmental change (Dall et al., 2012). Although consistent differences in behaviour between individuals are often observed, animals can also adjust behaviour with age (Réale et al., 2007) and plastically adapt behaviour to different ecological situations and/or contexts (Coppens et al., 2010; Dingemanse & Wolf, 2010; Stamps & Groothuis, 2010). For example, in a context of predation, individuals may alter their levels of activity and refuge use in the presence of different predators (e.g., mud crabs, *Panopeus herbstii*: Hughes et al., 2014). Behavioural plasticity is not contrary to the existence of personality, as long as behavioural differences among individuals do not disappear. For example, all individuals may adjust their levels of aggression in a context-dependent way, but the differences in aggressiveness among those individuals remain consistent (Dall et al., 2004; Sih et al., 2004a). When individuals behave according to their personality type and show limited plasticity, this may prevent them from behaving optimally according to the environmental circumstances; in those cases, the individuals' behavioural type might restrict their range of behavioural possibilities, leading to possible deviations from the 'optimal' behaviour (Sih et al., 2003; Bell, 2007).

When plastic phenotypic traits change over an environmental gradient, or across different ecological or social contexts, this can be studied using the concept of reaction norms (e.g., Dingemanse et al., 2010b; Kluen & Brommer, 2013). Behavioural reaction norms describe the direction and magnitude of changes in behavioural phenotype produced by individuals with the same genotype experiencing different environmental or social conditions (Nussey et al., 2007; Dingemanse et al., 2010a; Kluen & Brommer, 2013). Examples of behavioural reaction norms can be the relationship between exploration and predation risk (Dingemanse et al., 2007), between boldness and temperature (Biro et al., 2010), or between aggressiveness and female breeding stage (Araya-Ajoy & Dingemanse, 2014).

Behavioural reaction norms provide information about the average behaviour of an individual and how it changes with environmental context, specifying the relationship between the response value and the environmental context (Dingemanse et al., 2010b). Studying behavioural reaction norms with repeated measures in individuals has shown how repeatability may be context-specific (Kluen & Brommer, 2013). If all individuals show a similar response to the environmental context, there is no variation in the reaction norm slopes across individuals, and so the ranking of individual response values will be maintained across contexts, and the behaviour will be repeatable both within and between contexts. On the other hand, if individuals respond differently to the environmental context (i.e., there is variation in behavioural plasticity), then the reaction norm slopes and the ranking of individual response values will both vary between the contexts, and the repeatability of the behaviour will be context-dependent (Kluen & Brommer, 2013).

One type of environmental changes particularly crucial for animal behaviour is seasonality. Seasonality occurs in several habitats that vary substantially, for example, from Autumn to Spring (Walton et al., 2011). In temperate habitats, Spring marks the transition from the ecologically severe conditions of Winter, with low temperature, typically fewer food resources (Gracceva et al., 2014), and no breeding in most animals (Eccard et al., 2011), to better ecological conditions where breeding peaks in most species. Animals living in seasonal habitats need to adapt their physiology and personality (Walton et al., 2011) to cope with this seasonal environmental fluctuations, with recurrent fluctuations in photoperiod, food abundance and temperature (Scherbarth & Steinlechner, 2010; Eccard et al., 2011), favouring the investment in reproduction at one time of the year and the investment in survival at other time of the year (Weil et al., 2015). For instance, studies showed that reproductive behaviours, as well as hormonal and physiological changes, are induced by photoperiod (e.g., Leboucher et al., 2012), and personality traits can vary with these changes (e.g., Koolhaas et al., 1999, 2010). Photoperiod – annual cycle of day lengths – appears to be the environmental signal that in many species triggers changes in gene

expression to produce the suite of season-specific physiological and behavioural adaptations (Walton et al., 2011).

Understanding how personality differences among individuals are affected by the changes between non-breeding and breeding seasons, especially in social species, could be instrumental to understand the role of personality differences and why personality has evolved. Gregarious species might be shaped by sexual selection under certain conditions (Oh & Badyaev, 2010) and social behaviour may influence behavioural strategies (e.g., Schuett & Dall, 2009; Aplin et al., 2014). If personality differences increase in the breeding season, these differences could be more useful during sexual interactions, having evolved to respond to social challenges associated with reproduction. On the other hand, if personality differences decrease in the breeding season, these differences may be more useful in non-sexual interactions, and those reproductive challenges select individuals to behave more similarly to each other (Kluen & Brommer, 2013), indicating mostly non-reproductive social functions for personality differences. Particularly in social species, seasonal changes when entering the breeding season may involve different social challenges, such as finding and competing for mates. Therefore, I hypothesized that social species may adjust their differences in personality in the breeding season, perhaps accentuating or decreasing those differences among individuals.

Despite the importance of seasonality for animal behaviour, there is yet little understanding about how personality differences among individuals are affected across seasons (Brommer, 2013; Kluen & Brommer, 2013; Belgrad et al., 2017; Thys et al., 2017). Various studies showed behavioural changes across seasons, for example in ground squirrels (*Citellus undulates*, Spring to Summer and Summer to Autumn: Semenova et al., 2001), common voles (*Microtus arvalis*, Winter to Summer seasons: Gracceva et al., 2014) and mud crabs (early to late spawning seasons: Belgrad et al., 2017). However, little is known about how personality differences among individuals are affected by those seasonal changes, as only very few empirical studies addressed this topic (e.g., Haage et al., 2013; Kluen & Brommer, 2013; Amy et al., 2017; Thys et al., 2017).

1.3 | STUDY SYSTEM AND OBJECTIVES

Here, to assess whether behavioural differences among individuals change between the breeding and the non-breeding season, I worked with a highly gregarious and social bird, the common waxbill (*Estrilda astrild*). The common waxbill is a small and highly gregarious finch in the Estrildidae family, native from Sub-Saharan Africa (Stiels et al., 2011). This species forages communally, establishes large

mist flocks year-round and behaves socially both in reproductive and non-reproductive seasons (Clement et al., 1993). This bird is granivorous and forages in low vegetation, favouring open and grassy habitats, usually in the proximity of water (Clement et al., 1993; Payne, 2010; Batalha et al., 2013), such as agricultural landscapes (Reino, 2005; Sullivan et al., 2012). In Iberia, where this species is invasive, waxbills use a distinct ecological niche from those of native passerines (Batalha et al., 2013). Common waxbills, both males and females, are incredibly ornamented, with a red breast plumage, a red stripe through the eyes made up of a plumage mask and a bright red bill that gives the species its common name (waxbill, in reference to red sealing wax; Clement et al., 1993; Cardoso & Reino, 2018; Figure 1). Male ornamentation is often a sexual signal, since in species with conventional sex roles males often use it to attract mates, and, accordingly, in the waxbill males are on average more ornamented than females (Cardoso et al., 2014b, 2014a). But female waxbills are also highly ornamented, and this mutual ornamentation affects both preferences for individuals of the opposite sex but also non-sexual social preferences among individuals of the same sex (Cardoso et al., 2014b). Thus, colour ornamentation in waxbills could be involved in diverse social functions, for example, cooperation, group protection from predation, thermoregulation at night and social competition for non-reproductive resources (Tobias et al., 2012; Cardoso et al., 2014b).

Personality studies in waxbills showed that exploratory behaviour and sociability differ in a correlated manner, where more explorative individuals are less attentive to a social stimulus while less exploratory individuals pay more attention to the same social stimulus (Carvalho et al., 2013). A sociability test (response to a mirror image) is one of the most repeatable behavioural assays in this species, with behavioural differences between individuals persisting through time, even when tested several weeks or some months apart (Carvalho et al., 2013; Funghi et al., 2015). Thus, exploration and sociability are considered to be part of a stable personality axis, related to the reactive-proactive axis, where reactive individuals are the ones more attentive to social stimuli, and the proactive individuals are the ones that are more active and explore more autonomously (Cardoso & Reino, 2018). Other studies found similar personality differences in the closely related (i.e., in the same family) zebra finch (Rosa et al., 2012; McCowan et al., 2015).

These personality traits in the common waxbill correlate with ecological differences among habitats across their distribution range in Portugal, suggesting that personality differences have adaptive significance (Carvalho et al., 2013), but the actual functions of these personality differences remain to be investigated. Also, these personality differences are not related to dominance hierarchies within waxbill social groups (Funghi et al., 2015). The hypotheses that I will explore here are whether personality differences are involved in breeding, in which case I expect an accentuation of personality differences in Spring, or whether personality differences are involved mostly in non-reproductive social interactions, in which case I expect an attenuation of personality differences in Spring. I tested within-individual repeatability in behaviour across two Autumns and one Spring and assessed if the mean behaviour changed within and between seasons. I expect that, since previous work described consistent personality differences among individuals, repeatability of behaviour will be high in the same context (in consecutive non-breeding seasons; i.e., Autumns in consecutive years). When considering different contexts, such as breeding and non-breeding seasons, personality differences could increase, which would indicate that personality differences are particularly relevant for breeding, decrease, which would suggest that personality differences are more relevant for non-breeding social interactions, or remain similar.

Figure 1. A common waxbill (*Estrilda astrild*) showing the red colour ornamentation in the plumage and bill.

2 | METHODS

2.1 | BIRD CAPTURES (AUTUMNS 2016 AND 2017) AND HOUSING

I worked with 15 males and 15 females' common waxbills captured during October 2016 with mist nests in agricultural fields near Póvoa de Varzim, and other 15 males and 15 females captured during September 2017, in agricultural fields near Apúlia, Portugal. Both capture periods were in Autumn, outside the peak breeding season. Each bird was marked with a numbered aluminium ring in the right leg and was weighted in the field. All of the captured individuals had a red bill, indicating that none were juvenile, and all females with a brood patch or forming an egg (noticeable by inspecting the abdomen) were released.

Captures took place during mornings, and birds were then transported in a large cage (36.5 cm x 21.5 cm x 35.5 cm) with perches, food and water to the aviary at CIBIO/InBio, Campus de Vairão, Vila do Conde (ca. 30 minutes' drive from the capture location). There, birds were housed in 6 cages, 5 individuals per cage (88.5 cm x 30 cm x 40 cm). Cages were open (with bars) along one of the long sides, had 4 perches, and were placed in an open aviary room exposed to natural weather and illumination, but sheltered from rain and direct sun. Natural light was complemented with full spectrum lamps in the ceiling with a photoperiod similar to natural light-dark cycle (lights on 30 minutes before sunrise, and off 30 minutes after sunset). Birds had *ad libitum* access to seeds (Versele-Laga Prestige Tropical Finches) in two long feeders (23 cm x 5.5 cm x 7.5 cm), long enough for all birds in the cage to feed simultaneously, access to water (2 water drinkers), mixed grit with crushed oyster shell (sand) and millet spikes. Except on weekends, I daily changed fresh water and removed seed husks, I provided bath water at least every second day and provided vitamins (Avigold Advance, Aviform) in the water drinkers twice per week. Cage boards were cleaned and perches were replaced once per week.

During the first days in captivity, I checked if the birds behaved normally and were able to eat the seeds. After all birds were captured, the final 6 bird groups were balanced between males and females (3 cages with 3 males and 2 females, and 3 cages with 2 males and 3 females). All birds adapted well to the cage, feeders, and water drinkers before beginning the behavioural tests. Behavioural tests took place between 26th October and 7th December 2016, and 2nd October and 22nd November 2017. Afterwards, on the 14th December 2016 and the 23rd November 2017, the birds were released

in an outside enclosure with semi-natural conditions, wearing a small passive Radio-Frequency Identification (RFID) tag on a leg ring. Birds from 2016 were recaptured from the outside enclosure for behavioural re-testing in Autumn 2017 (from the 17th October to the 16th November 2017), and birds from both years were recaptured for re-testing again in Spring 2018 (from the 2nd May to the 1st June 2018).

In the large outside enclosure (ca. 235 m^2; Figure 2A), birds lived in semi-natural conditions: abundant vegetation, netted ceiling, large feeders hanged from a wall, and several perches near the feeding area. The outside enclosure was connected to an inside dormitory room (ca. 4 m^2; Figure 2B) via a small open window (18 x 10 cm), which the birds used to sleep and shelter from the cold. This small room (dormitory) had vegetation, a small heater to make night temperature milder, and full spectrum lamps in the ceiling with a photoperiod matching the natural light-dark cycle (lights on 30 minutes before sunrise, and off 30 minutes after sunset).

2.2 | BIRDS RECAPTURES (AUTUMN 2017 AND SPRING 2018)

I built a trap using a birdcage (36.5 cm x 21.5 cm x 31 cm) with one feeder inside, and an electronic system based on a programmable Arduino 1.8.4 board, an RFID antenna and a small motor that drops a curtain over the cage entrance (Figure 3). I programmed the trap for a selective recapture of birds in the outside enclosure and, at the end of each capture day, I reprogrammed the trap not to repeat previous captures. For birds to habituate to the trap, it was left untriggered for a period within 2 and 4 weeks immediately before the recaptures in the outside enclosure, with feeders and perches inside and/or outside the cage. I started the recaptures when most of the birds began to use the recapture cage regularly.

Figure 2. Aviary facilities where birds were housed. **(A)** Large outside enclosure with semi-natural conditions: abundant vegetation, netted ceiling, natural light. **(B)** Inside dormitory room connected with the outside enclosure by a small open window.

Figure 3. Recapture trap system. **(A)** Electronic system. **(B)** Inside view of the birdcage used for the recaptures. **(C)** Outside view of the birdcage used for the recaptures.

Recaptures were carried out, daily whenever possible, from 17th October to 16th November 2017 (Autumn recaptures) and from 2nd May to 1st June (Spring recaptures). The Spring recaptures occurred during the time of the year corresponding to the peak of breeding for common waxbill in Iberia (Sanz-Aguilar et al., 2015). I hanged the birdcage either on the wall next to the large feeders, on the floor under the feeders, or in an area that the birds used often in the middle of the aviary, near a wall. During the recaptures period, access to the large feeders was blocked (from 09.30 a.m. to 04.00 p.m.), encouraging the birds to feed in the trapped birdcage. One week after the Spring recaptures started, capture rates with the birdcage diminished, and I began to recapture the birds inside the dormitory room, where I provided food to attract them. Whenever a small group of birds entered the room, I closed the dormitory window with a piece of sponge, turned off the lights to calm the birds, and captured some of them with a net. I installed a small camera (Xiaomi Yi Action Camera) transmitting real-time images from the trap cage or dormitory window so that I could remove the birds as soon as they were trapped. When the small camera battery ran out, the monitoring was made *in loco*. For each trapped bird, I checked whether it had already been tested, or if it was a female with eggs, and in any of those cases I released it. If not, I put the bird in an paper bag and transported it to the test room, where the personality tests were performed, with a maximum waiting time of 20 minutes. After each test, the birds were again released in the outside enclosure through the dormitory window.

2.3 | BEHAVIOURAL ASSAYS

Behavioural tests were first performed during the time that birds were in birdcages after capturing from the wild, 30 birds in 2016 and 30 in 2017, and repeated in two rounds separated by ca. 6 and 7 weeks, respectively. Tests took place between 09.30 a.m. and 01.00 p.m., a period of high activity in birds (Palmgren, 1949). Behavioural tests were also performed to the recaptured birds from

the outside enclosure, 23 in the Autumn of 2017 and 35 in the Spring of 2018, and those took place between 10.00 a.m. and 04.00 p.m. to allow enough time for the recaptures. All tests were video recorded and behaviours quantified from the videos.

I performed two different behavioural assays: mirror test to assess response to a social stimulus (mirror image), and tonic immobility test to evaluate fear towards a potential predator (a human).

2.3.1 │ Mirror Test

The mirror test is a well-established behavioural assay in many species and was used several times in past research on common waxbills (Carvalho et al., 2013; Funghi et al., 2015). The mirror image is frequently used as a substitute for live conspecifics for behavioural assays in a range of other species as well (Cattelan et al., 2017). While in other species the mirror test can elicit aggressive responses (e.g., zebra finches: Wuerz & Krüger, 2015; jungle crows, *Corvus macrorhynchos*: Kusayama et al., 2000), in common waxbills it elicits non-aggressive social responses (Carvalho et al., 2013; Funghi et al., 2015), which is also the case in some shoaling fish species (e.g., Budaev, 1997; reviewed in Cattelan et al., 2017). Following previous protocols used in common waxbills (Carvalho et al., 2013; Funghi et al., 2015), the mirror test was conducted in a small birdcage (24.5 cm x 17 cm x 15 cm) with three equally distanced perches. The cage was placed 73.4 cm above the floor and in the centre of a closed, empty and illuminated with full spectrum lamps in the ceiling room (1.97 m x 1.97 m x 2.35 m). One end of the cage was covered by a mirror (17 cm x 15 cm) and the other end was covered by a fixed cardboard. Initially, the mirror was covered with a removable cardboard, that could be pulled with a nylon string from outside the testing room and kept hanged near the ceiling. The bird being tested was unable to see outside the testing room. A video camera recorded each test, which consisted of five minutes with the mirror covered, followed by five minutes with the mirror exposed. Videos were analysed using Observer XT11 (Noldus Information Technology, Wageningen, The Netherlands), and I quantified the following behavioural traits separately for before and after exposing the mirror:

- *Position relative to mirror*: Quantified dividing the cage in 5 different areas in relation to the mirror (Figure 4; 1: closest to mirror; 2: close to first perch after mirror; 3: close to the middle perch; 4: close to the perch more distant from the mirror; 5: closest to the opposite side of the mirror). I calculated a weighted average time (sum of area codes times the duration of permanence there, divided by the total duration) as an index of proximity to the mirror, which can vary from 1 (always near the mirror) to 5 (always far from the mirror).

- *Time facing the mirror*: Proportion of time that the bird's head was facing the mirror (i.e. within a 90˚ angle centred in the direction of the mirror).

- *Duration of grooming*: Proportion of time the bird was involved in cleaning the bill or the feathers.

- *Duration of resting*: Proportion of time the bird was in typical resting position with the plumage bulked.

- *Number of vocalizations*: Number of contact calls made (not counting other types of vocalizations; contact calls differ from other types of calls by being a sharp, abrupt 'pit' or 'tchick' or 'jip' and not a soft 'chip'; Clement et al., 1993; Payne, 2010).

- *Changing locations in the cage*: Number of switching positions along the horizontal axis (5 different positions relative to mirror), the depth axis (hanging on near the wall, not on the wall, and on distal wall), and the vertical axis (floor, perch, and hanging on top of cage). In each axis, changes to an adjacent area were counted as 1, changes to non-adjacent areas were counted as the number of crossed areas, and those counts were summed across all axes.

- *Fast movements*: Proportion of time the bird spent flying or hopping continuously, without stopping.

Figure 4. Birdcage used in the mirror test. Cage divided into 5 different areas in relation to the mirror: 1: closest to mirror; 2: close to first perch after mirror; 3: close to the middle perch; 4: close to the perch more distant from the mirror; 5: closest to the opposite side of the mirror.

Using data from all mirror tests, I first compared each of the seven behaviours between the periods before and after exposing the mirror, in order to choose which behavioural traits to use for quantifying response to the mirror image. Since the data were non-normal for all variables, I performed Wilcoxon signed-rank tests for paired samples. Vocalizations, fast movements and changing locations in the cage augmented significantly after exposing the mirror (V = 639, N = 60 birds, P = 0.01; V = 0, N = 60 birds, P < 0.001; V = 5016, N = 60 birds, P < 0.001, respectively). The other four behaviours did not change significantly after exposing the mirror or were never observed: position relative to mirror (V = 6534, N = 60 birds, P = 0.21), time facing the mirror (V = 7060, N = 60 birds, P = 0.19), duration of grooming (V = 75, N = 60 birds, P = 0.41) and duration of resting (not observed). Even though time facing the mirror did not increase significantly after exposing the mirror for our data, previous work found significant increases with the mirror exposed (Carvalho et al., 2013), and the trend in our data was in the predicted direction. Therefore, I quantified the responses to the mirror images using both the three behaviours that showed significant increases after exposing the mirror (vocalizations, fast movements and changing locations) and also time facing the mirror, as follows.

Using data from the periods with the mirror exposed, I checked the distribution of the data for each of the four behaviours selected above and transformed three to reduce kurtosis and approach normality. The numbers of vocalizations and changing locations had right-skewed distributions, so I performed a logarithmic transformation (log (x+1)). The number of fast movements also had a right-skewed distribution but a narrow range of variation, and so I first multiplied by 1000 before the log(x+1) transformation. Time facing the mirror had a platykurtic distribution, which cannot easily be normalized, and was not transformed. With these four behavioural variables, I ran a Principal Component Analysis (PCA) to obtain a single score of response to the mirror test. The first Principal Component (PC1) explained 63% of the variation and had an eigenvalue larger than 1 (2.53). The loadings of the behavioural variables on PC1 were positive and high for fast movements (0.84), changing locations (0.86) and number of vocalizations (0.71), and negative and high for time facing mirror (-0.78). This pattern of trait loadings on the mirror test PC1 was similar to previous work with waxbills (Carvalho et al., 2013; Funghi et al., 2015). I used this PC1 as the score of response to the mirror test, with high values indicating more movements and vocalizations but looking less often to the mirror, and low values indicating a more reactive response of looking to the mirror and doing fewer movements and vocalizations. All statistics were conducted in R v.3.4.0 software environment (R Core Team, 2017) using RStudio v.1.1.414 (RStudioTeam, 2016).

2.3.2 │ Tonic Immobility Test

Tonic immobility is a behaviour whereby an animal enters a state of apparent paralysis triggered by overturning the body, and it may be involved in predator-prey relationships, as a defensive reaction towards predators (Gallup et al., 1971; Edelaar et al., 2012). It is often used as an index of fear in a variety of taxa (Gallup, 1979). The tonic immobility test was made immediately after each individual's mirror test. After removing the bird from the mirror test cage, I gently placed the bird on its back, with its side facing the observer, on a wooden platform (5 cm x 5.1 cm x 1.7 cm), 91 cm above the floor, in the centre of the test room (197 cm x 197 cm x 235 cm) (Figure 5). The observer stayed silent and still approximately 25 cm from the platform during the time that the bird stayed immobile and recorded the time that the bird took to overturn and fly away up to a maximum of 60 seconds. The distribution of the tonic immobility data was continuous but had a peak at 0 seconds and other at 60 seconds, which is called a ceiling and floor effect, and for this reason, I could not transform this variable.

2.4 │ STATISTICAL ANALYSES

The following statistical analyses were performed using the PC1 scores of the mirror test and the time recorded in the tonic immobility test, also in the R software environment using RStudio. The distribution of data does not approach normality, because the mirror test data has a leptokurtic distribution and the tonic immobility test data showed a distribution with ceiling and floor effect. Therefore, all the analyses below used non-parametric approaches.

Figure 5. Setup for the tonic immobility test.

2.4.1 │ Repeatability of behaviour within and between seasons

I estimated within-individual repeatability for each of the two behavioural assays between the two rounds of the test in the first Autumn of each bird. I also estimated within-individual repeatability of behaviour between the first and second Autumn, and also between seasons (Autumn vs Spring). For the repeatability between rounds within the same season (the first Autumn of each bird), I used all 60 individuals housed in birdcages (30 in 2016, plus 30 in 2017). For the repeatability between Autumn 2016 and Autumn 2017, I used the 23 individuals that were tested in 2016 and that I could recapture in the Autumn of 2017 for re-testing, and I compared the mean between the two rounds of assays in the Autumn of 2016 with the single assay on the Autumn recapture of 2017. To estimate the repeatability between Autumn and Spring, I used the 35 individuals that I could recapture in the Spring of 2018: for each bird I first calculated the mean between the two rounds of assays in their first Autumn, then, for those birds measured in the Autumn of 2016 and recaptured in the Autumn of 2017, I calculated the mean between the 2016 average and the 2017 recapture, and finally I compared this final Autumn value with the single assay in the Spring recapture of 2018. In all cases, I estimated repeatability using only two measurements per individual, always in the same two contexts; this is the most straightforward situation for estimating repeatability, and repeatability equates to computing a simple Intra-class correlation (ICC; Bell et al., 2009). Since the behavioural data is not normally distributed, I calculated the ICC non-parametrically by using a Spearman rank-order correlation coefficient.

2.4.2 │ Comparison of mean behaviour

I tested for changes in mean behaviour values, for each of the two behavioural assays, using Wilcoxon signed-rank test, paired by individual birds. I compared behaviour between the Autumn 2016 and Autumn 2017, and between Autumn and Spring. To compare Autumn 2016 with Autumn 2017, I used the 23 individuals tested in 2016 and recaptured in the Autumn of 2017, using the same data as above for the repeatability between the Autumns of 2016 and 2017. When comparing Autumn with Spring, I used the 35 individuals that were recaptured in Spring 2018, again using the same data as above for the repeatability between Autumn and Spring.

2.4.3 │ Comparison of behavioural variation

To test if the behavioural differences between individuals were identical, increased or decreased from one year to the following, or from Autumn to Spring, I performed the Fligner-Killeen test of homogeneity of variance. As above, I used the 23 individuals tested in 2016 and recaptured in the Autumn of 2017 from the comparison between the Autumns of 2016 and 2017, and I used the 35 individuals recaptured in Spring 2018 for the comparison between Autumn and Spring. Unlike above, I did not average values across the multiple assays in Autumn but instead used only the first behavioural assay in Autumn for each bird. This is because averaging across multiple measurements reduces measurement error and could, therefore, bias the test by decreasing the variance of the population relative to that in the recaptures (which only have one behavioural assay).

2.4.4 │ Correlation between behaviour and behavioural change

Finally, I tested whether behavioural differences among individuals predicted their changes through time, either from one Autumn to the next or from Autumn to Spring. For the comparison between the two Autumns, I again used the same data as for the repeatability between Autumns for the 23 individuals captured in 2016 and recaptured in the Autumn of 2017; for the comparison between Autumn with Spring, I used the same data as for the repeatability between Autumn and Spring for the 35 individuals that were recaptured in Spring 2018. I correlated the mean behaviour of each individual (the mean of the two Autumns, in the first test, or the mean between Autumn and Spring, in the second test) with their changes in behaviour (the difference between the Autumns of 2017 and 2016, in the first test, and the differences between Spring and Autumn, in the second test) using Spearman rank-order correlation coefficient. In these correlations, I used the mean behaviour rather than the initial behaviour, because using initial behaviour is prone to the problem of "regression to the mean", whereby statistical tests are biased to find decreases of high initial values and increases of low initial values (Kelly & Price, 2005). Using the mean behaviour between the two-time points rather than the initial value effectively solves this "regression to the mean" bias.

3 | RESULTS

3.1 | Changes in behaviour within and between seasons

Within the same season, I found that the repeatability of behaviour in the mirror test between the two rounds in the same Autumn was 0.61 (Intra-class correlation, using Spearman rank-order correlation: $r_s = 0.61$, N = 60 birds, P < 0.001; Figure 6A). The repeatability between the Autumns of 2016 and 2017 was also high and significant ($r_s = 0.44$, N = 23 birds, P = 0.037; Figure 6B), and the mean behaviour between the Autumns of 2016 and 2017 did not change significantly (Wilcoxon signed-rank test: V = 104, N = 23 birds, P = 0.31; Figure 7). Behavioural variation between birds was identical between the Autumns of 2016 and 2017 (Fligner-Killeen test of homogeneity of variance: $\chi^2 = 0.065$, N = 23 birds, P = 0.80; Figure 7; see Appendix I Table 1). Also, the mean behaviour of individuals in the mirror test did not predict behavioural changes from one Autumn to the next (Spearman rank-order correlation: $r_s = 0.04$, N = 23 birds, P = 0.85; Figure 8).
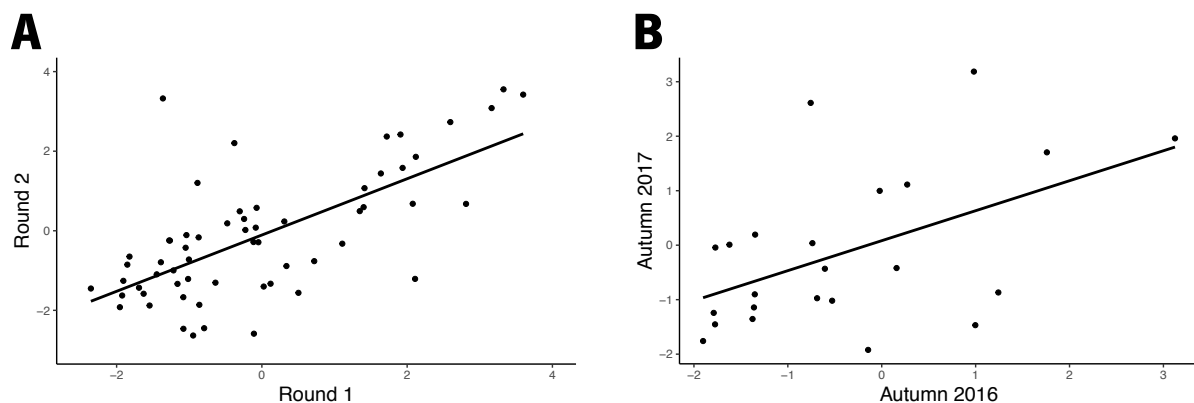

Figure 6. Repeatability of behaviour in the mirror test. **(A)** Intra-class correlation between round 1 and round 2. **(B)** Intra-class correlation between Autumn 2016 and Autumn 2017.

Comparing Autumn and Spring, within-individual repeatability of behaviour in the mirror test remained high and significant ($r_s = 0.62$, N = 35 birds, P < 0.001; Figure 9), despite the mean behaviour of individuals having changed significantly, becoming on average more proactive in the Spring (V = 188, N = 35 birds, P = 0.04; Figure 10). Behavioural variation in the population also increased significantly from Autumn to Spring ($\chi^2 = 4.120$, N = 35 birds, P = 0.04; Figure 10; see Appendix I Table 1), meaning that behavioural differences between individuals were accentuated. Finally, the mean behaviour of
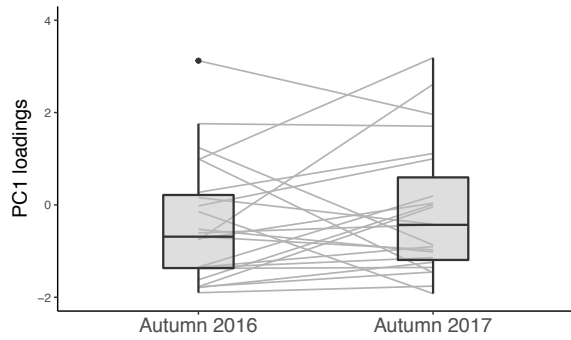
Figure 7. Changes in mean behaviour and in behavioural variation in the mirror test between Autumn 2016 and Autumn 2017.
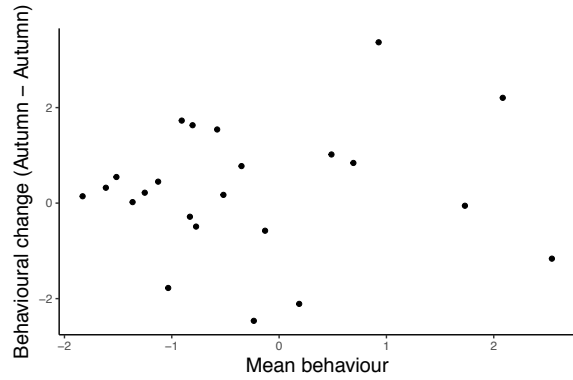
Figure 8. Correlation between behaviour and behavioural change in the mirror test from Autumn 2016 to Autumn 2017.

individuals was significantly and positively correlated with their behavioural changes from Autumn to Spring (r_s = 0.51, N = 35 birds, P = 0.002; Figure 11), meaning that the individuals already more proactive in the Autumn were the ones increasing the most in proactive behaviour towards Spring.

Figure 9. Repeatability of behaviour in the mirror test. Intra-class correlation between Autumn and Spring.

Figure 10. Changes in mean behaviour and in behavioural variation in the mirror test between Autumn and Spring.

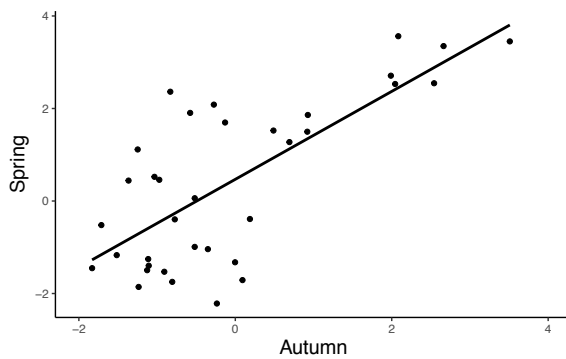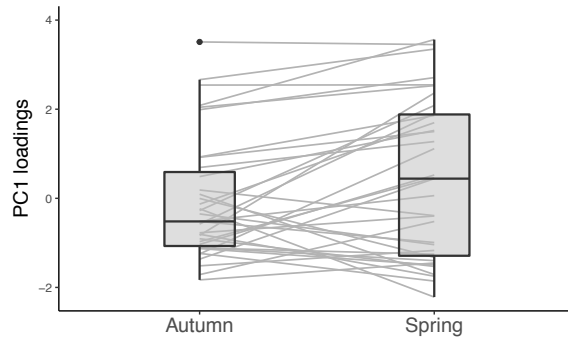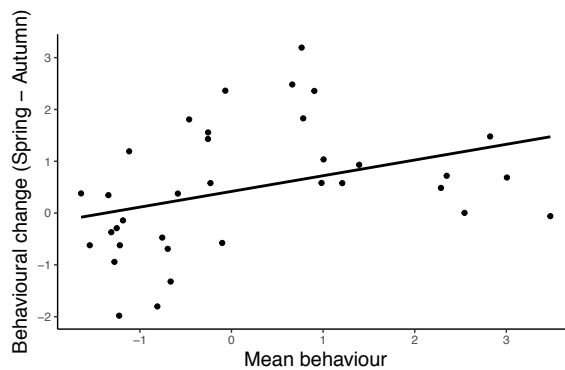**Figure 11.** Correlation between behaviour and behavioural change in the mirror test from Autumn to Spring.

In the tonic immobility test, the repeatability of behaviour was significant between the two rounds in the same Autumn (r_s = 0.37, N = 60 birds, P = 0.003; Figure 12A), and also between the Autumns of 2016 and 2017 (r_s = 0.52, N = 23 birds, P = 0.01; Figure 12B). The mean behaviour in the tonic immobility test did not change significantly from one Autumn to the next (V = 159, N = 23 birds, P = 0.14; Figure 13), nor did the variance in the population (χ^2 = 2.718, N = 23 birds, P = 0.10; Figure 13; see Appendix I Table 1). The mean behaviour of individuals also did not predict behavioural changes from one Autumn to the next (r_s = 0.02, N = 23 birds, P = 0.92; Figure 14).

Figure 12. Repeatability of behaviour in the tonic immobility test. **(A)** Intra-class correlation between round 1 and round 2. **(B)** Intra-class correlation between Autumn 2016 and Autumn 2017.

Figure 13. Repeatability of behaviour in the tonic immobility test. Intra-class correlation between Autumn 2016 and Autumn 2017.

Figure 14. Correlation between behaviour and behavioural change in the tonic immobility test from Autumn 2016 to Autumn 2017.

Comparing Autumn and Spring, within-individual repeatability in the tonic immobility test remained high and significant (r_s = 0.53, N = 35 birds, P = 0.001; Figure 15), and the mean behaviour did not change (V = 1393, N = 35 birds, P = 0.10; Figure 16). In this same test, the behavioural differences between individuals decreased significantly from Autumn to Spring (χ^2 = 4.076, N = 35 birds, P = 0.04; Figure 16; see Appendix I Table 1). The mean behaviour of individuals did not predict their behavioural changes from Autumn to Spring (r_s = -0.02, N = 35 birds, P = 0.89; Figure 17).
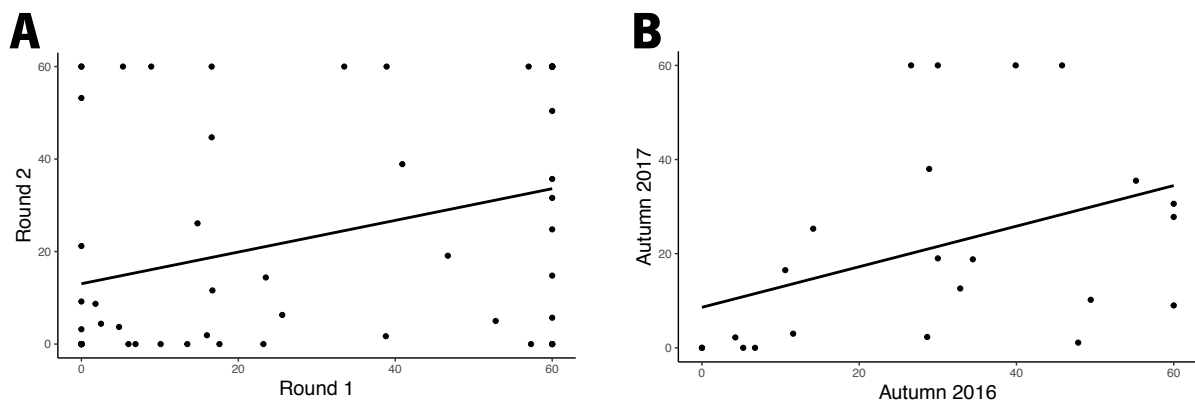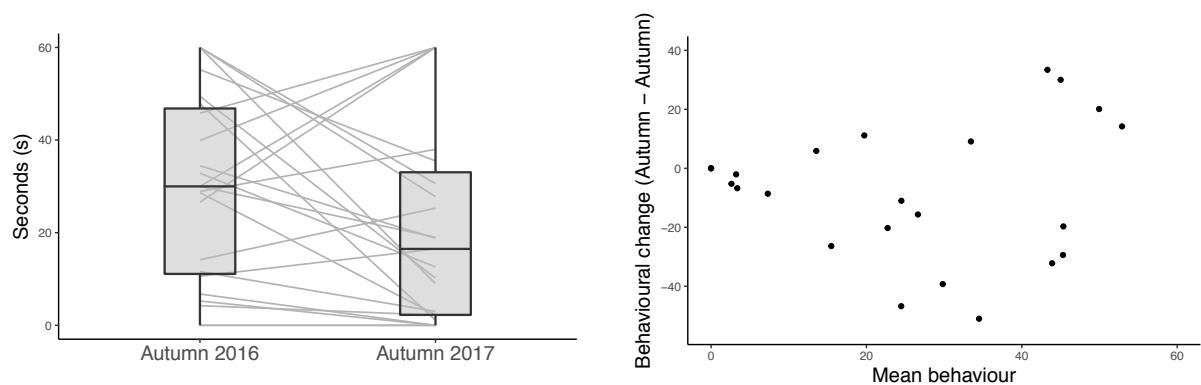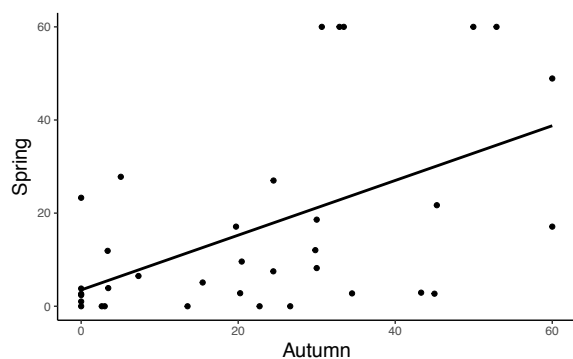
Figure 15. Repeatability of behaviour in the tonic immobility test. Intra-class correlation between Autumn and Spring.
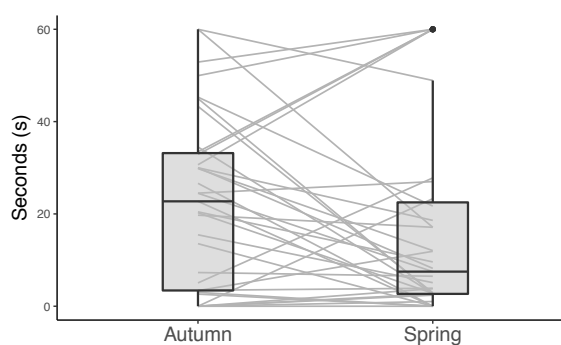
Figure 16. Changes in mean behaviour and in behavioural variation in the tonic immobility test between Autumn and Spring.
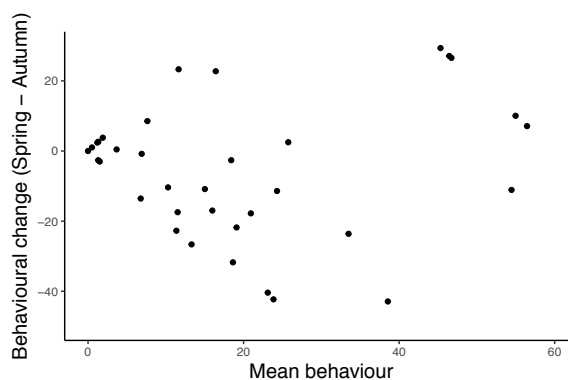
Figure 17. Correlation between behaviour and behavioural change in the tonic immobility test from Autumn to Spring.

3.2 | Sex-specific differences in behaviour

In Appendix II, I give results of similar analyses to the above, only conducted separately for each sex. Here, I only note the cases where results for one sex differ qualitatively from the overall results above. This is, when a significant effect in the main analysis above was not found in at least one of the sexes separately, or when there was a significant effect in sex-specific analysis that was not found in the main analysis.

Although I found individually-repeatable behaviour in the mirror test between the Autumns of 2016 and 2017, testing this separately for each sex, behaviour was repeatable only for males (males: r_s = 0.72, N = 10 birds, P = 0.05; females: r_s = 0.18, N = 13 birds, P = 0.55).

Similarly, comparing Autumn and Spring, the overall results showed repeatable within-individual behaviour in the mirror test, but for each sex individually, this was only repeatable in males (males: r_s = 0.83, N = 17 birds, P < 0.001; females: r_s = 0.29, N = 18 birds, P = 0.25). Also, the change in mean

behaviour that I found from Autumn to Spring was only significant for males (males: V = 34, N = 17 birds, P = 0.045; females: V = 67, N = 18 birds, P = 0.44), and behavioural variation between Autumn and Spring was no longer significant when analysing each sex separately (males: χ^2 = 0.07, N = 17 birds, P = 0.79; females: χ^2 = 2.62, N = 18 birds, P = 0.11). Additionally, the correlation between the mean behaviour of individuals and behavioural change from Autumn to Spring was only significant in females (r_s = 0.54, N = 18 birds, P = 0.02), although this correlation also approached significance in males (r_s = 0.45, N = 17 birds, P = 0.07).

In the tonic immobility test, I found within-individual repeatable behaviour between the Autumns of 2016 and 2017, but behaviour was not significantly repeatable when analysing the sexes separately (males: r_s = 0.59, N = 10 birds, P = 0.08; females: r_s = 0.23, N = 13 birds, P = 0.46). Also, I found that behavioural variation between birds remained identical between one Autumn and the next but, analysing females separately, variation decreased from Autumn 2016 to Autumn 2017 (χ^2 = 4.65, N = 13 birds, P = 0.03).

Comparing Autumn and Spring, the mean behaviour in the tonic immobility test did not change but, testing the sexes separately, mean tonic immobility decreased in females (females: V = 119, N = 18 birds, P = 0.047; males: V = 77, N = 17 birds, P = 1). I found that behavioural variation decreased significantly from Autumn to Spring but, analysing the sexes separately, this was true only in females (females: χ^2 = 4.16, N = 18 birds, P = 0.04; males: χ^2 = 0.92, N = 17 birds, P = 0.34).

4 | DISCUSSION

Animal personality refers to behavioural differences between individuals that are consistent across time and contexts (Réale et al., 2007). Animals exhibiting personality differences can also plastically adapt their behaviour in response to environmental changes (e.g., Gracceva et al., 2014). I conducted two behavioural assays on a gregarious bird, the common waxbill, to understand whether personality differences change plastically from the non-breeding to the breeding season. An accentuation of personality differences in the Spring would suggest that animal personality has essential sexual functions, while an attenuation of personality differences would indicate that personality differences are involved mostly in non-social or non-reproductive social interactions. I also tested within-individual repeatability in behaviour across two Autumns and one Spring and assessed if the mean behaviour changed within and between seasons.

I found that behaviour in assays related to sociability (mirror test) and fear (tonic immobility test) was repeatable within and between seasons and that mean behaviour and behavioural variation in the population remained identical from one Autumn to the next. Between different seasons, individuals changed their behaviour assayed in the mirror test, becoming on average more proactive in the Spring than in the Autumn, whereas in the tonic immobility test mean behaviour remained identical. Importantly, I found that behavioural differences between individuals in the mirror test increased from Autumn to Spring, with the behavioural types of different individuals predicting their between-season change in behaviour, while in the tonic immobility test behavioural differences were attenuated in the Spring.

4.1 | Seasonal changes in the mirror test

The mirror test is a well-established behavioural assay in many species to study either aggressive behaviour (e.g., jungle crows: Kusayama et al., 2000; zebra finches: Wuerz & Krüger, 2015) or sociability (e.g., common waxbills: Carvalho et al., 2013; Funghi et al., 2015; several fish species: reviewed in Cattelan et al., 2017). Mirrors are frequently used as social stimuli in a range of species, as substitutes for live conspecifics (Cattelan et al., 2017), and in common waxbills, the mirror images elicit non-aggressive social responses (Carvalho et al., 2013; Funghi et al., 2015). Past research also found that social and exploratory behaviours differ in a correlated manner, this is, more exploratory birds pay less attention to the mirror image, while less exploratory birds spend more time looking at the mirror image

(Carvalho et al., 2013). In this way, sociability and exploration are considered part of a stable behavioural syndrome (Cardoso & Reino, 2018), which is in line with individual personalities differing along a reactive-proactive axis, widespread across several animal species (Carvalho et al., 2013; Aplin et al., 2014).

Previous studies revealed that common waxbills in mirror test assays showed repeatable behaviour when tested several weeks apart (Carvalho et al., 2013; Funghi et al., 2015). When I tested within-individual repeatability within the same season, I confirmed these past results. Additionally, I tested the repeatability of behaviour one year apart (from Autumn 2016 to Autumn 2017) and across seasons (Autumn to Spring) and I found that in both situations the behaviour was highly repeatable, extending past results and showing that waxbill personality types persist across seasons and even one year apart. As expected, the mean individual behaviour and the behavioural variation between birds from one Autumn to the next did not change. This means that even after one year, both the mean behaviour and the behavioural differences between individuals remained identical. A study with European starlings found repeatability of behaviour across seasons (Autumn and Spring) and across a 2-year period (Thys et al., 2017). These findings indicate stable animal personality in two gregarious bird species, where consistent behavioural differences between individuals are maintained across long periods of time and different contexts (Réale et al., 2007; Dingemanse et al., 2012). Consistent differences between individuals in social behaviour could be ecologically relevant, as they may influence dispersal (Cote & Clobert, 2007), disease transmission (Barber & Dingemanse, 2010), competition for breeding territories (Farine & Sheldon, 2015) or reproductive success (Oh & Badyaev, 2010).

When birds were re-tested in the Spring, I found that they had, on average, become more proactive in the breeding season. Proactive individuals, often called "fast-explorers", are usually bolder, more aggressive (Sih et al., 2004a; Groothuis & Carere, 2005; Aplin et al., 2014) and, in the case of waxbills, pay less attention to social stimulus (Carvalho et al., 2013; Funghi et al., 2015) than reactive individuals. According to past work on waxbills (Carvalho et al., 2013; Funghi et al., 2015), I also confirmed that birds paying less attention to the mirror image were the ones who moved and vocalized more during the test.

One possible reason for this seasonal change in mean behaviour is that proactive strategies may be favoured during the breeding season, when bolder or more aggressive behaviour might allow fast exploration, access to resources and reproduction opportunities (Eccard & Rödel, 2011), such as finding a mate or defending a territory (Eccard & Herde, 2013). In fact, a review by Smith and Blumstein (2008) emphasized that boldness and exploration are usually related to high reproductive success. This result is in concordance with other studies. In common voles, it was found that individuals captured in the

Spring were bolder than animals captured during different seasons (Eccard & Herde, 2013); European mink (*Mustela lutreola*) became bolder and more explorative in the breeding season (Haage et al., 2013), and explorative behaviour was higher in the Spring than in the Autumn in great tits (Dingemanse et al., 2002, 2012) and in ground squirrels (Semenova et al., 2001). However, contrary results were found in a study with males of European starlings, where novel environment exploration and sociability (measured through the time they spent near the nestbox) were higher in the Autumn than in the Spring (Thys et al., 2017). Together, these findings prove that animal personality and behavioural plasticity are not incompatible, as consistent differences among individuals can be maintained despite the individuals' mean behaviour adjusting to environmental changes (Dingemanse et al., 2012).

The behavioural variation in the population increased from the Autumn to the Spring, which means that, although consistent, behavioural differences between individuals accentuated. Indeed, I predicted that behavioural differences would augment in Spring if animal personality has essential sexual functions. This accentuation in behavioural differences between birds suggests that animal personality may have evolved, in part, as an adaptation to social challenges involved in breeding, such as pair formation, sexual interactions, or others. Particularly in gregarious species, seasonal changes when entering the breeding season may involve different social challenges since, in addition to managing the ongoing non-sexual interactions within the groups, animals now need to, for example, find and compete for mates.

Although some studies have compared individual behavioural differences across contexts (reviewed in Brommer, 2013a; Hall et al., 2015; reviewed in Killen et al., 2016), very few looked at changes in those individual behavioural differences between the breeding and the non-breeding seasons. My results showed that, although personality differences between common waxbills were consistent from the non-breeding to the breeding season, these differences increased in the breeding season. Three studies in other species found no changes in individual behavioural differences across times of the year (great tits: Dingemanse et al., 2012), or between rainy (breeding) and dry (non-breeding) seasons (Namibian rock agamas, *Agama planiceps*: Carter et al., 2012), or between mating (breeding) and foraging (non-breeding) seasons (Belding's ground squirrels, *Urocitellus beldingi*: Dosmann & Mateo, 2014). Contrary to my findings, Kluen and Brommer (2013) found that variance across blue tits (*Cyanistes caeruleus*) was lower in the breeding season for neophobia-related behaviour, although behavioural differences between individuals were not repeatable and thus not a personality trait. Similarly, in striped mice (*Rhabdomys pumilio*), between-individual variation, although consistent, was lower during the breeding season for activity in females and for aggressiveness in males (Yuen et al., 2015). My study

is, thus, one of the first to compare personality differences between the breeding and non-breeding seasons and, to my knowledge, the first showing that those personality differences can be accentuated towards the breeding season. More studies are needed to understand these different results across species and behavioural traits.

Often, individuals from the same population vary their level of behavioural plasticity (Sih & Bell, 2008; Coppens et al., 2010; Dingemanse et al., 2010b). I found that the mean behaviour of individuals was significantly and positively correlated with the amount of behavioural change from Autumn to Spring, with more proactive individuals being the ones changing behaviour most towards Spring. This means that personality differences in the common waxbill consist not only in differences in behaviour among individuals, but also in correlated differences in the seasonal plasticity of those behaviours. Similar results, albeit not related to season, were found in Ural owls (*Strix uralensis*), where more aggressive individuals defending their nests were the ones better able to adjust their level of aggressiveness to variation in prey density, and also had higher reproductive success (Kontiainen et al., 2009).

When I analysed each sex separately, results were overall similar, but there were also some differences, perhaps because of lower statistical power when analysing only one sex. One interesting difference was that only in males was the behaviour in the mirror test significantly repeatable between seasons (either the two Autumns, or from Autumn to Spring), and only in males did behaviour change on average from Autumn to Spring. In a study with the domestic canary (*Serinus canaria*), male behaviour also appeared to be more repeatable than female behaviour during the breeding season (long-day photoperiods; Amy et al., 2017). Also, in European mink, males became bolder and more exploratory in the breeding season (Haage et al., 2013). In both cases, these sex differences are consistent with a sexual function of animal personality since, in species with conventional sex roles, males should experience stronger sexual selection on secondary sexual traits, and thus should show stronger behavioural differences towards the breeding season.

4.2 | Seasonal changes in the tonic immobility test

Tonic immobility is a widely used behavioural assay to assess fear, and it may be a defensive reaction towards predators (Gallup et al., 1971; Edelaar et al., 2012). While in other species tonic immobility is related to the reactive-proactive personality axis, where reactive individuals stay longer in tonic immobility (Erhard et al., 1999; Cockrem, 2007), in the common waxbills individual differences in tonic immobility is not related to the reactive-proactive personality axis as captured by exploration and mirror assays (Carvalho et al., 2013).

This behavioural assay was shown before to be repeatable over a period of several weeks (Carvalho et al., 2013; Funghi et al., 2015). I confirmed and extended these results by showing that differences in tonic immobility were repeatable even from one Autumn to the next or towards Spring. Birds did not change their mean behaviour on this assay between the two Autumns, and behavioural variation among individuals remained identical. Towards Spring, birds did not change their mean behaviour on this assay either.

Contrary to results with the mirror test, behavioural differences among individuals decreased towards Spring. This means that increased behavioural variation in Spring, as I found on the mirror test, is not a general consequence of, for example, higher overall activity in Spring. The contrasting seasonal patterns for the mirror and tonic immobility assays indicate that seasonal changes in among-individual differences are behaviour specific, and that increased variation in Spring is specific to the mirror assay (a personality assay in waxbills). As for tonic immobility, the decreased variation in the Spring suggests that among-individual differences are not particularly adaptive in the reproductive context and may even be mostly involved in non-reproductive social interactions. Similar results were found in blue tits neophobia-related behaviour, where variance across individuals was lower in the breeding season compared to the non-breeding season (Kluen & Brommer, 2013).

When analysing each sex separately, again, results were overall similar with some exceptions mostly attributable to lower statistical power when analysing only one sex. Two unexpected results were that, when analysing females alone, mean tonic immobility decreased from Autumn to Spring, and that behavioural variation among females decreased from the first Autumn to the next, being perhaps an age effect.

5 | FINAL REMARKS

The main result of this study, which focuses on how personality differences between individuals changed from Autumn to Spring, showed that personality differences among common waxbills increased in the Spring. This accentuation in personality differences was unique to behavioural traits related to the reactive-proactive axis of common waxbills (mirror test), and not a general effect of season on behaviour since behavioural differences did not augment in another behavioural assay (tonic immobility).

Increased personality differences in Spring could indicate that these differences are important and more useful in the breeding season. Especially in gregarious species, as the common waxbill, entering in breeding season may involve different social challenges such as pair formation, competition for mates, sexual interactions, or others. Understand how animal personality changes with breeding may give important cues on the function of personality. My work showed that common waxbills have stable personality differences and that is one of the first to suggest that personality differences are particularly important in the breeding context.

6 | LITERATURE CITED

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Table 1. Change in behavioural variation within the population from one Autumn to the next or from Autumn to Spring, in each of the two behavioural assays.

Season	Mirror test		Tonic immobility test	
	σ^2	P	σ^2	P
Autumn 2016	1.802	0.799	701.385	0.348
Autumn 2017	2.055		467.460	
Autumn	2.146	0.042 *	667.341	0.043 *
Spring	3.188		430.260	

The results are from the Fligner-Killeen test of homogeneity of variance.

σ^2 is the variance within the population when tested in each season.

P is the statistical significance of the Fligner-Killen test.

* p<0.05

In this appendix, I give results of similar analyses to the results section, only conducted separately for each sex.

Within the same season, I found that the repeatability of males' behaviour in the mirror test was high and significant both between rounds (r_s = 0.65, N = 29 birds, P < 0.001) and between the Autumns of 2016 and 2017 (r_s = 0.72, N = 10 birds, P = 0.02), but the repeatability of females' behaviour was high and significant only between rounds (r_s = 0.52, N = 31 birds, P = 0.003) and not significant between the Autumns of 2016 and 2017 (r_s = 0.18, N = 13 birds, P = 0.55). For either sex, the mean behaviour between the Autumns of 2016 and 2017 did not change significantly (males: V = 19, N = 10 birds, P = 0.43; females: V = 37, N = 13 birds, P = 0.59) and the behavioural variation between birds was also identical between the same Autumns (males: χ^2 = 0.0003, N = 10 birds, P = 0.99; females: χ^2 = 0.015, N = 13 birds, P = 0.90). In this test, the mean behaviour of individuals of each sex did not predict behavioural changes from one Autumn to the next (males: r_s = -0.14, N = 10 birds, P = 0.71; females: r_s = 0.09, N = 13 birds, P = 0.76).

Comparing Autumn and Spring, the within-individual repeatability of behaviour in males was high and significant (r_s = 0.83, N = 17 birds, P < 0.001), whereas in females it was not significant (r_s = 0.29, N = 18 birds, P = 0.25). The mean behaviour in the mirror test changed in males from Autumn to Spring (V = 34, N = 17 birds, P = 0.045) but not in females (V = 67, N = 18 birds, P = 0.44). The behavioural variation between birds remained identical for either sex (males: χ^2 = 0.07, N = 17 birds, P = 0.79; females: χ^2 = 2.62, N = 18 birds, P = 0.11). Finally, the mean behaviour of females was significantly and positively correlated with their behavioural changes from Autumn to Spring (r_s = 0.54, N = 18 birds, P = 0.02; Figure X), whereas this correlation was also positive but did not reach significance for males (r_s = 0.45, N = 17 birds, P = 0.07).

In the tonic immobility test, the repeatability of males' behaviour was high and significant between the two rounds (r_s = 0.51, N = 29 birds, P = 0.005) and not significant between the Autumns of 2016 and 2017 (r_s = 0.59, N = 10 birds, P = 0.08). In females, within-individual repeatability was not significant both between rounds (r_s = 0.19, N = 31 birds, P = 0.32) and between the Autumns of 2016 and 2017 (r_s = 0.23, N = 13 birds, P = 0.46). The mean behaviour between the Autumns of 2016 and

2017 did not change in either sex (males: V = 29, N = 10 birds, P = 0.48; females: V = 58, N = 13 birds, P = 0.15) and behavioural differences between females decreased significantly from Autumn 2016 to Autumn 2017 (χ^2 = 4.65, N = 13 birds, P = 0.03) while behavioural variation in males remained identical from one Autumn to another (χ^2 = 0.002, N = 10 birds, P = 0.96). Also, the mean behaviour of individuals did not predict behavioural changes from Autumn 2016 to Autumn 2017 in either sex (males: r_s = 0.24, N = 10 birds, P = 0.51; females: r_s = -0.16, N = 13 birds, P = 0.60).

Comparing Autumn and Spring, the within-individual repeatability of behaviour was high and significant in either sex (males: r_s = 0.58, N = 17 birds, P = 0.01; females: r_s = 0.50, N = 18 birds, P = 0.03). The mean behaviour only changed from Autumn to Spring in females (females: V = 119, N = 18 birds, P = 0.05; males: V = 77, N = 17 birds, P = 1) and the behavioural variation decreased significantly from one season to another in females (χ^2 = 4.16, N = 18 birds, P = 0.04) while in males remained the same (χ^2 = 0.92, N = 17 birds, P = 0.34). Finally, in the tonic immobility test, the mean behaviour of individuals did not predict behavioural changes from Autumn to Spring in either sex (males: r_s = 0.05, N = 17 birds, P = 0.85; females: r_s = 0.06, N = 18 birds, P = 0.81).