Survival of the smartest? An inquiry into behavioural character displacement in a *Passer* species.

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Abstract

Character displacement can happen where two closely related species live in the same area and compete over the same resources. The ecological displacement that usually precedes the character displacement may force the species to change their foraging strategy, which could put a certain selective pressure on behaviour.

Italian sparrows (*Passer italiae*) may be experiencing such a selective pressure where it lives in sympatry with the closely related Spanish sparrow (*Passer hispaniolensis*).

In this study I have used stable isotopes to compare the diets of two sympatric populations of Italian sparrows and performed controlled behavioural experiments on sympatric Italian and Spanish sparrows to look for species differences.

I found evidence for ecological displacement of the sympatric Italian sparrows, and between-species differences in exploratory behaviour.

Although additional behavioural studies of allopatric populations are necessary for testing the hypothesis of behavioural character displacement, hopefully this study can be a stepping stone for such future studies.

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1. Introduction

Character displacement is when closely related species diverge from one another where they live in the same area (sympatry) relative to where they live in different areas (allopatry). Sharing the same space makes relatively similar species more different from each another. That is, when in the same area they tend to "displace" one another ecologically, physiologically or behaviourally in one or more traits (Brown and Wilson 1956).

As closely related species often overlap in important traits such as habitat and food preferences, they are predicted to compete over these resources in sympatry (Brown and Wilson 1956). This competition may lead to an ecological displacement as a result of one or both species experiencing selection for changing their niche in such a way that the overlap of the competitors' niches (and thus competition) is reduced (Reif et al. 2018; Peers, Thornton, and Murray 2013).

Changes in niche sometimes require new or adjusted adaptations to foraging. Among the well-known examples of this are the three-spine sticklebacks (*Gasterosteus* spp.) where closely related species have developed different morphologies adapted to exploiting different resources in the same lake (Schluter 1995). Another example is two closely related species of *Plethodon* salamanders that have different jaw mechanics adapted to catching different types of prey in sympatry but not in allopatry (Adams and Rohlf 2002).

However, changes in morphology is not the only way for a species to respond to competition. For instance, a species may instead respond by adopting new foraging strategies. Certain behaviours may be more adequate than others and natural selection may thus favour the behavioural changes best suited for exploiting new resources.

Behavioural traits can have substantial heritability (Dingemanse et al. 2003; Sol et al. 2005) and consequences for fitness, and are thus likely targets for natural selection (Bell and Sih 2007; Karlsson Green et al. 2015; Laine et al. 2016) and character displacement. For instance, innovative behaviour can be advantageous when a species is adapting to novel conditions (Sol et al. 2005) and may therefore be targeted by character displacement when closely related species come in to secondary contact. A recent study (Sætre et al. 2017) indicates that such behavioural character displacement may be affecting a population of Italian sparrows (*Passer italiae*) living in the nature reserve of Lago Salso in the Gargano peninsula in east-central Italy. After the population experienced secondary contact with the closely related Spanish sparrow (*P. hispaniolensis*) in 2013 it has diverged genetically from that species at genes known to be involved in learning and cognition.

The Italian sparrow is a homoploid hybrid species that originated from past episodes of hybridization between the Spanish sparrow and the house sparrow (*P. domesticus*) (Hermansen et al. 2011; Elgvin et al. 2017). The three species are seed eating birds and are relatively similar in morphology and feeding ecology, although the Italian and House sparrow

are more associated with humans than is the Spanish sparrow, which normally occupy more mesic habitats (Summers-Smith 1988; Anderson 2006). That is, the Italian sparrow and house sparrow share a human commensal niche whereas the Spanish sparrow is "wilder" However, in farmland they may still occur together in sympatry. This is the case in certain places in the Gargano peninsula, where the Spanish sparrow established breeding colonies for just a little more than 20 years ago (Eroukhmanoff et al. 2014). The Italian sparrow population in Lago Salso, however, was allopatric until 2013.

When Sætre and colleagues started collecting genetic and morphological data from the Italian sparrow population at Lago Salso in 2012 the birds were seen feeding in large flocks both at a cereal field near the field station of Lago Salso and in a farm area associated with the station where a poultry pen was a popular feeding site. Then, after a group of Spanish sparrows settled in Lago Salso in 2013 a few noteworthy things happened with the Italian sparrow population (Sætre et al. 2017):

1) Habitat segregation: Italian sparrows were driven away from the cereal filed (likely chased off by the Spanish sparrows) in which they previously fed, becoming confined to the areas near the farm, mainly feeding from the poultry pen.

2) Reduced population size and body condition: Both effective and census population size was reduced (by 40% and 61% respectively) and the birds got a lower body mass-to-tarsus length ratio.

3) Genetic displacement: The Italian sparrows in Lago Salso diverged from the Spanish sparrow, particularly at genes involved in learning and cognition, in accordance with the theory of character displacement (Brown and Wilson 1956).

The genetic divergence that followed the settlement of the Spanish sparrow in Lago Salso was found to be paralleled in other and slightly older sympatric populations of the Italian sparrow in the Gargano peninsula. That is, the Italian sparrows that have lived in the same area as the Spanish sparrow for some 20 years were genetically more different from Spanish sparrows than were allopatric ones (Sætre et al. 2017).

This raises the question of whether there exists any phenotypical displacement that reflects this displacement of alleles? What consequences does sympatry have for their ecological niches? Has there been selection for a certain phenotype in the Italian sparrow population displacing it further from the Spanish phenotype? Which trait(s) have in that case been selected for and is thus being displaced? So far, no morphological displacements have been found (Eroukhmanoff et al. 2014; Sætre et al. 2017). As already mentioned, the loci that had diverged the most from the Spanish sparrow were genes associated with brain development, photoreception, learning, motricity and cognition in other vertebrate species (some of them birds) (Enright et al. 2014; Sugino et al. 2005; Xu et al. 2011; Brunkhorst et al. 2005; Seeher et al. 2014, but see Sætre et al. 2017 for the list of genes in question). Thus, the question is whether there is a displacement in any behavioural trait related to cognition?

However, how do we measure cognitive traits? The problem starts with the definition itself; there is no clear-cut and generally accepted definition of cognition in the literature. Yet one

widely accepted understanding of cognition is as ways in which animals take in sensory information, process, retain and act on it (Shettleworth 2001; Morand-Ferron, Cole, and Quinn 2016). This implies that variation in cognition can be due to everything from variation in sensory predispositions to variation in motor skills. Such a broadly defined quality is hard to measure directly. Traditionally, however, researchers have obtained measurements of cognitive traits through observing how animals behave.

Cognition is assumed to underlie certain kinds of behaviours involved in problem solving performance (Cole, Cram, and Quinn 2011; Ferron et al. 2016). One problem with obtaining a measure of cognition from such behaviours is that although an individuals' problem-solving performance in one task may be consistent over time (Medina-García, Jawor, and Wright 2017), performances in different types of tasks often appear not to be correlated. This may indicate that different tasks involve different aspects of cognition and that cognition might be a target too broad to hit with just one type of task. Some studies do find correlations among traits linked to cognition (Bouchard, Goodyer, and Lefebvre 2007; Boogert et al. 2011), some do not (Medina-García, Jawor, and Wright 2017; Anderson et al. 2017), whereas others have mixed results: Although performances in different cognitive tasks may not show much correlation, principal component analysis explaining most variation in performances in different tasks sometimes point to something like a general cognitive ability (Isden et al. 2013). Thus, it is debatable how much it is possible to infer about an animal's cognition from its performance in a problem-solving task (Rowe & Healy 2014). Yet, any problem-solving task will conceivably reveal something about some cognitive process and even if we cannot get the whole picture, one piece of it may yield more understanding than no piece.

What kind of task is suited to target at least one aspect of cognition? According to Shettleworth (2001) and Ferron (2016), one that requires an animal to demonstrate one or more of the faculties cognition is considered to comprise. This would include showing itself capable to take in information (sensing) and act on it (motricity) in such a way that it seems likely that the information has been taken into the actions' account (retaining and processing). Preferably the task should also be novel, in order to minimize the chance of the action being a result of "pre-programmed" behaviour, or more of a direct stimulus-response, that excludes the processing aspect of cognition.

Tasks that typically have been used for such purpose are extractive foraging tasks because, in addition to incorporating the requirements just mentioned, they are also ecologically relevant.

Some examples from behavioural studies of House sparrows include tasks involving transparent food containers covered by either a lid or a piece of paper, or with food trapped above a slot. The birds are then challenged to find a way to flip open the lid, pierce through the paper or pulling the slot to access the food (Papp et al. 2014; Bókony et al. 2014)

Tasks for bigger birds, like the Carib grackle (*Quiscalus lugubris*), could consist of flicking open a hinged food container by probing at the right places near the hinge (Overington et al. 2011).

All these tasks require the animal to interact with a novel device, process the devices' "response" to that interaction and adjust its next action to that response. In the latter example,

this means that the bird must notice that the opening of the container increases the closer to the hinge he probes.

The relationship problem-solving behaviour and personality is not well established. Personality is defined as consistent individual differences over time and across context and, although individual differences in performance in tasks like these appear consistent, at least over time, it is debated whether problem-solving performance should be considered part of personality or not. Traditionally they are treated as separate phenomena (Morand-Ferron, Cole, and Quinn 2016).

Studies of the relationship between personality and problem-solving behaviour have yielded mixed results, which may have to do with its complexity; the relationship may vary with other factors, such as age (Zidar et al. 2018). There have been found positive (Overington et al. 2011), negative (Lermite, Peneaux, and Griffin 2017) and no (Cole and Quinn 2012) correlations between exploratory behaviour and problem-solving performance.

One well-studied personality trait is that is both repeatable and heritable is exploratory behaviour (Dingemanse et al. 2003). Studying exploratory behaviour typically involve placing the test subject in a new, unfamiliar space, observing how fast it covers the different areas of this space. This trait is loosely linked to cognition in the sense that it facilitates an animal's encounter with new information about its surroundings (Carere and Locurto 2011; Sih and Del Giudice 2012).

Whether exploratory behaviour should be used to correct for or treated as an additional measure of cognition remains an open question. In either case, measuring exploratory behaviour along with problem-solving is a way of broadening the understanding of an animal's cognitive processes.

To start the investigation of a possible behavioural character displacement, I've looked into clues about diet through stable isotope analyses and run behavioural experiments, testing both problem solving and exploration, on Italian and Spanish sparrows from the sympatric populations of Masseria Mustazzo. We chose Masseria Mustazzo over Lago Salso because the species have been sympatric for longer in the former population, so potential differences in behaviour are expected be more emphatic and easier to detect.

Given that few behavioural studies of these two *Passer* species have been done, it is hard to know exactly which behaviours to look for in order to get good comparative measurements of exploration and problem-solving behaviour, but previous studies of House sparrows have inspired the current study (Liker and Bokony 2009; Bókony et al. 2014))

In this study I

1) Do an analysis of stable nitrogen and carbon isotopes in the feathers of sympatric Italian and Spanish sparrows, to see what consequences sympatry might have for their diets. Isotope analysis is a relatively non-invasive method of inferring differences in diet, as the feather stable isotope ratio reflects the stable isotope ratio in their food sources (Hobson and Clark 1992).

2) Design controlled behavioural experiments for wild-caught Italian and Spanish sparrows in captivity, to evaluate potential species differences in behaviour related to problem solving and exploration.

2. Materials and methods

2.1 Study species and study area
Italian and Spanish sparrow are both members of the genus *Passer*, of relatively similar size, both measuring around 16 cm and typically weighing in the range of 26-30 grams. Males of both species have chestnut red crown and nape and a black bib. The males' species are distinguished by the Spanish sparrow male's more extensive bib and black streaking on the flanks (lacking in the Italian sparrow male).

The females of the two species are uniformly brown, and although the Spanish sparrow female tend to have darker flanks than the Italian sparrow female, they show no reliable species differences in plumage (or other morphological traits).

Both the Italian and the Spanish sparrow are seed-eating, gregarious species, but they have some obvious behavioural differences; the Spanish sparrow is migratory, whereas the Italian sparrow is sedentary (like the House sparrow), and the Italian sparrow is more of a human commensal than the Spanish sparrow.

I've studied sparrows from Masseria Mustazzo and from Lago Salso, both located in the Gargano peninsula (province of Manfredonia, South-east of Italy), about 6 kilometers apart from each other. Their ecological composition is quite similar; both comprising a cereal field and a farm area (with chickens and chicken food/ poultry pen).

In Masseria Mustazzo the two species have lived in sympatry for about two decades (Eroukhmanoff et al. 2014). In Lago Salso, sympatry is (as mentioned in the introduction) more recent (Sætre et al. 2017).

2.2 Isotopes
Sampled from both Italian and Spanish sparrows in Masseria Mustazzo in 2015, from the still allopatric Italian sparrows in Lago Salso in 2012 and from the same population in sympatry with the Spanish sparrow years 2015, 2016 and 2017. All feathers were collected in spring time (May-June).

The feathers were sampled by capturing sparrows in mist nets and pulling the tertiary remige (a wing feather). This is done as part of a larger sampling procedure including taking blood, body measurements and ringing.

Isotope data from Mass. Mustazzo and Lagos Salso years 2012 and 2015 had already been obtained Eroukhmanoff and colleagues. The isotope data from Lago Salso 2016 and 2017, I obtained myself by cutting small pieces (~1mg) of the collected feathers (with a scalpel, weighing them on a microbalance, folding them into small tin capsules and placing them (in randomized order) onto a welled plate before sending them for analysis (at Jahren laboratory, UiO). For each sampled individual, I got the stable isotope ratios of both carbon and nitrogen.

These ratios represent the relationship between the ratio of the heavier isotope (^{13}C for carbon, ^{15}N for nitrogen) to the lighter isotope (^{12}C and ^{14}N) and a standard ratio for these isotopes (R_{STD}). This is how they are calculated:

$$\text{Nitrogen stable isotope ratio: } \delta^{15}N = (^{15}N/^{14}N)/^{15}R_{STD} - 1) *1000$$

$$\text{Carbon stable isotope ratio: } \delta^{13}C = (^{13}C/^{12}C)/^{13}R_{STD} - 1) *1000$$

2.3 Behaviour

2.3.1 Capture and housing

Study subjects: Male Italian (n = 9) and Spanish (n= 12) were collected in mist nets on June 5th and 6th (outside breeding season), 2018, from the (sympatric) populations in Masseria Mustazzo. All individuals were ringed, weighed and measured (tarsus length and beak length and width) upon capture before they were transported to their housing aviaries at the study site in Lago Salso.

At the study site, the Italian and the Spanish sparrows were kept in two separate, adjacent, (partially sheltered) outdoor aviaries ($\approx$ 4 (w) x 6 (l) x 2,5 (h) -m), each equipped with perches in all top corners, two roosting trees and two birdbaths (shallow plastic plates [$\varnothing \approx$ 50 cm]). During acclimation, food (a mix of millet, canary seeds and sunflower seeds) and water were provided *ad libitum* (food from treys placed on two wooden pedestals $\approx$ 110 cm above the ground, water from 3 metal bowls placed on the ground).

2.3.2 Experimental Protocol

The Experiments were carried out between September 15th, and October 7th, 2018, in two test aviaries (adjacent to the housing aviaries) with the same dimensions and an overall similar setup as the housing aviaries (four corner perches, two wooden pedestals).

Individuals of the two species were tested in separate aviaries at the same time, species switching test aviaries for each trial (first trial Italian in aviary 1, Spanish in aviary 2, second trial Italian in aviary 2, Spanish in aviary 1, and so on).

We transferred the birds between housing aviary and test aviary by capturing them with a hand net and transporting them in small cloth bags.

Two different experiments were conducted in this period; 1) A personality test aiming to measure exploratory behaviour, and 2) a foraging task aiming to measure problem solving skills.

Both experiments were recorded with an action camera mounted on the inside of each test aviary. The personality test was also observed and recorded in real time by an observer hiding outside the test aviary behind a green mesh. It eventually became apparent that the birds could notice the observer outside the aviary, so it was decided that the problem-solving experiment be recorded with cameras only.

The personality test was the first experiment to be carried out. During the 13 days this experiment lasted, all the birds were provided food from the feeding boards (placed on the ground in their housing aviaries) that were to be used in the problem-solving task, in order to familiarize them with this apparatus.

Personality test: Exploratory behaviour

This test consisted of three parts; 1) exploration of a small, unfamiliar cage, 2) escaping from this cage and 3) exploration of the test aviary following escape from the cage.

In order to level the birds' motivation, they were deprived of food; approximately two hours before test start, all food was removed from both housing aviaries. The food was replaced as soon as the test individuals had been collected from the housing aviaries.

Before test start, both test aviaries were prepared with food in a tray n the right pedestal and water in two metal bowls on the ground.

We tested one individual (from each species) at a time, introducing it into a small cage (40 (w) x 120 (l) x 40 (h) -cm) placed inside the test aviary, equipped with four perches and two water dispensers. Eleven minutes after introduction (one minute of "acclimation" + ten minutes of recordings), a door on the side of the cage was opened by means of a transparent fishing line (pulled by an observer hiding outside the test aviary), permitting escape from the cage and into the test aviary for further exploration.

After the door was opened, the bird was given 30 minutes to find the exit. If the bird managed to escape within this time limit, it was given 60 minutes to explore the aviary. If the bird did not succeed in escaping, it was guided out by one of the observers and the experiment discontinued.

After all observations were done, the test birds were recaptured from the test aviaries and released into their respective housing aviaries.

Initially this test was run twice a day; one at ten in the morning, the other at four in the afternoon, but the protocol eventually had to be adjusted due to stress inflicted upon the birds during capture. Ideally, all of the individuals would have done two trials each, but because of this adjustment, only six individuals repeated the trial.

Data collected from cage and exit

I defined 16 different areas of the cage (4 perches + 2 water dispensers + 5 ground areas + 5 wall areas) and recorded i) number of areas visited, ii) total number of flights/transitions between areas, iii) number of visits to the ground, iv) exit/ no exit, v) latency to exit the cage.

To correct for arbitrary movements, I also calculated vi) number of areas visited more than 5% and vii) 10% of the total number of times the bird transitioned. The variable exit/ no exit was weighed with 1 for exit and 0 for no exit. Exit latency was recorded in number seconds passed from the door opening to the bird escaping (for the ones who did not escape, exit latency was weighed with 1800 seconds)

Figure 1: Exploratory behaviour experimental set-up.

Data collected from test aviary exploration

From the aviary exploration test, I recorded i) whether or not the bird visited the ground, ii) latency to visit the ground for the first time, iii) number of visits to the ground, iv) whether or not the bird drank water, v) latency to the first drink, vi) number of drinks, vii) total number of flights and viii) number of areas visited (out of 9 different areas defined; 4 perches, 4 corners and a metal bar in the back of the aviary, ground not included)

Considering that the birds did in fact notice the observer outside the aviary, I also created a variable including all the visits to the front of the aviary (that is the part of the aviary closest to the observer), with intention of using this as a proxy for boldness.

The variables for ground visit – "yes or no", and drink – "yes or no", were weighed with 1 for "yes" and 0 for "no". A visit to an area was defined by landing in that area. For the individuals that never went to the ground or drank water the latencies were weighed with 3600 seconds.

Foraging task: Problem solving behaviour

In this experiment, the birds were to feed from a wooden board (~ 45 (w) x 45 (l) x 5 (h) -cm) with 16 wells drilled into it (in 4 x 4 rows), each well ~ 4 cm deep and ~4 cm in diameter (see picture below). A small transparent plexiglass lid was attached to each well with a screw, in such way that it could easily slide to the side. All the wells were filled with the same food as the birds had been fed over the summer. The task consisted in (after being accustomed to feed from this board with uncovered wells) finding a way to open the plastic lids in order to reach the food inside the wells.

Figure 2: Feeding board used in the problem-solving experiment

Birds were captured from their housing aviaries the day before the test and placed in the test aviaries for ~22h of acclimation. During acclimation, the birds were provided food from the feeding board (attached to the left pedestal, elevated ~110 cm above the ground) during the day. For motivational purposes, the feeding board was removed ~1h before sunset, depriving the birds of food overnight. The food was replaced with closed lids ~1h after sunrise (that is, when the test starts)

Most, but not all, of the birds seemed to accept the feeding board quite quickly.

Three birds from the same species were tested together (except from the last trial where only two birds were tested together) in the same test aviary. Two of the test individuals were

marked with water-based colors (one green and one orange) before being released in the test aviary. This would allow an observer (in this case myself) to recognize the individuals on video.

Before test start, I mounted the cameras in each test aviary before introducing the feeding boards with closed lids. The test started as soon as I had left the aviary.

The tests then ran for 60 minutes, during which I recorded (from the videos), each individual's i) latency to visit the board for the first time, ii) latency to the first attempt, iii) number of attempts, iv) number of pecks, v) total number of visits to the board, vi) total time spent on the board, vii) number of unique wells attempted at, and viii) success in opening a lid.

I defined an attempt as one or more pecks (beak touching plexiglass) on one lid, meaning that several consecutive pecks on one lid were counted as one attempt. I defined a peck as a brief strike with the beak on the lid. (one bird sometimes kept its beak fixed at one point on the lid while revolving the well. Such activity was weighed with 10 pecks). A visit was defined by landing onto the board (not counting the small flights some birds occasionally used to relocate themselves on the board). Total time spent on the board, I obtained by adding the durations of all the visits the individual paid the board. The number of unique wells attempted at was how many of the 16 different wells on the board the individual had attempted at the end of the test.

Based on these recordings, I also calculated each individual's ix) attempt intensity (pecks per attempt), x) diligence (attempts per minute spent on board) and xi) average length of visit (total time spent on board/ number of visits). I also noted, for each visit, whether or not the bird was the first one to arrive at the board, termed xii) pioneering.

If an individual never visited the board (and thus never gave any attempts to open a lid) both latencies were weighed with 3600 seconds. If an individual visited, but never attempted, attempt latency was weighed with 3600 seconds.

The test was repeated once for most groups (except for two groups who did the test three times, and the last group of two sparrows who only was given one trial), the second test being carried out on the consecutive day, in the same test aviary.

When the tests had been carried through and recorded on video, all the test birds were recaptured from the tests aviaries and replaced in their respective housing aviaries.

2.4 Data handling and analyses

To register and process the data I used Excel and a standard Windows text editor. For statistical analyses I used R version 3.3.1 where I set the alpha level of significance to $p \leq 0.05$ for all tests. The data included both parametric and non-parametric variables (normality tested with both Q-Q plots and Shapiro Wilks-test). Comparing differences in means between groups, I ran t-tests for the parametric variables and Wilcoxon rank sum tests (Mann-Whitney

U test) for the non-parametric ones. Comparing differences in variance, I used the Fligner-Killeen test (robust against non-parametric data and outliers). On all binary data, I used Fisher's exact tests to compare groups and probit regression when treated as response variables. When correcting for multiple testing, I used Holm's adjustment of p-value.

2.4.1 Isotopes

I used isotope data from male sparrows only (as females' species in sympatric populations is uncertain). I looked at population means, variances and densities of stable carbon and nitrogen isotope ratios (annotated $\delta^{13}C$ and $\delta^{15}N$, respectively)

I did a species comparison in Mass. Mustazzo, and the Italian sparrows' time series from Lago Salso with the distribution in Masseria Mustazzo. Sample counts ar presented in the table below.

	Lago Salso	Mass. Mustazzo	
Year	*P. italiae* (N)	*P. hispaniolensis* (N)	*P.italiae* (N)
2012	7	-	-
2015	15	16	15
2016	16	-	-
2017	15	-	-

Table 1: Isotope sample count

2.4.2 Behaviour

Exploratory behaviour experiment

Data from cage and exit:

A total of 23 trials were run, 6 of which were replicates. To get an indication of repeatability, I tested for differences between the first and the second trial of these 6 individuals.

I considered using the average values of the 6 individuals that did the test twice. However, I made the decision of only including the values from their first, trial, keeping all the individuals' test condition as similar as possible.

On this data, I first tested for difference in proportion of individuals who managed to exit the cage within 30 minutes.

Then I ran a Principal Component Analysis (PCA), excluding the exit data, before comparing the species' mean and variance of all variables (including PC1 and PC2).

Finally, I looked for predictors for exit success, using a probit regression model for binomial data, with all the variables included in the PCA as independent variables.

Aviary data

Here I first looked for species' differences in proportion of ground-visitors and proportion of drinkers (Fisher's exact test for both). Then I ran two PCAs; first including all numeric variables, then one excluding the latencies to visit the ground and to drink. Finally, I compared the species' means and variance of all variables (including PC1 and PC2 of the latter PCA)

Problem solving experiment

A total of 18 individuals (11 Spanish and 7 Italian) were tested in this experiment, and all of them (except for one Spanish sparrow, tested on the last day) went through at least two trials. Some of them never visited the board (in any of the trials), so I first tested the species' difference in proportion of visitors (Fisher's exact test). Then I removed the non-visitors from the dataset, which left me with 15 individuals, before proceeding with the analyses. As there were no significant differences between the first and second trial, I averaged the values (of all variables) from the first two trials of all visitors and included the individual who was only tested once (meaning that it was not the average values, but values from this individual's first trial that were used).

I chose to exclude the calculated/derived variables (intensity, diligence, average length of visit, and attempt per visit), as they were closely correlated to the raw variables, before running a PCA. I then tested for species' differences in mean and variance of all variables, including PC1 and PC2.

Once I had run all the (quantitative) tests on the whole sample of 15 visitors, I tried to correct for the disparity between the Italian (n=5) and the Spanish (n=10) sample sizes by randomly sampling 5 Spanish individuals 20 times, running the same tests for each sample.

Finally, I tested for difference in success rate (binary) between the species.

Correlations

In addition to comparing the species' behaviour in these experiments, I looked for correlations (Spearman's rank) between exploration and problem solving in variables, PC1 and PC2.

2.5 Confounding factors

Before running relevant tests, I checked whether factors such as time of day (afternoon or morning for the exploration experiment), test aviary (1 or 2) or observer (out of three different ones in the exploration experiment) had a significant effect.

Problem solving experiment:

The individual measurements in the problem-solving experiment are partially pseudoreplicates, considering that social effects are not corrected for.

In the cases a lid was opened, the access to food affected the sparrow's behaviour on the board. Thus, I considered measurements such as times spent on board and number of attempts as invalid for comparison in the time interval from the lid was opened until the end of the test. So, to make the data from comparable for the whole duration of the test, I extrapolated their behaviour for the remaining time of test duration, from the behaviour measured before a lid was opened, by averaging the value (y) of each variable per minute before lid opening, and multiplying it by 60, so that the new value (x) would be: $x = (y/42) * 60$.

In one group of Italian Sparrows, the video from the first 20 minutes of their second trial was lost. I had recordings for 60 minutes from this group, but this was "skewed" 20 minutes relative to the other trials,

The last test (of Spanish sparrows) was done with only two birds, and group size might have an effect to the sparrow's behaviour (indeed; group size is known to have an effect on problem-solving performance (Liker and Bokony 2009).

2.6 Ethical note

Capture, housing and experimental procedures were all authorized by the Italian Institute for Environmental Protection and Research (ISPRA), the Regional Council of Puglia and Gargano National Park.

One of the Spanish sparrows died in the housing aviary on the day of capture, and one Italian sparrow died in the housing aviary during the period of observation. The cause of death is unknown, but possibly a combination of old age and stress. This is considered a relatively low mortality rate for a captive sparrow experiment (Papp et al. 2014).

None of the birds showed any signs of physical pain during capture, handling or testing, and were always treated as carefully as possible.

After observations, all birds were given a visual health check by a veterinarian, before they were transported back to and released at the site of capture.

3 Results

3.1 Isotopes
Masseria Mustazzo

Only stable nitrogen isotope ratios (δ^5N) showed significant differences in mean ($p = 7.868$e-06) and variance ($p = 0.0012$) -
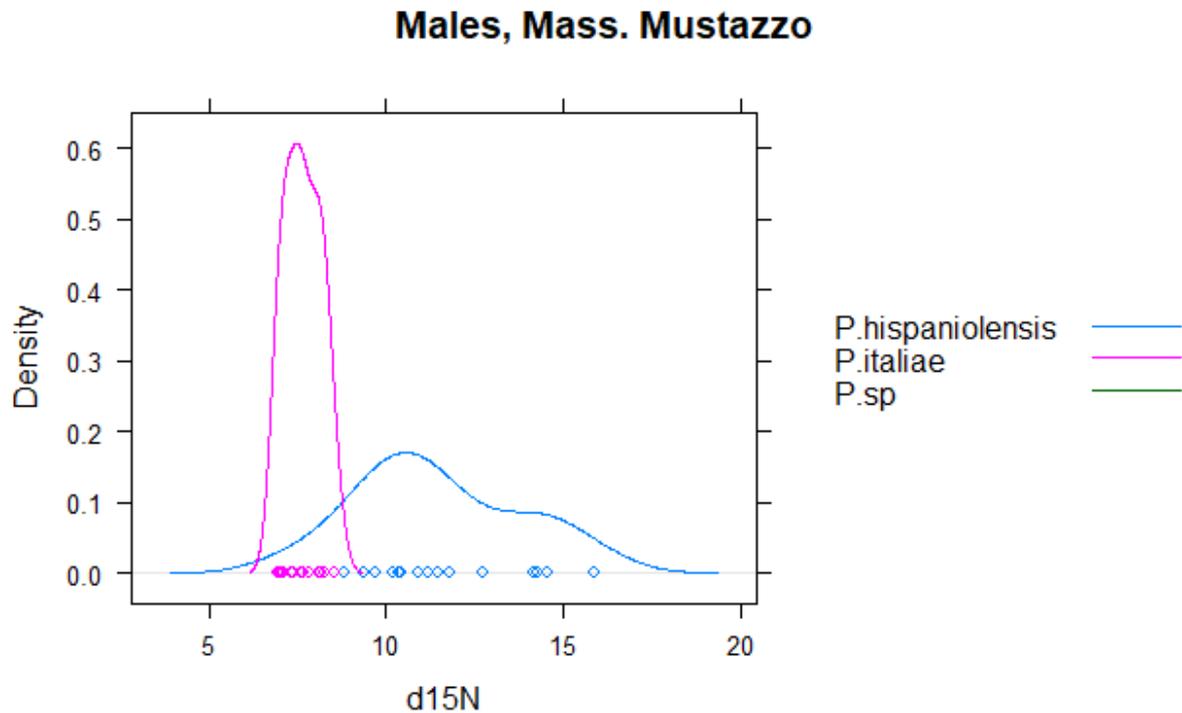
Figure 3: Densities of stable nitrogen isotope ratio in Masseria Mustazzo. The two species show a displacement in nitrogen isotope ratio.

Lago Salso, Italian population time series

There were no significant differences between any of the years in either δ^{15}N or δ^{13}C. The change in mean and variance over the years did however show some interesting trends:

A steady decrease in the mean value δ^{15}N, from 2012 to 2017. The variance increases from 2012 to 2015, remains relatively steady until 2016, but decreases drastically between 2016 and 2017.

δ^{13}C also decreases in mean and variance from 2012 to 2017, but there is no clear pattern in change in variance over the same time period.
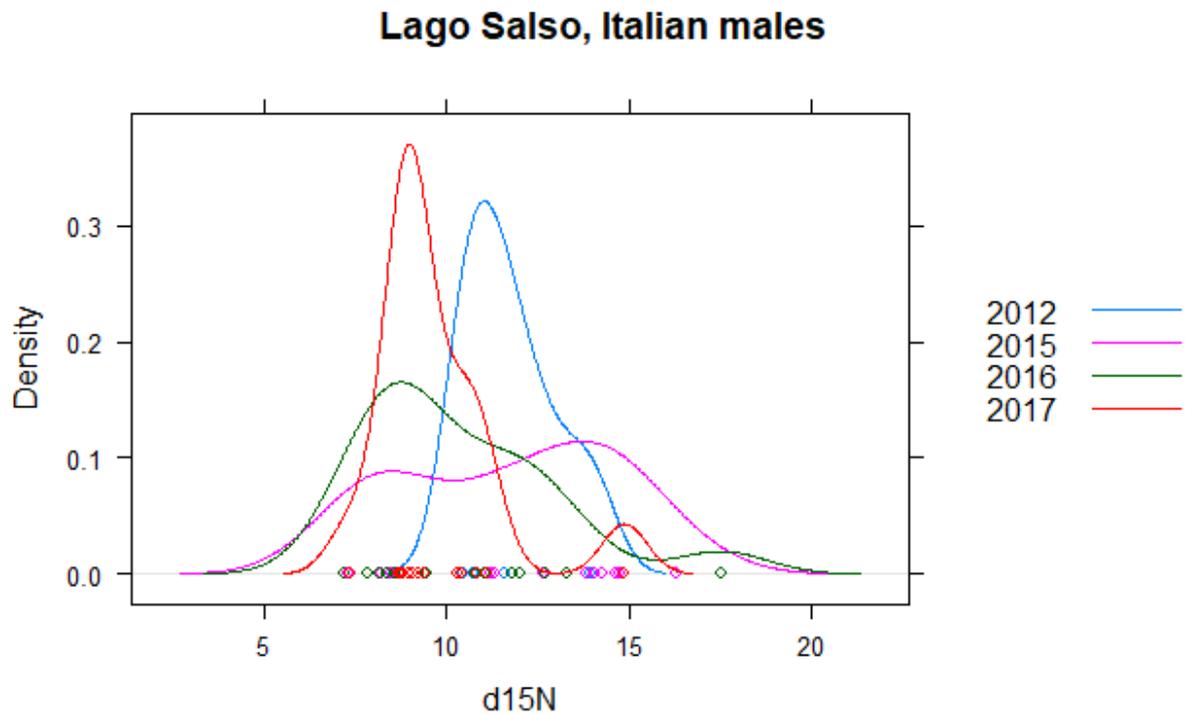
Figure 4: δ^{15}N densities in Lago Salso (2012 and 2015-2017). Over time, the ratio moves towards a lower mean, and the variance is heavily reduced between 2016 and 2017, trending towards the density in the Italian sparrow population in Masseria Mustazzo.
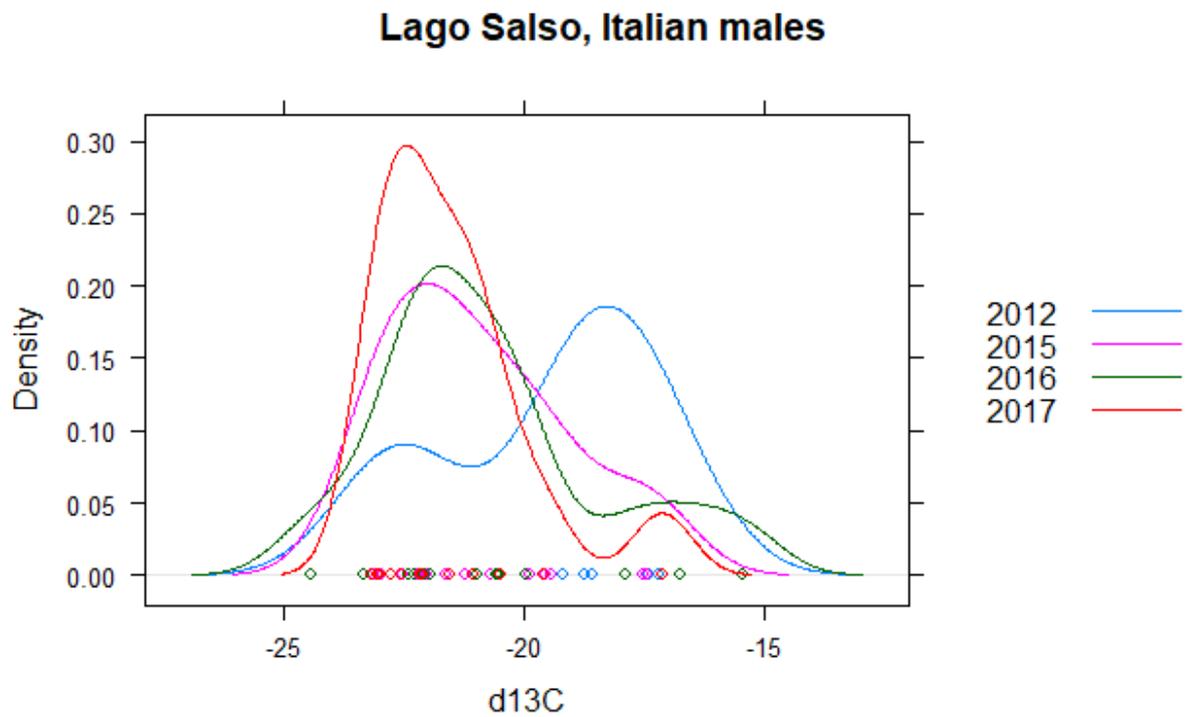

Figure 5: δ ^{13}C densities in Lago Salso (2012 and 2015-2017).

	δ ^{15}N		δ ^{13}C	
	Mean	**SD**	**Mean**	**SD**
2012	11.72	1.25	-19.47	2.26
2015	11.70	2.96	-20.96	1.87
2016	10.35	2.66	-20.25	2.37
2017	9.71	1.73	-21.53	1.60

Table 2: Lago Salso isotope ratios, means and standard deviations

3.2 Behaviour

3.2.1 Exploratory behaviour

Cage exploration and exit

When comparing the first and second trial of the 6 individuals who repeated the test, I found no significant differences in any of the recorded variables. Although this is an indication that the sparrows' behaviour in the cage is repeatable, since the test was repeated for such a small proportion of the individuals, I chose to only include data from their first trial in the analysis. (meaning that all the results presented here are from the first trial).

Exit/no exit:

	P. hispaniolensis	*P. italiae*
Exit	6	5
No exit	4	3

Table 3: Number of birds who exited (and not) from the cage.

No significant differences (P = 1) in proportion of escapers.

The video of one of the Spanish escapers was lost, so this individual is not included in further analyses of behavior in the cage (but is included in the analyses of behavior in the aviary, as I have live recordings from that experiment).

PCA (exit data excluded):
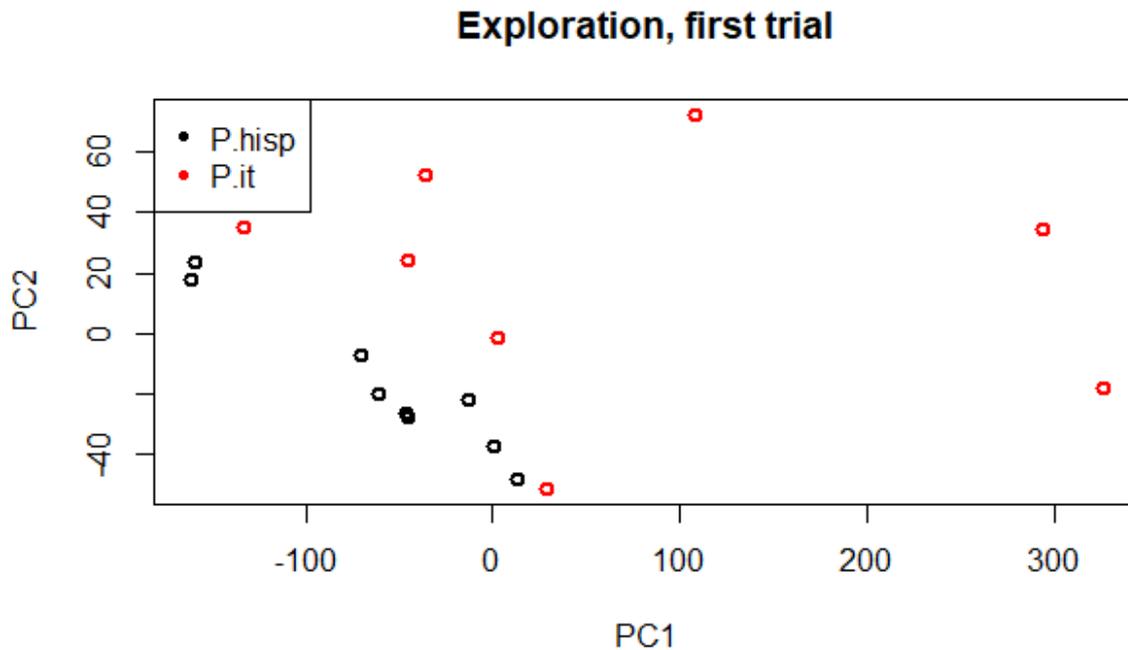
Figure 6: PCA of cage exploration, exit data excluded

The differences in between the species was significant in the mean of PC1 ($p = 0.046$), but not of PC2 ($p = 0.055$). Although the variance was higher for the Italian sparrows in both PC1 and PC2, it was not significantly different from the Spanish sparrows' variance.

The Italian sparrows visited more areas ($p = 0.003$) and went to the ground more often ($p = 0.0024$) than the Spanish sparrow, with hardly any overlap (see boxplots), number of areas ranging from 11 to 16 in the Italians and from 6 to 14 in the Spanish, number of visits to the ground ranging from 5 to 182 in the Italians and from 0 to 26 in the Spanish (by comparison, only one Italian sparrow visited the ground fewer than 26 times).

The Italian sparrows also had a higher mean number of flights/ transitions; however, this did not correlate with number of areas visited. Running a GLM showed that number of flights/ transitions had an, although significant, very small effect on number of areas visited.

(interestingly, the Italian sparrow that did the fewest transitions (190) was one out of two sparrows who visited all 16 areas of the cage)

No predictor for exit success:

The probit regression showed that neither variable, or PC1 or PC2 explained exit success.

| Variable | P. hispaniolensis | | P. italiae | | Wilcoxon (T-test) | Holm's correction |
	Mean	SD	Mean	SD	P	P
Areas visited (N)	10.00	2.65	13.88	1.89	0.006 (0.003)	(0.015)
Areas visited (N) > 5% of transitions	4.33	1.22	6.50	1.60	0.012 (0.008)	(0.032)
Areas visited (N) > 10% of transitions	2.56	0.73	4.25	0.89	0.002	0.014
Transitions (N)	276.56	67.17	382.88	155.72	0.163	0.489
Visits to the ground (N)	5.00	5.81	84.38	65.74	0.0024	0.014
Exit/ No exit	0.56	0.53	0.63	0.52	0.822	0.91
Exit latency (s)	1143.11	790.54	823.13	850.98	0.455	0.91

Table 4: Cage exploration means, standard deviations and *p*-values for differences in means.
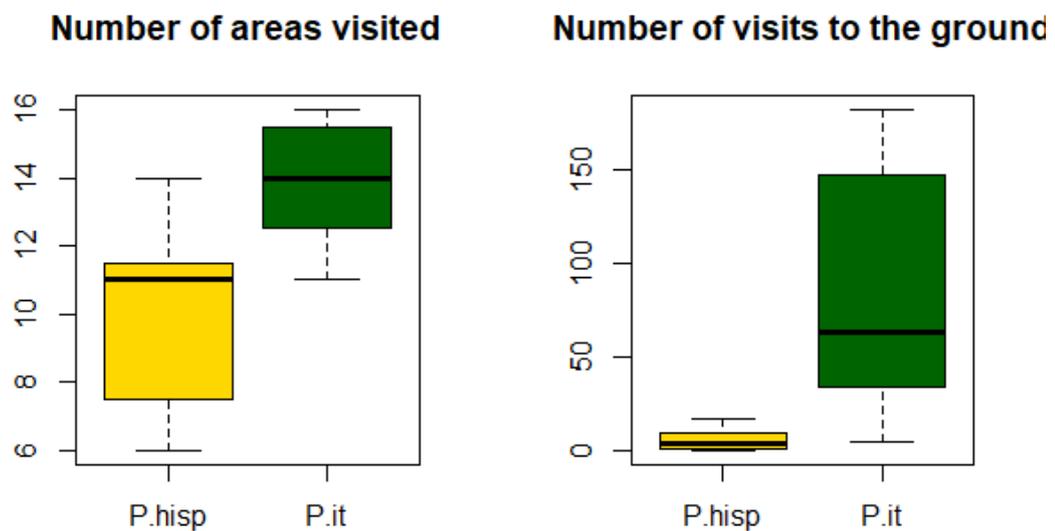
Figure 7: Cage exploration box plots of number of areas and number of ground-visits.
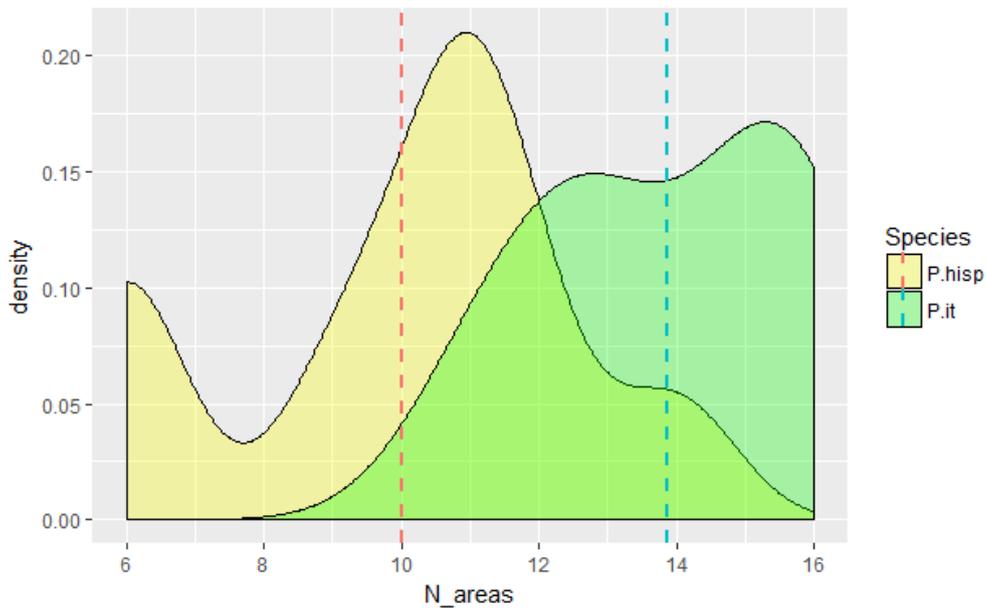
Figure 8: Density plot of number of areas visited (Spanish yellow, Italian green), dashed lines representing the group means.
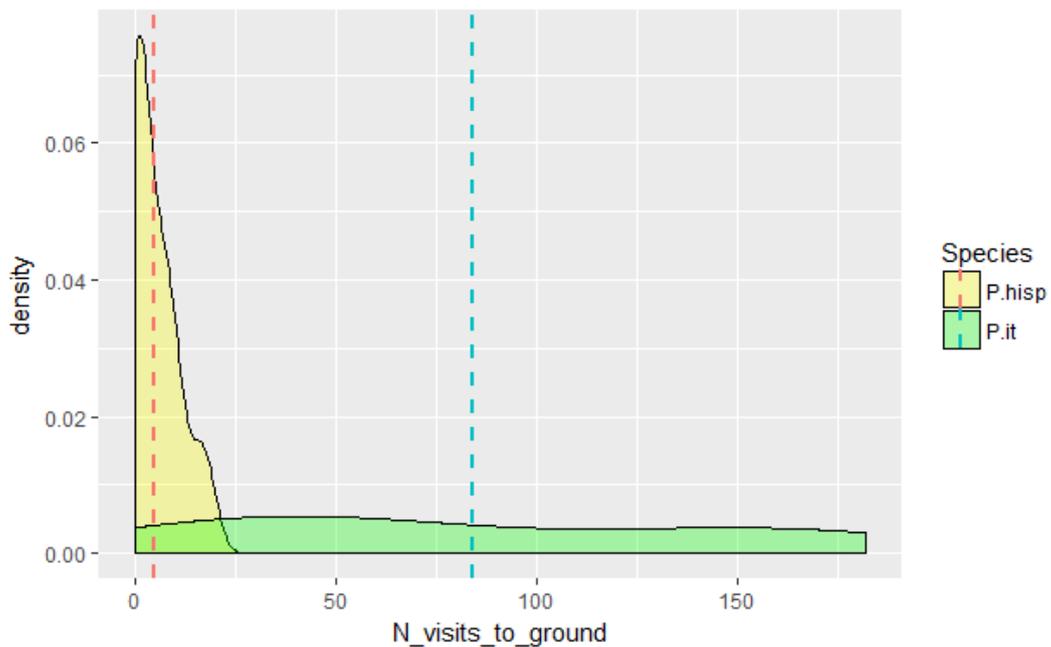
Figure 9: Density plot of number of visits to the ground (Spanish yellow, Italian green), dashed lines representing the group means.

Aviary exploration

The number of individuals who managed to escape from the cage determined the sample size for this experiment, which was 11 in total; 6 Spanish and 5 Italian. All of the 5 Italian

sparrows (who managed to escape the small cage) visited the ground at least once, and all of them drank water from the metal bowls on the ground.

3 of the 6 Spanish sparrows (who escaped the cage) visited the ground at least once, and 2 of these drank water.

Only one individual – an Italian sparrow, ate food from the pedestal in this experiment.

	P. hispaniolensis	*P. italiae*
Visited ground	3	5
Did not visit ground	3	0

Table 5: Representing number of aviary ground-visitors

The difference between the species was not significant ($p = 0.18$).

	P. hispaniolensis	*P. italiae*
Drank water	4	5
Did not drink water	2	0

Table 6: Representing number of drinkers in the aviary test

Neither this difference was significant ($p = 0.06$)

There were no significant differences (not in means nor in variances) between the species in either variable, nor in PC1 or PC2.

Variable	P. hispaniolensis		P. italiae		Wilcoxon (T-test)	Holm's correction
	Mean	**SD**	**Mean**	**SD**	**P**	**P**
Ground visit (yes or no)	0.50	0.55	1.00	0.00	0.099	0.594
Latency to visit the ground (s)	3100.00	690.04	1406.00	961.09	0.021 (0.013)	(0.104)
Visits to the ground (N)	0.83	1.17	2.60	1.82	0.073 (0.105)	(0.594)
Latency to drink (s)	3280.00	648.07	2310.20	696.85	0.031	0.217
Drinks (N)	1.50	2.81	3.00	3.39	0.156	0.594
Flights (N)	411.33	383.50	782.80	315.94	0.082 (0.112)	(0.594)
Areas visited (N)	5.50	1.05	6.20	1.30	0.449 (0.363)	(0.726)
Visits to the front (N)	33.83	47.54	28.00	31.27	0.784	0.780

Table 7. Aviary exploration: Means, standard deviations and *p*-value for differences in means between the species

3.2.2 Problem solving behaviour

3 of the 18 birds tested, never visited the board in any of their trials.

	P. hispaniolensis	*P. italiae*
Visitors (N):	10	5
Non-visitors (N):	1	2

Table 8: Number of individuals who did and did not visit the feeding board during the experiment.

The difference in proportion of visitors between the species was not significant ($p = 0.53$)

(However, I did find a significant difference between test aviaries. All the non-visitors were tested in test aviary 2).

Success

Only two individuals - both of them Spanish sparrows, ever managed to open a lid during the problem-solving experiment. The species' difference in success rate was not significant ($p = 0.52$)

Behaviour on the board

The PCA of the numeric variables showed significant between species differences in means of both PC1 ($p = 0.034$) and PC2 ($p = 0.049$). Although not significant, Spanish sparrows also had greater variance than the Italians in both PC1 and PC2.

The Spanish sparrows did (on average) spend significantly more time on the board ($p = 0.01$), attempted at a larger number of wells ($p = 0.02$) and gave more pecks ($p = 0.05$) than the Italian sparrows. The Spanish sparrows also showed a greater variance for most of the variables, but the difference in variance was only significant in number of attempts ($p = 0.018$).

When correcting for the discrepancy of sample size, by running the same test with 5 randomly sampled Spanish sparrows 20 times, I only got significant differences 12 times for total time spent on board, 6 times for number of wells and 5 times for number of pecks.

The figures and table below are from the original sample of 10 Spanish and 5 Italian sparrows.
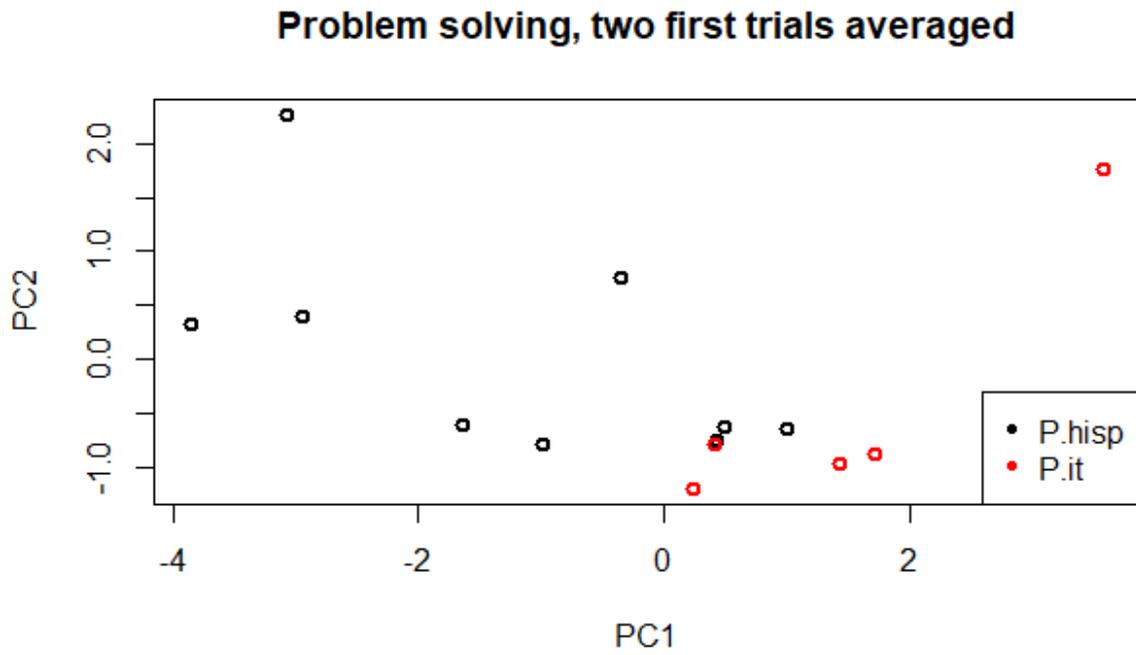
Figure 10: From PCA of the numeric variables recorded in the problem-solving experiment
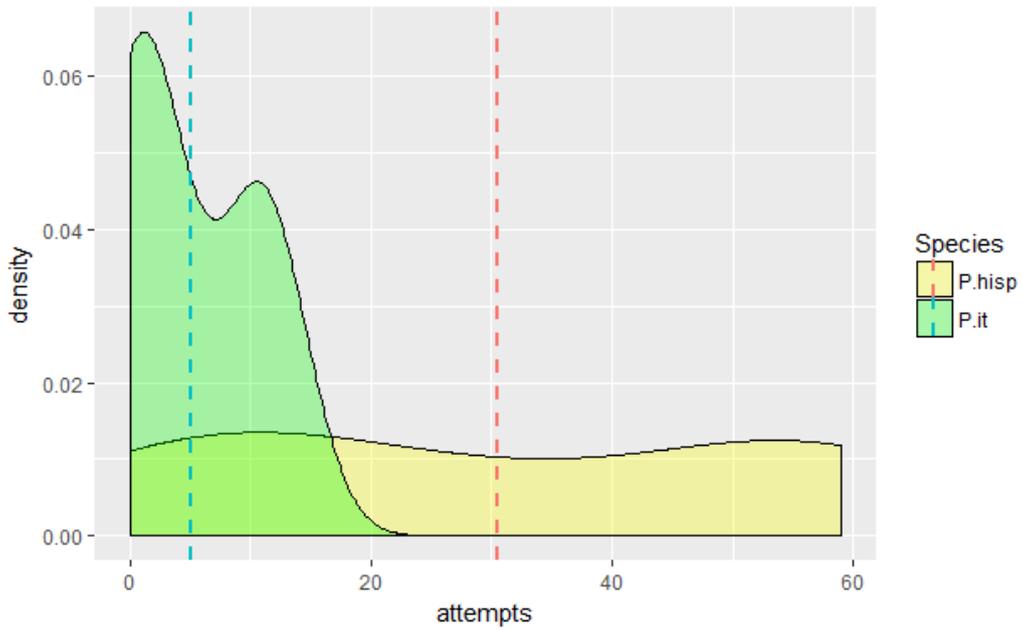
Figure 11: Density plot of number of attempts, with dashed lines representing group means.

Variable	P. hispaniolensis		P. italiae		Wilcoxon (T-test)	Holm's correction
	Mean	**SD**	**Mean**	**SD**	**P**	**P**
Visit latency	737.50	1092.01	917.80	1508.04	1	1
Attempt latency	1080.40	1103.01	1535.50	1326.45	0.540	0.450
Attempts (N)	30.45	23.78	5.00	5.52	0.086	0.516
Pecks (N)	80.70	88.57	10.30	12.55	0.050	0.450
Visits (N)	12.83	9.29	5.90	3.54	0.125 (0.060)	(0.450)
Total time spent on board (s)	205.58	119.56	69.10	56.61	0.037 (0.010)	(0.120)
Wells (N)	8.3	5.02	2.80	2.93	0.050 (0.020)	(0.200)
Intensity (pecks/ attempt)	2.32	1.45	1.43	1.03	0.178 (0.195)	(0.585)
Diligence (attempts/ min spent on board)	7.91	6.45	3.02	3.16	0.111	0.555
Avg. length of visit (s)	17.50	11.01	9.17	6.73	0.141	0.564
Pioneering	0.63	0.29	0.62	0.36	0.902	1
Attempts per visit (N)	2.15	1.44	0.62	0.63	0.066 (0.013)	(0.143)

Table 9: Problem solving behaviour means and variances (of the original sample). P-values are from the tests comparing differences in mean.

3.2.3 Correlations

I found no correlations between problem solving behaviour and exploratory behavior (not between any of the variables, nor between PC1 and PC2 of problem solving with PC1 and PC2 of exploration), not across species, nor within species.

4 Discussion

With this study I have found indications of dietary displacement of Italian and Spanish sparrows living in sympatry. I have also found species differences in the behaviour of sympatric Italian and Spanish sparrows, particularly expressed in exploratory behaviour.

I did not find any correlation between exploratory behaviour and problem-solving performance.

Below, I discuss these results in more detail.

4.1 Isotopes

I found a difference in stable nitrogen isotope ratio (δ^{15}N) in the feathers of the two sparrow species living in sympatry in Masseria Mustazzo; the Italian sparrows had a lower mean value and less variance than the Spanish sparrows. Although this reflects the δ^{15}N in their diets (Hobson and Clark 1992), it is hard to infer anything specific about diet based on solely on isotope composition. The heavy nitrogen isotope ^{15}N tends to accumulate in the food chain, raising the values of δ^{15}N (Cabana G. and Rasmussen J. B. 1994; Hobson 2007), so one possibility is that the Spanish sparrows are fed insects of a higher trophic as nestlings, or that they tend to incorporate more insects in their diet. On the other hand, considering that all sampled individuals were adults, that isotope composition in their sampled feathers reflects isotope composition in their diet of only half a year before sampling (Runemark et al. 2018), and that both species are mainly granivores for most of their lives, it is also likely that the difference is a result of eating seeds from plants grown in different soils (Evans 2001). Either way, this result is a solid indication that these sympatric populations of Italian and Spanish sparrows exploit different food sources.

In the recently sympatric Italian sparrows in Lago Salso, the population mean and the variance of δ^{15}N is approaching that of the Italian population in Masseria Mustazzo, which has been sympatric with the Spanish sparrow for about two decades more. It appears that the diet of the Italian sparrow in Lago Salso is in some aspect becoming more similar to that of the Italian sparrow population in Masseria Mustazzo.

These results indicate that the niche of the Italian sparrow is displaced in sympatry with the Spanish sparrow. This is also is also in accordance with Sætre and colleagues' report of strong habitat segregation occurring after the settlement of the Spanish sparrows in Lago Salso.

The fact that the Italian sparrow has a lower variance δ^{15}N in sympatry, and that it is lower than that of the Spanish sparrow, also indicate that it occupies a narrower niche. This is in line with previous ecological studies showing that when two closely related species (with similar

preferences in habitat use) occur together, their niche preferences change nd that one of the species tend to be more ecologically displaced than the other (Peers, Thornton, and Murray 2013; Reif et al. 2018).

Thus, there is reason to believe that the Italian and the Spanish sparrows, in sympatry, face different challenges in foraging, which in turn might have implications for their behaviour.

4.2 Behaviour
4.2.1 Exploratory behaviour
Here I found that the Italian sparrows were more exploratory than the Spanish sparrows, in the sense that they explored more areas than the Spanish sparrows in the cage test. The Italian sparrows were also slightly more active, but this was not significant. As there were no correlations between number of areas visited and number of transitions, exploration of the cage was not an artefact of activity. Although it was only significant in number of visits to the ground, the Italian sparrows also had an overall higher variance in all variables, meaning that they had greater inter-individual differences in exploratory behaviour than the Spanish sparrows.

It is plausible that the two species' general differences in ecology have shaped their behaviour differently. The Italian sparrow is, as mentioned in the introduction, more associated with humans than the Spanish sparrow, and there is some evidence that more urban species tend to be more exploratory (Thompson et al. 2018; Frynta et al. 2018) and less responsive to predation risk (Tsurim, Abramsky, and Kotler 2008) than their non-urban relatives, meaning that a human commensal have a more "bold" phenotype.

The fact that the Italian sparrows showed more variance in exploratory behaviour, could also be consistent with their commensal nature; urbanization tends to increase inter-individual variation in birds (Møller 2010; Thompson et al. 2018)

Another possible reason for the relatively higher variation in personality among individuals in the Italian sparrow is that it as a hybrid has more standing genetic variation than its parent species (Seehausen 2013; Sætre et al. 2017), and more genetic variation in a population usually means more variation in phenotype.

One possibly influential factor on the sparrows' behavior is stress. During the experiments all the sparrows were exposed to relatively stressful situations, from being handled by a human, to being in an unfamiliar, relatively constrained environment. Such events are likely to induce endocrinal stress responses (Weaver, Gao, and McGraw 2018), which in turn could affect their behaviour (Baugh et al. 2013; Moyers et al. 2018; Arnold et al. 2016).

The hormonal response to stressful situations may differ between the species. Linking this up to what is known about the Italian and Spanish sparrows' differences in ecology (namely that the Italians are more commensal); some have found no correlation between stress response and urbanization (Weaver, Gao, and McGraw 2018) others have found that urban birds a have a lower stress response to human handling (Atwell et al. 2012). If this is the case for the Italian and the Spanish sparrows, the Italian sparrows might have been less stressed during the experiment, which in turn could have been the reason for their higher exploration rate in that

situation (Atwell et al. 2012). Then it is also possible that some of the inter-individual variation in the Spanish sparrows' behaviour can have been masked by a response to stress.

As I have no any measurement of stress response from this experiment, I cannot say for certain which role stress played in the sparrows' behaviour in this experiment. However, considering the possible relationship between human commensalism and stress response, and between stress response and exploratory behaviour, could be interesting for future studies. Whatever the proximate mechanisms underlying the exploratory behaviour of the Italian and Spanish sparrows in these experiments, their differences are worth further investigations.

No predictor for exit

The proportion of birds who managed to escape from the cage, was roughly the same for both species (62% of the Italian and 60% of the Spanish sparrows)

A little surprising, neither activity level (number of transitions) or exploration (number of areas) inside the cage predicted the birds' exit success in either group. This makes exit success a questionable measure of exploratory behaviour. Is escape just a chance event? Adjustments to the experimental design may improve the exit success' value as a measure of exploration. Firstly, the door of the cage could be bigger (the door used in this experiment was about 15 x 15 cm). Secondly, the timing of opening the door could have been better.

Some anecdotal evidence suggests that 10 minutes is too long to explore a small cage. This seemed true at least for some birds who started out behaving really exploratory, covering most areas in just a few minutes, but eventually their movements became more monotonous, as if "giving up". Shortening the time of the cage exploration should thus be considered in future experiments of this kind.

However, the possibility that the escapers in this experiment had some undetected behavioural quality in common should not be excluded.

Aviary exploration

Although no significant differences between the Italian and the Spanish sparrows were found in this test, the species differences in behaviour the aviary did to some degree reflect those in the cage in the sense that the Italian sparrows visited the ground more readily than the Spanish sparrows.

We must keep in mind, that this sample is already biased by only including individuals who managed to escape from the cage. Even though it was not correlated with the behaviour in the cage, escape might have selected individuals on some undetected quality. If so, this could have made these samples more similar to each other than the groups they were selected from.

4.2.2 Problem solving behaviour

First, the problem with groups of birds not visiting the board should be addressed. There were no significant species differences in proportion of non-visitors. The test aviary did however have a large effect (all non-visit groups were tested in test aviary number 2.) and is a source of

error that should be considered for future experiments in these aviaries. It is possible that the birds have found food elsewhere in this aviary, that we did not see. If future experiments are to be carried out in these aviaries, they should be thoroughly raked and examined between each test round.

Further I discuss the problem-solving behaviour of the birds who visited the board (5 Italian and 10 Spanish)

The Spanish sparrows were generally more active on the feeding board, they spent significantly more time on the board and made more attempts than the Italian sparrows. These differences were not as expressed when correcting for the discrepancy in sample size, and the only result that could be considered significant is the difference in time spent on the board. It was interesting however, that in contrast to exploratory behaviour, Spanish sparrows shoed more interindividual variation in problem-solving behaviour than the Italian sparrows.

Unlike exploratory behaviour, problem-solving behaviour does not seem to correlate with urbanization (Kark et al. 2007; Papp et al. 2014), and the results from this experiment is thus not inconsistent with what we know of the species' general ecology, the Italian being the most "urban" of the two.

One factor that can affect the birds' problem-solving performance is their physiological state; more hungry animals will often be more eager to solve the task (Rowe and Healy 2014), so if the two species have different basal metabolic rates, this could also lead to differences in motivation.

Only two birds managed to open a lid, and there were no predictors for success (nor was there anything noteworthy in the successful problem-solvers' behaviour), so these appear to have been "lucky" events. Thus, it is hard to say anything about the sparrows' problem-solving skill or performance based on their success in this experiment.

I did, however, make some interesting off the record observations of the sparrows' behaviour during the problem-solving task. Some sparrows seemed to be more "creative" in their attempts to open the lids. Where most birds just pecked away at the lids, two birds (one Spanish and one Italian) nibbled on the screw by which the lid was attached (when pecking seemed futile). Another alternative strategy applied by one Spanish sparrow was fixing its beak at one point in the middle of the lid and circling around it. This individual at one point also tried using its leg.

These types of performances are indicative of, and thus be important for measuring, problem-solving skill, but they are hard to objectively quantify. They could, however, give ideas for how to better adjust this experiment to the sparrows' capabilities.

4.2.3 Behavioural correlations

The fact that no correlations were found between exploratory behaviour and problem-solving is consistent with the literature. It also indicates that exploratory behaviour may not be necessary to correct for when testing problem-solving skills in sparrows.

4.2.4 Closing remarks on behaviour

Ideally, the sample sizes would have been larger, and more trials would have been run over a longer period of time in both experiments. More and better adjusted problem-solving tasks would also have contributed to get a better understanding of how the sparrows approach a problem.

5 Conclusion and future prospects

To my knowledge, this is the first study comparing the behaviour of the Italian and the Spanish sparrow in a controlled experiment. I found that the Italian sparrow in this setting expresses a more exploratory phenotype than the Spanish sparrow, but the proximate mechanisms for this phenotypical difference remains unknown.

Although the problem-solving experiment yielded inconclusive results, I think that a more solid sample size and some adjustments to the experimental design could give a decent measure of problem-solving performance.

It is hard to draw any conclusions on either species' cognitive faculties, or how these vary across the species. However, the sparrows' willingness and different approaches to solve a problem are promising for future studies aiming to measure the problem-solving behaviour of these sparrow species.

The most important next step in the investigation of behavioural character displacement of the Italian sparrow is to compare between-species differences in sympatric populations with those of allopatric populations, and also to look for differences between sympatric and allopatric populations of Italian sparrows. Bigger between-species differences in sympatric populations, and general differences between sympatric and allopatric Italian sparrows would support the hypothesis of behavioural character displacement.

With this preliminary study, I hope to encourage the continuation of this inquiry.

References:

Adams, D. C., and F. J. Rohlf. 2002. "Ecological Character Displacement in Plethodon: Biomechanical Differences Found from a Geometric Morphometric Study." *Proceedings of the National Academy of Sciences* 97 (8): 4106–11.

Anderson, Rindy C., William A. Searcy, Susan Peters, Melissa Hughes, Adrienne L. DuBois, and Stephen Nowicki. 2017. "Song Learning and Cognitive Ability Are Not Consistently Related in a Songbird." *Animal Cognition* 20 (2): 309–20.

Arnold, Kathryn E., Katherine A. Herborn, Lindsay J. Henderson, Aileen Adam, Lucille Alexander, and Neil Evans. 2016. "Individual Variation in Corticosterone and Personality Traits in the Blue Tit Cyanistes Caeruleus." *Behaviour* 153 (13–14): 1611–37.

Atwell, Jonathan W., Gonçalo C. Cardoso, Danielle J. Whittaker, Samuel Campbell-Nelson, Kyle W. Robertson, and Ellen D. Ketterson. 2012. "Boldness Behavior and Stress Physiology in a Novel Urban Environment Suggest Rapid Correlated Evolutionary Adaptation." *Behavioral Ecology* 23 (5): 960–69.

Baugh, Alexander T., Kees van Oers, Marc Naguib, and Michaela Hau. 2013. "Initial Reactivity and Magnitude of the Acute Stress Response Associated with Personality in Wild Great Tits (Parus Major)." *General and Comparative Endocrinology* 189: 96–104.

Bell, Alison M., and Andrew Sih. 2007. "Exposure to Predation Generates Personality in Threespined Sticklebacks (Gasterosteus Aculeatus)." *Ecology Letters* 10 (9): 828–34.

Bókony, Veronika, Ádám Z Lendvai, Csongor I Vágási, Laura Pa, ˘ Tras¸, Tras¸, D Péter, L Pap, József Németh, et al. 2014. "Necessity or Capacity? Physiological State Predicts Problem-Solving Performance in House Sparrows". 2014. *Behavioural Ecology*. 25 (1): 124-135-

Boogert, Neeltje J, Rindy C Anderson, Susan Peters, William A Searcy, and Stephen Nowicki. 2011. "Song Repertoire Size in Male Song Sparrows Correlates with Detour Reaching, but Not with Other Cognitive Measures." *Animal Behaviour* 81 (6): 1209–16.

Bouchard, Julie, William Goodyer, and Louis Lefebvre. 2007. "Social Learning and Innovation Are Positively Correlated in Pigeons (Columba Livia)." *Animal Cognition* 10 (2): 259–66.

Brown, W. L., and E. O. Wilson. 1956. "Character Displacement." *Systematic Zoology* 5 (2): 49.

Brunkhorst, Adrian, Mattias Karlén, Jiaqi Shi, Monika Mikolajczyk, Mark A Nelson, Madis Metsis, and Ola Hermanson. 2005. "A Specific Role for the TFIID Subunit TAF4 and RanBPM in Neural Progenitor Differentiation."

Cabana G., and Rasmussen J. B. 1994. "Modelling Food Chain Structure and Contaminant Bioaccumulation Using Stable Nitrogen Isotopes." *Nature* 372: 255–57.

Carere, Claudio, and Charles Locurto. 2011. "Interaction between Animal Personality and Animal Cognition." *Current Zoology*. Vol. 57.

Cole, Ella F., Dominic L. Cram, and John L. Quinn. 2011. "Individual Variation in Spontaneous Problem-Solving Performance among Wild Great Tits." *Animal Behaviour* 81 (2)

Cole, Ella F, and John L Quinn. 2012. "Personality and Problem-Solving Performance Explain Competitive Ability in the Wild." *Proceedings of the Royal Society B: Biological Sciences* 279 (1731): 1168–75.

Dingemanse, Niels J, Kees van Oers, Arie J van Noordwijk, Christiaan Both, and Piet J Drent. 2003. "Repeatability and Heritability of Exploratory Behaviour in Great Tits from the Wild." *Animal Behaviour* 64 (6): 929–38.

Elgvin, Tore O., Cassandra N. Trier, Ole K. Tørresen, Ingerid J. Hagen, Sigbjørn Lien, Alexander J. Nederbragt, Mark Ravinet, Henrik Jensen, and Glenn Peter Sætre. 2017. "The Genomic Mosaicism of Hybrid Speciation." *Science Advances* 3 (6).

Enright, Jennifer M, Karen A Lawrence, Tarik Hadzic, and Joseph C Corbo. 2015. "Transcriptome Profiling of Developing Photoreceptor Subtypes Reveals Candidate Genes Involved in Avian Photoreceptor Diversification HHS Public Access." *J Comp*

Eroukhmanoff, F., T. O. Elgvin, M. F. Gonzàlez Rojas, F. Haas, J. S. Hermansen, and G. P. Sætre. 2014. "Effect of Species Interaction on Beak Integration in an Avian Hybrid Species Complex." *Evolutionary Biology* 41 (3): 452–58.

Evans, R. Dave. 2001. "Physiological Mechanisms Influencing Plant Nitrogen Isotope Composition." *Trends in Plant Science*. 6(3): 121-126.

Frynta, Daniel, Barbora Kaftanová-Eliášová, Barbora Žampachová, Petra Voráčková, Jovana Sádlová, and Eva Landová. 2018. "Behavioural Strategies of Three Wild-Derived Populations of the House Mouse (Mus m. Musculus and M. m. Domesticus) in Five Standard Tests of Exploration and Boldness: Searching for Differences Attributable to Subspecies and Commensalism." *Behavioural Processes* 157 (July): 133–41.

Morand-Ferron, Julie, Ella F. Cole, and John L. Quinn. 2016. "Studying the Evolutionary Ecology of Cognition in the Wild: A Review of Practical and Conceptual Challenges." *Biological Reviews* 91 (2): 367–89.

Møller, Anders Pape. 2010. "Interspecific Variation in Fear Responses Predicts Urbanization in Birds." *Behavioral Ecology* 21 (2): 365–71.

Hermansen, Jo S., Stein A. Sæther, Tore O. Elgvin, Thomas Borge, Elin Hjelle, and Glenn Peter Sætre. 2011. "Hybrid Speciation in Sparrows I: Phenotypic Intermediacy, Genetic Admixture and Barriers to Gene Flow." *Molecular Ecology* 20 (18): 3812–22.

Hobson, Keith A, and Robert G Clark. 1992. "Assessing Avian Diets Using Stable Isotopes II : Factors Influencing Diet-Tissue Fractionation." *The Condor* 94 (1): 189–97.

Hobson, Keith A. 2007. "Stable-Carbon and Nitrogen Isotope Ratios of Songbird Feathers Grown in Two Terrestrial Biomes: Implications for Evaluating Trophic Relationships and Breeding Origins." *The Condor* 101 (4): 799–805.

Karlsson Green, K., S. Harris, E. I. Svensson, F. Eroukhmanoff, and L. B. Pettersson. 2015. "Rapid Changes in Genetic Architecture of Behavioural Syndromes Following Colonization of a Novel Environment." *Journal of Evolutionary Biology* 29 (1): 144–52.

Isden, Jess, Carmen Panayi, Caroline Dingle, and Joah Madden. 2013. "Performance in Cognitive and Problem-Solving Tasks in Male Spotted Bowerbirds Does Not Correlate with Mating Success." *Animal Behaviour* 86: 829–38.

Laine, Veronika N., Toni I. Gossmann, Kyle M. Schachtschneider, Colin J. Garroway, Ole Madsen, Koen J. F. Verhoeven, Victor de Jager, et al. 2016. "Evolutionary Signals of Selection on Cognition from the Great Tit Genome and Methylome." *Nature Communications* 7 (1): 10474.

Lermite, Françoise, Chloé Peneaux, and Andrea S. Griffin. 2017. "Personality and Problem-Solving in Common Mynas (Acridotheres Tristis)." *Behavioural Processes* 134: 87–94.

Liker, A., and V. Bokony. 2009. "Larger Groups Are More Successful in Innovative Problem Solving in House Sparrows." *Proceedings of the National Academy of Sciences* 106 (19):

Medina-García, Angela, Jodie M Jawor, and Timothy F Wright. 2017. "Cognition, Personality and Stress in Budgerigars." *Behavioral Ecology* 28 (6): 1504–16.

Overington, Sarah E, Laure Cauchard, Kimberly-Ann Côté, and Louis Lefebvre. 2011. "Innovative Foraging Behaviour in Birds: What Characterizes an Innovator?" *Behavioural Processes* 87: 274–85.

Papp, Sándor, Veronika Bókony, Ernő Vincze, Bálint Preiszner, and András Liker. 2014. "A Comparison of Problem-Solving Success between Urban and Rural House Sparrows." *Behavioral Ecology and Sociobiology* 69 (3): 471–80.

Peers, Michael J L, Daniel H Thornton, and Dennis L Murray. 2013. "Displacement in Canada Lynx and Bobcat Evidence for Large-Scale Effects of Competition: Niche Subject Collections." *Proc. R. Soc. B* 280 (1773).

Reif, Jiří, Radka Reifová, Anna Skoracka, and Lechosław Kuczyński. 2018. "Competition-Driven Niche Segregation on a Landscape Scale: Evidence for Escaping from Syntopy towards Allotopy in Two Coexisting Sibling Passerine Species." *Journal of Animal Ecology* 87 (3): 774–89.

Rowe, Candy, and Susan D Healy. 2014. "Measuring Variation in Cognition." *Behavioral Ecology*. 25(6): 1287-1292.

Runemark, Anna, Laura Piñeiro Fernández, Fabrice Eroukhmanoff, and Glenn-Peter Sætre. 2018. "Genomic Contingencies and the Potential for Local Adaptation in a Hybrid Species." *The American Naturalist* 192 (1): 10–22.

Schluter, Dolph. 1995. "Adaptive Radiation in Sticklebacks: Trade-offs in Feeding Performance and Growth1" *Ecology*. Vol. 76.

Seeher, Sandra, Bradley A Carlson, Angela C Miniard, Eva K Wirth, Yassin Mahdi, Dolph L Hatfield, Donna M Driscoll, and Ulrich Schweizer. 2014. "Impaired Selenoprotein Expression in Brain Triggers Striatal Neuronal Loss Leading to Coordination Defects in Mice" 462 (1): 67–75.

Shettleworth, Sara J. 2001. "Animal Cognition and Animal Behaviour." *Animal Behaviour* 61 (2): 277–86.

Sih, Andrew, and Marco Del Giudice. 2012. "Linking Behavioural Syndromes and Cognition: A Behavioural Ecology Perspective." *Philosophical Transactions of the Royal Society B: Biological Sciences*.

Sol, Daniel, Richard P. Duncan, Tim M. Blackburn, Phillip Cassey, and Louis Lefebvre. 2005. "Big Brains, Enhanced Cognition, and Response of Birds to Novel Environments." *PNAS* 99 (7): 4141–42.

Sugino, Ken, Chris M Hempel, Mark N Miller, Alexis M Hattox, Peter Shapiro, Caizi Wu, Josh Huang, and Sacha B Nelson. 2006. "Molecular Taxonomy of Major Neuronal Classes in the Adult Mouse Forebrain." *NATURE NEUROSCIENCE* 9 (1).

Summers-Smith, J. Denis. 1988. *The Sparrows: A Study of the Genus Passer*. T & AD Poyser.

Sætre, Glenn Peter, Angélica Cuevas, Jo S. Hermansen, Tore O. Elgvin, Laura Piñeiro Fernández, Stein A. Sæther, Camilla Lo Cascio Sætre, and Fabrice Eroukhmanoff. 2017. "Rapid Polygenic Response to Secondary Contact in a Hybrid Species." *Proceedings of the Royal Society B: Biological Sciences* 284 (1853).

Thompson, Megan Joy, Julian Claude Evans, Sheena Parsons, and Julie Morand-Ferron. 2018. "Urbanization and Individual Differences in Exploration and Plasticity." *Behavioral Ecology* 29: 1415–25.

Tsurim, Ido, Zvika Abramsky, and Burt P. Kotler. 2008. "Foraging Behavior of Urban Birds: Are Human Commensals Less Sensitive To Predation Risk Than Their Nonurban Counterparts?" *The Condor* 110 (4): 772–76.

Xu, Jun, and Megan Andreassi. 2011. "Reversible Histone Methylation Regulates Brain Gene Expression and Behavior."

Zidar, Josefina, Alexandra Balogh, Anna Favati, Per Jensen, Olof Leimar, Enrico Sorato, and Hanne Løvlie. 2018. "The Relationship between Learning Speed and Personality Is Age- and Task-Dependent in Red Junglefowl". 2018. 72 (10).