



UNIVERSIDADE DE ÉVORA

ESCOLA DE CIÊNCIAS E TECNOLOGIAS

DEPARTAMENTO DE BIOLOGIA

**Study of behavioural syndromes of *Sylvia melanocephala* in
Mitra |**

Patrícia Beltrão dos Santos |

Orientação: Doutor Rui Lourenço |

Doutor Carlos Godinho |

Doutor Pedro Pereira |

Mestrado em Biologia da Conservação

Dissertação

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Estudo das síndromes comportamentais da população de *Sylvia melanocephala* da Herdade da Mitra

Resumo

O Homem, ao longo do tempo, tem vindo a alterar os ecossistemas. Diversas espécies apresentam personalidade e síndromes comportamentais que, por sua vez, parecem influenciar o estabelecimento das espécies em ambientes alterados pelo Homem. Nós estudámos o comportamento de 30 toutinegras-de-cabeça-preta *Sylvia melanocephala* através de quatro testes. O nosso objetivo era perceber se esta espécie apresenta consistência comportamental e se os comportamentos estudados em quatro testes se encontram correlacionados. Nós também pretendíamos perceber se o habitat poderia influenciar o comportamento dos indivíduos. Os nossos resultados mostraram que esta espécie apresenta consistência comportamental. Para além disso, o habitat parece influenciar o comportamento dos indivíduos, onde indivíduos mais agressivos e exploradores se encontram em habitats ótimos. Os comportamentos de fuga associados ao teste do espelho e do predador apresentaram-se correlacionados bem como os comportamentos de agressão e ousadia.

Study of behavioural syndromes of *Sylvia melanocephala* in Mitra

Abstract

Humans have been altering the ecosystems. Animal personality/behavioural syndromes appear to have an important role in the establishment of a species in Human-altered habitat. We studied the behaviour of 30 Sardinian warblers *Sylvia melanocephala* using four different tests. We wanted to understand if this species shows behavioural consistency and if the behaviours across the four tests are correlated. We also wanted to see if the habitat (natural vs. human-altered areas) may influence individual behaviour. Our results suggest that the Sardinian warbler shows behavioural consistency regarding the four tests. In addition, the habitat appears to influence the behaviour, as individuals that were more aggressive and explorative lived in optimal habitats. The escape behaviours associated with the presence of the conspecific (mirror image) and predator were correlated, as were also the aggressive and boldness behaviours.

Introduction

Ecosystems have been suffering changes that result from human activities. Many of these changes are harmful to the wildlife, which creates the need for the conservation of biodiversity. The animal behaviour field research can assume an important role in wildlife conservation. One of the focus of this research field is to understand differences in individual response to different ecological contexts, which includes learning ability and the strategies that individuals adopt in order to maximize fitness. These aspects are all essential to wildlife conservation as they can bring new knowledge and help to make a conservation strategy successful. However, it is important to note that wildlife conservation area integrates more research fields besides animal behaviour (Festa-Bianchet and Apollonio 2003).

Animals can show consistency in their individual behaviour (e.g. more aggressive, less bold) across time and/or situations, which has been designated as “animal personality” (Gosling 2001; Dall et al. 2004; Réale et al. 2007). Animal personality has been studied in several taxonomic groups, including mammals (Réale and Festa-Bianchet 2003), birds (Amy et al. 2010), reptiles (Carter et al. 2012), amphibians (Kelleher et al. 2017), fishes (Brown et al. 2008) and insects (Logue et al. 2009). The behaviours presented by individuals can be defined according to the ecological context (Sih et al. 2004). Réale et al. (2007) considered five different behavioural categories: (1) "exploration-avoidance" when individuals are confronted with a new situation; (2) "shyness-boldness" when individuals are facing a predator; (3) "activity"; (4) "aggressiveness", agonistic interactions to a conspecific; (5) "sociability," non-aggressive interaction with conspecifics. Two or more of these different behaviours may be correlated, which constitutes a “behavioural syndrome” (Stamps and Groothuis 2010; Garamszegi et al. 2012; Jandt et al. 2014). Individuals' personality may be affected by several factors such as sex, age and body size (Gustafsson 1988; Groothuis and Carere 2005; Funghi et al. 2015). Several studies have shown that animal personality and behavioural syndromes, influence the fitness of individuals (Dingemanse et al. 2004; Duckworth 2006). Moreover, behavioural syndromes can generate trade-offs with many ecological implications for species (Sih et al. 2004). For example, a more active individual will be able to collect more resources but will also become more susceptible to predation (Sih et al. 2012). Behavioural syndromes may also sometimes be associated with the lack

of behavioural plasticity, which is extremely important in rapidly changing environments (Sih et al. 2004). Behavioural plasticity allows the individuals to respond quickly to changes in the environment, where species that show more plastic behaviours have more success in colonizing new habitats (Sol and Lefebvre 2000; Sol et al. 2002).

Humans have changed the ecosystems, including habitat degradation and fragmentation, alteration of the abiotic conditions and introduction of exotic species (Mcdonnell and Hahs 2015). The behaviour of individuals assumes a key role in the capacity to thrive in human-altered habitats (Sol et al. 2002, Fogarty et al. 2011). However, some individuals exhibit unsuitable behaviours in these environments which ultimately can result in population decline (Schlaepfer et al. 2002; Sih and Del Giudice 2012). The role of personality in the establishment of species in human-altered habitats has been studied by several researchers (Tuomainen and Candolin 2011; Sih et al. 2011; Sih et al. 2012). However, there are contradictory results, where the same behaviour is favoured in some cases but not in others (Sol et al. 2011; Bókony et al. 2012). Therefore, the study of animal personality and behavioural syndromes in populations affected by habitat modification can contribute to the conservation of the species (Sih et al. 2012).

Birds have complex behaviours, which makes them interesting study models (Aplin et al. 2013, Jacobs et al. 2014). The Sardinian warbler *Sylvia melanocephala* a small passerine from Mediterranean Europe with resident, and territorial habits which feeds mainly on insects, but can also consume fruits (Bas et al. 2005; De Juana and Garcia 2015). The Sardinian warbler favours sites with shrub cover, maquis and garrigues but can also be found in human-altered habitats, such as gardens and orchards which are sub-optimal habitats (Shirihai et al. 2001; Equipa Atlas 2008). Moreover, this species presents sexual dimorphism (figures 1 and 2) and the adults and juveniles have different plumage, which allows to study the influence of sex and age in the behaviour. There is little information about the behaviour of the Sardinian warbler, which constitutes a gap in the scientific knowledge. In the study area, its population size allows the capture of an acceptable number of individuals with a relatively low effort.

Within the broad context of animal personality, the aims of this work were to understand if the individuals of Sardinian warbler differed in their behavioural responses when submitted to the same stimulus; if individuals show behavioural consistency regarding the context (e.g. exploration context) and if the behaviours are correlated

between different contexts; and if the behaviour of individuals is related to the habitat when considering natural habitats and human-altered habitats. For this purpose, the behaviour of the individuals was studied using four behavioural tests: (1) exploration (figure 3), (2) mirror (figure 4); (3) predation (figure 5); (4) tonic immobility (figure 6).

The choice of the experimental design was complex as it would involve many small details. In the beginning we started doing the tests in the field but it was essential to minimize all the potential factors influencing the behaviour (as the position of the sun). Therefore, the tests were conducted in the laboratory. The size of the cage was based on literature, adjusted for the size of the study species (Sardinian warbler). The individuals of another study site were submitted to the behavioural tests to understand what could be improved and to adjust small details. I spent about twenty-five days doing fieldwork, sixty days analysing the video data, fifteen days working with statistical analysis and forty days writing the master thesis. There was a total of 38 sampling sites distributed by a natural and a human-altered habitat (figure 7).



Figure 2 - Female of Sardinian warbler



Figure 1 - Male of Sardinian warbler



Figure 3 - Cage of the exploration test

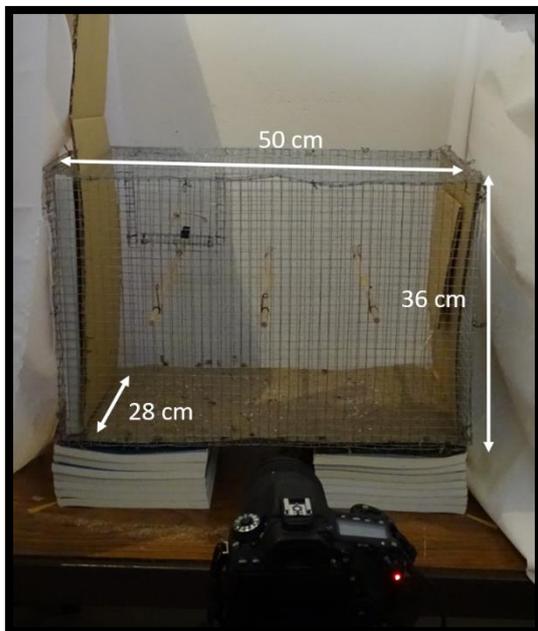


Figure 4 - Cage of the mirror test

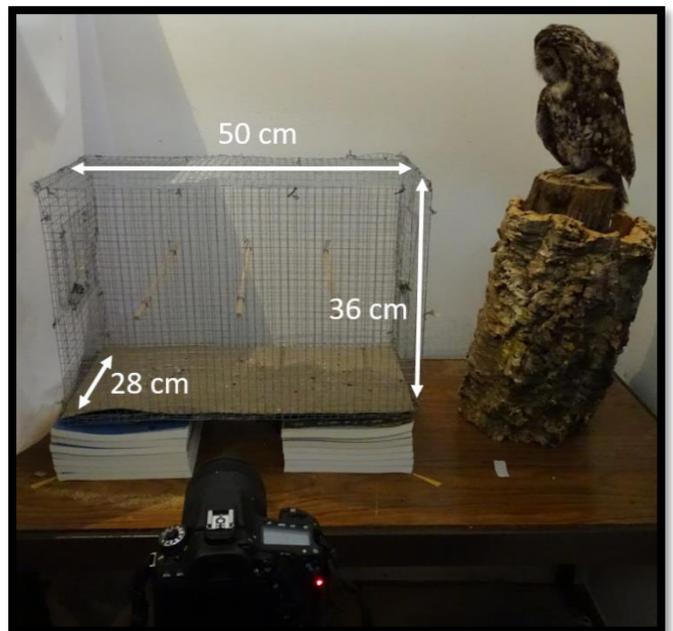


Figure 5 - Cage of the predator test

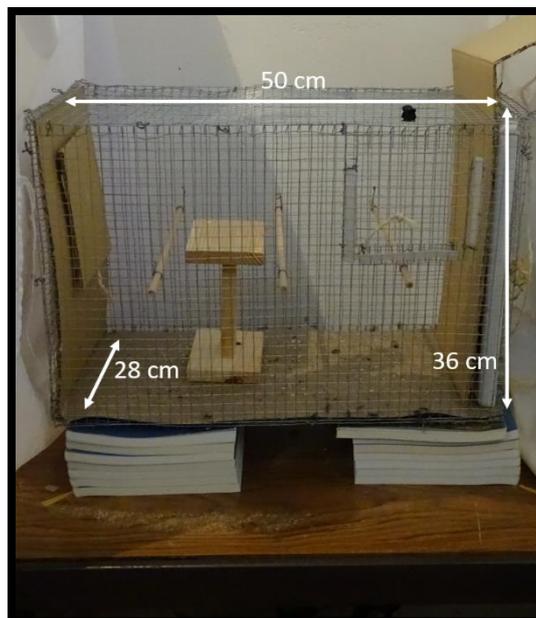


Figure 6 - Cage of the tonic immobility test

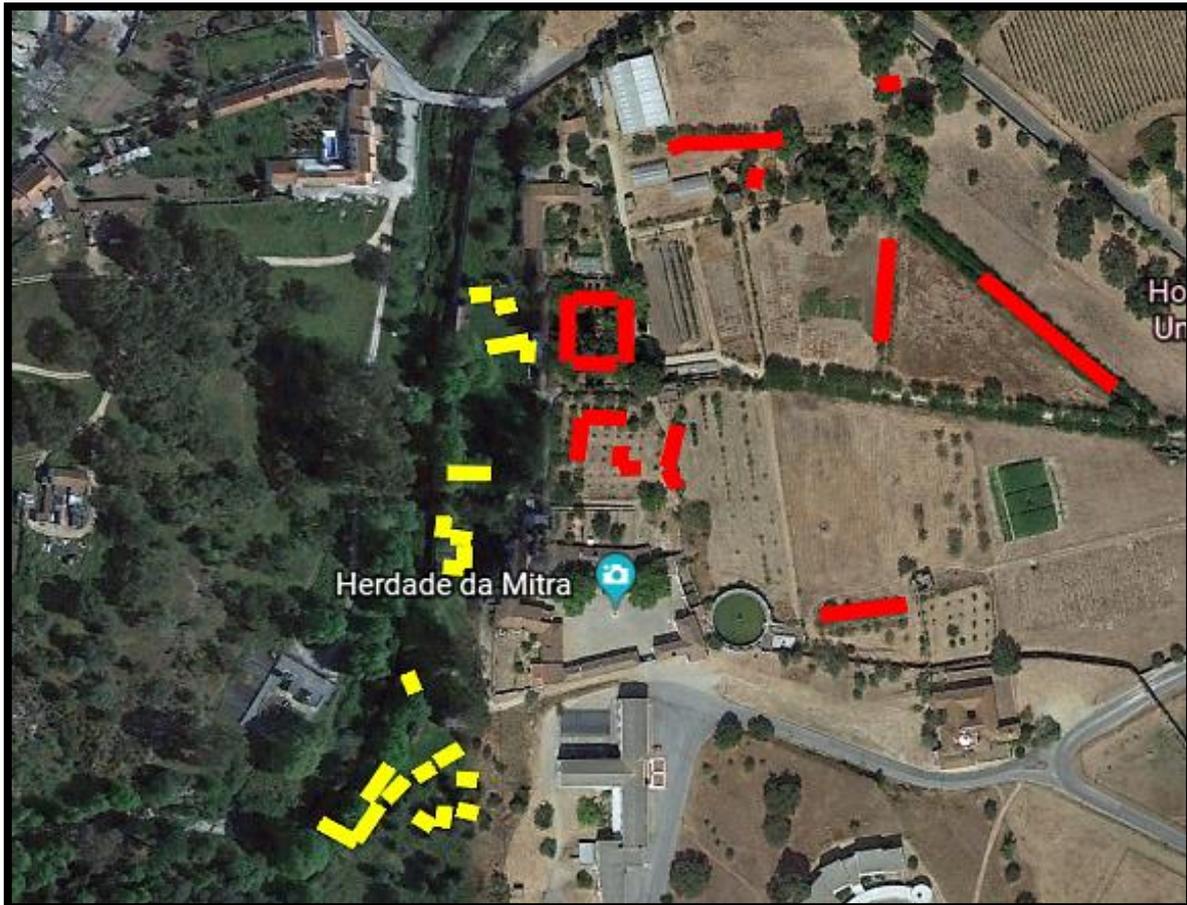


Figure 7 – Sampling sites of the Sardinian warblers' individuals in Mitra (yellow – natural habitat; red – human-altered habitat)

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Research article

Study of behavioural syndromes of *Sylvia melanocephala*

Patrícia Beltrão, Carlos Godinho, Rui Lourenço, Pedro Pereira

Abstract

Humans have been inducing changes on the environment and altering the ecosystems. Species adapt differently to these changes, and personality/behavioural syndromes appear to have an important role in the establishment of the species in human-altered habitats. We studied the behaviour of Sardinian warblers *Sylvia melanocephala* across four different tests (exploration, mirror, predator, and tonic immobility). We wanted to understand if this species shows behavioural consistency and if the behaviours across the four tests are correlated. We also wanted to see if the habitat (natural vs. human-altered areas) may influence the individuals' behaviours. Our results suggest that the Sardinian warbler has behavioural consistency regarding the four tests. In addition, the habitat appears to influence the behaviour, as individuals that were more aggressive and explorative lived in optimal habitats. The escape behaviours associated with the presence of the conspecific (mirror image) and predator were correlated, as were also the aggressive and boldness behaviours. This study suggests that animal personality can be relevant in conservation biology, allowing to understand the species behaviour towards different habitats. *Key words:* animal personality; Sardinian warbler; exploration; aggressiveness; habitat.

Introduction

Animals have shown consistent individual behaviours across time and/or situations, which has been designated as “animal personality” (Gosling 2001; Dall et al. 2004; Sih et al. 2004; Réale et al. 2007). Personality has been studied in several taxonomic groups, including mammals (Réale and Festa-Bianchet 2003), birds (Amy et al. 2010), reptiles (Carter et al. 2012), amphibians (Kelleher et al. 2017), fishes (Brown et al. 2008) and insects (Logue et al. 2009). Different behaviours can be correlated across time or contexts, which constitutes a “behavioural syndrome” (Stamps and Groothuis 2010; Garamszegi et al. 2012; Jandt et al. 2014). The fitness of individuals is also related to personality and behavioural syndromes (Dingemanse et al. 2004) which can have

implications for species ecology and evolution (Sih et al. 2004). Associated with the behavioural syndromes is the lack of plasticity in behaviour, which can assume a high importance in rapidly changing environments by Human action (Sih et al. 2004). Behavioural plasticity allows the individuals to respond quickly to changes in the environment, where species that show more plastic behaviours have more success in colonizing new habitats (Sol and Lefebvre 2000; Sol et al. 2002).

The study of behaviour is important for species conservation, as it affects, for example, individual's fitness, reintroduction success of captive-bred animals and the ability of the species establishment in certain habitats (Bremner-Harrison et al. 2004; Conrad et al. 2011; Sih et al. 2004). The human population has been introducing environmental changes in habitats, sometimes drastically (McDonnell and Hahs 2015). Fragmentation or habitat loss, ecological invasions, new abiotic conditions are just some examples of the new challenges that species are facing (Sih et al. 2012). However, species can adapt to these changes differently and behaviour appears to have an important role in this, where it can have detrimental or favourable consequences to species (Sih et al. 2011). Animal personality in human-altered habitats has been studied but there are contradictory results, with the same behaviour being favoured in some cases but not in others (Sol et al. 2011; Bókony et al. 2012).

In birds, personality can be affected by different individual traits, such as body size, sex and age (Gustafsson 1988; Groothuis and Carere 2005; Funghi et al. 2015). For instance, exploratory behaviour differs between sexes in zebra finches (*Taeniopygia guttata*) but not in great tits (*Parus major*) (Dingemanse et al. 2002; Schuett and Dall 2009). In the common waxbill (*Estrilda astrild*) it is body size that influences the response to conspecifics, where larger individuals are more dominant and aggressive (Funghi et al. 2015). Age can also have an important effect on the behaviour in some species, such as in great tits (Carere et al. 2005), but not in others, like common waxbills (*Estrilda astrild*) (Carvalho et al. 2013).

Birds have shown complex behaviours and can be studied in captive conditions, which makes them suitable study models for animal behaviour research (Atwell et al. 2012; Jacobs et al. 2014). The Sardinian warbler (*Sylvia melanocephala*, Gmelin, 1978) is a small resident passerine that can be found in Mediterranean Europe, having a widespread distribution in Portugal (Equipa Atlas 2008; De Juana and Garcia 2015). This

species lives in habitats that have garrigues, maquis and shrubs but also in human-made habitats, such as orchards and gardens (De Juana and Garcia 2015). The Sardinian warbler is a territorial species (Bas et al. 2005) and it feeds mostly on insects (Shirihai et al. 2001). It has already been found behavioural consistency in neophobic behaviour and exploratory behaviour towards a novel object for this species (Mettke Hofmann et al 2005). However, there is no information about other behaviours and about what influences them.

Within the broad context of animal personality, the aims of this work were to understand if the individuals of Sardinian warbler differ in their behavioural responses when submitted to the same stimulus; if individuals show behavioural consistency regarding the context (e.g. exploration context) and if the behaviours are correlated between different contexts; and if the behaviour of individuals is related to the habitat when considering natural habitats and human-altered habitats. For this purpose, the behaviour of the individuals was studied using four behavioural tests: (1) exploration, (2) mirror; (3) predation; (4) tonic immobility.

Methods

This study took place in the experimental estate of the University of Évora – Herdade da Mitra, located in Évora, South Portugal. The area has a Mediterranean climate and is characterized by natural habitats (woodlands and scrublands) and human-altered habitats (gardens and orchards). Fieldwork was carried out between November 2017 and February 2018 outside the breeding season of the Sardinian warbler. We used mist nests to capture a total of 30 individuals of Sardinian warbler, which were then submitted to the behavioural tests (first trial). Individuals were banded with a ring with a unique alfa-numerical code. We recaptured 9 males of the 30 previously studied individuals, and these were resubmitted to the behavioural tests (second trial). The first and the second trial were separated by a minimum interval of 15 days to avoid learning (Herborn et al. 2010; Schuett et al. 2011; Edelaar et al. 2012). To evaluate the relationship between behaviours and the habitat, we captured the individuals in two habitat types: natural and human-altered.

Before the birds were submitted to the behavioural tests, we collect morphometric measures including: the length of the (1) wing, (2) tarsus, (3) third primary feather

(Svensson 1992), (4) bill, (5) the distal length of the bill, (6) bill gape width (Hulsman 1981), and (7) weight. The first three measures are considered a good indicator of body size (Jenni and Winkler 1989; Wyllie and Newton 1994; Wiklund 1996; Galván et al. 2012). The bill measurements can reflect dominance as it is used as a weapon and weight can be related to body condition (Serpell 1982; Petrie 1988). We also identified the sex and age of the individuals: sex was determined by the observation of plumage colour and pattern (13 individuals were females and 17 were males) and age was determined through feather traits (Svensson 1992) (20 individuals were first calendar-year individuals and 10 were adults). After the collection of biometric data, the birds were submitted to the four tests by the following order: exploration test, mirror test, predator test and tonic immobility test. The tests were conducted between 09:00 and 17:00 hours and all of the behaviours were recorded in video. The videos were coded using BORIS “Behavioral Observation Research Interactive Software” (Friard and Gamba 2016).

Exploration test

The exploratory behaviour consists in the reaction of individuals when they are facing new situations, such as new habitat (Réale et al. 2007). The exploration test (ET) was conducted in a rectangular cage of 150x50x50 cm (length x width x height; wire mesh 1x1 cm) which was visually and acoustically isolated. The cage was equally and transversally divided by an opaque white card with three equidistantly perches in each half and had a green carpet in the floor. During the experiment, each individual was placed during 1 hour for acclimatisation with access to one half of the cage and with access to fly larvae. After the acclimatisation period, ten minutes of recording started after we covered and prevent the access to food and, simultaneously, removed the opaque white card. This allowed the bird to explore the entire cage (test period adapted from Herborn et al. 2010). We chose this design in order to discriminate the exploratory behaviour (Corey 1978; Carter et al. 2013). We recorded two variables as a measure of exploratory behaviour: “movements-ET” and “time-ET”. The first variable consists in the number of movements in the novel side of the cage. A movement was defined as a flight between two different perches or between a perch, the cage walls and/or the floor. The variable “time-ET” consists in the time spent by the individuals in the novel side of the cage.

Mirror test

The mirror test measures the aggressiveness of an individual towards a conspecific (Réale et al. 2007). For the mirror test (MT) the bird was placed in a rectangular cage of 28x50x36 cm (length x width x height; wire mesh 1x1 cm) with 3 perches equally distant and a brown carpet covering the floor. The mirror was placed on one of the small sides. The first perch was the closest to the stimuli (mirror) and the third the furthest. The cage was visually and acoustically isolated. For acclimatisation, the bird spent 10 minutes in the cage before the start of the recording with the mirror covered with an opaque cardboard. After that period, the bird was video-recorded during 5 minutes with the mirror covered (control period). Then, the mirror was exposed by removing the cardboard with a string and the bird was recorded 5 minutes more (test period adapted from Carvalho et al. 2013).

We selected two variables that allowed us to understand the effect of the mirror on the individuals. The variable “movements-MT” consists in the difference in the number of movements between the test period and the control period. The variable “perch3-MT” consists in the difference between the time spent on perch 3 during the test period and the time spent on perch 3 during the control period. We also chose one variable (aggressive-MT) that is related only to the test period because it comprised aggressive behaviours towards the mirror. In the “aggressive-MT” variable, we included the frequency of two aggressive behaviours demonstrated by the individuals: open the bill directly towards the mirror (i.e. the opponent) and physical attack which are indicators of great aggressiveness among conspecifics in insectivorous passerines with territorial habits (Andrew 1961; Blurton Jones 1968; Verbeek et al. 1996).

Predator test

The reaction of the individuals towards the predator reflects shyness-boldness behaviour (Réale et al. 2007). The predator test (PT) was conducted in a rectangular cage of 28x50x36 cm (length x width x height; wire mesh 1x1 cm) with 3 perches equally distant and a brown carpet covering the floor. The first perch was the closest to the stimuli (predator) and the third the furthest. It was also visually and acoustically isolated from the rest of the environment. For this test, we used a taxidermic tawny owl (*Strix aluco* (L.)) dummy. The tawny owl is a common predator in the study area, and it often

includes passerines in the diet (Manganaro et al. 2000; Balčiauskienė et al. 2005; Santos et al. 2013). The birds had an acclimatization period of 10 minutes followed by 5 minutes of the control period (predator covered) and 5 minutes of the test period (predator exposed). This last 10 minutes (control and test period) were video-recorded. There was a distance of 30 cm between the predator and the side of the cage near it (experiment adapted from Edelaar et al. 2012).

In this test, we selected two variables which enabled us to see the effect that the predator had on the individuals' behaviour: "movements-PT" and "near-PT". The variable "movements-PT" consists in the difference in the number of movements between the test period and the control period, as in the mirror test. The variable "near-PT" expresses the difference between the time spent close to the predator (sum of the time in perch 1 and the cage floor near the owl dummy) in the test period and in the control period.

Tonic immobility test

Tonic immobility (TI) expresses boldness towards a predator (Réale et al. 2007; Edelaar et al. 2012). For the tonic immobility test the bird was dorsally placed on a platform inside a rectangular cage of 28x50x36 cm (length x width x height; wire mesh 1x1 cm). The bird was held gently in the dorsal position for 30 seconds in order to enter into tonic immobility. After that period, the researcher's hands slowly released the bird. If the bird stayed in the same position for more than 5 seconds we considerate that it entered into tonic immobility. If not, we repeated this procedure up to a maximum of five times (adapted from Jones et al. 1994; Edelaar et al. 2012). We had one individual in the first trial that, after repeating the procedure five times did not enter into tonic immobility. So, this individual was excluded from the analysis involving this test. We also had one individual in the second trial in the same condition, therefore it was excluded from the analysis involving the same trial. During the test, the researcher would stare, without making any noise or movement, at the bird in order to simulate a predator (Gallup 1977; Gallup and Rager 1996).

We selected one variable that enabled us to understand the individuals' behaviour in this test: "number-TI". This variable consists in the number of repetitions until the bird entered in tonic immobility.

Ethical note

This study was conducted under a permit from the legal authority in Portugal – Instituto de Conservação da Natureza e das Florestas (ICNF). No birds were injured in order to do this work. The handling of the birds was conducted accordingly to the ringers' guide of this institution (ICNF) and North America (North American Banding Council 2001).

Statistical analyses

In order to verify if the explanatory variables were strongly related to each other (collinearity), we applied a Spearman's rank correlation (continuous variables) or chi-squared test (categorical variables). None of the variables in the study had a correlation value superior to $|0.7|$, so they all were included in the analysis. The variables age, sex, and habitat were categorical, whereas the other variables (wing length, tarsus length, third primary feather, bill length, distal bill length, bill gape width and weight) were continuous.

To analyse our data, we use AIC-based model selection approach – multimodel inference (Burnham and Anderson 2002). We chose this approach because it incorporates the model selection uncertainty (Burnham et al. 2011). We used the above-mentioned explanatory variables to explain the behavioural differences between individuals in the four tests. We used generalised linear models for each dependent variable (10) described above. Because only the individuals of the first trial were included ($N=30$), we limited our models to a maximum of three explanatory variables (Harrell 2001). We ran all possible models, including the null model as a measure of model fitness. We did not exclude any explanatory variable from the multimodel inference analysis because all of them have a priori biological meaning in this context. Also, this procedure allows every explanatory variable to be represented equally in the set of possible models. For each response variable, the output is a set of possible models, ranked by their AICc values (Akaike information criterium corrected for small sample sizes). The $\Delta AICc$ (difference in AICc) and the Akaike weight (w_i) were used to compare models. We considered as competing models those with $\Delta AICc$ inferior to 2 (Burnham and Anderson 2003). We also calculated the relative importance of explanatory variables (sum of the w_i in all models including a given variable). For the model averaging we used

the zero method in order to analyse which explanatory variable had the strongest effect (Nakagawa and Freckleton 2010). Models were validated for goodness of fit through the model diagnostic plots. In order to see if the behaviours shown by the individuals in the different tests were correlated, we used Spearman's rank correlation. Behavioural consistency was evaluated across the two trials, using Wilcoxon signed-rank test. For these two analyses, we used a significance value of 0.05.

All the statistical analyses were conducted in R version 3.3.1 (R Core Team 2016), with the packages "MuMIn" (Barton 2009), "gplots" (Warnes et al. 2016), "asht" (Fay 2017) and "psych" (Revelle 2016), "Mass" (Ripley et al. 2013).

Results

Exploration test

Movements-ET – The set of 17 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, tarsus length, third primary feather length, distal bill length, bill gape width, weight, age, habitat (Table 1). The null model was included in the best models (indicating that the predictor variables may have little explanatory power). Bill gape width appeared to be the predictor with the strongest relationship with the number of movements on the novel side (RVI = 0.47). The larger the width the less explorative the birds were. Tarsus length was the second most important variable (RVI = 0.41), and together with the variables wing length and weight, it suggests that individuals with larger body size explored more.

Time-ET – The set of 6 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, third primary feather, bill gape width, weight, sex, age and habitat (Table 1). The null model was not included in the best models. Bill gape width appeared to be the predictor with the strongest influence on the time spent on the novel side of the cage (RVI = 1). Where individuals with a larger width explored less. This measure was present in every model obtained for this variable. Weight was present in four of the best models, suggesting to be the second more important predictor (RVI = 0.61). Heavier individuals explored less. The other predictors only appeared once in the set of the competing models. Nevertheless, these variables may have influenced the time spent on the novel side. The larger the wings the less explorative the birds were; males, first calendar-year individuals or individuals that live in human-altered habitats tended to be

Table 1. Results of the multimodel inference approach for the variables used in the exploration test

	Movements-ET		Time-ET	
	RVI	Direction	RVI	Direction
Wing length	0.25	+	0.18	-
Tarsus length	0.41	+		
Third primary feather length	0.16	+	0.11	+
Distal bill length	0.08	-		
Bill gape width	0.47	-	1	-
Weight	0.22	+	0.61	-
Sex			0.21	-
Age	0.09	-	0.11	-
Habitat	0.05	-	0.11	-

less explorative; finally, individuals with longer third primaries tended to explore more (Table 1).

Behavioural consistency across trials – The exploratory behaviour presented by the individuals appeared to be consistent across the two trials (movements-ET: Hodges-Lehmann estimator = -11.50, P=0.08; time-ET: Hodges-Lehmann estimator = -13.00, P=0.09).

Mirror test

Movements-MT – The set of 4 competing models ($\Delta AICc < 2$) included the explanatory variables third primary feather, bill length and habitat (Table 2). The null model was included in the best models (indicating that the predictor variables may have little explanatory power). The length of the third primary feather had the high relative importance influencing the number of movements done by individuals (RVI = 0.27). The bigger the length of the feather the more movements were done by individuals when showed the mirror. The habitat and the bill length also appeared to influence the number of movements. Individuals with bigger bills or that live in human-altered habitats moved less upon the mirror.

Table 2. Results of the multimodel inference approach for the variables used in the mirror test

	Movements-MT		Perch3-MT		Aggressive-MT	
	RVI	Direction	RVI	Direction	RVI	Direction
Wing length			0.1	–	0.19	+
Tarsus length			1	–		
Third primary feather length	0.27	+	0.25	–		
Bill length	0.14	–			1	+
Distal bill length			0.8	–	0.19	+
Weight			0.1	+		
Age			0.21	+		
Habitat	0.22	–			0.2	–

Perch-MT – The set of 7 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, tarsus length, third primary feather length, distal bill length, weight and age (Table 2). The null model was not included in the best models. Tarsus length had the greater importance in measuring the repellent effect of the mirror (RVI = 1). Individuals with bigger tarsus length would be less repelled by the mirror. This effect seems to be the same for the wing length and third primary feather length. The distal bill length also appeared to have a strong influence (RVI = 0.8), suggesting that individuals with bigger measures would be less repelled by the mirror. Finally, the age and the weight were included in the best models, suggesting that first calendar-year individuals or heavier individuals would be repelled by the mirror.

Aggressive-MT – The set of 4 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, bill length, distal bill length and habitat (Table 2). The null model was not included in the best models. Bill length takes a primary role in influencing the aggressive behaviours (RVI = 1). The bigger the length of the bill the more aggressive the Sardinian warblers were. This is also true relating the distal width of the bill. The data also suggested that individuals with bigger wings and that live in natural habitats were more aggressive.

Table 3. Results of the multimodel inference approach for the variables used in the predator test

	Movements-PT		Near-PT	
	RVI	Direction	RVI	Direction
Wing length			0.1	–
Tarsus length	0.15	–		
Bill length	0.1	+	1	+
Distal bill length			0.24	–
Bill gape width	0.22	+		
Weight			1	+
Sex	0.25	+	0.12	–
Age			0.27	+
Habitat	0.13	–		

Behavioural consistency across trials – Sardinian warblers showed behavioural consistency across the two trials (movements-MT: Hodges-Lehmann estimator = -17.00, P=0.33; perch3-MT: Hodges-Lehmann estimator = -120.50, P= 0.10; aggressive-MT: Hodges-Lehmann estimator = -0.00, P= 0.75).

Predator test

Movements-PT – The set of 7 competing models ($\Delta AICc < 2$) included the explanatory variables tarsus length, bill length, bill gape width, sex and habitat (Table 3). The null model was included in the best models (indicating that the predictor variables may have little explanatory power). The variable sex assumed the strongest importance in relation to the number of movements (RVI = 0.25), with males moving more upon the predators than females. Bill length and bill gape width had a positive relation with the variable “movements-PT”. On the contrary, the variable tarsus length had a negative relation with the “movements-PT”. Individuals that live in human-altered habitats tended to move less upon the predator.

Table 4. Results of the multimodel inference approach for the variables used in the tonic immobility test

	Number-TI	
	RVI	Direction
Wing length	0.07	–
Tarsus length	0.63	+
Third primary feather length		
Bill length		
Distal bill length		
Bill gape width	0.48	–
Weight		
Sex	0.21	–
Age	0.07	–
Habitat		

Near-PT – The set of 5 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, bill length, distal bill length, weight, sex and age (Table 3). The null model was not included in the best models. Weight and bill length (RVI = 1) influenced the time spent near the predator, where individuals with smaller bill length and weight were repelled by the presence of the predator. Age, distal bill length, sex and wing length also appeared to have an effect on time spent near the predator. In adults, individuals with larger distal bill length, wing length or males were more repelled by the predator

Behavioural consistency across trials – The behaviour showed by the individuals seemed to be consistent across the two trials (movements-PT: Hodges-Lehmann estimator = -0.51, $P=0.91$; near-PT: Hodges-Lehmann estimator = -58.50, $P=0.10$).

Tonic immobility test

Number-TI – The set of 8 competing models ($\Delta AICc < 2$) included the explanatory variables wing length, tarsus length, bill gape width, sex and age (Table 4). The null model was included in the best models (indicating that the predictor variables may have little explanatory power). Tarsus length appeared to have the strongest influence on the number of times that took an individual to entered in tonic immobility (RVI = 0.63). The

bigger the measure the more times it took to be in tonic immobility. The other four variables that entered in the top models had a negative relation with the number of times that it took to be in tonic immobility. The bigger the wing length or the bill gape width the less number of times it took to be in tonic immobility. Furthermore, males or first calendar-year individuals also took less number of times to enter in tonic immobility.

Behavioural consistency across trials – The behaviours presented by the individuals was consistent across the two trials (number-TI: Hodges-Lehmann estimator = 0.00, $P=0.75$).

Correlation between tests

The variables movements-MT and movements-PT in the predator and mirror tests were correlated ($r_s=0.44$, $P=0.02$). Individuals that moved more upon the mirror also moved more when facing the predator. Furthermore, the variable aggressive-MT (mirror test) and the variable number-TI (tonic immobility test) appeared to be also correlated ($r_s=0.37$, $P=0.05$). Individuals that express more aggressive behaviours took longer to enter in tonic immobility.

Discussion

According to our tests Sardinian warblers seem to differ in their behaviour depending of several individual traits. We verified the existence of behavioural consistency, suggesting that animal personality is possibly marked in this species. We also found that the individual movement behaviour seems to be positively correlated between tests, as aggressiveness and boldness (tonic immobility). In addition, we observed that the exploration and aggressive behaviours were apparently related with habitat type.

Sardinian warblers showed consistent behaviours across time, and consequently it indicates a marked personality, regarding the four behavioural tests: (1) exploration, (2) mirror; (3) predation; (4) tonic immobility. This has ecological implications since personality can affect fitness (Dingemanse et al. 2004; Smith and Blumstein 2008). Our results showed that less exploratory and less aggressive individuals live in human-altered habitats. This might seem contradictory to other studies, where passerine birds that are more exploratory and aggressive are better suited to cope in human-altered habitats (Evans et al. 2010; Sol et al. 2011). However, in this study, the two habitat types are very

close to each other and individuals could go from one habitat to another. Our results may be explained based on optimal and suboptimal habitats, where birds that live in human-altered habitats (suboptimal) are displaced from the more natural habitats (optimal) by dominant birds (Krebs 1971; Murray 1971; Robertson 1972). There is often a positive relation between dominance and exploratory behaviour (Verbeek et al. 1996; Dingemanse and De Goede 2004; Cole and Quinn 2012). This could explain why individuals in natural habitats are more explorative. Also, individuals that explore more are usually better in defending a high-quality territory (Both, Dingemanse, Drent, & Tinbergen, 2005). Accordingly to Luttbeg & Sih (2010), species that live in high-quality habitats should be more explorative, and thus able to obtain more resources. Also, individuals that live in optimal habitats should have to spend a greater effort to defend the territories (Fretwell 1972). These individuals would be more aggressive and would displace the defeated individuals to the human-altered habitat (Verner 1977; Silverin 1998).

Individuals that made more movements when facing the mirror also moved more when facing the predator. The movements made by the individuals appear to express escape behaviours, as in other studies with birds (Gallup et al. 1971; Keer-Keer et al. 1996; Edelaar et al. 2012). This behaviour could have important fitness consequences, influencing antipredator behaviour or intra-specific competition (David et al. 2011). Individuals that are more aggressive tended to take more tries to enter in tonic immobility. This means that more aggressive individuals are also bolder. This behavioural syndrome has been recorded and studied in several animal groups, such as fishes, birds and mammals (Bell and Sih 2007; Dochtermann and Jenkins 2007; Evans et al. 2010). Depending on the environmental characteristics (i.e. patterns in predation risk and food resources), behaviours can be advantageous or disadvantageous (Sih et al. 2004; Powell and Gartner 2011; Sih et al. 2012). Therefore, individuals will be restricted to certain type of habitats accordingly with the behaviours presented (Duckworth 2006; Sih et al. 2004). The differences in behaviour of individuals according to the habitat are very important to species conservation, as it allows predicting the species reaction to human-altered habitats (Powell and Gartner 2011).

Exploratory behaviour was influenced by several traits. In our study, Sardinian warblers with smaller bill gape explored more, probably because they are more restricted in

relation to prey-size items comparing with birds with larger bill gapes (Hulsman 1981; Saunders et al. 1995; Kloskowski 2003). Therefore, birds with smaller bill gape may need to explore more in order to find suitable size-prey items. Also, lighter birds would not probably feed for a longer time than heavier birds, and so they may be compelled to be more explorative to find food. The Sardinian warbler's adults have larger territories than first calendar-year individuals (Bas et al. 2005) and it is possible that this influences positively their ability to explore. Adults are dominant and have more experience than juveniles in many insectivorous passerines species (Hogstad 1987; Enoksson 1988; Sandell and Smith 1991), which may also explain why adults explored more comparing with juveniles. We found that males were less explorative than females, which might seem contradictory since in many passerines species males are dominant over females (Hogstad 1987; Enoksson 1988). Nevertheless, Sardinian warbler's males defend their territory in winter (Cramp and Brooks 1992) and therefore males may be less exploratory than females. Aggressive behaviour, as exploratory behaviour, is related positively with dominance (Noble 1939). Individuals with larger body and bill size were more aggressive and less repelled by the mirror. The body size acts as a clue for the fighting ability and in many species, larger individuals have a competitive advantage over smaller individuals (Parker 1974; Petrie 1988; Funghi et al. 2015). The Sardinian warblers use the bill as a weapon, so its size is also a clue for the fighting ability (Serpell 1982; Petrie 1988), explaining our findings for bill measurements. Adults tend to be dominant and have more experience than first calendar-year individual (Arcese and Smith 1985; Sandell and Smith 1991), which are less experienced in confrontations, and therefore would try to keep a greater distance from the opponent (Arcese and Smith 1985). In turn, adults have a higher probability to have encountered a predator, as they have more life experience. It is possible that they would identify the tawny owl a greater threat than first calendar-year individuals, that tended to be more naïve (Enoksson 1988; Carlson et al. 2017). We could not find an individual trait that explained the variation for tonic immobility response. We would expect similar results to the predator because they both measure the same trait (boldness Réale et al. 2007). Nevertheless, tonic immobility test is much more invasive than the predator test, since it involves handling restraint. So, it is possible that the explanatory variables affecting the response of the predator test may be different from those affecting tonic immobility. Tonic immobility could be related with

physiological characteristics, as corticosterone response (Cockrem 2007). Corticosterone responses levels (high or low) and its plasticity affects the capacity of birds to cope with new stimuli and therefore, with environmental changes (Cockrem 2013). Future studies would be needed to understand the how behaviour and corticosterone response may affect the establishment of individuals in human-altered habitats.

In this study, we found that Sardinian warbler shows consistent behaviours across time. We also found that habitat and behaviour are related to each other, where individuals less exploratory and less aggressive live in human-altered habitats. In a changing world, ecosystems and habitats are being altered and it is important to understand if behaviour assumes a key role in the establishment of individuals in new areas. Furthermore, is important to understand how behaviour can be advantageous or disadvantageous in different types of habitats.

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Final remarks

Sardinian warblers appeared to have individual differences regarding exploratory behaviour, aggressive behaviour, and boldness behaviour, which suggests a role for animal personality in this species. They also showed two behavioural syndromes which has ecological and fitness implications. The habitat type occupied by Sardinian warblers were related with their behaviour. Individuals that were more aggressive and explorative inhabit the optimal places. These individuals may be displacing the others to suboptimal habitats (Krebs 1971; Murray 1971). The role of personality in human-altered habitats as begin to attract many researchers (Sih et al. 2004; Sih and Del Giudice 2012), which can bring new field knowledge on how to conserve and protect species in these new habitats.

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Appendix

Table 5. Set of best models obtained for the variable time-ET

Explanatory variables	df	Log-likelihood	AIC _c	ΔAIC _c	Akaike weight
Bill gape width + weight	4	-142.60	294.79	0.00	0.28
Bill gape width + sex	4	-142.89	295.38	0.59	0.21
Bill gape width + wing length	4	-143.05	295.71	0.91	0.18
Bill gape width + age + weight	5	-142.07	296.64	1.85	0.11
Bill gape width + third primary feather + weight	5	-142.07	296.65	1.85	0.11
Bill gape width + habitat + weight	5	-142.12	296.74	1.94	0.11

Table 6. Model averaging results obtained for the variable time-ET

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	29.93	11.95	12.31	2.43	0.012	
Bill gape width	-2.03	0.76	0.80	2.55	0.01	1
Weight	-0.61	0.60	0.61	1.02	0.31	0.61
Sex	-0.31	0.65	0.66	0.47	0.64	0.21
Wing length	-0.07	0.18	0.18	0.41	0.68	0.18
Age	-0.07	0.30	0.31	0.24	0.81	0.11
Third primary feather	0.012	0.05	0.05	0.23	0.82	0.11
Habitat	-0.06	0.25	0.26	0.23	0.82	0.11

Table 7. Set of best models obtained for the variable movements-ET

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
Wing length	3	-111.97	230.86	0.00	0.11
Bill gape width + tarsus length	4	-110.69	230.98	0.12	0.10
Bill gape width	3	-112.17	231.25	0.40	0.09
Weight + tarsus length	4	-111.10	231.80	0.94	0.07
Weight	3	-112.55	232.03	1.17	0.06
Third primary feather	3	-112.60	232.13	1.27	0.06
Wing length + tarsus length	4	-111.38	232.36	1.50	0.05
Age	3	-112.78	232.48	1.62	0.05
Bill gape width + habitat + tarsus length	5	-109.99	232.49	1.63	0.05
Bill gape width + third primary feather + tarsus length	5	-110.00	232.49	1.63	0.05
Bill gape width + third primary feather	4	-111.46	232.52	1.66	0.05
(Null)	2	-114.09	232.63	1.77	0.05
Bill gape width + age	4	-111.53	232.66	1.81	0.04
Bill gape width + weight + tarsus length	5	-110.10	232.70	1.85	0.04
Bill gape width + wing length	4	-111.58	232.76	1.90	0.04
Distal bill length + wing length	4	-111.63	232.86	2.00	0.04
Distal bill length + weight + tarsus length	5	-110.18	232.86	2.00	0.04

Table 8. Model averaging results obtained for the variable movements-ET

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-7.16	14.50	14.77	0.46	0.63	
Wing length	0.09	0.18	0.19	0.46	0.64	0.25
Bill gape width	-0.59	0.83	0.84	0.70	0.48	0.47
Tarsus length	0.34	0.50	0.51	0.67	0.50	0.41
Weight	0.18	0.39	0.40	0.44	0.66	0.22
Third primary feather	0.03	0.08	0.08	0.32	0.75	0.16
Age	-0.08	0.32	0.32	0.25	0.80	0.09
Habitat	-0.04	0.20	0.20	0.176	0.86	0.05
Distal bill length	-0.16	0.71	0.72	0.23	0.82	0.08

Table 9. Set of best models obtained for the variable movements-MT

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
(Null)	2	-179.42	363.28	0.00	0.37
Third primary feather	3	-178.47	363.86	0.58	0.27
Habitat	3	-178.71	364.34	1.05	0.22
Bill length	3	-179.13	365.18	1.90	0.14

Table 10. Model averaging results obtained for the variable movements-MT

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-146.09	380.36	389.05	0.38	0.71	
Third primary feather	2.75	5.9	6.02	0.46	0.65	0.27
Habitat	-8.95	23.69	24.22	0.37	0.71	0.22
Bill length	-4.23	18.4	18.97	0.22	0.82	0.14

Table 11. Set of best models obtained for the variable perch3-MT

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
Distal bill length + third primary feather + tarsus length	5	-177.07	366.65	0.00	0.25
Distal bill length + tarsus length	4	-178.54	366.68	0.03	0.25
Distal bill length + age + tarsus length	5	-177.90	368.30	1.65	0.11
Tarsus length	3	-180.74	368.40	1.75	0.10
Age + tarsus length	4	-179.43	368.46	1.81	0.10
Distal bill length + weight + tarsus length	5	-178.03	368.56	1.91	0.10
Distal bill length + wing length + tarsus length	5	-178.04	368.57	1.92	0.10

Table 12. Model averaging results obtained for the variable perch3-MT

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	1901.01	864.78	889.98	2.14	0.03	
Distal bill length	-151.91	114.07	116.79	1.3	0.19	0.8
Third primary feather	-3.17	6.73	6.84	0.46	0.64	0.25
Tarsus length	-57.06	27.62	28.9	1.98	0.05	1
Age	11.17	28.98	29.57	0.38	0.71	0.21
Weight	2.53	11.57	11.88	0.21	0.83	0.1
Wing length	-1.28	5.91	6.07	0.21	0.83	0.1

Table 13. Set of best models obtained for the variable aggressive-MT

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
Bill length	3	-64.30	135.53	0.00	0.42
Bill length + habitat	4	-63.68	136.96	1.44	0.20
Distal bill length + bill length	4	-63.73	137.07	1.54	0.19
Wing length + bill length	4	-63.77	137.13	1.61	0.19

Table 14. Model averaging results obtained for the variable aggressive-MT

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-27.35	13.18	13.7	2	0.05	
Bill length	1.76	0.81	0.84	2.09	0.04	1
Habitat	-0.17	0.45	0.46	0.37	0.71	0.2
Distal bill length	0.35	0.99	1.02	0.34	0.73	0.19
Wing length	0.05	0.14	0.14	0.33	0.75	0.19

Table 15. Set of best models obtained for the variable movements-PT

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
(Null)	2	-174.27	352.99	0.00	0.25
Tarsus length	3	-173.52	353.97	0.98	0.15
Sex	3	-173.58	354.09	1.09	0.15
Habitat	3	-173.69	354.31	1.32	0.13
Bill gape width	3	-173.79	354.51	1.51	0.12
Bill gape width + sex	4	-172.61	354.82	1.83	0.10
Bill length	3	-174.00	354.93	1.94	0.10

Table 16. Model averaging results obtained for the variable movements-PT

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-48.39	383.52	391.76	0.12	0.9	
Tarsus length	-4.11	12.97	13.23	0.31	0.76	0.15
Sex	9.69	22.83	23.29	0.42	0.68	0.25
Habitat	-4.12	15.18	15.53	0.27	0.79	0.13
Bill gape width	9.86	26.51	27.11	0.36	0.72	0.22
Bill length	2.33	12.72	13.12	0.18	0.86	0.1

Table 17. Set of best models obtained for the variable near-PT

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
Bill length + age + weight	5	-171.42	355.35	0.00	0.27
Bill length + weight	4	-172.93	355.46	0.11	0.26
Bill length + weight + distal bill length	5	-171.55	355.60	0.25	0.24
Bill length + weight + sex	5	-172.21	356.91	1.57	0.12
Bill length + weight + wing length	5	-172.40	357.30	1.96	0.10

Table 18. Model averaging results obtained for the variable near-PT

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-2026.18	738.03	763.92	2.65	0.01	
Bill length	105.2	36.51	38.15	2.76	0.01	1
Age	17.19	34.32	34.89	0.49	0.62	0.27
Weight	57.47	24.22	25.25	2.28	0.02	1
Distal bill length	-28.63	62.82	63.89	0.45	0.65	0.24
Sex	-5.21	18.95	19.39	0.27	0.79	0.12
Wing length	-1.15	5.04	5.17	0.22	0.82	0.1

Table 19. Set of best models obtained for the variable number-TI

Explanatory variables	df	Log-likelihood	AIC _c	Δ AIC _c	Akaike weight
Tarsus length	3	-29.00	64.96	0.00	0.18
(Null)	2	-30.30	65.06	0.10	0.18
Bill gape width + tarsus length	4	-27.75	65.17	0.22	0.17
Bill gape width + tarsus length + sex	5	-26.60	65.80	0.84	0.12
Bill gape width	3	-29.43	65.83	0.87	0.12
Tarsus length + sex	4	-28.36	66.38	1.42	0.09
Age	3	-29.94	66.85	1.89	0.07
Bill gape width + tarsus length + wing length	5	-27.16	66.93	1.97	0.07

Table 20. Model averaging results obtained for the variable number-TI

	Estimate	SE	Adjusted SE	z	p-value	RVI
(Intercept)	-5.92	11.73	12.02	0.49	0.62	
Tarsus length	0.56	0.58	0.59	0.95	0.34	0.63
Bill gape width	-0.67	0.91	0.93	0.73	0.47	0.48
Sex	-0.17	0.43	0.44	0.39	0.7	0.21
Age	-0.04	0.21	0.22	0.17	0.86	0.07
Wing length	-0.01	0.08	0.08	0.19	0.85	0.07

Table 21. Spearman's rank correlation values between response variables (p- value for Spearman's rank correlation)

	time-ET	movements-ET	movements-MT	pearch3-MT	agonistic-MT	close-PT	movements-PT	number-TI
time-ET	1.00 (0.00)	0.74 (0.00)	0.05 (0.81)	-0.15 (0.43)	-0.17 (0.39)	-0.30 (0.11)	-0.09 (0.64)	0.07 (0.71)
movements-ET	0.74 (0.00)	1.00 (0.00)	-0.08 (0.67)	-0.15 (0.44)	0.01 (0.96)	-0.04 (0.83)	-0.08 (0.68)	0.05 (0.79)
movements-MT	0.05 (0.81)	-0.08 (0.67)	1.00 (0.00)	0.29 (0.13)	-0.35 (0.06)	-0.26 (0.17)	0.44 (0.02)	0.26 (0.17)
pearch3-MT	-0.15 (0.43)	-0.15 (0.44)	0.29 (0.13)	1.00 (0.00)	-0.15 (0.44)	0.18 (0.36)	0.24 (0.20)	-0.06 (0.75)
agonistic-MT	-0.17 (0.39)	0.01 (0.96)	-0.35 (0.06)	-0.15 (0.44)	1.00 (0.00)	0.15 (0.45)	-0.17 (0.39)	0.37 (0.05)
close-PT	-0.30 (0.11)	-0.04 (0.83)	-0.26 (0.17)	0.18 (0.36)	0.15 (0.45)	1.00 (0.00)	-0.11 (0.57)	-0.05 (0.81)
movements-PT	-0.09 (0.64)	-0.08 (0.68)	0.44 (0.02)	0.24 (0.20)	-0.17 (0.39)	-0.11 (0.57)	1.00 (0.00)	-0.14 (0.47)
number-TI	0.07 (0.71)	0.05 (0.79)	0.26 (0.17)	-0.06 (0.75)	0.37 (0.05)	-0.05 (0.81)	-0.14 (0.47)	1.00 (0.00)