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juvenile Northern Bald Ibis (*Geronticus eremita*) -  
An observational and experimental study.”

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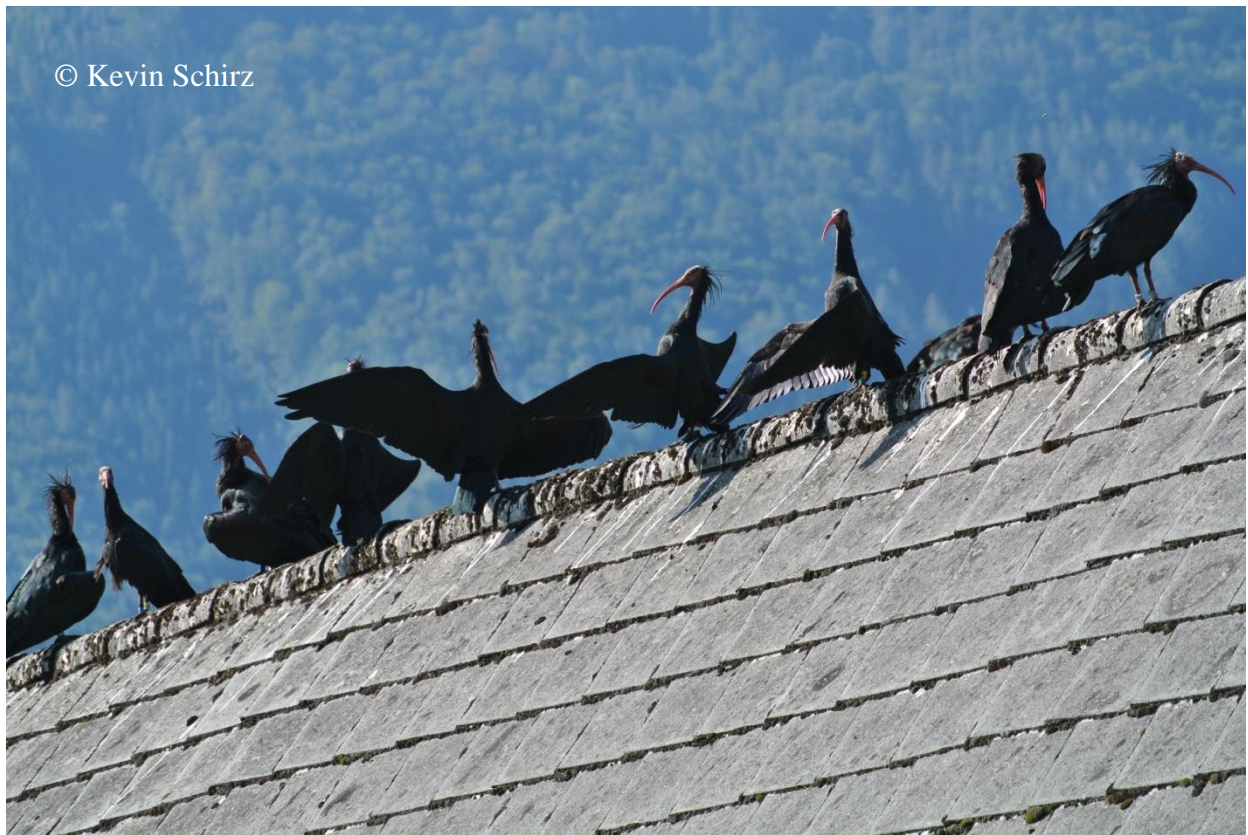


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*„Leben ist ein informationsgewinnender Prozess“*  
*„Life is an information-gaining process“*  
by Prof. Dr. Konrad Lorenz





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## Zusammenfassung (Abstract in German)

Die Nahrungssuche durch in gruppenlebende Individuen kann aufgrund der vielen Nahrungs-Konkurrenten kostspielig sein. Gruppen bieten aber auch einige Vorteile, wie etwa einen erhöhten Schutz vor Raubtieren. Hamiltons "selfish herd theory" liefert eine Erklärung dafür, warum Tiere Gruppen bilden. Nach dieser Theorie steigt das Risiko von Raubtieren angegriffen zu werden mit der Entfernung zum nächsten Gruppenmitglied, das Risiko ist zudem bei Individuen die sich an den Rändern der Gruppe aufhalten höher als bei den Individuen in zentralen Positionen. In Bezug auf den Zugang zur Nahrung können Verteilung der Nahrungsressourcen sowie das Alter und der soziale Rang von Gruppenmitgliedern, die Position eines Individuums innerhalb einer Gruppe beeinflussen, da es mit Artgenossen um den Zugang zur Nahrung konkurriert.

Der Begriff "Persönlichkeit" steht für konsistente Verhaltensreaktionsprofile auf eine Reihe externer Reize. Konsistente Verhaltensphänotypen wie Persönlichkeit haben messbare Auswirkungen auf das Überleben und die Fortpflanzung eines Individuums und tragen somit zur Persistenz von Populationen, Arten und der biologischen Vielfalt bei. Bisher wurde nicht viel über die Rolle der Persönlichkeit als Faktor für die räumliche Position eines Individuums innerhalb einer Gruppe oder den Zugang zur Nahrungsressource geforscht. Es ist möglich, dass verschiedene Persönlichkeitstypen Unterschiede in ihrem Verhalten der räumlichen Ausbreitung zur Nahrungssuche sowie Nahrungserwerb aufweisen. Das Ziel dieser Studie ist es zu testen, ob Persönlichkeitstypen von juvenilen Waldrappen (*Geronticus eremita*) ihre räumliche Position bei der Nahrungssuche und ihren Zugang zur Nahrung beeinflussen. Die Persönlichkeit dieser Tiere wurde bereits während der Nestlingsphase bis zum 30. Tag experimentell gemessen. Ich beobachtete 19 juvenile Waldrappe mit bekanntem Persönlichkeitswert, als sie sechs Monate alt waren und in freier Wildbahn nach Nahrung suchten. Die Persönlichkeit der 19 Waldrappe überspannte eine Persönlichkeitsachse von passiv bis aktiv.

Um die räumliche Lage während der Nahrungssuche im Untersuchungsgebiet (Molln in Österreich) zu messen, habe ich mehrmals am Tag vier Transekte gescannt und die räumliche Verteilung jedes gesichteten Vogels innerhalb der Gruppe in Relation zu den anderen Individuen aufgezeichnet. Als die Vögel im Herbst ins Grünau-Tal zurückkehrten, führte ich einen experimentellen Futtersuchversuch durch. Ich stellte hierfür Futterschalen gefüllt mit der gleichen Futterqualität in einer Reihe auf ein Feld. In der Behandlungsgruppe *eins* platzierte ich drei Futterschalen und in der Behandlungsgruppe *zwei* platzierte ich zwei Schalen (simulierte Ressourcenknappheit). Jede Schale wurde mit einer Kamera gefilmt, um später die Latenz zu messen, mit der sich ein juveniler Waldrapp der Schale nähert, und um die agonistischen Wechselwirkungen während der Fütterung mit einer Kodierungssoftware zu analysieren.

Die Ergebnisse sind wie folgt: Es gab eine Auswirkung der Persönlichkeit auf ihr räumliches Auftreten innerhalb einer Gruppe. Passive Juvenile befanden sich eher im Zentrum der Gruppe und aktive Juvenile an der Peripherie. Es gab auch einen statistisch signifikanten Effekt der Gruppenausbreitung auf die Anzahl und Entfernung der nächsten Gruppenmitglieder pro Juvenile, aber keinen Effekt der Persönlichkeit auf die Entfernung zum nächsten Nachbarn. Neun juvenile Waldrappe kehrten nicht in das Wintergebiet zurück und könnten Raubtiere zum Opfer gefallen sein. Ich verglich die modale Position in der Gruppe und die Persönlichkeiten dieser neun Vögel und stellte fest, dass die fehlenden Vögel eher aktive Juvenile aus der Peripherie waren. Während der Fütterungsexperimente gab es keinen Einfluss der Persönlichkeit auf die Latenz bei der Annäherung an die Fütterung. Passive Juvenile erhielten jedoch deutlich mehr agonistische Wechselwirkungen als aktive Vögel.

Diese Studie trägt zu unserem Verständnis bei, wie die Persönlichkeit einer bedrohten Vogelart mit dem Überleben von Juvenilen in einer wichtigen Lebensphase in Verbindung gebracht werden kann.

## Abstract

Foraging in groups can be costly because of the many food competitors. But living in a group also offers foragers benefits, such as increased protection from predators. Hamilton's 'selfish herd theory' provides an explanation for why animals form groups and also makes predictions about the nearest neighbour distance. According to this theory, the risk of predation increases with the distance to the next group member, and the risk of predation is higher for individuals at the edges of the group than for those in central positions. Concerning food access, the distribution of food resources and the age and social rank of an individual may influence its position within a group as it competes with conspecifics to access food.

The term 'personality' is shorthand for the fact that individuals within a group show a range of different, but at the individual level, consistent behavioural response profiles to external stimuli. Consistent behavioural phenotypes such as personality have measurable effects on survival and reproduction and thus contribute to the persistence of populations, species and biodiversity. To date, not much research has been done on the role of personality as a factor affecting an individuals' spatial position within a group or its access to food. It is possible that different personality types show different foraging spatial location and behavioural access to food resources. The aim of this study is to test whether the personality types of juvenile northern bald ibis (*Geronticus eremita*) influence their foraging spatial position and their access to food. The personality was experimentally measured during the nestling phase until day 30, and I observed 20 juvenile ibis with known personality score when they were juveniles aged six months old, foraging in the wild. The personality of the 20 birds spanned a personality axis from passive to active.

To measure spatial location during foraging in the Molln area (summer area of the birds), I scanned the study area along four transects and recorded the spatial distribution of every bird sighted, also relative to other birds in the group. When the birds returned to the Grünau valley (spring/winter area) in autumn, I conducted an experimental food trial. I placed food trays in a line on a field; the trays were filled with the same quality of food but the treatment *two* condition consisted of two presented food trays (simulating resource scarcity) in the treatment *one* condition with three trays. The different trials were video recorded to later measure the latency for a juvenile to approach the tray, and to analyze the agonistic interactions during feeding.

There was an effect of juvenile personality on its spatial occurrence within a foraging group. Passive juveniles were more likely to be in the centre of the foraging group and active juveniles at the periphery. There was also a statistically significant effect of group spread on the number and distance to the next group member per juvenile, but no effect of personality on the nearest neighbour distance. Nine juveniles did not return to the spring/winter area, and hence could have been depredated. I compared the spatial position within the group and personality of these nine birds and found that missing birds were more likely to be active birds from the periphery. During the feeding experiments, there was no effect of personality on the latency to approach to feed. However, passive birds received more agonistic interactions than active birds.

This study contributes to our understanding of how personality in a threatened bird species could be linked with survivorship of juveniles across a key life stage.

# 1 Introduction

## 1.1 Foraging ecology

Natural selection favours a variety of behavioural strategies that enhance feeding efficiency, survival and fitness (Pyke, Pulliam, & Charnov, 1977). However, there can be a tension between natural selection on individual behavioural traits on the one hand and their efficacy within a group setting. For example, individuals that forage in groups with con- or heterospecifics often carry high costs and it is therefore questionable what strategies an individual can use to reduce such costs. These costs can be expressed as enhanced competition over food (i.e. Bautista, Alonso, & Alonso, 1998) or an elevated risk of parasite transfer (i.e. Brown & Brown, 2004). In addition to costs, foraging in a group may have many benefits for an individual, most notably reduced predation risk and enhanced feeding rate in some circumstances. For instance, in Alaska moose (*Alces alces gigas*) predation risk increases with distance from cover; Molvar & Bowyer (1994) showed that moose joining larger groups could select high quality foraging sites far from cover whereas solitary moose foraged at low quality foraging sites close to cover. In foraging Japanese macaques (*Macaca fuscata*), there were differences in an individual's feeding rate in relation to feeding group size that were mediated by social vigilance; feeding rate was highest for intermediate group size when both social monitoring and food competition were lowest compared to the case when group size was very small or very large (Kazahari & Agetsuma, 2010). Thus, many trade-offs (e.g. between predation risk and feeding rate) may influence an individual's behaviour in groups of different sizes.

Hamilton's 'selfish herd theory' is based on fundamental processes that underpin the fitness benefits of why animals form groups (Hamilton, 1971). This theory predicts that selection will favour individuals that maintain close proximity to other conspecifics as well as central positions within a group. These predictions are based on observations that predation risk increases with the distance to the nearest neighbour, and predation risk is higher for individuals at the edges of the group as they are the most accessible and closest prey from the predator's two-dimensional perspective (e.g. lion-prey relationship). Also under conditions of vertical predation, when predation occurs from above or below the group (e.g. fish schools, bird flocks), there is evidence that predators are more successful when targeting prey at the periphery (Hamilton, 1971; Quinn

& Cresswell, 2006). Some concepts used to describe the predation-associated benefits to individuals of group living include ‘dilution effect’ (predator can capture only one prey at a time, see Morgan & Colgan, 1987), ‘many eyes theory’ (more individuals to observe the environment, see Molvar & Bowyer, 1994) or the ‘predator confusion effect’ as prey flee in different directions (Olson et al., 2013).

The second major driving force influencing group living dynamics is food resource acquisition. Group living may result in more efficient food source exploitation by individuals (Rubenstein, 1978), and this translates into fitness because the net intake rate of energy has been shown to be positively correlated with fitness (reviewed in Pyke, 1984). The distribution of food resources also plays a role in foraging decisions. Generally, when a food source has a patchy distribution in the environment, knowledge of the quality, location and size of food sources becomes valuable information related to feeding efficiency (Clark & Mangel, 1983). Information sharing among group members increases access to patchy high quality food sources, and confers an additional benefit to individuals living in a group. For instance, guppies (*Poecilia reticulata*) in larger groups were faster at finding food by using passive cues emitted from successful foragers (guppies respond to the food discovery of others) (Day et al., 2001). Black-billed gulls (*Larus bulleri*) use active emitted recruitment signals produced by group members that have knowledge about the location of new food patches (leader behaviour) and follow them from their colony site (information centre) to the feeding ground. Because each colony member may act as leader, the ensuing feeding efficiency may benefit each individual in the colony (Evans, 1982). Other social roles in foraging groups include producer and scrounger concepts. Individuals in foraging groups may either actively search for food and therefore act as producer or they adopt the scrounger strategy and join successful producers (often using social information); scroungers may displace producers, feed on their food, or steal, in some cases using aggressive behaviour (e.g. carib grackles: Morand-Ferron, Giraldeau, & Lefebvre, 2007). Scrounger behaviour may depend on hunger level (Lendvai et al., 2004), social dominance (Liker & Barta, 2002), and may increase with group size (Coolen, 2002).

The distribution pattern of food resources also plays a role in selecting optimal behavioural strategies in order to enhance feeding efficiency. When food sources are widely distributed but occur in small patches, individuals may do better foraging alone (Clark & Mangel, 1983). For instance, Ryer & Olla (1995) found that juvenile walleye pollock (*Theragra chalcogramma*) changed their strategy from group foraging to foraging alone when food was widely but patchily

distributed. The animal that reached the food patch first generally depleted it quickly; in this way, it is not worthwhile for other individuals to pay attention to other foraging cues when food is widely but patchily distributed. Solitary foraging animals may also benefit from reduced incidence of scrounger interference (Elbroch et al., 2017). Finally, cooperatively feeding individuals can increase feeding efficiency if they capture larger prey, as for instance in lions (Stander, 1992), or by startling hidden prey, which make them more catchable as they disperse (Peres, 1992).

Age and social rank are factors that predict an animal's position within a group. In general, yearling individuals are less able to compete against older individuals in a group, and often younger animals are subordinates in agonistic or competitive interactions (reviewed in Huntingford, 2013). During group movement, the safest position is the back-centre of the group, whereas the front-centre should be the most profitable (Janson, 1990). Individuals in front positions are also more likely to be the leader, and they influence the moving direction of the group (Bumann & Krause, 1993). Rarely are young and subordinate individuals group leaders (Norton, 1986), and hence they experience elevated predation risk as the consequence of their spatial position in a group during movement. Individuals that occupy a central spatial position in a foraging group have been shown to experience lower predation risk at the cost of increased feeding competition (Hirsch, 2011). Given that subordinates and juveniles tend to be supplanted from the best feeding sites by dominant food defenders (Hirsch, 2007), the prediction is that subordinate individuals are more likely to occupy peripheral positions in a group (e.g. yellow baboons *Papio cyanocephalus*; Collins, 1984). Individuals in peripheral spatial positions may experience higher predation risk during feeding (e.g. ring-tailed coatis: Hirsch, 2011).

Consequently, foraging groups exhibit a variety of dynamics that are the sum of a range of different strategies by individuals to increase survival and feeding efficiency. Diverse behavioural phenotypes including 'personality' may be selected for to achieve a balance between the costs and benefits of group living (Aplin et al., 2014).

## 1.2 Personality

The term ‘personality’ is short hand for consistent behavioural response profiles to a set of external stimuli (Dingemanse & Réale, 2005). In general, animals show variation between individuals in their response intensity towards the same environmental stimuli, and the same individual shows a consistent pattern of response profile to different sets of stimuli (Gosling, 2001). Thus, at the individual level, there may be a narrow response plasticity and consistency of a behavioural strategy over a lifetime (Sih, Bell, & Johnson, 2004). Many animal species from varied taxa have been shown to exhibit these behaviourally consistent personality profiles, including mammals (e.g. Hudson et al., 2011; Bremner-Harrison, Prodohl, & Elwood, 2004), birds (e.g. Drent, Van Oers, & Van Noordwijk, 2003; Aplin et al., 2014; David, Auclair, & Cézilly, 2011; Dall, 2004); reptiles (e.g. Siviter et al., 2017), amphibians (e.g. Kelleher, Silla, & Byrne, 2018); fishes (e.g. Sneddon, 2003), cephalopod molluscs (e.g. Sinn et al., 2001) and arthropods (e.g. Kralj-Fišer & Schuett, 2014). When behavioural traits in individuals are repeatable, correlate with each other across tasks, and are consistent across time, they are referred to as animal “personality” (Gosling & John, 1999; Van Oers et al., 2004). These traits may be favoured by natural selection as an adaptive strategy to survive and reproduce in a changing environment (Sih, Bell, & Johnson, 2004). Along the behavioural axis from docile to aggressive, traits must covary to qualify as personality traits; for example, boldness and aggression scores should correlate during different ontogenetic life stages (Bell & Stamps, 2004; Van Oers et al., 2004).

Genes and environment interaction effects are a source of variation that could influence the expression of personality across life stages. For instance, Bell & Stamps (2004) found a shift in the level of aggression across the life stages of three-spined sticklebacks (*Gasterosteus aculeatus*) due to environmental factors experienced during development to adulthood. In contrast, in great tits (*Parus major*), researchers found no evidence of shifting personality traits in exploration behaviour with age, and in this system, personality was stable across a lifetime (Dingemanse et al., 2002).

The personality axis from docile to bold has also been categorised by researchers as falling along an axis from passive personality type (or passive strategy) to active personality type (or active strategy) (Martins et al., 2007; Dingemanse et al., 2004). An active personality type tends to score highly in aggressive behaviour, risk-taking with predators, and fast exploration in novel

environments (Bell & Stamps, 2004; Van Oers et al., 2004), whereas a passive personality type has lower reaction scores during conflict and less exploration/engagement with unfamiliar objects or situations (Wilson et al., 1993) and is slow in exploring novel environments (Guillette et al., 2011). Some of these traits show different social associations across species; for example, aggressive behaviour was linked with dominance rank in great tits (Verbeek, 1996), but not in big horn sheep (Réale et al., 2000). Personality traits can be heritable in some species, as shown in great tits across generations (Van Oers et al. 2004). Evidences of the heritability of single behavioural components of personality support this assumption and come from studies that analysed large sample sizes (see Bouchard & Loehlin, 2001). From the perspective of mechanism, studies have found a link between hormones and personality traits. For example, Zebra finches (*Taenopygia guttata*) with high corticosterone level were faster in exploring the environment and took more risks than individuals with low levels (Martins et al., 2007).

Context depended trade-offs between growth and mortality in an individual's life history may select for the combination of personality types in a system when there are different costs and benefits of personality-strategies for survivorship and reproduction (Wolf & Weissing 2010). For instance, on the one hand, active personality types may have a higher mortality rate due to greater conspicuousness toward predators (e.g. foraging on the periphery) (Aplin et al., 2014) than passive personality types. On the other hand, active personality types may be better able to compete for food (Sih, Bell, & Johnson, 2004) and become leaders given faster exploration of the environment (Dingemanse & De Goede, 2004). During foraging, bold individuals are more likely to lead moving groups; they are more likely to be 'producers' and have a higher food intake rate compared with shy individuals who are more likely to be 'scroungers' (i.e. barnacle geese, Kurvers et al., 2010). In great tits, bold individuals were more likely to show exploratory behaviour and increase travel distance to new foraging sources (Dingemanse et al., 2003). Other processes could sustain the diversity of personality types in a group, including the benefits of social signalling (e.g. individuals signal future behavioural pattern) and social niche specialisation (e.g. reduces social conflicts; see also Bergmüller & Taborsky, 2010).

The persistence of personality types in a population could be maintained by frequency dependent selection (Wolf & Weissing, 2010) and can be conceptualised through classical game theory such as the Hawk-Dove model. When natural selection acts on the frequency of a given behavioural strategy that under current conditions confers the highest fitness (play 'Hawk'), this increases the success of that strategy to a tipping point until there are too many 'Hawks' and the

‘Dove’ strategy increases. The behavioural strategies or personalities oscillate in an evolutionary stable mix of strategies (ESS) within the population (Sigmund & Nowak, 1999).

### *1.3 Motivation & study species*

Consistent behavioural phenotypes like personality have measurable effects on survivorship and reproduction and hence contribute to the persistence of populations, species, and biodiversity (Sih et al., 2004). There are growing calls to better understand how personality may play a role in protecting wildlife populations (Bro-Jørgensen, Franks, & Meise, 2019). However, few studies have examined the role of personality in threatened species. For instance, Richardson et al. (2019) studied effects of personality in a threatened bird, the hihi (*Notiomystis cincta*), and discovered that bold juveniles were more likely to survive. Other researchers, such as De Azevedo & Young (2006), caution that bold hand-reared greater rhea (*Rhea americana*) may be less optimal for reintroduction because of greater dispersal and approach towards risky unfamiliar areas in the wild. A similar situation was found in re-introduced bold swift foxes (*Vulpes velox*), which travelled greater distances from their refuge sites and were more likely victims of road kills due to less fear toward novel stimuli (Bremner-Harrison et al., 2004). Hence the personality in a given context or environmental condition is important for wildlife conservation programs for different reasons. Understanding the role of personality with respect to foraging behaviour could be an important tool for conservation management in threatened species, because it could help to predict the future responses of populations in a changing environment, or help select individuals for reintroduction in the wild, with the goal to increase or maintain a stable population.

The focal species in this study is the endangered northern bald ibis (*Geronticus eremita*, Linnaeus, 1758); it is so classified in the IUCN Red List (2019) and became extinct in Europe 350 years ago. With its eye-catching long and slightly curved beak, this ibis species is well adapted to forage as a tactile hunter in meadows. When foraging, the birds forage together in groups and catch invertebrates but also small vertebrates by probing the ground with their beaks.

The birds are known to display a variety of complex social interactions between group members across the year (Böhm & Pegoraro, 2011). In addition to small migrating populations in Syria and Turkey, at last 95% of free-living birds are concentrated in a sedentary subpopulation in Morocco, where they suffer from changes in farming on the feeding grounds and human



disturbance (Bowden et al., 2008; BirdLife International, 2020). In order to prevent the extinction of this endangered species in the wild, several international institutions and organisations established *in situ* restoration programs for maintenance of populations in Syria, Morocco and Turkey, also *ex situ* breeding operations for reintroduction of this bird species back to suitable habitats in their indigenous regions in Europe (BirdLife International, 2020). The process of reintroduction has involved the study of free-flying hand raised birds, also in partnership with the Konrad Lorenz Research Center, the ‘Alpenzoo Innsbruck’ and the ‘Waldrappteam’. The aim was to collect information for establishing migratory ibis colonies (i.e. from Burghausen and Kuchl), that currently successfully migrate to the wintering range in Orbetello (Italia) (Fritz & Unsöld, 2015; Fritz, 2004).

#### *1.4 Aim of the study*

The aim of this study is to test if the personality of juvenile northern bald ibis is associated with patterns of foraging in the field and during experimental food trials. I use two approaches.

(1) I measure the relative spatial occurrence (group position, nearest neighbour distance) of colour-banded free-flying juvenile northern bald ibis foraging in the wild. I predict that six month old juveniles that had previously been identified as passive or less exploratory when they were 30 day old chicks (Pühringer-Sturmayr et al. in prep.) would have a different spatial position in the group, which is predicted to be more central and these birds have many close neighbours compared with juveniles identified as active or more exploratory.

Furthermore, I predict that more active birds on the periphery would be more likely to experience risk and hence be missing from the over-wintering population.

(2) I measure the latency to feed and the intensity of feeding behaviour at experimental food trays. I predict that passive, less exploratory, juveniles will have a longer latency to feed and more likely be the recipients than donors of agonistic behaviour.

## 2 Methods

### *2.1 Study animals and study site*

The free-living colony of northern bald ibis (NBI) at the Konrad Lorenz Research Center (KLF) in Grünau im Almtal (Upper Austria) are the descendent birds from 1997 when chicks from zoos in Vienna and Innsbruck were brought to the KLF (Tuckova, Zisser, & Kotrschal, 1998) in accordance with the European Breeding Programme (EEP) (Böhm, 1999). With the established bird colony, the social behaviour of these birds could be examined in order to maintain the know-how for introductory projects in Morocco and Spain.

Currently (2019), the population of free-living northern bald ibis at the KLF is 53 individuals. The NBI colony comprises 33 Adults and 20 Juveniles that hatched in the year 2019, at the time of data collection for this project. The focal NBI colony is sedentary but flies every year short distances from the Almtal region (47°51'11.58"N, 13°57'22.16"E) to two small villages in the Alps of Upper Austria in summer. The birds spend the summer season foraging exclusively on agricultural meadows in those villages (Zoufal et al., 2007). The village Molln (47°53'5.46"N, 14°15'25.78"E) and the adjoining Leonstein (47°53'42.49"N, 14°13'52.00"E) are located approximately 23km straight flight distance from the Almtal region. The birds return to the Almtal region in autumn where they are provided supplementary food in a large open-access aviary at the Herzog-von-Cumberland game park; the supplemental feeding is provided because of poor natural food abundance during winter (Sorato & Kotrschal, 2005). The focal birds in this study are 19 of 20 juvenile NBI that were reared in 2019 (year of hatch). From a previous study on the personality of these same birds by Pühringer-Sturmayr et al. (in prep.), we classed 9 birds as 'passive' as assessed by novel arena test, three birds as 'normal', and seven birds as 'active' (Table 1). All birds were individually marked with coloured rings on their legs for individual identification (Table 1).

**Table 1:** The birds have been assigned either an individual ID Number (ID No.) or name (name).

<i><b>ID No</b></i>	<i><b>name</b></i>	<i><b>sex</b></i>	<i><b>hatching date</b></i>	<i><b>left foot</b></i>	<i><b>right foot</b></i>	<i><b>mesured personality</b></i>
<b>1</b>	<i>Kiri</i>	female	14.04.2019	yellow-ALU	black-midblue	<b>passive</b>
<b>2</b>	<i>Konstanze</i>	female	16.04.2019	yellow-ALU	black-yellow	<b>normal</b>
<b>3</b>	<i>Kadisha</i>	female	11.04.2019	yellow-ALU	orange-darkblue	<b>passive</b>
<b>4</b>	<i>Kilian</i>	male	13.04.2019	yellow-ALU	orange-purple	<b>active</b>
<b>5</b>	<i>Margot</i>	female	13.04.2019	yellow-ALU	darkblue-yellow	<b>active</b>
<b>6</b>	<i>Monsti</i>	male	17.04.2019	yellow-ALU	darkblue-silver	<b>passive</b>
<b>7</b>	<i>Monika</i>	female	19.04.2019	yellow-ALU	darkblue-black	<b>active</b>
<b>8</b>	<i>Quintessa</i>	female	15.04.2019	yellow-ALU	yellow-green	<b>passive</b>
<b>9</b>	<i>Quiecks</i>	male	15.04.2019	yellow-ALU	yellow-silver	<b>active</b>
<b>10</b>	<i>Udine</i>	female	14.04.2019	yellow-ALU	white-purple	<b>passive</b>
<b>11</b>	<i>Ursula</i>	female	15.04.2019	yellow-ALU	white-brown	<b>passive</b>
<b>12</b>	<i>Udessa</i>	female	17.04.2019	yellow-ALU	white-silver	<b>passive</b>
<b>13</b>	<i>Sonia</i>	female	16.04.2019	yellow-ALU-green	black	<b>normal</b>
<b>14</b>	<i>Sybille</i>	female	17.04.2019	yellow-ALU-green	red	<b>passive</b>
<b>15</b>	<i>Simi</i>	female	19.04.2019	yellow-ALU-green	yellow	<b>active</b>
<b>16</b>	<i>Sombrera</i>	female	12.04.2019	yellow-ALU	silver-black	<b>passive</b>
<b>17</b>	<i>Tarzan</i>	male	13.04.2019	yellow-ALU-yellow	brown	<b>active</b>
<b>18</b>	<i>Till</i>	male	14.04.2019	yellow-ALU-yellow	white	<b>active</b>
<b>19</b>	<i>Timur</i>	male	17.04.2019	yellow-ALU-yellow	midblue	<b>normal</b>

## 2.2 Data collection

The data collection was divided into two approaches to interrogate foraging behaviour of NBI: (1) observations on meadows, and (2) experimental food trials.

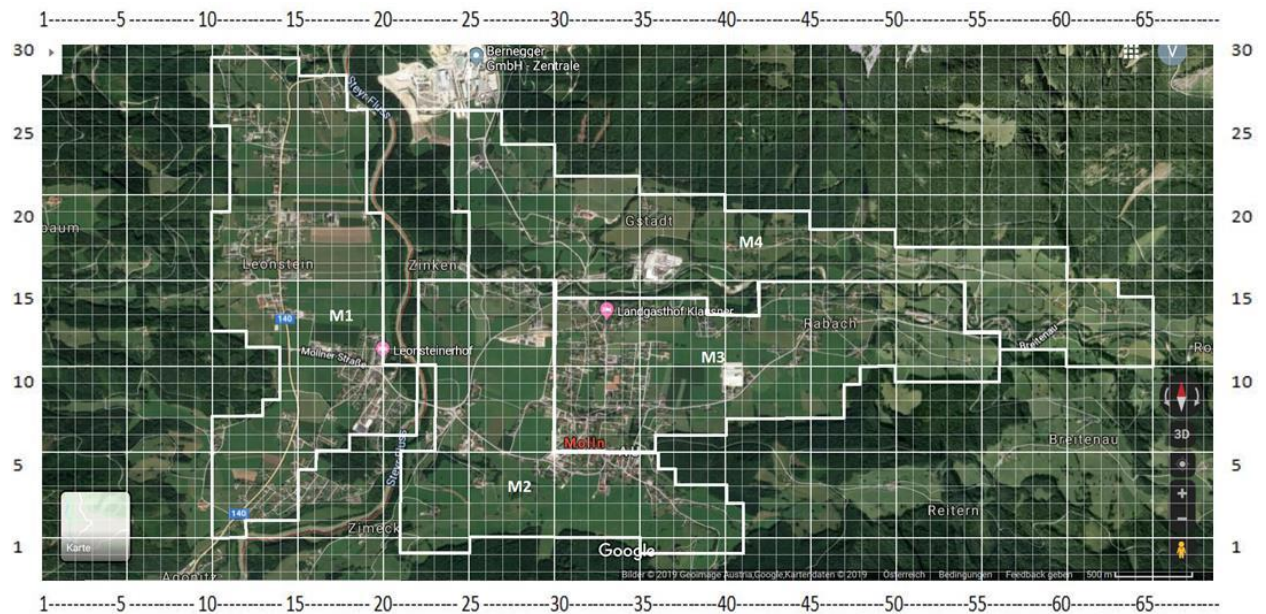
### 2.2.1 Observations of free-flying birds foraging in the wild

To obtain information on the relative spatial occurrence (group position, nearest neighbour distance) of the juvenile NBI foraging in the wild in relation to their personality, transect sampling was done in Molln and Leonstein during August and September 2019. I used transect sampling to detect the presence of northern bald ibis foraging on 12 days (Table 2).

**Table 2:** The sampling effort of the field observations. The 12 days for the observations were randomly chosen, but mostly occurred twice per week. The sampling time and the number of group sightings on the meadow were different per day.

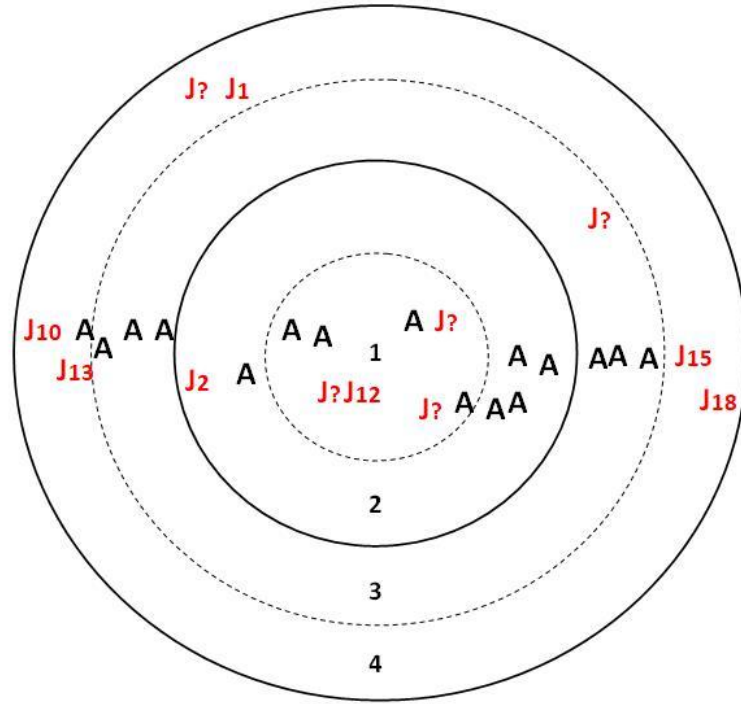
<i>Day</i>	<i>Date</i>	<i>Sampling Time</i>	<i>Group Sightings</i>
<b>1</b>	12.08.2019	6h20min	3
<b>2</b>	13.08.2019	6h	4
<b>3</b>	19.08.2019	7h30min	4
<b>4</b>	20.08.2019	7h15min	7
<b>5</b>	25.08.2019	5h	5
<b>6</b>	26.08.2019	5h	6
<b>7</b>	29.08.2019	6h	5
<b>8</b>	02.09.2019	5h30min	11
<b>9</b>	03.09.2019	6h	9
<b>10</b>	09.09.2019	5h30min	12
<b>11</b>	10.09.2019	6h	7
<b>12</b>	16.09.2019	5h15min	10
<b>Total:</b>		<b>64h05min</b>	<b>84</b>

Four transects were defined (three in Molln and one in Leonstein) with similar size, which covered several meadows where NBI are likely to occur (derived from previous observations in this region, KLF long-term records). To record the location of the birds within the transects, I used the computer software *Google Earth Pro* (Google LLC 2001, v7.3.2) to create a map for the region; I created a virtual grid generated with Adobe *Photoshop* (Adobe Inc., v. CC2019) above the picture. Each mesh of the grid corresponded to a 100 m x 100 m location in the landscape (total 803 meshes in 4 transects; Figure 1). These meshes were ticked on the plan when a group was sighted and the numbers of the XY - coordinates of meshes were noted (Figure, 1).



**Figure 1:** The map for transect surveys during data collection in the field. The boundaries of transect M1 – M4 are labelled in white. The numbers on the x and y axis enable a quick location notation of each sighting.

Each transect was sampled at least 4 times by car on the two observation days. If a group was detected in meadows, the birds' spatial positions were noted on paper using the instantaneous focal sampling method aided by a Swarovski Scope (SWAROVSKI ATS 65 HD). Each group was separated by any other group if the distance between the outer-most bird to the next bird was at least 50m. To record the spatial distribution of the NBI birds within the group, the spatial position of each bird was scored by hand on a sheet of paper consisting of a circle figure divided into four 25% zones based on the overall spread of the group. Zones 1 and 2 refer to the centre (inner and outer centre) of the group, whereas zones 3 and 4 refer to the periphery (inner and outer periphery) (delimited by sub-circles; Figure 2).



**Figure 2:** Circle figure. Lines separate the Zones 1-4. ‘A’ denotes the position of an adult within the group (labelled in black), ‘J’ denotes the position of a juvenile within the group (labelled in red). The associated number with the ‘J’ is the ID number of the juvenile; the question mark means that the identification was not possible for this individual.

During each sighting, the observation received a unique trial number, geographical position coordinates, weather condition (cloudy, partly cloudy and sunny), temperature (degrees centigrade), the estimated distance from the road (m), the observer’s position relative to the centre of the group (m), the size of the meadow where the group was located ( $m^2$ , derived with the Google Earth Pro polygon function), the estimated group spread (m), the total number of birds in the group, and the number of adults and juveniles in the group. Furthermore, the distance of nearest neighbour (juvenile or adult from identified juvenile) and the number of nearest neighbours within a 5m radius around the identified juvenile were estimated.

The juveniles were well distinguishable from the adults due to the bright *neoptil* plumage on the head and the lancet-shaped feathers on the neck, which are shorter in the juvenile (compare Figure 3 and 4).



**Figure 3:** Adult Northern Bald Ibis (© Kevin Schirz)



**Figure 4:** Juvenile Northern Bald Ibis (© Kevin Schirz)

### *2.2.2 Observations of free-flying birds during experimental food trials*

To test whether personality has an effect on foraging behaviour, an experimental food trial was carried out. The start of the experiment was originally scheduled for early October (generally when the NBI colony returns from the summer area), but was delayed due to unusually warm weather conditions until late November (2019), which was associated with a delay in the return of the birds. The warm weather conditions seemed to have resulted in adequate food resources in the wild during late autumn. The food experiment took place at the Konrad Lorenz Research Centre in Grünau im Almtal and lasted 10 days in total. Generally, the birds are used to receiving their supplemental food on the meadow in front of the KLF (47°48'51.56"N, 13°56'53.80"E), where the supplemental food is distributed over the meadow from a yellow pail. This familiar feeding site of the NBI was used for the experiment. High quality food was used: 1kg insects (desert locusts, cockroach, crickets, zophobas), 0.5kg minced chicks and 1.5kg minced beef heart (3kg in total per feeding), to entice the majority or all NBI to come to the feeding. Trays of 90cm in diameter were used in the experiment to present the food.



The feeding experiment took place between 8:00 and 10:00 am when at least 1/3 of the flock and at least one juvenile was present. If fewer birds arrived at the site, the trays were filled but no data were collected. The experiment started when the first bird landed on the meadow and ended after 45 minutes. To make sure that no bird noticed the upcoming feeding event and landed on the meadow before the trays and the cameras were placed in the correct position, I placed the trays already filled with food adjacent to the experimental site.

The experiment was divided in two conditions to simulate different situations of food availability: (1) treatment 1 (resource abundance): three food trays presented to the birds, and (2) treatment 2 (resource scarcity): two food trays presented to the birds. During the experiment, the food trays were placed in a line with 5m distance in between and were filled with the same food quality and quantity. Experimental and control trials were randomized over days. The randomization was calculated with R (R Core Team, 2016). The 10 trials occurred in the following order: treatment 1, treatment 1, treatment 2, treatment 1, treatment 1, treatment 2, treatment 2, treatment 2, treatment 2 and treatment 1. To start the experiment, one of us placed two (treatment 2) or three (treatment 1) prepared trays on the meadow after that a second person carried the yellow pail from the KLF towards the meadow and placed it at the feeding site (the birds followed that person with the pail to the meadow). A second feeding took place after the experiment on the same day in the aviary in the game park, during which no data were collected, to ensure that all birds received adequate food.

Three cameras (Nikon1 J1 with a 30-110mm NIKKOR objective, Canon Legria HF G10 and Panasonic HC-V808) were placed on the edge of the meadow (arranged in a line, with 17m distance from feeders) and were focused on the trays (each camera on one tray) under consideration of a 1,5m radius that surrounded each tray (defined with barbeque sticks, Figure 6). This radius was the spatial distance where the behavioural conditions of each juvenile that joined the feeding experiment could be recorded for subsequent focal sampling analysis.

For analyzing the 450 min recorded behavioural categories (45 min per day for 10 days) I used the computer software *Solomon coder beta* (©Andras Péter, v. 19.08.02). I focused on agonistic interactions such as pecking, threatening, defensive threatening, threat greeting, displacing and fighting (see *Ethogram*, Table 3) between juveniles and between juveniles and adults. To quantify the behavioural response, I measured the frequency of behaviours. Each focal juvenile



that participated in a feeding event was observed at least 1 time to at most 6 times removing food from the tray.



**Figure 6:** Shows the experimental setup where one camera is focusing the right tray that is surrounded by NBI.

### 2.3 Ethogram

The Ethogram was created using *ad libitum* observations with a common binocular (USCAMEL WD 10x42) during the field observations in order to acquire unambiguous definitions of each behaviour (Table 3). The observed behaviours were compared against the Ethogram according to Pegoraro (1992).

<i>Behavioural context</i>	<i>Sub-category</i>	<i>Description</i>
<i>Attention</i>	<i>vigilance</i>	The bird stopped its activity while freezing for a moment in an upright position, then mostly right and left movements of the head or/and tilting the head to one side follows (1 eye look up). Sometimes irregular emitted “Gruh-Calls” with slightly open beak.
<i>Consumption</i>	<i>foraging</i>	The beak is always in front of the body when moving with different speed on foot; the entire body is more or less horizontally aligned. The head is slightly lowered, with each step a jerky forward movement of the head (optocollic nystagmus),

		<p>eyes looking down. Poking with beak forward and sideways into the ground during movement (in locomotion direction) without stopping or with stopping locomotion. When stopping, the bird mostly poking several times into the ground or pulls on the prey with its beak deeply in the ground by moving the head upward with jerky movements (then the whole body twitches with each movement). Sometimes the bird is rushing forward for a short distance with stretched neck, lowered head, slightly opened peak and accelerating speed (faster movements of feet) on prey. The prey is often crushed with the beak and is swallowed as a whole through a fast upward movement of the beak which is more or less slightly open, or sometimes ingests while the beak is still down. During foraging, the colony members often organized in a line in order to float the prey.</p>
<b>Comfort behaviour</b>	<i>drinking</i>	The bird dives its slightly open beak in the water (about half of the beak), then it raises its beak out of the water at a steady speed until the beak stops in a vertical position. During the upward motion, the bird starts to clack with its beak with movements of the throat. Sometimes with head shaking after drinking.
	<i>resting</i>	Standing on one leg (the other leg is angled and hidden in the plumage) or sometimes on two legs, with its beak between the wings on its back or with slightly retracted head (beak is then in front of the body). Seldom resting with bent legs flat on the ground (perching, sometimes with angled wings which slightly stretched from the body, beak is then in front of the body).
	<i>self-preening</i>	Snapping the feathers with the beak or pulled through the beak from bottom to the feathers top; between the wings, on the wings, the chest (then with erected body and angled head in order to reach the chest with the beak), tail feathers and back. Self-preening behaviour is shown sometimes while they stand on one foot.
	<i>cleaning</i>	The bird is shaking the body with fluffy plumage; short flapping of the wings, snuffing and head shaking and wiping beak on objects with tilted head movements.
	<i>yawning</i>	The bird has wide open beak.
	<i>stretching</i>	The bird open and holds one wing sideways (the other wing remains angled) and the foot on the same side as the open wing, is pulled backwards. Body position is upright. After that, the bird sometimes yawns with wide open beak.
	<i>scratching</i>	Rapid movement of claws on the head, neck and beak or by turning the head back and rubbing the top of the head against the back.

<b>Affiliative behaviour</b>	<i>bathing</i>	In puddles or shallow water elsewhere. The bird going in the water until it reaches the ventral side of the body (the legs are then more or less under water). After that the bird shakes its plumage and body parts (quick of the bird's wings which remain angled, head and tail shaking). The bird is then completely wet.
	<i>sunbathing</i>	Steeplly erect body and more or less splayed wings towards the sun. Mostly with "Nickhaut Blinkern".
	<i>preening invitation</i>	Greeting behaviour with "Chrup-calls" or repeated soft quacking "Gräh-calls". Slow movement to another bird, then the bird remain in front of the beak of the other in a horizontal body position with lowered head for few seconds. Usually, the interaction partner responds with the same call behaviour when "Chrup-call".
	<i>greeting</i>	Repeating sipping "Chrup-calls". Head is down, back is horizontal. The head and its beak swayed a bit downwards (head pattern is clearly visible) and again upwards (jerky nodding). Sound was emitted during the upward movement. Calls in 1-2 sec intervals. Sometimes the other birds begin then to call.
	<i>presenting nest-material</i>	Repeated soft quacking (nagging). The sound was emitted with the head slightly lowered, the head is jerky nodding. The bird has leaves, straw, moss or something in its beak and drops it in front of another bird which responds with nodding too. Sometimes the other bird takes the material with his own beak and keeps it awhile.
	<i>bill-shaking</i>	One bird grabs the other bird's beak with its own beak, then both shake the head and nod while they are still in contact with the beaks.
<b>Agonistic behaviour</b>	<i>allopreening</i>	Reciprocal soft nibble with the beak on plumage: on head, chest and back. Sometimes the bird poking deeply in the plumage between the wing and body from the other. Often one bird tilts its head while preening the other bird, the other bird meanwhile holds still. Sometimes with crossing their necks when both partners preen each other.
	<i>contact sitting</i>	Standing on one leg (the other leg is angled and hidden in the plumage) or sometimes on two legs, with its beak between the wings on its back or with slightly retracted head (beak is then in front of the body) tightly next to each other. Sometimes with body contact.
	<i>threatening</i>	The bird stretches its beak jerkily forwards against another bird but does not touch it. Sometimes the bird tilts its head during movement, so that the curved beak stops laterally of the other bird's body.

	<i>threat greeting</i>	Sipping “Chrup-calls” during beak movement from a more or less horizontal position up to an almost vertical position and again back. The call was then emitted during the upward movement, sometimes afterwards with beak lowering (double calls). Movements and calls are repeated.
	<i>defensive threatening</i>	The bird often freezing in its movements in a head down position with fluffy plumage (especially breast and back) and erect collar for few seconds.
	<i>pecking</i>	The bird snaps with its slightly opened beak to the other bird with or without contact to the body.
	<i>fighting</i>	The birds are biting each other intensively in bill or body, often with beak fencing before. Then they disrupt the behaviour and stand more or less face to face with erect bodies and collar with raised head until they begin to bite again.
	<i>scrounging</i>	Stealing food from the beak of the other. Often associated with displacing (see <i>displacing</i> ).
	<i>displacing</i>	One Bird is running toward another bird (head down) and displacing the bird from them feeding or resting place. Sometimes the other bird fleeing with relatively upright body with fast pace or jumping short distances away with short flapping of the wings. Displacing can also appear when one bird (donator) doesn’t really show agonistic behaviour, while the other bird (receiver) makes room for him.
<b>Appeasing</b>	-	While interacting with another bird: The appeasing bird looking permanently away, yawning or pretend roosting.
<b>Locomotion</b>	<i>walking</i>	Body is a bit upright, the head is looking forward and the beak is closed. Movement on feet with different speed and direction (during foraging the colony members are often organized in a line to float the prey).
	<i>flying</i>	Depending on the size of the group, the birds fly either in a V-formation or in an oblique line. One bird is always at the top of the formation, the others are laterally offset behind. While flying over a meadow, some group members fall sideways to the ground, but don’t reach it and fly then back to the rest of the group. Before landing, the birds mostly circle over the meadow for a while. While landing, the birds glide in direction ground and beat the wings forward with an upright body position above the chosen landing spot (the feet are then stretched forward), in order to slow down the speed until they fall on their feet. After landing, they angle the wings.

**Table 3:** The observed behaviours are categorized in terms of context.

## 2.4 Statistical analysis

To perform all statistical tests and graphs, I used the statistical software R (R Core Team, 2016). The graphs were created with the “qqplot2” package (Wickham, 2009), the statistical models with the “lme4” package (Bates et al., 2015) and “lmerTest” package (Kuznetsova et al., 2017) for p-value determination.

(1) To explore the spatial occurrence of the juvenile NBI during field observations, I calculated the proportion of identified juveniles in the four zones using the “plyr” package (Wickham, 2011). The effect of personality on the spatial distribution of juveniles along the zones was tested using linear by linear association test with the modal zone per bird (most common zone with one value per bird). A principal components analysis (PCA) generated with “prcomp” (Becker et al., 1988) was used to calculate a variable for proximity with PC scores extracted from the components with an eigenvalue of 1.574 that explained 78.7% of the variance; there were high factor loadings for nearest neighbour (m) (-0.89) and number of juveniles (0.89). The PC-scores were used as the response variable in the generalized linear mixed model (GLMM) which tested factors affecting the number and proximity of nearest neighbours (AIC: 387.013, 392.686). Personality and Group Spread were predictors (fixed effects), while the Individual ID was a random effect.

(2) Nine juveniles went missing from the post-fledging to winter season. Hence I compared their spatial occurrence (modal zone) during foraging and personality to test the hypothesis that birds on the periphery or more active birds would be more likely to experience risk and hence be missing from the over-wintering population. Cramer’s V (package: DescTools; Signorell, et mult. al., 2019) was used to measure the relationship between the modal zone and the missing status. I used likelihood ratio test (package: lmttest; Zeileis & Hothorn, 2002) to examine the significance. To calculate the percentage change of missing birds compared to birds that returned/survived I used the following formula:

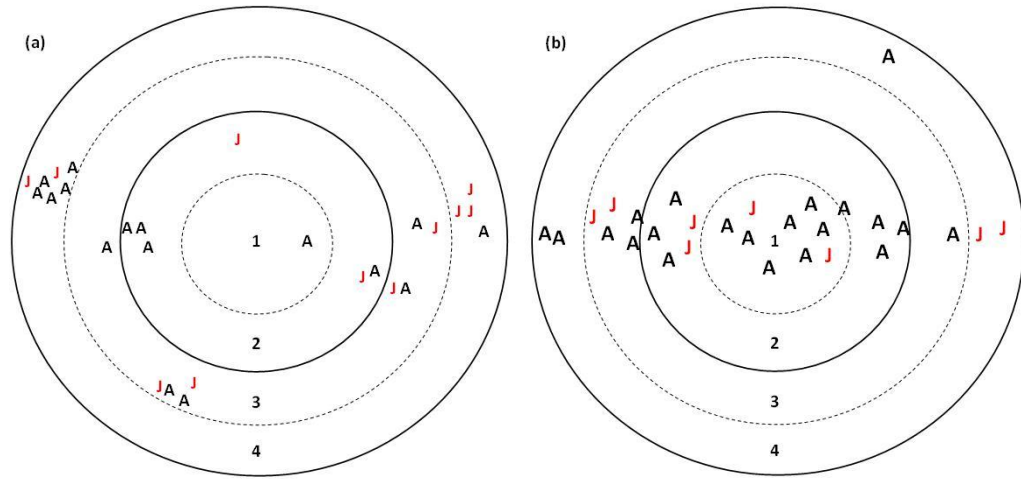
$$\text{Percentage Change} = \frac{\% \text{ missing} - \% \text{ returned}}{\% \text{ returned}} \times 100$$

(3) For investigating the time in response to feed for the different personality types, I did a second PCA with the different latency measurements – the time a bird used to reach the 1.5m radius around the tray and tray itself (i.e. when the bird takes food from the tray). I extracted a PCA component for latency to respond with an eigenvalue of 1.235 (61.77% of variance explained, factor loadings: 0.786 for latency to arrive and -0.786 for latency Tray); I used t-tests to compare differences in conditions (treatment 1 and treatment 2) with the derived PC-scores for each personality type (passive, normal, active). To explore the effects of experimental condition and personality on agonistic behaviours donated and received during feeding trials, I conducted a third PCA on behaviours donated and received to compare these patterns across personality types. The eigenvalue of the behaviour PCA was 1.235, explained 61.7% of the variance and had high factor loadings for the frequency of donated agonistic behaviour (-0.73) and received agonistic behaviour (0.73). I used personality, sex and condition as fixed effects in GLMMs in relation to PC - latency of response in the first model (AIC: 358.657, 364.314) and on agonistic behaviour in the second model (AIC: 383.514, 389.171). The response variables were the PC-scores, and individual ID was a random effect. Differences between adult and juvenile birds in the frequency of agonistic behaviours received and donated were tested with ANOVA.

### 3 Results

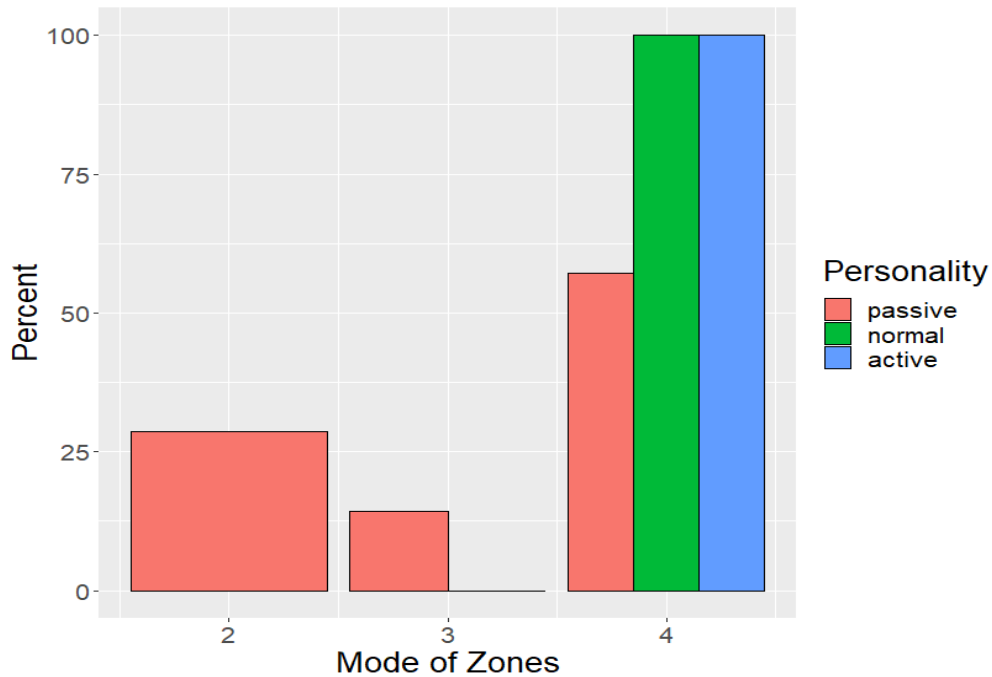
#### *3.1 Transect sampling*

There were 84 sightings of NBI groups from 12 days of transect sampling. The observed groups had an average  $\pm$  SE size of  $32 \pm 15$  birds (range: 4 - 53) with  $12 \pm 6$  juveniles, an average spread of  $28 \pm 17$  m (range: 1 – 100m). The average and SE number of sightings per identified juvenile (coloured rings were visible) was  $8.3 \pm 3$ . The entire colony (N=53) was observed in all four transects several times (M1 = 7x, M2= 50x, M3= 12x, M4= 15x). There was variation in spatial patterns (Figure 7).



**Figure 7:** Two examples of distribution patterns from 84 observations of NBI groups, showing common observed spatial distribution patterns of NBI groups: (a) sub-group formation within a wide spread group of estimated 50m spread on a meadow - 16 Adults (A), 11 Juveniles (J); (b) a group with linear formation on a meadow with a spread of estimated 10m – 21 Adults (A), 8 Juveniles (J).

There was a significant effect of personality (passive, normal, active) on the modal zone of occurrence (linear by linear association,  $p = 0.037$ ,  $df = 1$ ). Passive juveniles were more likely to be in the centre of the group and active individuals were more likely to be on the periphery (Figure 8).



**Figure 8:** Comparing the proportion of the personalities from the identified juvenile birds across the four zones (spatial occurrence), the passive birds were more likely to be in the centre (28.6% in zone 2, 14.3% in Zone 3 and 57.1% in zone 4) of the group than normal- and active birds, which were observed more often in the outer periphery (Zone 4) in 100% of cases. Compared with the passive, the normal and active birds were almost two times as likely to be in the outer periphery (Zone 4). Despite some individuals occurred also in zone one, they were mostly observed in the other zones (mode of zones) - therefore zone one is excluded.

Using GLMM, there was a statistically significant effect of group spread on the number and distance of nearest neighbours ( $p = 0.003$ ,  $df = 132$ ) per juvenile, but no effect of personality ( $p = 0.104$ ,  $df = 132$ ) or juvenile ID ( $p = 0.273$ ,  $df = 132$ ) (Table 4). If the group spread was greater, so was the nearest neighbour distance, without a measurable effect of personality on the number and distance of nearest neighbours.



**Table4:** Shows the coefficients of the generalized linear mixed model of number and distance of nearest neighbours in foraging juvenile NBI. The test statistic was t for fixed factors and z for random factors. Personality and group spread were fixed effects; individual ID was a random effect. The significant effect is labelled in bold.

<i>Response variable</i>	<i>Final model</i>	<i>Coefficients</i>	<i>Estimate</i>	<i>SE</i>	<i>Test statistic</i>	<i>p-value</i>
<b>PC Neighbours</b>	Personality Group Spread	Intercept	0.507	0.2628	1.929	0.056
		Personality	0.402	0.2451	1.639	0.104
		<b>Group Spread</b>	<b>-0.021</b>	<b>0.0069</b>	<b>-3.046</b>	<b>0.003</b>
		Individual ID	0.085	0.077	1.096	0.273

### 3.2 Foraging zone and personality of the missing juveniles

(1) There was a non-significant positive association between the modal zone of a juvenile during foraging in a group and its status as ‘missing’ from the winter flock (Likelihood ratio  $p = 0.462$ , Cramer’s  $V = 0.302$ ), which means that there was a trend that birds are more likely to go missing in a certain zone.

(2) There was also a non-significant positive association between the spatial occurrence of personalities (passive, normal, active) within a group and the status as ‘missing’ (Likelihood ratio  $p = 0.560$ , Cramer’s  $V = 0.239$ ), which means that there was a trend that certain personalities were more likely to go missing.

Comparing the percentage of juveniles that survived post-fledging and were seen in the winter flock per modal zone during foraging (zone 1: 9.1%, zone 2: 9.1%, zone 3: 9.1%, zone 4: 73%) with the percentage of missing birds (zone 1: 0%, zone 2: 11.1%, zone 3: 0%, zone 4: 89%), juveniles on the periphery in zone 4 were 0.2 times more likely to go missing (21.9% change). In passive juveniles, 33% were missing from the winter flock (4 birds); in more active juveniles, 5 birds or 50% were missing (22.2% of normal and 44.4% of active juveniles). Thus, more active birds were 0.5 times more likely to be missing than passive birds (51% change).

### 3.3 Feeding experiment

Of the 53 colony members with  $N = 19$  juveniles, a total of 43 birds with  $N = 9$  juveniles participated in the feeding experiment (Table 5) (11 juveniles in total – 1 juvenile bird without personality measurements, 1 focal juvenile bird that was observed but never joined the experiment).

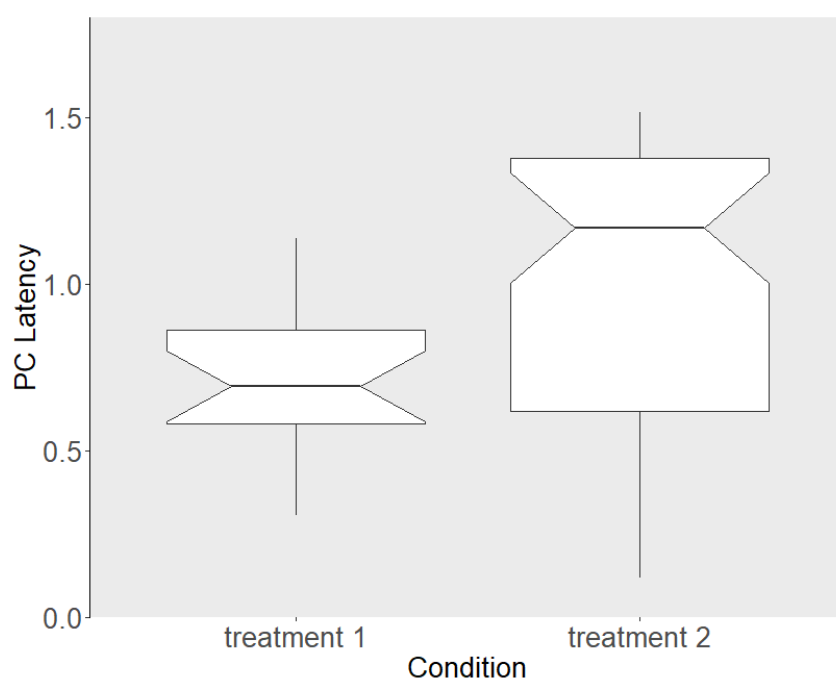
**Table 5:** An overview of the juveniles that joined the feeding experiment (individual number [ID No.], name), with assigned personalities (passive, normal, active) and number of observations during the 10 feeding trails (#observations per individual / #trails).

<i>ID No.</i>	<i>name</i>	<i>personality</i>	<i>frequency of observations</i>
4	Kilian	active	3/10
5	Margot	active	2/10
8	Quintessa	passive	5/10
10	Udine	passive	6/10
12	Udessa	passive	6/10
13	Sonia	normal	1/10
16	Sombrera	passive	3/10
18	Till	active	4/10
19	Timur	normal	5/10

GLMM analysis to explore the effects of the experimental conditions and personality on latency to feed found a significant effect of treatment group ( $p = 0.001$ ,  $df = 131$ ) but not personality ( $p = 0.438$ ,  $df = 131$ ) (Table 6). A bird's latency to feed was higher under the treatment 2 food conditions than under the treatment 1 conditions (Figure 9).

**Table 6:** Shows the coefficients of the generalized linear mixed model of latency to feed. The test statistic was t for fixed factors and z for random factors. Personality, sex and treatment group were fixed effects; Individual ID was a random effect. Treatment group had a significant effect on latency to feed (labelled in bold).

<i>Response variable</i>	<i>Final model</i>	<i>Coefficients</i>	<i>Estimate</i>	<i>SE</i>	<i>Test statistic</i>	<i>p-value</i>
<b>PC Latency to feed</b>	Personality Sex Treatment group	Intercept	-0.026	0.3828	-0.069	0.945
		Personality	-0.362	0.4649	-0.778	0.438
		Sex	0.249	0.4293	0.579	0.563
		<b>Treatment group</b>	<b>0.592</b>	<b>0.1585</b>	<b>3.736</b>	<b>0.001</b>
		Individual ID	0.200	0.156	1.279	0.201



**Figure 9:** Comparative boxplot in which the treatment groups (treatment 1= resource abundance left boxplot [N = 9 individuals], treatment 2 = resource scarcity right boxplot [N = 8 individuals]) plotted against each other in relation to PC latency (y-axis).

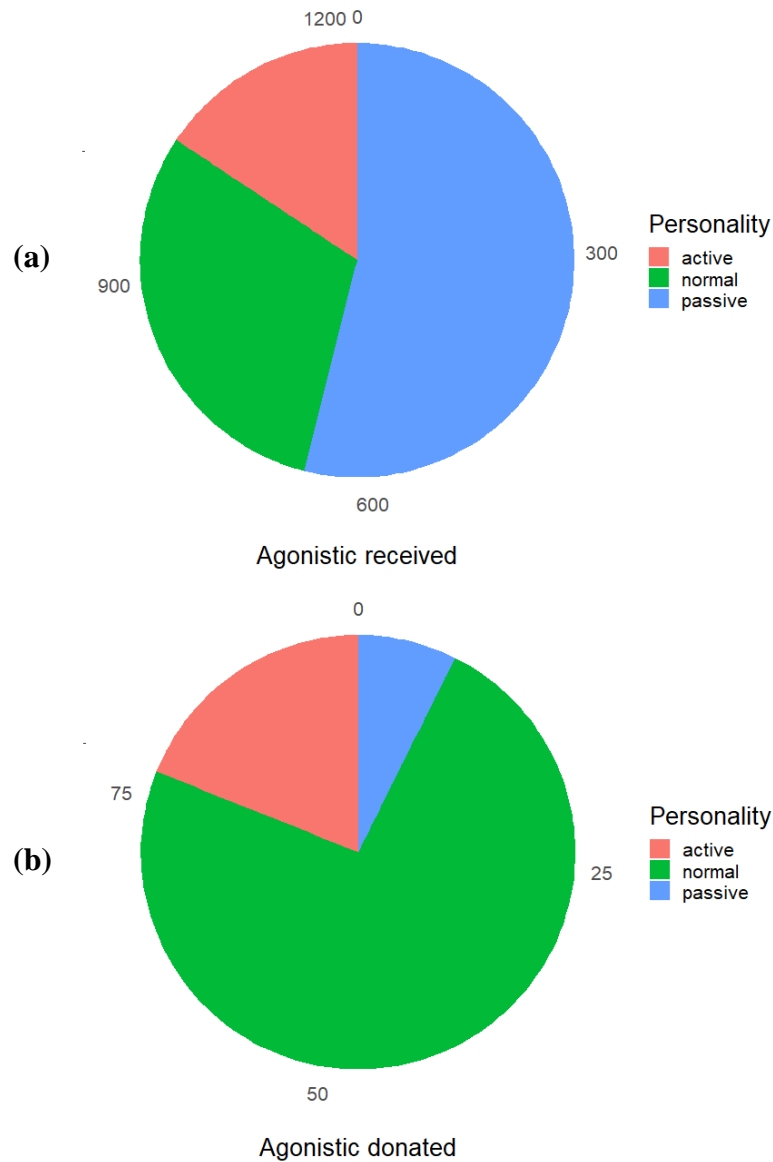
**Table 7:** Observed agonistic behaviour in juveniles during the feeding experiment, in accordance with the Ethogram (Table 3). The most common behavioural subcategory is highlighted in bold.

<i>Agonistic behaviour in juveniles</i>		
<i>Subcategory</i>	<i>Received (mean)</i>	<i>Donated (mean)</i>
displacing	<b>0.70</b>	0.14
pecking	<b>0.38</b>	<b>0.60</b>
threatening	0.16	<b>0.25</b>
threat greeting	0.14	0.13
fighting	0.04	0.02
scrounging	0.00	0.03

GLMM analysis to explore the effects of treatment group and personality on agonistic behaviours donated and received found a significant effect of personality ( $p = 0.018$ ,  $df = 131$ ) but not treatment group ( $p = 0.557$ ,  $df = 131$ ) (Table 8). Passive birds were more likely to receive more agonistic behaviours from others than active birds (Figure 10).

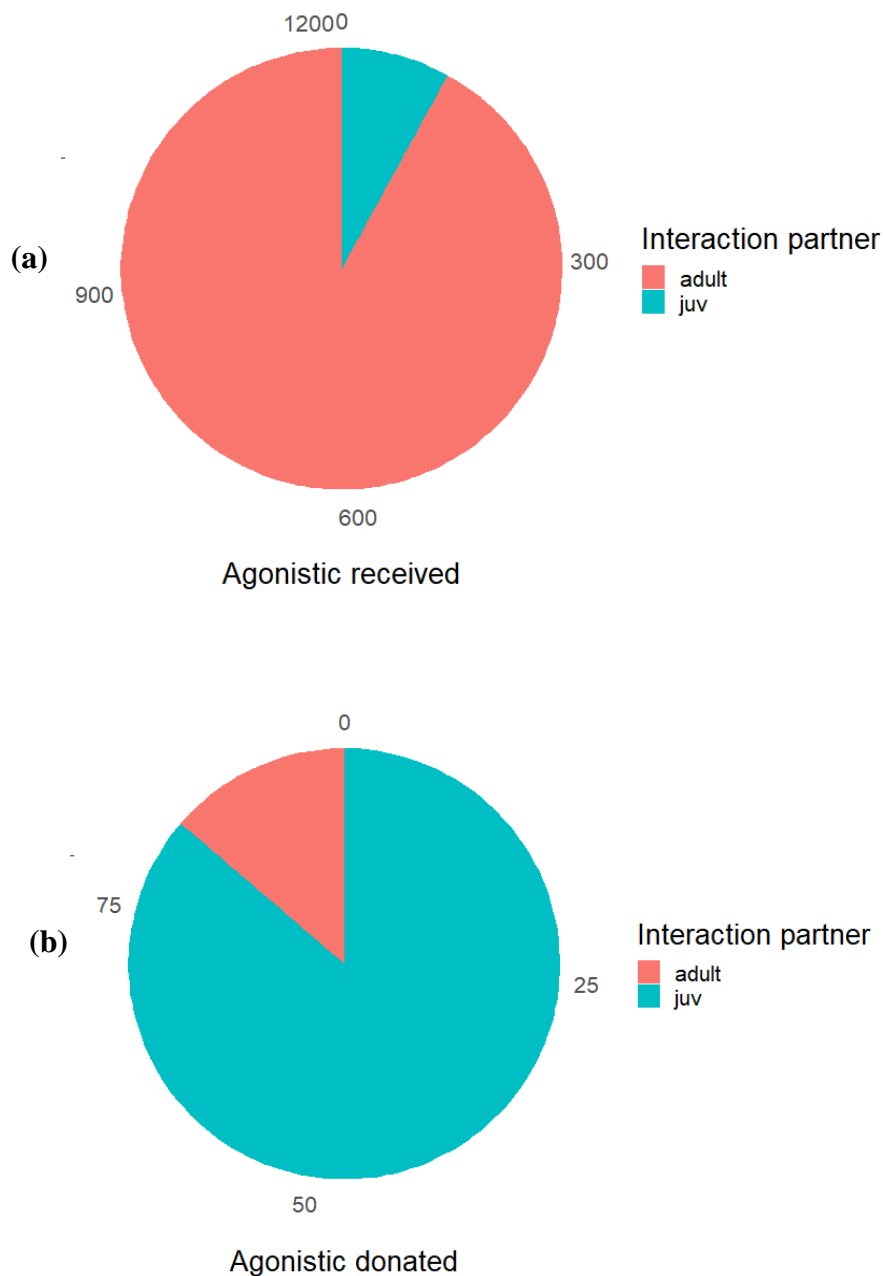
**Table 8:** Show coefficients of the generalized linear mixed model of number of agonistic interactions received at feeder in foraging juvenile NBI. The test statistic was  $t$  for fixed factors and  $z$  for random factors. Personality, sex and treatment were fixed effects; individual ID was a random effect. Personality had a significant effect on the number of agonistic interactions received.

<i>Response variable</i>	<i>Final model</i>	<i>Coefficients</i>	<i>Estimate</i>	<i>SE</i>	<i>Test statistic</i>	<i>p-value</i>
<b>PC Agonistic behaviour</b>	Personality Sex Treatment group	Intercept	-0.096	0.1680	-0.572	0.569
		<b>Personality</b>	<b>0.469</b>	<b>0.1959</b>	<b>2.394</b>	<b>0.018</b>
		Sex	-0.165	0.2393	-0.691	0.491
		Treatment group	-0.105	0.1787	-0.589	0.557
		Individual ID	0.200	0.156	1.279	0.201



**Figure 10:** The pie charts illustrate the sum of agonistic behaviour (a) received and (b) donated by juveniles during social interactions, shown per personality type (passive, normal, active). The passive juveniles received the most agonistic interactions (blue) compared with the fast active juveniles (red), while the more active juveniles donated the most agonistic behaviours (green and red).

The ANOVA tested the differences in frequency of agonistic behaviours received and donated between adults and juveniles. The juveniles received significantly more agonistic behaviour from adults ( $p = 9.87\text{e-}13$ ) and donated significantly more agonistic behaviour to other juveniles ( $p = 0.0014$ ) (Figure 11).



**Figure 11:** The pie charts illustrate the sum of agonistic behaviour (a) received and (b) donated by juveniles (blue) during social interactions with adults (red).

## 4 Discussion

This study aimed to test the effects of personality on the spatial occurrence and foraging behaviour of juvenile northern bald ibis during the post-fledging period. The main findings are that juvenile personality was associated with spatial occurrence during foraging in the wild and agonistic behaviour at experimental feeding trays. (1) During group foraging observations, passive juveniles occupied more central foraging positions and active juveniles occupied more peripheral foraging positions. (2) During experimental feeding trials, passive juveniles received more agonistic behaviour from other northern bald ibis compared with active juveniles.

The findings of this study align with patterns found in other studies, whereby bold exploratory individuals tend to be on the periphery of groups. Aplin et al. (2014) examined the spatial distribution of wild great tits (*Parus major*) during foraging trips for birds with experimentally determined personality. Passive individuals were more likely to have close neighbours and occur in the centre of the group and active individuals were more likely to be leaders at the edge of the group. They interpreted the findings based on individual decision making, in which the individuals trade-off the benefits and costs of being at the periphery or in central positions of the group which depends on their personality type. According to this study, the periphery offers less competition for food but higher predation risk for the great tits, whereas the central position offers anti-predation strategies and social foraging cues but elevated competition for food. In case of NBI, we also found that active juveniles were at the periphery, perhaps to better exploit novel food sources with reduced food competition. In terms of feeding efficiency, being on the periphery may only be advantageous for the NBI when food items are small and evenly distributed, so that the birds can be spatially separated and have lower intraspecific competition over food (Hirsch, 2007). The food sources of the NBI are mainly earthworms and arthropod larvae (Zoufal et al., 2007) which are thought to be randomly distributed along the meadows' soil (Poier & Richter, 1992; Weidemann, Stiedl, & Kalmring, 1990). For this reason, NBI do not need to aggregate on a single spot for foraging in the wild and instead their spatial distribution could exploit the wide distribution of potential prey in the ground. Passive birds might profit from anti-predator strategies in rather central positions and receive more foraging cues from group members, which could be tested in future studies.

Anti-predator behaviour can be the target of selection, because it is partly heritable and is modified through experience with predators (Magurran, 1990; Blumstein, 2006). The NBI individuals may favour foraging in groups in spite of increased competition given high predation risk. In the related white ibis (*Eudocimus albus*), vigilance increased on the spatial periphery because the individuals there were under more predation pressure than those in the centre. The birds in the centre had higher feeding efficiency because they spent less time in vigilance (Petit & Bildstein, 1987). But in contrast to this assumption, Blanchard, Sabatier, & Fritz (2008) suggest that the reduced vigilance in the centre of a group could have another meaning. They conclude that impala (*Aepyceros melampus*) in the centre of a group decrease their vigilance because of within-group competition. The risk to lose the feeding patch through group members due to vigilance is then high. In the case of the NBI, a vigilant bird may have higher risk of being displaced from the feeding patch. In fact, the most common interactions within a group during the feeding trials were displacement (0,7) followed by agonistic pecking (0,38). Previous observations of ibis groups found that displacement among birds was more frequent than fights (Kopij, 1998). This suggests that the prevalence of agonistic and displacement behaviour in the northern bald ibis is a key behaviour to regulate individual access to resources in a foraging context.

The NBI is known to be a hierarchical species in which the adults dominate over juveniles (Serato & Kotschral, 2006). Notably, some passive juveniles were also observed on the periphery (Figure 8). One explanation for the occurrence of passive juveniles on the periphery could be stronger competition with dominant adults within central positions, which forced the subdominant juveniles regardless of their personality to the edges - despite the possible preference of passive juveniles to stay more central. Animals on the front edge in moving groups should have a better access to food when foraging for invertebrates (Hirsch, 2007; Janson, 1990), especially when the NBI are grouped in a linear formation in order to disturb and chase the prey on the meadow (Kushlan, 1978 in: Böhm & Pegoraro, 2011). The feeding experiment of this thesis shows that the juveniles received the most agonistic behaviour from adults during feeding (Figure 11, a.), which is comparable with a former study that investigated feeding behaviour of NBI (Czerny, 2018). Generally, the NBI juveniles are subject to aggression by adults, whereby the encounter probability may be influenced by their personality and/or position in the group (Thaler, Ettel & Job, 1981). In the wild, the competitive factor over food would be weaker because the food is randomly distributed (Morrell & Romey, 2008), but in addition, the adults could act selfishly to defend the best places in the centre where they are better protected against



predators (Hamilton, 1971). For instance, Whitfield (1985) observed age-related differences in foraging behaviour in juvenile turnstones (*Arenaria interpres*), who foraged rather on the periphery of the group where they were more likely attacked by sparrowhawks (*Accipiter nisus*) as adults seemed to ‘monopolize’ the centre. In fact, the group size of the NBI colony in this study decreased from 53 to 43 birds (10 birds lost) after returning to the wintering area in Grünau, and nine of the missing birds were juveniles. So, it is possible that these juveniles were victims of predation because of their peripheral position in the group. In fact, the juveniles on the periphery were more likely to go missing and 50% of missing birds had active personalities. According to Fritz et al. (2017), in addition to depredation, collisions and electrocution on power lines may have been a cause of death and may occur when birds (mostly juveniles and subadults) disperse. The last case is also discussed in Bowden et al. (2008), where the juveniles of the NBI colony flew to multiple destinations after leaving the summer site in 2016. The missing birds in this study were also mainly juveniles, which supports the assumption that these birds might be more susceptible to predation, vagrancy or death for other reasons. One adult NBI of the present study colony was known to have been depredated by a northern goshawk (*Accipiter gentilis*) (personal observation), as the predation event was observed. Thus, for all these reasons, the different personalities may use different strategies for food acquisition in the wild in which the normal and active juveniles may profit from decreased competition in a risky periphery, which makes them possibly more vigilant, while the slow exploring birds profit from lowered time spent in vigilance and thus longer time investing in foraging on safer central positions, though with increased competition over food in those areas. Further research on vigilance and feeding efficiency in association with the spatial position in the NBI is needed.

An alternative interpretation for the peripheral spatial positions could also be that juveniles were more exploratory than adult birds in a foraging context. Spiezo et al. (2018) found a difference in exploration trait of captive northern bald ibis, with more resting adults and more foraging juveniles. Hence, the juveniles examined in this thesis could have spread out on the meadow during foraging while the adults were resting.

In contrast to my expectations, personality had no significant effect on the distance and number of nearest neighbours. Passive juveniles did not have more group members in close vicinity than normal or active juveniles. However, group spread had a significant effect on nearest neighbour distance. A previous study that monitored foraging behaviour in NBI in the desert of Syria found that NBI were grouped in a more or less loose arrangement, and the inter-bird distance was

generally a few meters while foraging (Serra et al., 2008), as observed in the present study. However, when the NBI were not foraging, they were usually close together and showed affiliative or comfort behaviour (personal observation; e.g. resting, sun-bathing, preening, social preening and pair sitting in breeding partners - according to Pegoraro, 1992). These observations suggest that NBI in a group may have been observed while relaxing with a small group spread or foraging with wider group spread. Future research could score the behaviour of each individual observed during foraging transect observations to ascertain the spread of behaviours within a group.

There remains some uncertainty about the accuracy of the data collected during the field observations. Other studies that focused on the spatial position of animals had the issue that the definition of ‘periphery’ and ‘centre’, especially in moving groups, is not easy to define; in some cases the group geometry was linear or the focal individuals changed their position frequently within the group (Frid, 1997; Stankowich, 2003). These challenges could also be felt during this study. Group patterns with unclear centre and periphery, such as in sub-groups (Figure 7, a) or in linear formations (Figure 7, b), possibly generated a bias in my results. For instance, when juveniles were located on the periphery within a sub-group and there was another sub-group less than 50m away (otherwise the next sub-group would be considered a separate group, see Methods). In linear formations, the group members at the central edges were recorded as birds in the inner zones of the circle despite their peripheral spatial positions. Furthermore, I often failed to identify individual juvenile IDs because of camouflaged rings due to high grass or uneven terrain (8 average identifications per focal juvenile out of 84 total sightings of groups) and I had less time for identifications in moving groups. Because the spatial pattern was changing quickly in such groups, I sometimes focused on juveniles on the edges to be sure to collect data from the periphery.

In terms of latency differences, the passive birds were more or less as fast as the active birds (Figure 9). Furthermore, the birds were significantly faster during the treatment 1 condition (three food trays presented) compared to the treatment 2 condition (two food trays presented). According to Phüringer-Sturmayr et al. (in prep.) the active NBI juveniles in this thesis were faster in exploring during Novel Arena exploration tests as they were 30 day old. Hence, an explanation for the equality in latency during the feeding trials could be that the personality axis from slow to fast explorer may have changed across development, as has been observed in some other animal species (e.g. slow birds getting faster, cp. great tits in: Carere et al., 2005). However, another study that tested the exploration trait of great tits with different approaches

found no correlations between tests but repeatable behaviour within one kind of exploration test. They suggest that the exploration behaviour is context specific and that the birds have no general exploration strategy (Arvidsson et al., 2017). Thus, the NBI could also react differently in different exploration tests.

Alternatively, the hunger level of the juvenile NBI could influence the time of response to feed, which requires further testing. According to Fehrer (1956), hungry animals may increase their exploratory activity. This suggestion was derived from testing food deprived albino rats (*Rattus norvegicus domestica*) that leave a familiar box to explore an unfamiliar box more readily than sated animals. In middle Europe, the soils usually freeze in winter and consequently NBI are then not capable to poke with their curved long bill in the ground to exploit food sources (Tuckova et al., 1998). The sedentary NBI colony in Grünau is therefore strongly reliant on daily supplemental feeding events at the game park during winter, in order to survive. Perhaps the higher energy demand in winter, that has also been found in other subtropical birds (Smit & McKechnie, 2010), in combination with the circumstance that the NBI juveniles are subordinates, may impact the juveniles' latencies regardless of their personality. While the focal birds got a second feeding in the aviary on the same day, it is possible that the adults defending the food resources were there as well and that juveniles are generally constrained to access food. In fact, the latency of juveniles increased when two feeding trays were carried out instead of tree, which suggests that the adults occupied the trays during the experimental condition more (Figure 9) causing the juveniles problems to reach the trays. According to Soma & Hasegawa (2004), social dominance has a relationship with foraging efficiency because dominants have priority access to resources, as examined for example in budgerigars (*Melopsittacus undulates*).

Among the NBI juveniles, there were significant differences between the personalities in the frequency of agonistic behaviour (Table 8). The fact that passive individuals received more agonistic behaviours at the experimental food trays, as found in this study, raises questions about correlations of behavioural traits within personality types. Perhaps active individuals use more aggressive foraging behaviour to access resources. The 'normal' and 'active' personalities donated the most agonistic behaviour to the other juveniles (Figure 10, b) in which agonistic pecking was the most common agonistic behaviour (Table 7), while the passive juveniles received the most agonistic interactions in comparison to the others (Figure 10, a). Agonistic behaviour was not dependent on sex (Table 8), which is similar to the results of another study that investigated behavioural symmetries between the sexes of NBI (Serato & Kotschral, 2006).

This suggests that the individual differences in agonistic behaviour may come from different personality types in the studied juveniles. Active juveniles acted more aggressively and expressed agonistic pecking (0.6) and threats (0.25) during these social stress conditions (Table 7). Further studies could test the consistency of aggressive behaviour in the active NBI, which would confirm a correlation between the fast exploring trait and aggression in this type of personality.

## 5 Conclusion

Although this study faced many difficulties in terms of assigning a bird's position in a moving foraging group and small sample sizes due to unpredictable events, the study gives insights into personality-associated behaviour within an NBI group. During field observations, passive birds occupied central foraging positions and active birds occupied peripheral foraging positions. Using experimental feeding trials, passive birds received more agonistic behaviour from other birds. Combined these findings point to a role of personality in shaping access to resources in a threatened bird species and highlight potential risk factors for a sub-set of the juveniles from food competition in the centre to predation risk on the periphery. It was interesting to see that the different personality types had more or less the same latencies in approaching a feeder, suggesting that the exploration trait is maybe context specific or not stable during individual ontogenesis, and hunger could play a role in feeding behaviour in autumn. Clearly, small sample size is a limiting factor in this study. However, small sample size is often an aspect of working with threatened species, though care is required in the interpretation of the findings.

Information about personality types of threatened species can be used in predictive models that forecast their survival under a range of changing environmental conditions. Through simple detour tests with freshly hatched birds, the level of exploration behaviour and other behavioural traits that correlate with exploration (i.e. boldness, aggression) can be measured. Decisions for release of individuals can be made in order to optimize the colony for introduction in the wild (McDougall & Reader, 2006). This study contributes to our understanding of how personality in a threatened bird species could be linked with survivorship of juveniles across a key life stage.

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