FORAGING BEHAVIOUR IN CAPTIVE RED KNOTS

The role of individual differences in the use of social information

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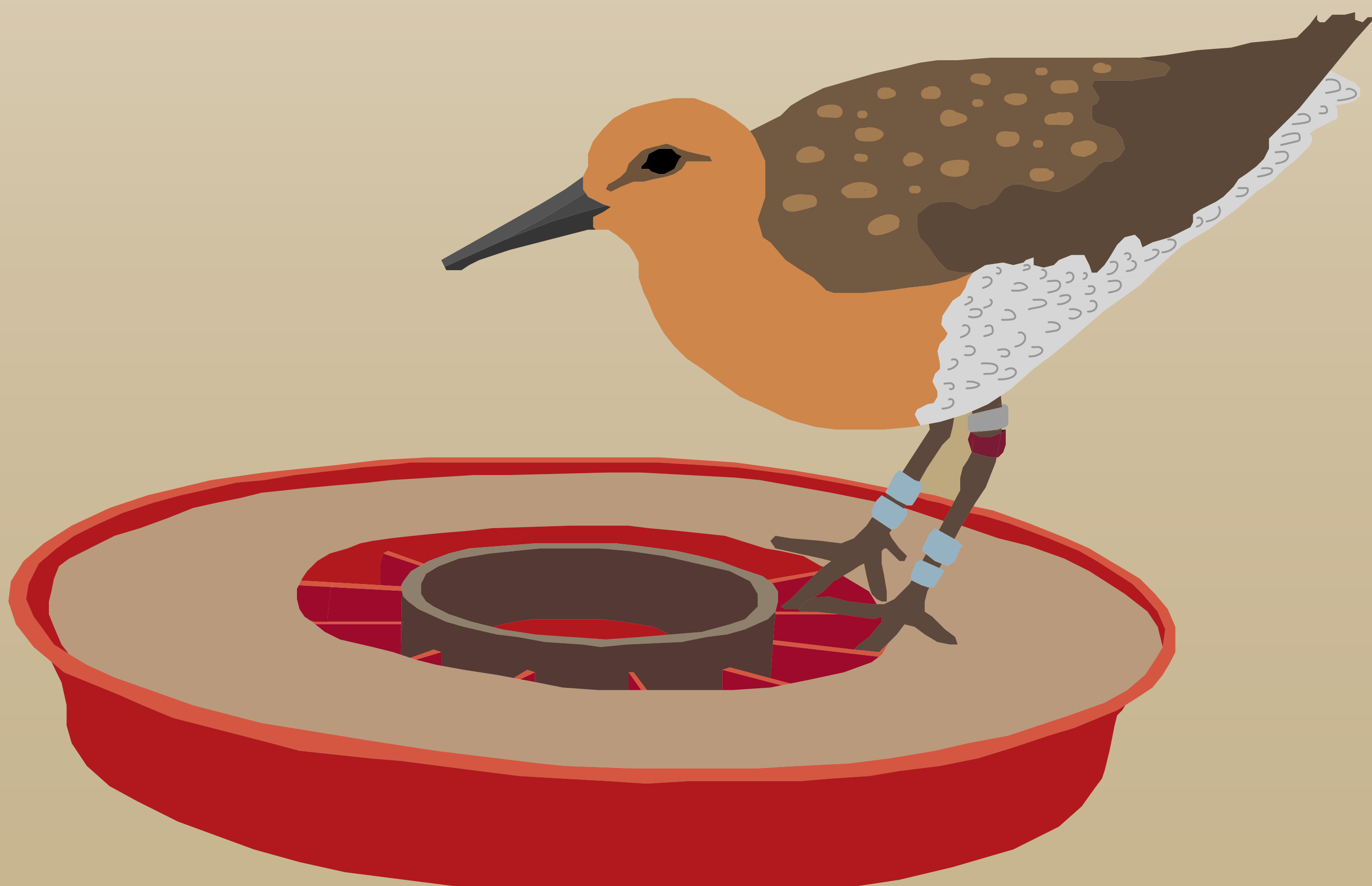

Foraging behaviour in captive red knots

The role of individual differences in the use of social information

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Abstract

Collective behaviour is widespread among animals, and through social learning, it provides individuals with ways to deal with rapid environmental change. Within the group, animals differ in personality and are engaged in networks of social interactions. The availability and spread of information about the location and quality of resource patches may depend on the distribution of personalities. Previous studies have found that individuals with exploratory personality are more likely to discover food patches; therefore, non-exploratory individuals could benefit from following explorers.

Calidris canutus islandica are suitable candidates for using public information to increase their foraging success, and consequently survival rates, because the benefits outweigh the costs. In fact, knots benefit from sharing foraging information while avoiding costs of competition, as food is abundantly but cryptically dispersed on the mudflats.

In this project, we investigate the use of social information by captive red knots, examining their foraging behaviour both alone and in the group. Several behavioural assays were conducted in the experimental shorebird facility at NIOZ (Texel, The Netherlands), where 21 patches were placed in a sandy arena, but only one contained prey items. Fifty captive red knots, whose exploratory personalities were previously assessed, were tested in this setup, firstly alone and subsequently in groups of 2, 3 and 4 total birds. For all trials, the fraction of time the focal bird took to discover the filled food patch was measured and identified as "searching time", which was analysed in relation to individual-level traits and group's characteristics.

The results unexpectedly show that exploratory personality does not influence foraging behaviour in any case. Nevertheless, all the birds became faster in finding the food when they were in a group. Most importantly, non-exploratory birds remarkably benefit from being with other individuals that share information about the food patch location through local enhancement.

This captivity study gave insights into the use of social information by knots and how their foraging behaviour changes from being alone to being in a group, highlighting the vital importance of group foraging, especially for non-exploratory individuals.

Keywords: Red knots, captivity, collective behaviour, animal personality, foraging information

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1 Introduction

1.1 Background

Collective behaviour (e.g., flocking) is widespread among animals, and several studies have pointed out that it has costs and benefits. On the one hand, grouping's main cost is competition for resources, which happens when the individual's intake rate decreases due to resource depletion and interference competition [1] [2]. On the other hand, an essential advantage of aggregation regards the increased safety from predation, as the shared vigilance for predators is higher [3] [4]. Moreover, it enables the transfer of information about foraging opportunities between individuals [5] through social interactions and thus, creating an information web where each individual is engaged in complex networks of social interactions [6].

Considering that resources are generally distributed unevenly within natural systems [7], social information about the location and quality of food patches is crucial in determining survival in the wild [6]. Therefore, group-living animals significantly benefit from sharing foraging information [8] [9], which is used for decision-making [10] and allows individuals to cope with rapid environmental change in a faster and more accurate way, through social learning [11] [12].

Within groups, animals differ from one another in their behavioural phenotypes, which designate their personality. In fact, animal personality describes and accounts for consistent behavioural patterns over time and/or context. One typically measured personality trait is exploration. Having an exploratory personality implies promptness to actively explore novel environments over long distances [13] [14], whereas non-exploratory personality assumes a more sedentary behaviour. The study of personality differences has proven useful in many fields, including conservation, and it is an essential addition to the understanding of animal ecology and evolution [15].

The variation in personality may drive collective behaviour [16] [17] as it can affect interactions among individuals within groups, determining social network structure [18].

Some studies have shown that exploratory individuals are more likely to discover food patches [13]. Therefore, non-exploratory individuals could benefit from following explorers [19], according to the local enhancement hypothesis [20], which consists in the attraction of searching individuals to groups of already-feeding birds [21]. This form of intraspecific interaction is usually regarded as the "producer/scrounger relationship", where non-exploratory birds are the scroungers that exploit resources provided by producers, which are exploratory individuals [22]. In this context, it is evident that the use of public information is essential for increasing foraging success and consequently, survival rates and population resilience. However, we still have little understanding of the relationship between individual-level personality traits, such as exploration behaviour, and the spread of information in a group [23]. Additionally, investigating how information is shared between individuals would provide useful insights into the field of movement ecology, as it affects decisions about when, where and how to move [24].

Studying these mechanisms in captivity allows behavioural observations and personality characterisation in controlled environments [25]. Furthermore, it is the starting point to understand how personality and environmental variation in resources affect collective behaviour. The results of such research will expand our knowledge on the networks of sharing the information and will be useful for further research in the wild, which might ultimately aid nature conservation. In fact, it has been previously shown that fundamental insights contribute to the conservation of red knots and the Wadden Sea in general (e.g., [26]).

1.2 Red knots

Calidris canutus, commonly called red knots, are medium-sized migrant shorebirds that have been studied at the Royal Netherlands Institute for Sea Research (NIOZ) for several decades. This thesis focuses on the subspecies *islandica* [27], which breeds in the Arctic during the summer (June-July) [28] [29], and spends the rest of the year in coastal areas of western Europe [29] [30] [31].

The Wadden Sea provides an important moulting habitat as well as a rich feeding habitat due to high densities of shellfish like Baltic tellins and cockles [32]. At high tide, they aggregate (roost) on the exposed areas of the mudflats in large and dense flocks and at low tide, they search for food in large groups of up to several thousand individuals [32]. Their diet mainly consists of small bivalves, especially mussels, clams, and cockles. Although they also consume amphipods, gastropods, marine worms, shrimps, and tiny crabs [33]. They feed by repeatedly inserting their bills in the wet sediment of the mudflat until they remotely touch-sense the prey's shell, over a distance of several centimetres [34]. This is possible due to a peculiar characteristic: pressure-sensitive organs at the tip of the bill [34]. Once the prey is found, knots swallow it whole and crush the shell with their strong muscular stomach (known as gizzard), which fragments are subsequently defecated [35] [36].

Red knots show a high degree of aggregation in the Wadden Sea, regularly foraging in groups of up to 15,000 individuals [32] and adjusting their space use based on the distribution of resources [37]. Since food patches are broadly and cryptically dispersed in the mudflats [38], knots can avoid costs of interference competition [39] [2] [40]. This makes them suitable candidates for using social cues to find places where the prey species are in high densities and, therefore, increase their foraging success [41]. This means that they constitute a great system to look at the link between personality and social foraging, because years of research allowed us to gain broad knowledge on their diet, habitat preferences, survival rates and, lately, personalities [42] [33] [43].

This bird species is an ideal study model even for practical reasons, as it copes very well with being in captivity (e.g., [44]) and the experimental shorebird facility of NIOZ is excellent for testing field-generated hypotheses of group composition and movement studies. Additionally, Bijleveld *et al.* [5] [45] have found that knots consistently differ in exploratory behaviour, which is measured as the speed of movement in a novel (but non-rewarding) environment, and that they are capable of detecting and using social information to increase their food-finding rate.

At the end of this investigation in captivity, the individuals will be released into the wild with a WATLAS (Wadden Sea Advanced Tracking and Localisation of Animals in real-life Systems) unique tag-ID (figure 2) to track their movement and habitat use in the Dutch Wadden Sea, in order to maximise the scientific gain from these animals.

In conclusion, collective behaviour and social learning in wild populations are vital to study, having the potential of increasing population resilience to the rapid global environmental change and threads as sea-level rise and habitat destruction. This aspect is particularly crucial for red knots considering that the population trend of these birds is declining [46] and that the IUCN Red List classifies *Calidris canutus* as a Near Threatened species [47].

1.3 Objectives

This experimental project on captive red knots aims at understanding how foraging behaviour (i.e., searching time for food-finding) is affected by individual traits (i.e., exploratory personality and body mass) and motivation (i.e., fasting time).

Moreover, we further investigate the differences between foraging alone and in a group. First, birds are tested alone to understand how individual-level traits affect the searching time for food-finding. Subsequently, birds are tested in groups of 2, 3 and 4 individuals to observe how social information on the location of resources is spread and how the group's characteristics (i.e., group size, mean group's personality) affect the individual's searching time.

In addition to the searching time, the time in side-aviary before entering the experimental arena is analysed in correlation with personality. Furthermore, the influence of the time in side-aviary on the searching time is also assessed for birds tested alone. Lastly, other aspects that may influence personality and/or searching time are examined, including body mass at capture, dominance and location of the food.

1.4 Research questions and hypotheses

The main research questions and relative hypotheses of this study are:

1) When an individual is alone:

(a) How do individual traits and motivation affect the searching time?

We hypothesise that exploratory individuals will have lower searching times compared to non-exploratory ones. Moreover, we predict that individuals with higher body masses will be slower because they are less motivated to find food and less exploratory [45]; and that longer fasting times will correspond to lower searching times, because of higher hunger level and motivation to find food.

(b) How does personality affect the time in the side-aviary?

We expect that exploratory individuals will spend less time in the side-aviary compared to non-exploratory ones. This is because exploratory individuals are usually bold, whereas non-exploratory are shy [48].

(c) Does the time in side-aviary influences the searching time differently for the two personality types?

We presume that the time in side-aviary will positively influence both exploratory and non-exploratory birds' searching time. Meaning that, regardless of their personality, birds that spend longer times in the side-aviary, will also be slower in finding the food, possibly due to shyness and/or low motivation.

2) When an individual is in a group:

(a) How do the group's characteristics, individual traits and motivation affect the searching time?

We predict that the searching time will decrease when the mean exploration speed of the group is higher. Meaning that the more the group is composed of exploratory individuals, the less time it will take for the focal bird to find the food, due to the spread of social information through local enhancement. For the same reason, it is also expected that an increased number of partners will result in lower searching times. Regarding body mass and fasting time, we hypothesise that they will have the same impact on the individual trials' searching time.

(b) How does personality affect the time in side-aviary?

We expect that exploratory individuals will spend less time in the side-aviary than non-exploratory ones, for the same reason previously mentioned.

3) How do different group sizes (from individuals alone to groups of four) affect the searching time of both exploratory and non-exploratory personalities?

We expect the searching time to decrease with larger group sizes for both personalities, with a significant difference from 1 (alone) to 2 (not alone), because of scramble competition and social facilitation. Furthermore, when looking at the two personalities separately, we hypothesise exploratory individuals to be on average faster than non-exploratory in finding the food.

2 Materials and Methods

2.1 Study species

Fifty *Calidris canutus* of the *islandica* subspecies were captured with mist-nets at night on the 29 October 2019 in the Dutch Wadden Sea, near the island of Griend, and then transported to NIOZ (Texel, The Netherlands; 53°00'12" N, 4°47'23" E).

Each individual is provided with a unique metal identification ring on the right tibia and three plastic coloured rings of a unique combination, symmetrical on both tarsi (see figure 1).

Figure 1: Red knot with a metal identification ring on the right tibia and three plastic coloured rings of a unique combination, symmetrical on both tarsi (RPY). © Aileen Roncoroni

A list of all these fifty birds that performed the behavioural assays can be found in appendix 6.1.

After the experiments, the birds were equipped with a WATLAS tag (see figure 2), as well as new coloured rings with another unique combination, and released back into the wild during summer 2020.

Figure 2: Red knot with a WATLAS tag glued with superglue on its back. © Selin Ersoy

Prior to the experiments, the exploratory personality of these individuals was assessed by PhD student Selin Ersoy. This is traditionally determined by studying individual movements after the introduction to a novel environment [48] [15]. Thus, she tested the birds inside an arena filled with water and containing wet sand patches. The trials were recorded by a camera placed on the ceiling, and the individual's movements were later automatically tracked with a computer software called idTracker [49]. The log_{10} of the mean speed (m/s) is then used as a measure for exploratory behaviour.

The birds were then separated into three groups to better visualise the differences and finding patterns in further analysis. Twenty individuals with higher exploration speeds are labelled as "exploratory", while the twenty with lower exploration speeds are considered "non-exploratory". The ten birds with exploration speeds in between are rated as "mid-exploratory" and were later excluded from the data analysis to better view the two main groups of personality: exploratory and non-exploratory. Figure 3 shows the fifty experimental birds with the relative exploration speed and therefore personality that were assessed by Selin Ersoy and Allert Bijleveld.

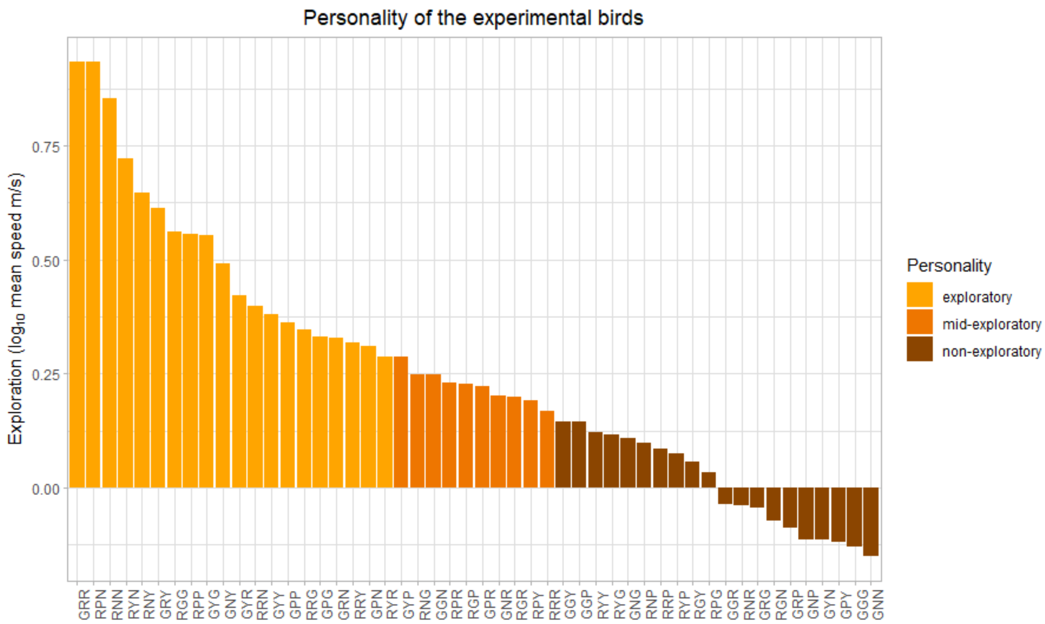


Figure 3: Graph showing the fifty experimental birds named over the coloured rings and their exploration speed and personality type.

2.1.1 Housing

The birds were housed in outdoor aviaries of NIOZ, Texel. These aviaries are approximately 4 m long, 2 m wide and 2.5 m high at one end, sloping down to a height of 1.9 m at the other end. There is a supply of running freshwater in a tray for drinking and bathing, and running saltwater on the coated concrete floors. Moreover, a stretch of sand collected from the Wadden Sea, covered in 5 cm saltwater resembles the knots' natural mudflat habitat, allowing them to probe the sediment.

These cages' composition was changed every day: after their trials, the birds were released to a different cage, randomly chosen. This allows them to get to know each other and prevents a particularly dominant bird from attacking the same individuals, hindering their feeding.

Lastly, once a week, the birds were weighed, their moult and plumage status scored, and their feet checked for small wounds or infections [50].

2.2 Experimental setup

2.2.1 Experimental shorebird facility

The experiments were conducted in the experimental shorebird facility of NIOZ, on the island of Texel (according to protocol 2000.04 of the DEC, the Dutch committee for animal experiments). It is characterised by an intertidal, climatised indoor arena; approximately 7 m long, 7 m wide and 3 m high, filled with sand. However, we separated it into two equal parts with a polyester sheet, and only employed one half for the experiments, reducing the real measure of length to 3.15 m. The three main reasons for this adjustment are that:

- it facilitates the usage of one single camera on the ceiling to film the trials from the top;
- it makes it easier for the observer to examine the birds during the trials;
- only groups of maximum four birds at a time were tested, so there is no need for a vast arena.

Adjacent to the experimental arena, there is an aviary (of 4 m long, 1.6 m wide and 2.5 m high), hereafter called "side-aviary", similar to the outside cages were the birds are housed, but without natural light. The side-aviary is useful to help the birds acclimatise before the trial and release them in the experimental arena with the aid of a sliding door. It has a supply of running freshwater in a tray and running saltwater on the floor, to keep the floor and the birds' feet clean.

2.2.2 Food patch

Twenty-one red trays (customarily used in captivity as feeders with a transparent plastic top) constitute the patches. However, only one actually contains food, hereafter called “food patch”, which location is randomly selected for each trial or group of trials, to avoid the possibility that birds learned its position.

The patches were designed with a beige disc on top and a ring at the centre, attached with velcro, to cover and hide the food. This prevents the birds from seeing whether the patch contains food from a distance, forcing them to look closely and underneath, consequently allowing us to know when a tray had been searched (see figure 4).

Figure 4: Food patch with food hidden under the disc and a bird eating from it. © Rosemarie Kentie

The distribution of the patches in the arena is showed in figure 5. The same distance between the patches was maintained for all trials as well as from the bottom, top and side walls.

Although in the wild, knots feed mainly on armoured mollusc prey that they swallow whole [33], they are fed with protein-rich trout food pellets in captivity (Produits Trouw, Vervins, France), hereafter called “trouvit”. These pellets are based on fish meal and contain a whole spectrum of balanced nutrients, vitamins and amino acids.

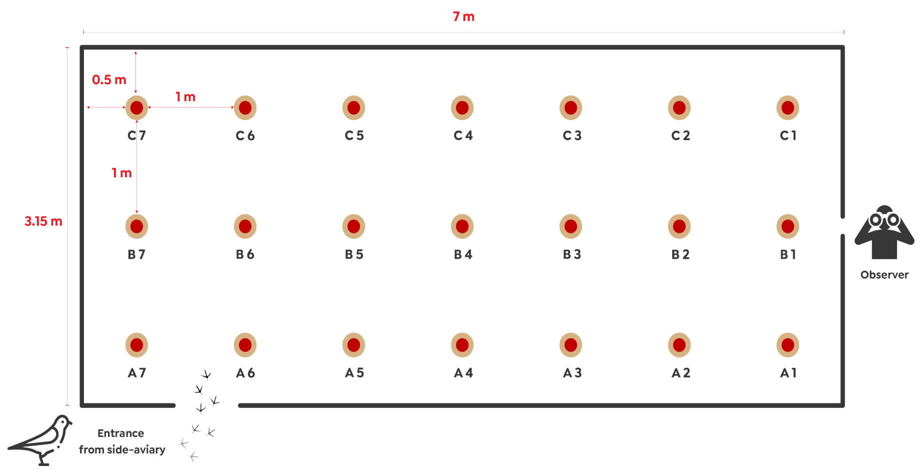
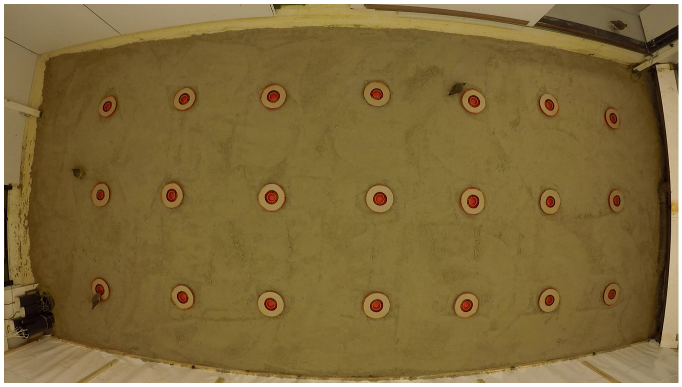


Figure 5: Illustration showing the arena with the location and "names" of the patches. © Dornaz Vazifehaali

2.2.3 Cameras

Three GoPro cameras were used to film the trials from different points of view (see figure 6):

- Top-camera (Hero 5) mounted on the ceiling, giving an overview of the whole arena from the top;
- Door-camera (Hero+) mounted in the side-aviary, to identify birds as they enter by their colour rings;
- Side-camera (Hero+) mounted on the side of the arena, close to the observer, to see interactions between individuals and to have a view of the entire arena from the side.



(a)

(b)

(c)

Figure 6: Views of the three GoPros: (a) top-camera (b) door-camera (c) side-camera. Screenshot captured at the same time. © Aileen Roncoroni

2.2.4 Training and tests

With the objective of getting the birds acquainted with the experimental setup, and teaching them that only one patch contains food, there was a three-week training period before the experiments. From the beginning of the training, all food trays in the outside aviaries were changed to be identical to those in the experimental arena. Moreover, the birds were released multiple times in the arena to habituate, in progressively reduced group sizes. Initially in big groups of 25 individuals and subsequently in smaller groups of 8 or less. Furthermore, the number of filled food patches in the arena was gradually reduced from 6 to 1, and the location shuffled every time.

After the training, we performed tests for a week where we released groups of four to one bird in the arena. The birds were deprived of food overnight, to motivate them to search for food in the arena during the tests. During these test trials, in contrast to the training, we meticulously followed the experiment's protocol and tested the cameras.

2.2.5 Experimental procedure

After a total of approximately four weeks where the birds had, on average, 11 trials (minimum 9 and maximum 12), they were ready to start with the real experiments. We performed a total of 200 trials (50 birds $\times$ 4 trials). For the first experiment, we tested the birds alone in the experimental arena. Whereas for the second experiment, each bird was tested in a group of 2, 3 and 4 total birds, and constituted the "focal bird", meaning that it was the only individual within the group which behaviour was subsequently analysed.

In order to induce standard hunger levels between birds, food was deprived of all outside aviaries every night. Knots are naturally accustomed to periods without food as they cannot feed around high tide nor during their non-stop flights of migration [32].

Each trial consisted of retrieving the focal bird (and the partners) from its aviary, measuring its body mass and letting it rest in the side-aviary (for minimum 4 and maximum 18 minutes, with an average of 11 minutes). Then, we remotely opened the sliding door that connects the side-aviary to the arena with a pulley mechanism, to let the bird enter. If the bird did not enter voluntarily after 2 minutes, we gently herded it in. The time from the door opening until the bird lands in the arena is defined as "time in side-aviary". All trials lasted 10 minutes and aimed to measure the "searching time" of the focal bird, namely the time from when it lands into the arena until it discovers the food patch filled with trouvit.

During the trials, an observer would note the first timestamp as the door was opened, the second as the focal bird landed in the arena and the third as it found the patch containing the food among the others (figure 7). Later, these times were double-checked with the aid of the recorded videos. Additionally, the observer wrote down any aggressive interaction between the birds or general remark (e.g., birds' behaviours, especially if unusual, unpredicted noises that could have disturbed them and potential malfunctioning of the cameras).

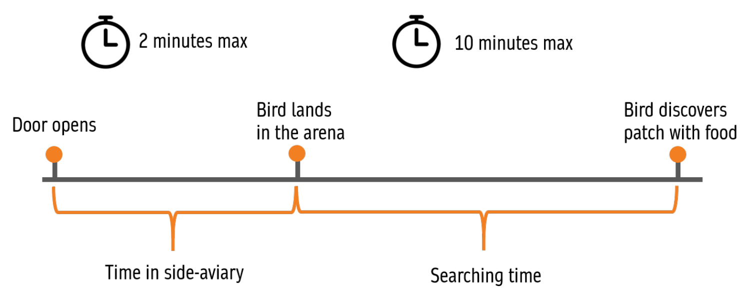


Figure 7: Timeline of the trials and timestamps. © Aileen Roncoroni

The detailed experiment protocol can be found in appendix 6.2.

2.3 Data analyses

Data analyses were carried out in R [51]. Generalised linear mixed model were conducted through the `lm` function, one by one to answer to each part of the research questions.

Firstly, the searching time of the birds tested alone constituted the response variable as a function of several explanatory variables: first personality, then body mass and lastly fasting time. The time in side-aviary was also used as the response variable with personality as the explanatory variable. Furthermore, the time in side-aviary was analysed in relation to the searching time, for the two personalities separately by conducting two separate linear models.

Secondly, the focal bird' searching time of the group trials was analysed firstly in correlation with the mean exploration speed of the group, then group size and lastly body mass and fasting time. Additionally, the time in side-aviary was used as the response variable with mean exploration speed of the group as the explanatory variable.

Thirdly, three linear models were performed where searching time was the response variable as a function of group size for both personalities together, then only for exploratory and non-exploratory individuals separately.

Lastly, to address the question of dominance, we registered every aggressive interaction that we observed over the experiment period to make a dominance rank by giving a dominance score to each individual through Elo ratings. Moreover, to analyse whether the location of the food patch influenced the searching time, we ran a mixed-effect model, using the searching time as the response variable and the food patch as a random effect (`searching_time ~ personality + (1|food_patch)`).

3 Results

3.1 Individuals alone

This section shows the results of the first experiment with individuals tested alone in the arena.

The data rejects the hypothesis proposed for the first research question showing that personality, in terms of exploration speed, does not influence the searching time for food-finding (figure 8 and table 1).

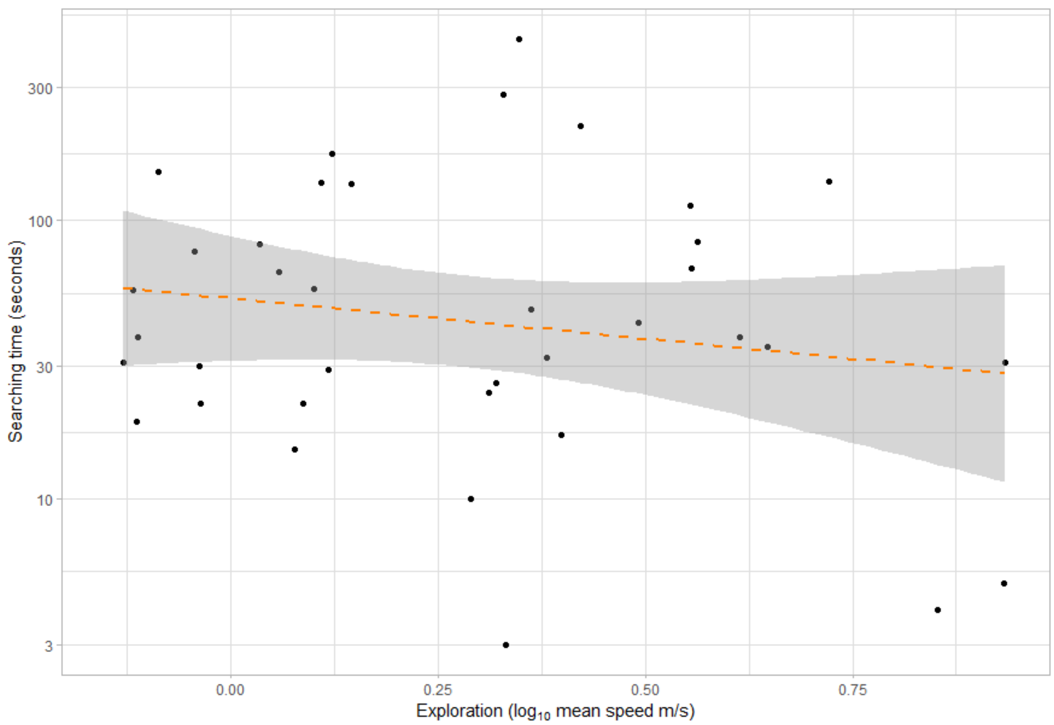


Figure 8: Correlation of searching time and exploration speed for all birds tested alone.

Body mass seems to play an important role as it has a negative effect on searching time, although the opposite effect was expected (figure 9 and table 1).

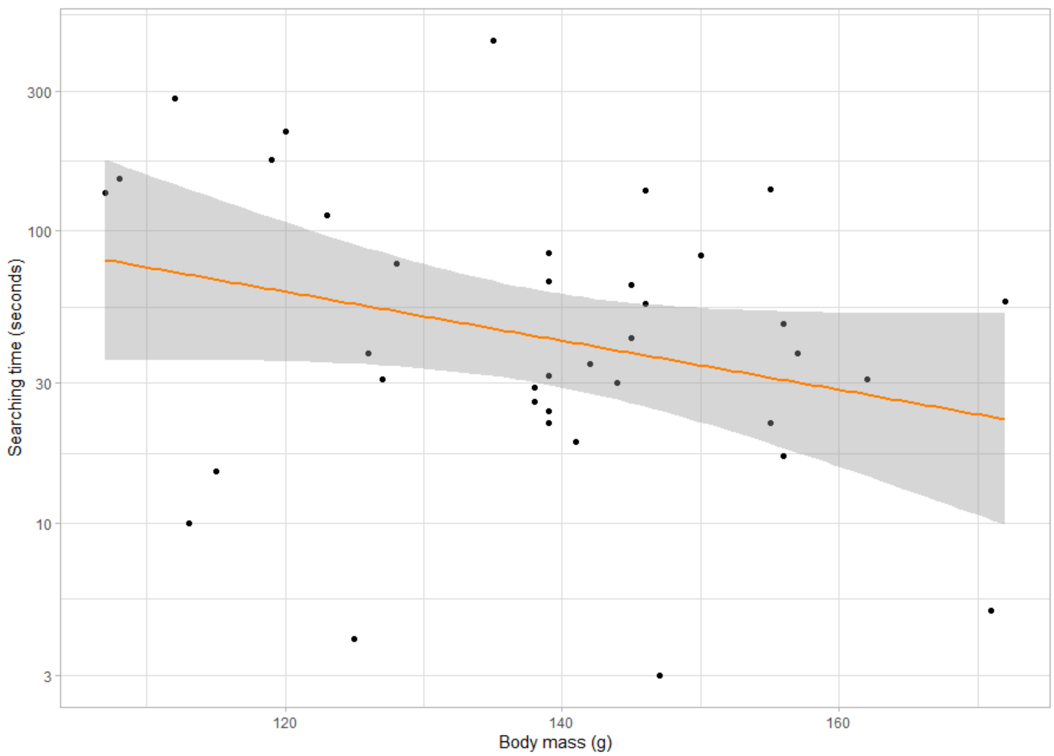


Figure 9: Correlation of searching time and body mass for all birds tested alone.

The same applies to fasting time, which is a proxy for motivation as it is defined as the time since the food was deprived in the outside aviary (the night before) until the bird found the food patch in the arena (figure 10 and table 1).

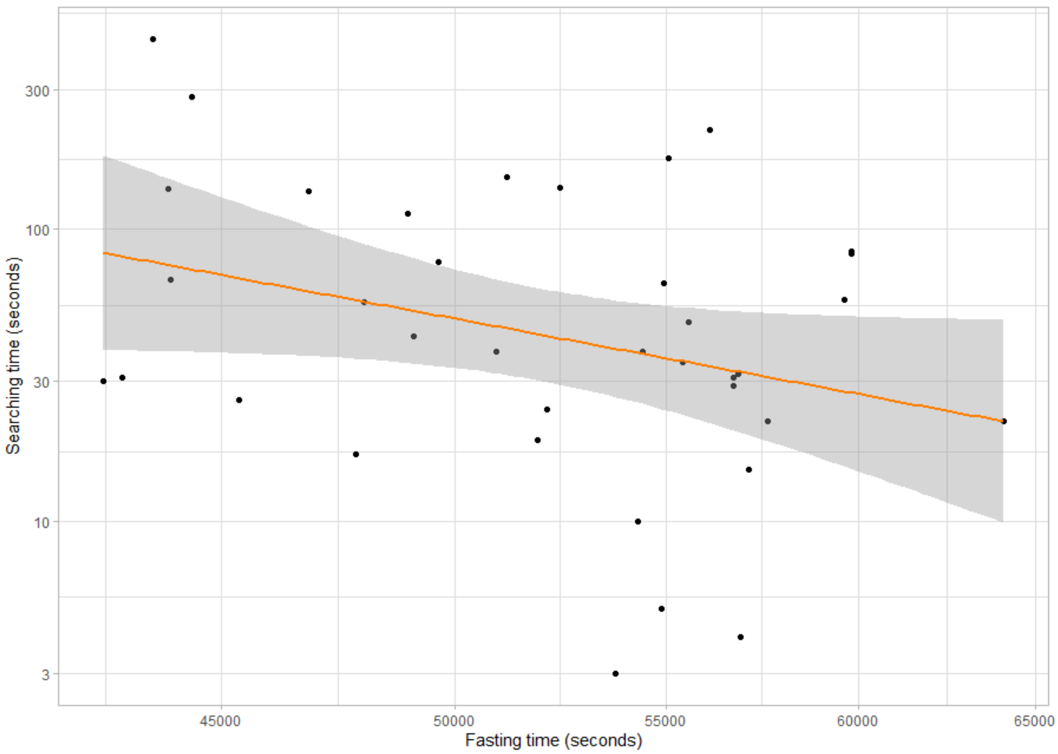


Figure 10: Correlation of searching time and fasting time for all birds tested alone.

When the birds are tested alone, personality seems to influence the time spent in the side-aviary before entering the experimental arena. In fact, exploratory individuals spend less time in the side-aviary compared to non-exploratory ones (figure 11 and table 1).

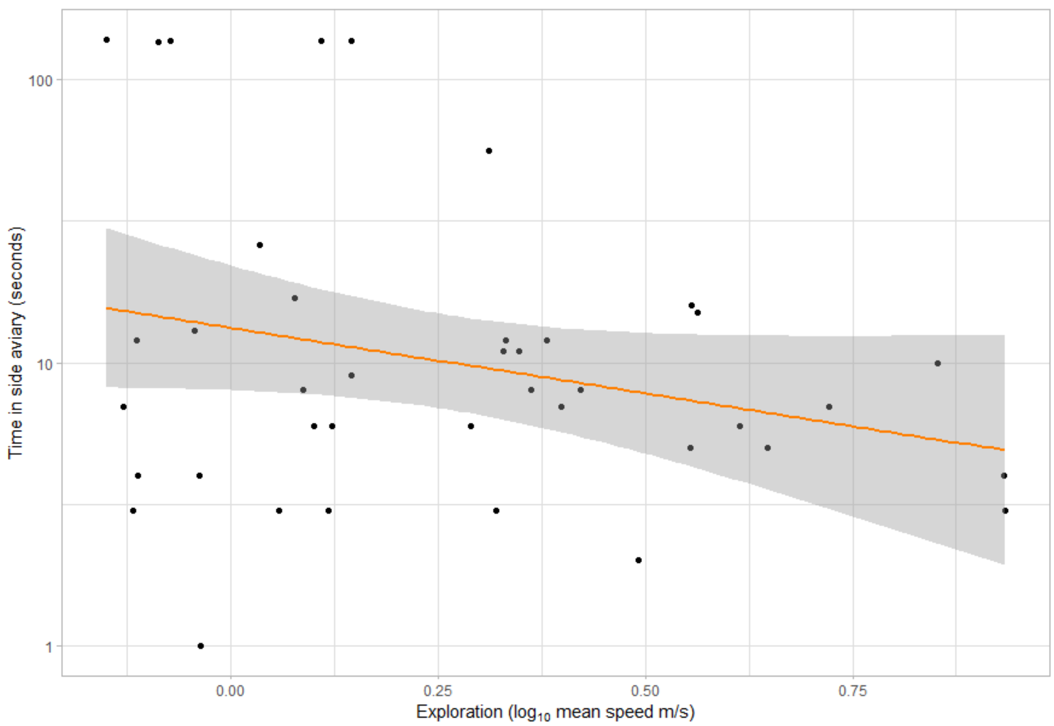


Figure 11: Correlation of time in the side-aviary and exploration speed for all birds tested alone.

When looking at the correlation between the time in side-aviary and the searching time, a different result is found for the two personalities. For non-exploratory birds, the time in side-aviary significantly affects the searching time: individuals that spend more time in the side-aviary took longer to find the food (figure 12, table 1). In the case of exploratory birds instead, the result is not significant (table 1).

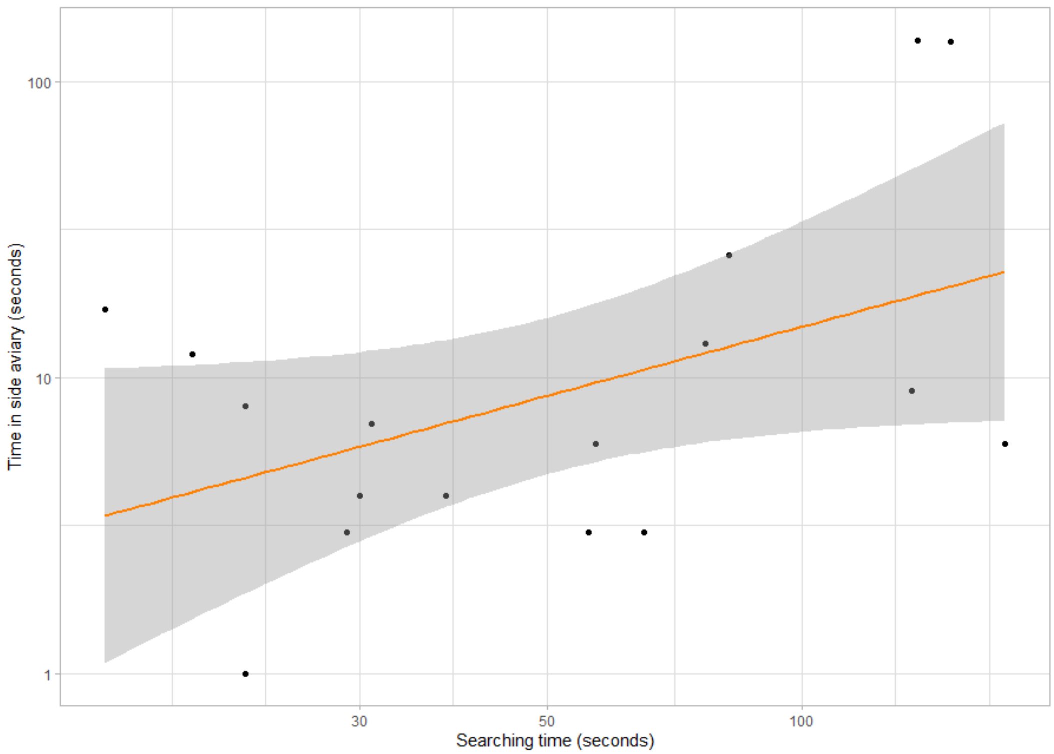


Figure 12: Correlation of time in the side-aviary and searching time for only non-exploratory birds tested alone.

Formula	**Estimate**	**SE**	***p*-value**
Searching time ∼ Exploration speed	-3.44	49.50	0.95
Searching time ∼ Body mass	-1.80	0.85	0.04
Searching time ∼ Fasting time	-0.006	0.003	0.04
Time in side-aviary ∼ Exploration speed	-48.46	21.81	0.03
Time in side-aviary ∼ Searching time (non-exploratory)	0.47	0.18	0.02
Time in side-aviary ∼ Searching time (exploratory)	-0.002	0.02	0.92

Table 1: Output of the `lm` functions in R for the analyses of the individuals alone.

3.2 Individuals in a group

In this section, the results of all group sizes (2, 3 and 4 total birds) are presented together. The graphs of the distinct groups are not displayed since the outcome was the same.

In accordance with the results of individuals tested alone, but contrary to the expectations of research question number 2, there is no significant correlation between the searching time of the focal bird and the mean exploration speed of the group (figure 13 and table 2).

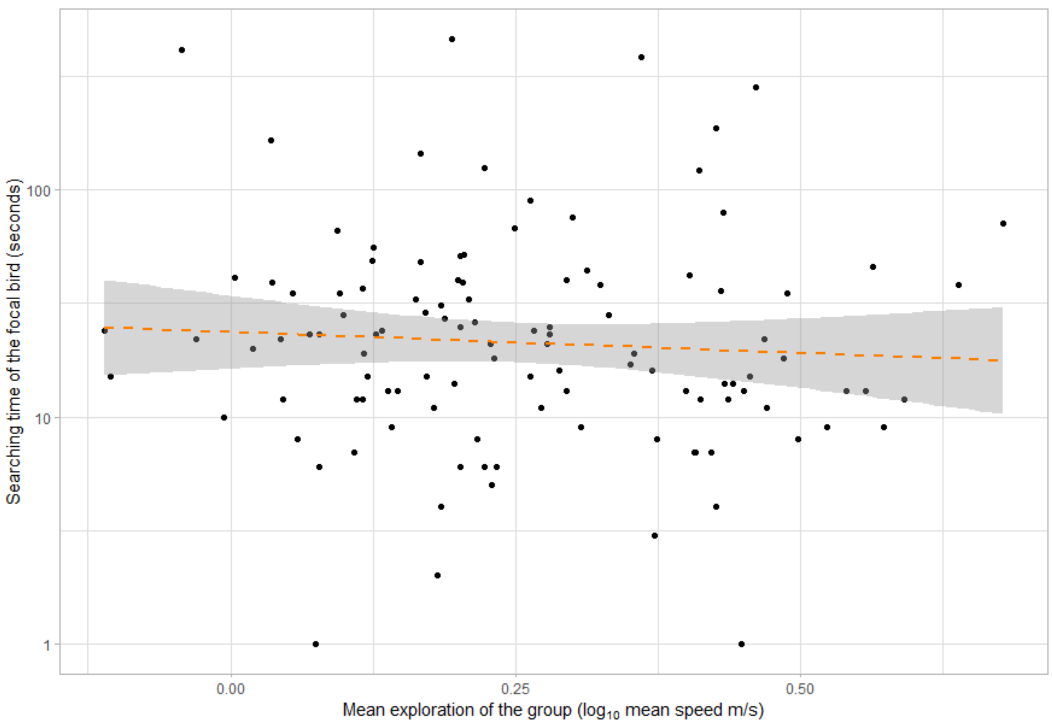


Figure 13: Correlation between searching time of the focal bird and mean exploration speed of the group.

In contrast to what was hypothesised, group size does not influence the searching time of the focal bird (figure 14 and table 2).

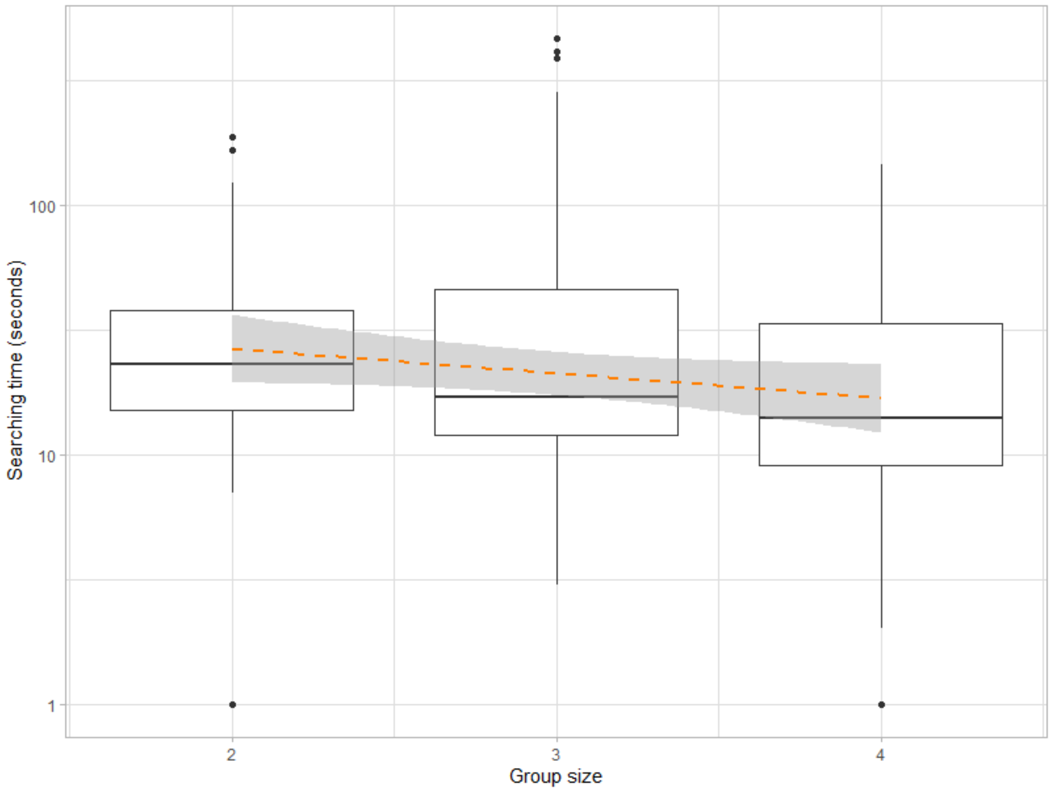


Figure 14: Correlation between searching time of the focal bird and group size.

Contrary to to what observed in individuals tested alone, body mass and fasting time do not have a significant influence on the focal bird when in a group (figure 15, 16 and table 2).

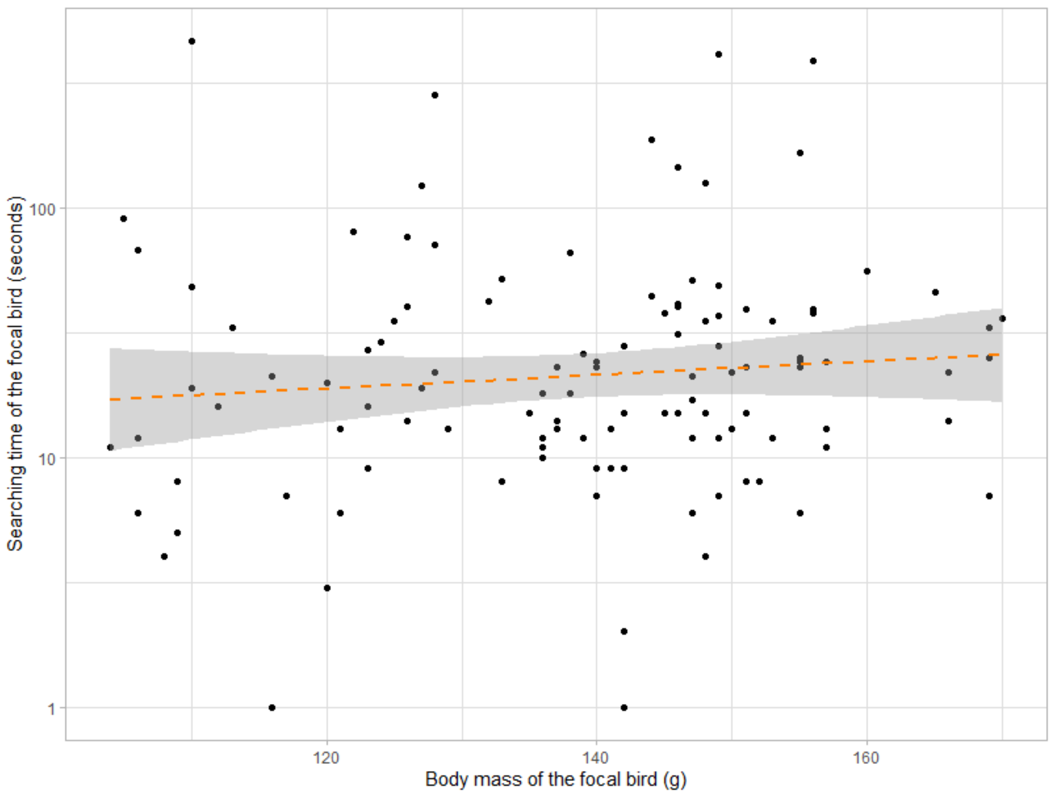


Figure 15: Correlation between searching time and body mass of the focal bird in a group.

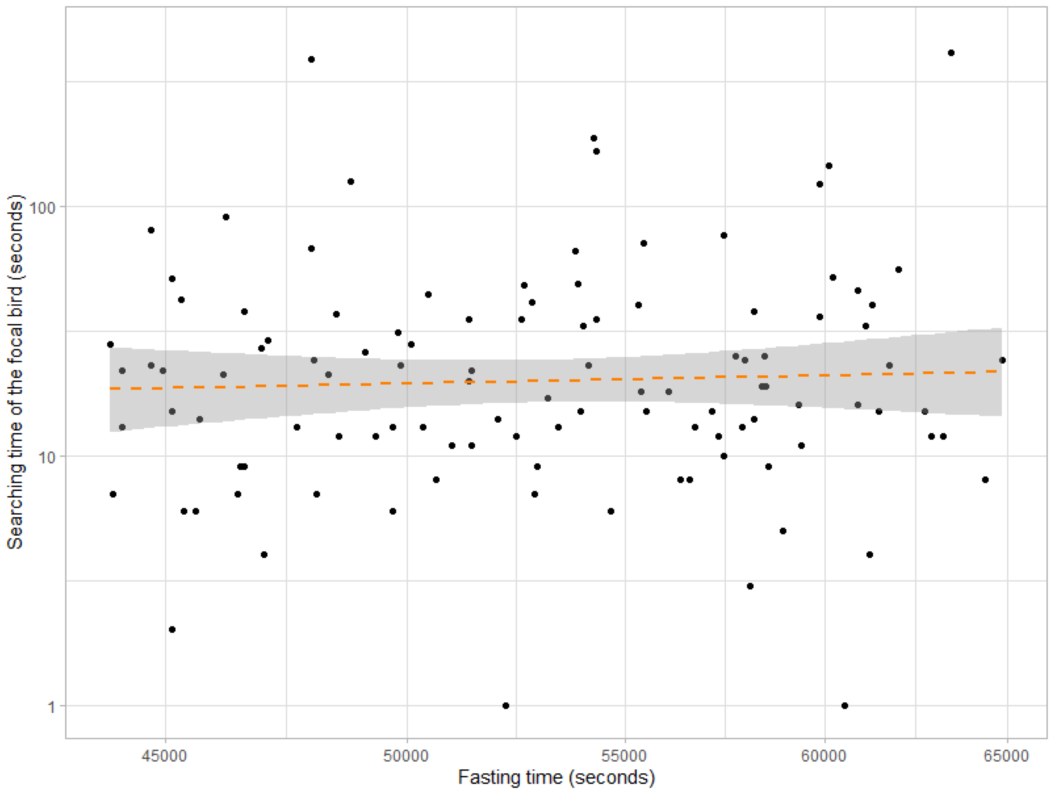


Figure 16: Correlation between searching time and fasting time of the focal bird in a group.

As opposed to the results obtained with individuals tested alone, the time that the focal bird spends in the side-aviary before entering the experimental arena is not correlated with the mean exploration speed of the group (figure 17 and table 2).

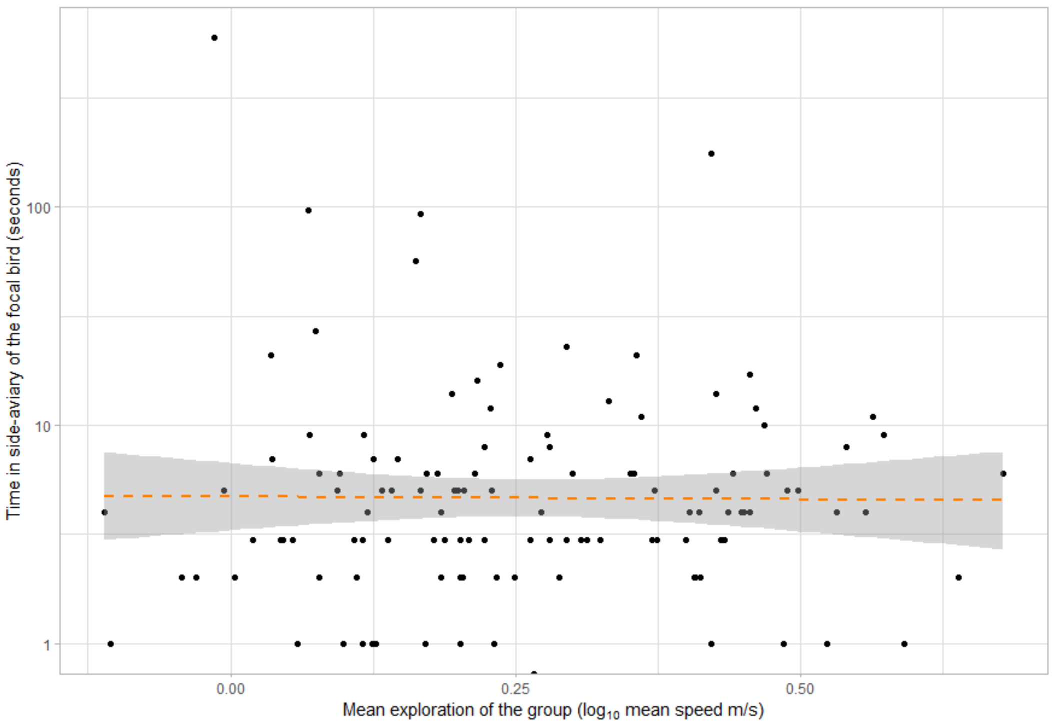


Figure 17: Correlation between time in the side-aviary of the focal bird and mean exploration speed of the group.

Formula	**Estimate**	**SE**	***p*-value**
Searching time ∼ Mean exploration speed	-21.33	41.55	0.61
Searching time ∼ Group size	-5.99	8.49	0.48
Searching time ∼ Body mass	-0.06	0.43	0.89
Searching time ∼ Fasting time	0.001	0.001	0.43
Time in side-aviary ∼ Mean exploration speed	-46.68	30.91	0.13

Table 2: Output of the `lm` functions in R for the analyses of the individuals in a group.

3.3 Comparison of individuals alone and in a group

This section displays a comprehensive analysis of individuals alone and in a group, performed to answer the third research question.

When looking at the two different personality types in group size 1 (individuals alone), we see that non-exploratory birds show longer searching times to find food than exploratory birds. However, their searching time decreases when there are other birds in the arena, to the point where they become even faster than exploratory individuals (figure 18 and table 3).

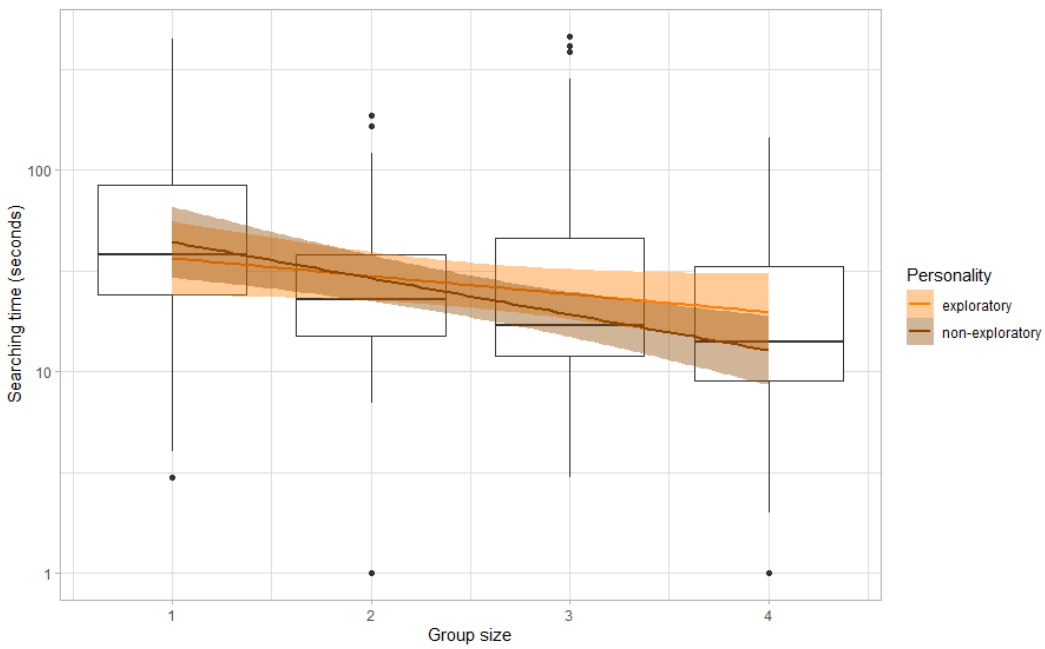


Figure 18: Correlation between searching time and group size, for the two types of personality.

Formula	Estimate	SE	p-value
Searching time ∼ Group size	-12.54	5.72	0.03
Searching time ∼ Group size (non-exploratory)	-13.59	6.02	0.03
Searching time ∼ Group size (exploratory)	-11.22	9.55	0.24

Table 3: Output of the `lm` functions in R for the comprehensive analysis of individuals alone and in a group.

3.4 Additional analyses

The other aspects that we investigated in order to make a comprehensive analysis of the collected data, as mentioned in chapter 1, did not show any significant result. For this reason, these additional analyses are listed in this separate section.

In addition to the body mass measured on the day of the trial, used in the results previously mentioned in this chapter, we also analysed the body mass measured when the bird was first captured. The results show that personality does not have any influence on the body mass at capture (Estimate = -9.47×10^{-6}, SE = 5.30×10^{-3}, p-value = 0.99).

The same result was found when analysing the effect of personality on the difference between the body mass measured at capture and the day of the experiment: there is no effect (Estimate = 4.08×10^{-4}, SE = 0.002, p-value = 0.89).

Furthermore, searching time is not influenced by the difference between the body mass measured at capture and the day of the experiment (Estimate = -1.12, SE = 0.86, p-value = 0.20).

In order to assess the dominance issue, we analysed the calculated dominance score in correlation with exploratory behaviour, body mass and searching time; however, it does not seem to affect any of these factors (respective p-values were: 0.52, 0.47 and 0.12). Moreover, within the groups, the partners' absolute and relative dominance were analysed, suggesting the absence of a significant influence of these variables on the focal bird's searching time (respective p-values: 0.09 and 0.06).

Lastly, the mixed-effect model results show that there is not a large effect of the food patch location on the searching time (7.73%, p-value = 0.83), opposed to what we expected.

4 Discussion

Our aim was to investigate how searching time for food-finding is affected by individual-level traits in birds alone and in the group.

The major discovery of this study is that, contrary to our prediction for research questions 1 and 2, exploration as a personality trait does not influence foraging behaviour in individuals alone (figure 8) nor in groups (figure 13).

Nevertheless, if we focus on the social aspect to answer research question 3, the results affirm that red knots benefit from social foraging. In fact, all birds become faster in finding the food when they find themselves in a group (regardless of what size), compared to alone (figure 18). This could be due to both competition for limited resources [52] [53] and social facilitation [54]. However, figure 18 also shows that non-exploratory birds have a steeper slope (although the confidence intervals overlap), potentially meaning that with increasing group size, they become even faster than exploratory individuals. This indicates that the former may benefit more from social foraging, as they are slow in finding the resources on their own and need others to get useful information, in contrast to the other personality type [13]. Furthermore, this proves that non-exploratory birds are flexible in responding to the social environment, whereas exploratory individuals are unresponsive to changes in the environment [48] [55].

In addition to the searching time for food-finding, we also analysed the time spent in the side-aviary before entering the arena. In this case, a correlation with personality is observed (at least with birds tested alone): exploratory individuals leave the side-aviary faster than non-exploratory ones (figure 11). Although this is an exciting discovery, the time in side-aviary is more related to boldness, while searching time to exploratory behaviour. In fact, boldness is often associated with an animal's reaction to a novel environment, which in this case would be the experimental arena [15].

This study also demonstrates the existence of a relationship between boldness and exploration, at least for non-exploratory birds. Figure 12 displays this correlation: individuals that spend longer times in the side-aviary, also take longer to find the food patch in the arena and vice versa. This finding is in agreement with various studies (e.g., [48], [56]) that have proved that these two personality traits are related in a way that exploratory individuals are bold and pro-active whereas non-exploratory ones are shy and reactive.

Verbeek *et al.* [48] also affirmed that there might be a trade-off between exploration speed and attention to the environment. On the one hand, bold birds explore quickly, which entails poor attention to the environment and a better adaptation to stable environments. Thus, this risk-prone attitude implies lower survival probability [57]. On the other hand, cautious birds explore slowly and therefore are able to react readily, which makes them better adapted to unstable environments [48].

Other than personality, we examined another individual-level trait in relation to searching time, more specifically body mass. In fact, physiological characteristics have been shown to vary among individuals [58] [59] and there is growing evidence that personality can be related to such components [60] [61] [62] [45].

We measured the focal bird's body mass over the experiment period before each trial. We observed a significant correlation between searching time and body mass in individuals (figure 9). However, the relationship is the opposite of the one predicted, which was that higher body masses would correspond to longer searching times, due to lower motivation. The observed relationship could derive from a positive feedback loop: individuals that are faster in finding the food get more chances to eat, and therefore, gain weight. In fact, the birds were deprived of food for more than 12 hours at night, so they only had a few opportunities to eat, namely in the arena during the trial and at the end of the experimental day for a few hours.

As part of the additional analyses, we did not find a correlation between exploratory behaviour and body mass over the period, although Bijleveld *et al.* [45] have found that exploratory birds are lighter than non-exploratory ones. A possible reason why this was not observed this time, could be that food is easily accessible for all individuals in captivity, without having to travel large distances to find preys, as it happens in the wild.

Most importantly, is it worth mentioning that the experiment period coincided with the fattening season before migration [44]. In this phase of the year, birds become remarkably active and gain weight, often doubling their average body mass before taking-off on a non-stop flight that takes several days [63]. This detail could also explain why we observed that all birds were generally fast in finding food, regardless of their personality.

As mentioned in chapter 2, food was deprived simultaneously for all the birds each evening, and they were starved throughout the night. However, due to the experimental day's logistics, some individuals had to wait longer before they could get the chance to eat in the arena, so all birds had different fasting times. When analysing this aspect in the trials of individuals alone, birds that have been food-deprived for longer show lower searching times (figure 10), according to the hypothesis for the first research question. This could be caused by higher hunger level and motivation to find food, which could overrule the effect of personality on the searching time.

Nonetheless, we see that neither body mass nor fasting time influence the searching time when the birds are tested in groups (figures 15 and 16). Likewise, time spent in the side-aviary is not affected by personality in the group scenario (figure 17).

This may relate to interference competition for resources, as it has been suggested by Bijleveld *et al.* [39], which induces all birds to become faster in order to find food before the others, masking individual differences.

In the field, aggressive interactions between knots are rarely observed [39]. This is because foraging areas on intertidal mudflats are extensive and allow them to spread out while remaining in a group [38] [64]. However, in captivity, limited space and fewer resources may make them more aggressive and territorial [39]. Indeed, we observed several aggressive interactions between the birds, both in the hosting aviaries (mainly when we provided them with food after the experimental day) and in the arena during the group trials. Therefore, those individuals that were very frequently showing territorial behaviours were assigned to a high dominance score and vice versa. We expected dominance to play a large role, for instance, in how much a bird can eat and thus gain weight. Nevertheless, the additional data analysis displays no significant correlation between dominance score and body mass, nor exploratory behaviour. Furthermore, the focal bird's searching time does not seem to be affected by the presence of one or more dominant partners. This is consistent with what was found by Bijleveld *et al.* [5]: there is no significant difference between dominant and subordinate birds in terms of exploiting public information, possibly because, in nature, resources patches are largely distributed in the vast environment.

Some food patches seemed to be easier to discover by the birds, so we believed that the food patch location might have influenced the searching time. More precisely, when the food was hidden inside the patches closer to the side-aviary (for instance, A6 and A7 in figure 5) it seemed to be found faster compared to when it was inside other patches. This might be related to the fact that the birds would mainly land in the arena right next to these patches. However, considerable variation in searching time was observed even at these particular patches, and the analysis showed that the food patch location does not influence the searching time. Moreover, it is worth mentioning that the patch containing trouvit was randomly selected for each trial with an R script. Therefore, a few patches were never used, while others were employed in more than one trial. This means that it is possible that the same bird found the food in the same patch, for example, twice. It remains unknown whether this detail could affect the searching time.

Investigating mechanisms of social foraging and making behavioural observations in captivity is more convenient and practical. However, many factors that contribute to individual variation in the wild are absent, namely competition for food and actual predation danger (e.g., [65] [66]), which constitutes a limitation. Nevertheless, in this case, it still serves as an indication of how information is transferred within social networks. Notably, we are interested in understanding this, since modern anthropogenic processes are causing the loss of information, including disruption to information processing and transmission (e.g., low urban signal-to-noise ratios [67] [68]). Additionally, Kraan *et al.* [38] demonstrated that the decline of suitable foraging areas for red knots, due to the human-induced habitat changes [29], leads to the reduction of the available information about their prey. These two joint declines culminate in a decreased survival of *islandica* knots in the Wadden Sea [38] as well as in other subspecies' staging areas [29].

5 Conclusions and Future Work

5.1 Conclusions

We have limited understanding of how particular animal personalities affect collective behaviour, social networks and information transfer in wild populations [23]. Investigating these aspects will help us understand how social learning can increase population resilience to rapid environmental changes.

This study had the aim to investigate what factors influence searching time for food-finding in captive red knots with different personalities (exploratory and non-exploratory). This was studied both in individuals alone and in groups while analysing its potential correlation with individual-level traits (i.e., personality, body mass), motivation (i.e., fasting time) and group's characteristics (i.e., group's mean personality and size).

The results unexpectedly show that exploration does not influence searching time in any case. However, other variables, namely body mass and fasting time, significantly affect searching time. Nevertheless, this was observed only in individuals alone and not in groups, which demonstrates how the group masks individual differences. Moreover, all the birds became faster in the presence of others, probably due to a balance of scramble competition [52] [53] and social facilitation [54].

Lastly, we found that non-exploratory birds benefit more from being in a group than exploratory individuals. This is because they need other individuals that share foraging information to increase their food-finding rates [5]. On the other hand, exploratory birds might also benefit from group foraging because of increased safety [3] [4], provided mostly by non-exploratory birds that have greater attention towards the surroundings [48] [55].

5.2 Future Work

To conclude, a number of recommendations for future developments of this study are suggested. Future research on personality and the use of social information in foraging would further develop and confirm these first findings.

It would be appropriate to compare the results obtained in this study with the boldness experiments performed about a month later by MSc student Hans Linssen, where he tested the same birds in a similar setup to assess their personality in terms of shy or bold. For instance, we question whether the same individuals that spent longer times in the side-aviary also resulted in being shy in a later investigation.

Other interesting topics for future work are site-fidelity and cognitive memory, which could be studied by analysing the videos and examine whether birds were going back to the patches where they had previously found food [69]. The fish-eye view from the top-camera can be easily transformed into a linear view with R, using a function for transforming pixel-coordinates to centimetres, making it suitable to successfully track the individuals in the whole arena with automated tracking software (e.g., [49]). Moreover, the same tool could give insights on the distance covered in the arena, the number of searched patches and amount of time spent feeding at the food patch by each focal bird and relate those to personality and dominance.

More ideas for future studies include analysing of the various behaviours, instead of merely considering the whole time from landing to discovering the food. For instance, searching (defined as moving from a patch to the other and inspecting the inside), moving (without checking the patches), watching (the surroundings while standing), interacting (both attacking and evading) and preening or sleeping, similarly to what was done by Bijleveld *et al.* [39].

Ultimately, this research should be carried forward assessing social foraging in the wild, thanks to recent technological advancements [70] [71]. This would contribute to fundamental research which could also be applied to the conservation and management of wild populations [71]. Moreover, tagged animals, and particularly migratory birds that travel long distances (see figure 2), give us the opportunity to monitor the impacts of the ongoing environmental changes on their distribution, habitat use and stopover sites [72].

6 Appendices

Updated: 27 June 2020

6.1 Bird list

Cage 1 to 5

Species: Kanoetstrandloper *(Calidris canutus)*
Red Knot

Total birds: 50 (5*10)

Project nr.: AVD8020020171505

Ring	Colour	Capture date	Location	Sex	Subsp	Age	Info
Z099.126	GGG	29-10-2019	Griend		isl	A	
Z099.128	GGN	29-10-2019	Griend		isl	A	
Z099.132	GGP	29-10-2019	Griend		isl	A	
Z099.133	GGR	29-10-2019	Griend		isl	A	
Z099.136	GGY	29-10-2019	Griend		isl	A	
Z099.140	GNG	29-10-2019	Griend		isl	A	
Z099.141	GNN	29-10-2019	Griend		isl	A	
Z099.142	GNP	29-10-2019	Griend		isl	A	
Z099.143	GNR	29-10-2019	Griend		isl	A	
Z099.146	GNY	29-10-2019	Griend		isl	A	
Z099.148	GPG	29-10-2019	Griend		isl	A	
Z099.151	GPN	29-10-2019	Griend		isl	A	
Z099.153	GPP	29-10-2019	Griend		isl	A	
Z099.155	GPR	29-10-2019	Griend		isl	A	
Z099.159	GPY	29-10-2019	Griend		isl	A	
Z099.162	GRG	29-10-2019	Griend		isl	A	
Z099.163	GRN	29-10-2019	Griend		isl	A	
Z099.165	GRP	29-10-2019	Griend		isl	A	
Z099.166	GRR	29-10-2019	Griend		isl	A	
Z099.167	GRY	29-10-2019	Griend		isl	A	
Z099.169	GYG	29-10-2019	Griend		isl	A	
Z099.174	GYN	29-10-2019	Griend		isl	A	
Z099.177	GYP	29-10-2019	Griend		isl	A	
Z099.178	GYR	29-10-2019	Griend		isl	A	
Z099.179	GYY	29-10-2019	Griend		isl	A	
Z099.180	RGG	29-10-2019	Griend		isl	A	
Z099.181	RGN	29-10-2019	Griend		isl	A	
Z099.182	RGP	29-10-2019	Griend		isl	A	

Z099.185	RGR	29-10-2019	Griend		isl	A	
Z099.186	RGY	29-10-2019	Griend		isl	A	
Z099.187	RNG	29-10-2019	Griend		isl	A	
Z099.193	RNN	29-10-2019	Griend		isl	A	
Z099.358	RNP	29-10-2019	Griend		isl	A	
Z099.360	RNR	29-10-2019	Griend		isl	A	
Z099.361	RNY	29-10-2019	Griend		isl	A	
Z099.362	RPG	29-10-2019	Griend		isl	A	
Z099.366	RPN	29-10-2019	Griend		isl	A	
Z099.368	RPP	29-10-2019	Griend		isl	A	
Z099.369	RPR	29-10-2019	Griend		isl	A	
Z099.370	RPY	29-10-2019	Griend		isl	A	
Z099.371	RRG	29-10-2019	Griend		isl	A	
Z099.372	RRN	30-10-2019	Griend		isl	A	
Z099.373	RRP	30-10-2019	Griend		isl	A	
Z099.374	RRR	30-10-2019	Griend		isl	A	
Z099.375	RRY	30-10-2019	Griend		isl	A	
Z099.376	RYG	30-10-2019	Griend		isl	A	
Z099.377	RYN	30-10-2019	Griend		isl	A	
Z099.378	RYP	30-10-2019	Griend		isl	A	
Z099.379	RYR	30-10-2019	Griend		isl	A	
Z099.380	RYY	30-10-2019	Griend		isl	A	

Standard checking: weekly control of feet, weight, breast- wing moult and any injuries.

6.2 Experiment protocol

Day before

- Assign focal birds to trials for the next day with an R-script and add that to excel files "trials" and "obs"
- In the "obs file", under the column "what", there are "switches", "exp", and "training". Each bird has a switch to assign it to the right aviary at the end of the day. The "exp" is the information for the trials the next day. The meaning of "training" is explained later.
- In the "trials" file there are the information on the "orderID", "food_patch", "switches" as well as space for the remarks etc.
- The procedure for assigning birds to trials and aviaries is to select between 10-15 trials a day, and keep them with 3-4 trials per aviary and maximally 12 birds (assign these aviaries in sequence from o1-o5).
- The focal birds have bird_type "f" and the partners to make the group sizes have "p". The birds that are not used in a trial (bird_type "s", for spare) are assigned to the last aviaries (usually o4-o6 depending on the number of birds in the trials).
- All birds will be in the arena once a day. At the end of the experiments, these spare birds are released into the arena (like a trial) for training in one or sometimes two big groups (again depending on the number of spare birds)
- Remove food in all aviaries the evening before at approximately 21:00 (timestamp "no_food")

Morning

- Prepare cameras (top-camera (fix securely), side-camera, door-camera)
- Add food to all trays and remove it (to make sure all patches smell the same)
- Prepare food patch (column "food_patch")
- Prepare six crates in w6 for releasing the birds in their aviaries after the training trial

- Provide food for an hour to the spare (training) birds in the outside cages

Batch of trials

- Catch all birds in one aviary approximately 15 min before the start of the trial (timestamp “catch” in ”trials” file)
- Weigh and fill-in “obs” file with timestamp
- Put the birds in crates per trial

Each trial

- Release experimental birds in side-aviary to habituate for ∼5 min (timestamp release)
- Check camera batteries (replace top-camera battery every 4 trials) and SD cards
- Clean arena, remove tracks and loose pellets from ground, and clean/fill food patches
- Switch trays: remove food from the current food patch, and fill the tray indicated in the column “patch_switch” and switch these two trays. This is to avoid visible cues to food (tracks and dirt from previous foragers)
- Start cameras (top, side door: 1440 wide 30 fps)
- Open sliding door (timestamp “door_open”)
- Timestamp “entry” to the arena
- If none of the birds leave after 2 minutes, go into the side-aviary and gently but swiftly herd them in (timestamp “herded_in”, or alternatively write “no”).
- Write down which bird is where to help match idTracker data to individuals later on
- Write down what bird is territorial, and if possible the interactions between the birds

- Trials should last at least 10 min, and from the moment that the last bird has discovered the food patch wait at least 2 minutes to give reward
- After 10 minutes (or more with the reward time) stop trial (also if birds have not found food after 10 min)
- If top-camera does not switch off: note top-camera end time in the remarks (for easy use in idTracker)
- Herd birds back into the side-aviary (switch off the light) and catch them
- Place crate with the birds near w6 for assignment to aviary crates (during next trial)
- Clean side-aviary

During trial

- Select and catch next experimental birds if needed
- Distribute birds that have been in trials between the six crates: one crate per aviary where they will be released for next day's trials
- If a bird's weight is lower than 105 put in a blue crate and feed after minimally one hour
- Copy video files to ZEUS
- Enter data, clean, prepare, etc.

End of the experimental day

- Do the training trial(s) with "spare" birds. These should last 15 minutes maximally.
- Put birds in crates sorted per cage
- Return birds to outside aviaries in compositions as the birds will be in trials the next day
- Do not immediately give food in aviaries to avoid not eating in arena and gorged in aviary

- Do dominance observations for 5-10 min per cage after giving food
- Empty SD cards, rename the files (e.g. "2020-04-20-test-trial-01-topcam.MP4") and put them on the external hard drive (move them to ZEUS as soon as possible thereafter)
- Charge batteries
- Prepare for next day

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