Effects of physical and social environment on zebra finches' foraging intensity

submitted by

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I certify that all material in this thesis/dissertation* which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

The zebra finch (*Taeniopygia guttata*) is the most widely used passerine bird in captive research, yet little work has been done in the wild where physical and social conditions are more variable and their behaviour can be investigated in an ecological context. Zebra finches forage on the ground and are vulnerable to predation by a range of terrestrial and aerial predators. In this thesis, I explore how the physical and social environment affects their foraging decisions in captivity and in the wild. The decision to feed in a particular patch is an attempt to optimise the costs and benefits of feeding at that location. I used giving-up densities (GUD) – the density of food remaining in a patch after the forager(s) have exploited it, to measure the perceived risk of zebra finches to a variety of experimental treatments. In captivity, I investigated how zebra finches' foraging intensity responded to characteristics of the captive environment such as the availability of perches, cover, and ground substrate. In the wild, I examined how their foraging intensity was affected by the distance to natural cover (vegetation) or their visual fields. I also explored effects of the local neighbourhood density of zebra finches in the wild. I further investigated captive zebra finches' foraging intensity in different sized groups, as a function of the proximity to, and behaviour of neighbouring flocks. I show that zebra finches forage more intensively when they are close to vegetation and perceive cover as protective. I also found that foraging intensity increased non-linearly with group size and mass and sex mitigated how social and physical environments affected foraging intensity. Overall, my finding suggest that while foraging, zebra finches place greater emphasis on their social, compared to physical environments. My thesis highlights the importance of taking into account a wide range of social factors when investigating foraging decisions by animals.

List of Contents

Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other University. All the research presented in this thesis has been carried out during October 2016 to October 2018. I am the principal contributor of all chapters within this thesis.

Contributions statement

I do declare that this thesis constitutes my original work, and has not been submitted or accepted for the award of a higher degree at another institution. No persons have contributed to this work that have not been given credit, including images and photo credit. All the work of previous scholars influencing this work are cited in the appropriate manner.

This thesis will be submitted to Macquarie University and Exeter University in accordance with the Cotutelle agreement dated 5th of July 2016.

The protocols to collect morphological measurements in Zebra Finches used in this thesis were approved by ethics committees at Macquarie University (ARA 2015/028-8).

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in the studies were in accordance with the ethical standards of the institution or practice at which the studies were conducted. The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

Sydney, 12/07/2019

Anika Immer

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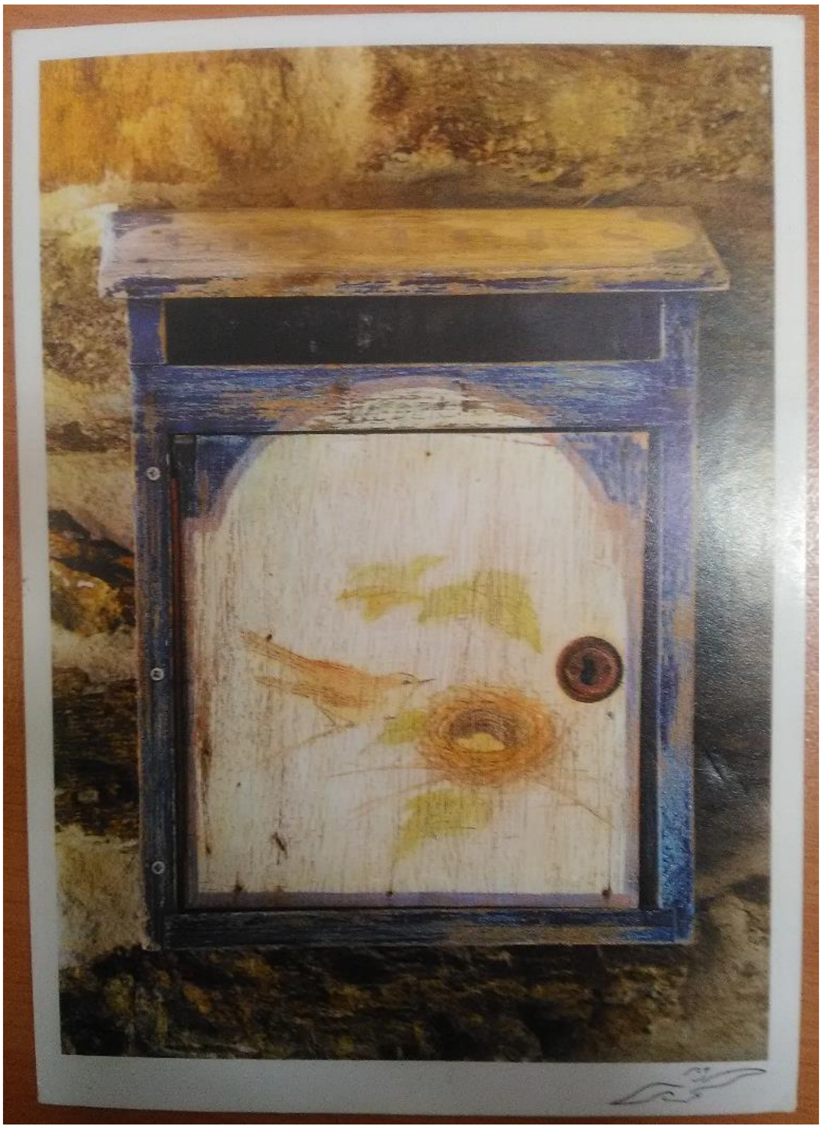
« Quelle aventure !!! J'ai bien fait de venir ! »



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	I	II	III	IV	V	VI	VII	VIII
CONCEPTION & DESIGN	AI	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI (95%), SG, SD	AI (90%), SG	AI
DATA COLLECTION		AI	AI	AI	AI	AI	AI	
ANALYSIS		AI	AI	AI	AI	AI	AI	
WRITING	AI	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI (90%), SG, SD	AI
OVERALL RESPONSIBILITY	AI	AI	AI	AI	AI	AI	AI	AI

CHAPTER I

General Introduction

In order to understand the evolution of individuals within a group, we are often trying to find an optimum whithin different behavioural strategies. However, in a changing environment, the theoretical best behavioural strategy can change, and several behavioural strategies can also co-exist. One of the main theoretical examples in behavioural ecology is the hawk-dove game (Maynard Smith and Price, 1973). In this game two different strategies, the hawk and the dove, compete over a resource. The dove will not fight and share the resource while the hawk will fight and get the whole resource if he wins, or lose the resource and potentially also become injured if he loses. Thereby, the best strategy for an individual depends on the other strategies, and their frequency in the population. Other activities could also have an array of possible behaviours with no best overall optimum per se but equivalent ways to cope with a situation. In a highly variable environment, there could be selection for flexibility, in which case a population would keep a large variance. Individual variation would then maintain variations of the entire population and thereby its adaptive potential and particularly it's resilience to change.

For different strategies to enhance individual survival, the balance between the costs and benefits for each strategy should be equivalent. Empirical work on foraging zebra finches (*Taeniopygia guttata*) suggest that temporal and/or spatial heterogeneity in resource distribution would contribute in maintaining different behavioural strategies (Tej and Dubois, 2018).

The zebra finch

Weighing 12 g in average, the zebra finch is the smallest, and one of the most widespread granivorous birds in the Australian arid zone (Morton and Davies, 1983). The Australian desert is characterised by scarce and erratic rainfalls, leading to primary production unpredictability (Morton et al., 2011). Zebra finches almost exclusively eat grass seeds (Morton and Davies, 1983), which is one of the most stable resources available in the arid environment (Brown et al., 1979). Zebra finches' foraging behaviour is strongly shaped by the fear of predation. They can be found in flocks of hundreds individuals (Zann, 1996). But they generally appear in much smaller group sizes, the most common group size being two (McCowan et al., 2015). Zebra finches are socially monogamous (Zann, 1996), and genetically mostly monogamous (Griffith et al., 2010).

Zebra finches have extensively been studied in captivity (review by Griffith and Buchanan, 2010). Indeed, they are extremely easy to breed in captivity in comparison to other passerine birds. They have become the avian equivalent of the lab rat in research labs across the world. As such, we know a great deal about a wide range of areas including basic biology, physiology and behaviour. Studying a well-worked model species is efficient: Based on years of studies and experiments, we can ask questions that are more specific and have a clearer view on what is feasible or not. However, little is known about zebra finches in their natural habitat, and most of those working on them in Europe and North America have no real understanding of the ecology and environment of the Australian arid zone. This has several consequences potentially affecting welfare as if we do not know what makes an environment safe for a zebra finch in their natural habitat; we cannot reproduce those conditions in captivity. Moreover, knowing relatively little from wild studies can have large impacts on the interpretation researchers do about captive zebra finches. One example is the finding that extra pair paternity was much lower in captivity than in the wild (Griffith et al., 2010). In this thesis, experiments were conducted both under laboratory conditions and in the wild.

Predation risk in foraging decisions: eating without being eaten

Foraging is the decision made at each point in time to balance the conflicting demands for (i) direct energy intake to survive and reproduce and (ii) for survival through predator avoidance. Foraging at a specific location is the decision made at each point in time that foraging right here, right now, is better than foraging somewhere else or at another time. Foragers might then select habitats in which they feel relatively safe. For example, for prey species, foraging close to vegetation (cover) is likely to decrease the perceived risk of predation. Foragers can also select the social context in which they operate. There is strong evidence that decisions are modulated by social context (Van Den Bos et al., 2013). In many prey species, social foraging is an important component of anti-predator behaviour (Giraldeau and Caraco, 2018). Foraging in groups typically decreases the per capita risk of being depredated (dilution effect, Delm, 1990), increases predator detection (many eye hypothesis, Pulliam, 1973), increases opportunities to hide behind conspecifics (Hamilton, 1971), and decreases predator lethality due to the confusion effect (Landeau and Terborgh, 1986).

To investigate how zebra finches use their environment in order to eat without being eaten, we used the giving up density (GUD) approach. This approach allows one to investigate the costs of foraging. A forager should exploit a food patch until the cost of foraging there and the benefits of exploitation are equal. The density of food left by the forager is called the GUD (Brown, 1988). GUDs can be measured using depletable food items mixed into a non-edible substrate in a container (Brown, 1988). A forager exploiting such a food patch gets diminishing returns because the more the forager eats the food items, the more the food density decreases and the more difficult it gets for the forager to find new food items. The GUD of a food patch reflects the GUD from the most efficient forager who visited it; GUD thereby often reflects the GUD of the last forager. If a less efficient forager visit the food patch last, this forager will give up before finding a food item. However, Brown (1988) suggested that GUD would be affected by the possibility of several individuals foraging. Furthermore, individual foragers with different states might also influence GUD (Bedoya-Perez et al., 2013; Brown, 1999).

As the GUD technique use depletable food patches, foraging missed opportunity cost are different than zero (Brown, 1999). This means that when a forager is in an environment with several depletable food patches, the forager will visit the different patches, because the cost of staying in a single patch increases with the number of food items already eaten. GUDs thereby quantify choices made by foragers. If a forager were given the choice to forage in non-depletable food patches (e.g. ad libitum food) the forager would give up because the gain of food in overall would be lower than the costs of foraging or will be too fat (which is costly). The decision to forage in a place would then be met once, at the beginning, and the forager would eat until another activity (other than foraging) would be of greater value. Depletable food patches quantitatively capture the foragers choice whereas non-depletable food patches capture it only qualitatively.

Using the GUD technique in artificial resources patches allows manipulations of a variety of variables while foragers remains in their natural environment (Brown, 1988). GUDs results allow an understanding of how a forager perceives all of the different parts of a complex environment. GUD methods have been used in a wide variety of taxa since the framework was introduced (Brown, 1988; Bedoya-Perez et al., 2013). Even if GUD have been used to study foraging birds very earlier on (Valone and Brown, 1989), most work has focused on mammals, essentially rodents and asocial foragers (Bedoya-Perez et al., 2013). However, Carthey and Banks (2015) provided empirical evidence that foragers visiting a food patch as a group affects GUDs, probably by decreasing predation risk.

Vigilance is a tool to balance food and safety while engaged in foraging (Brown, 1999). In a risky situation, animals might allocate more time to vigilance, which decreases their foraging activity. Animals would thereby need more time to eat the same amount of food, this is likely to result in higher GUD (Brown, 1999). However, vigilance does not necessarily correlate with GUDs (Morris and Vijayan, 2018).

In summary, zebra finches evolved in an unpredictable and patchy environment and are often seen foraging in groups. I hypothesised that zebra finches use both physical and social aspects of their environment in order to eat without being eaten. In this thesis, I investigated the role of physical and social environment of foraging decisions in the zebra finch. We used zebra finches because they are the most widely studied bird in behavioural work in the lab, and yet we do not understand much about their natural ecology and motivation for behaviour. The insight from this work will help to interpret and direct new captive research. The zebra finch also provides a useful model system for understanding behaviour in any social prey species, and therefore helps us to understand the drivers behind social behaviour generally in such animals.

Chapters description

In a first attempt to investigate GUD in zebra finches, I conducted experiments on simple physical changes in the cages: availability of perches, cage floor and presence of cover (Chapter II). By measuring the balance of cost and benefits of a food patch, the GUD approach is an interesting perspective from which to investigate welfare questions. Once the GUD protocol was operational in captivity, I focused on the only physical aspect affecting captive zebra finches: the presence of cover. I investigated how the distance of cover affected zebra finch foraging choices in their natural environment (Chapter III). I also explored the potential effects of weather conditions and neighbouring conspecific density. As zebra finches were foraging more intensively close to cover in the wild but less intensively behind cover in captivity, I investigated how they would be affected by cover blocking their sightlines without providing refuge (chapter IV). I also considered the potential effects of food patch elevation and ease of escape.

Zebra finches generally forage in groups. This might influence how they make foraging decisions. I investigated if zebra finches would forage more intensively next to small or larger flock sizes and if this choice was affected by their own group size (Chapter V). I also examined their foraging choices regarding neighbours' behaviour. I then further inspected the link between GUD and group size, along with individual mass and mass similarity within groups (Chapter VI). As increasing evidence was found that individual characteristics might influence one foraging behaviour and the foraging behaviour of conspecifics, I explored if the sexual identity and the pair bond of dyads would affect their foraging efficiency (Chapter VII).

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CHAPTER II

Giving up density as a tool to study welfare in captive birds

Abstract

Animal welfare is an important issue both in terms of delivering ethical treatment of animals and through its influence on the quality of research for those animals studied in a captive situation. The zebra finch is the most widely used passerine bird in captive research, in addition to being commonly kept as cage or aviary birds. Surprisingly, to date, few studies have examined the welfare of these birds in captivity, even though they have the potential to act as a model for captive animals more generally. Here, we have used the giving up density framework (hereafter GUD) to investigate how the behaviour of zebra finches in captivity responds to characteristics of the captive environment such as the availability of perches, cover, and ground substrate. The GUD approach uses an animals' foraging decisions to provide information on its perceptions of different environmental contexts. In a prey species, such as the zebra finch, this insight comes because an individual will balance the cost and benefit of feeding at specific locations that vary in riskiness. Relatively more food will be consumed in a context in which an individual feels comfortable, whereas they will 'give up' on a risky patch more readily. Our results show that zebra finches' perceived risk was higher when behind cover, while we found the effects of the floor substrate and number of available perches to be weak. Our results suggest that the use of giving up densities is a straightforward and relevant way to determine environmental features in which zebra finches feel safer, and this new approach can add an important new tool to explore welfare questions in captive animals, improving conditions and ultimately well-being.

Keywords: Zebra finch; Foraging; Environmental features; Welfare; Landscape of comfort

Introduction

One of the key challenges in animal welfare is in recognizing the extent to which an animal feels positive, negative or ambivalent towards a particular stimulus or situation (Dawkins, 1988). In songbirds such as the zebra finch *Taeniopygia guttata*, different ways of assessing welfare have been suggested from the direct measure of the level of stress hormones to direct assays of behaviour such as song rate (Yamahachi et al., 2017). Here, we suggest that a method, quite widely used in ecological studies (Brown, 1988), – the giving up density paradigm (hereafter GUD) - may provide insight into the way in which elements of the holding environment are positively and negatively perceived by birds.

The decision to feed at a specific location is made through a balance of the cost and benefits of feeding there. In prey species, the decision to leave a foraging patch is largely determined by the value provided by continuing to forage (related to the density of food encountered) against the risk of remaining in that situation. The GUD (the density of food remaining in standardised patches after an animal has exploited them) is a result of the trade-off between foraging and fear at a particular location (Brown, 1988). By revealing how fearful or comfortable an animal feels in a particular context, the GUD paradigm has the potential to provide important information about the quality of the captive environment in a way that is very un-invasive because it is can be easily assayed through the measurement of food density in experimental foraging patches. Troxell-Smith et al. (2017a, b) describes it as “Landscape of comfort”. This is preferable to more invasive methods such as hormone sampling, or more logistically challenging or time-consuming behavioural assays (e.g. measuring behaviour directly).

Although the zebra finch is a widely used model species in behavioural, genetic and neurological research (Griffith and Buchanan, 2010), relatively little work has focused on their welfare (e.g. Collins et al., 2008; Yamahachi et al., 2017). However, a number of common environmental features have been suggested to positively affect welfare in caged zebra finches. For example, positive welfare outcomes have been suggested for increasing the number of perches as zebra finches take refuge on the perches (Yamahachi et al., 2017, Jacobs et al. 1995); the presence of cover (Collins et al., 2008); and having food enrichment on the floor of cages (Olson et al., 2014). The floor of a cage itself can either be an open wire mesh (facilitating cleaning), or a hard substrate. Whilst the welfare outcomes of this profoundly different cage flooring have apparently not been examined in the zebra finch, the floor substrate was found to influence the risk perception measured through GUDs in wild squirrels (Thorson et al., 1998), in wild goats (Shrader et al., 2008) and in wild Namaqua mouse (Abu Baker and Brown, 2012). In several field studies, distance to cover was found to affect GUDs in rodents and birds (Molokwu et al., 2010, reviewed in Brown and Kotler, 2004). The availability of perches are considered as they are known to be a refuge for zebra finches. Distance to refuge has been found to affect GUDs in wild hyrax (Druce et al., 2006) and in wild marmots (Monclùs et al., 2015).

Here, we investigated whether zebra finches would forage more intensively (leave lower GUDs) on one side or the other of the cage. Experimental features were added and removed from one side of the cage and zebra finches were given the choice to forage on either the left or right. Individuals may vary in how comfortable they feel in their captive exhibit space (Tetley & O’Hara, 2012; Troxell-Smith et al., 2017a) and enrichment can affect individuals differently (Ings et al., 1997). Therefore, we investigated the extent to which any preferences were general in the whole population, or were individually based. We also considered the possibility that environmental features would ‘carry-over’ after the salient features were removed. Both of these potential characteristics need to be considered in an evaluation of the utility of the GUD paradigm as a tool to provide positive welfare outcomes.

We tested if three features (cover, number of perches and ground substrate) in the cages of zebra finches affected their foraging intensity. We expected them to forage more intensively with more perches as perches provide safety. We expected them to eat more on the covered part of the cage as they would feel protected from potential predators (in our case, humans). Finally, we expected them to forage more intensively on the paper ground as the surface they hop on around the foraging patch is then flat.

Material and Methods

Experiments were conducted from October to December 2016 at Macquarie University. In total, 64 domesticated (32 male and 32 female), and 48 wild derived (26 male and 22 female) zebra finches were used in the experiments. All work was conducted in cages with dimensions 61cm wide x37cm high x 28cm deep. Each cage had a solid metal back and sides but the front, top and bottom were each composed of wire mesh panels. Birds were housed with another companion bird of the same sex in a cage and had ad libitum access to commercial finch seeds, water and grit. Birds were paired for one month before trials and then remained together for the entire duration of experiments in their respective cage where they were tested. We weighed the birds before trials with a spring balance as GUDs can be affected by forager's size (Cozzoli et al., 2018).

We conducted three separate experiments, each with 2 treatments. Cages were separated in half, with a feature added to one side. Birds then had free access to both sides of the cage (Figure 1A). Experiment 1 involved covering half of the front of the cage with brown packaging paper so that the birds could not see outside and leaving the other half uncovered (Figure 1D). Experiment 2 involved adding two perches on one side, making four perches in one half and two on the other half (Figure 1B). Experiment 3 involved covering half of the cage floor with brown packaging paper on the inside of the wire panel and the other half was left as a wire mesh panel (Figure 1C).

On a trial day, birds had no access to food for 2 hours (8am to 10am), then they could forage in the food patches for 2 hours (10am to 12 am), during which they were left completely undisturbed in the holding room. Food patches consisted of aluminium trays (16cm long x 8cm large x 2cm deep) filled with 0.6g of white French millet seeds mixed through 100mL of construction sand. In order to conceal any food items that could be visible, 25mL of sand was then poured on the top. At the end of each trial, the experimental patches were removed and the birds were again given access to their ad libitum seed in an aluminium tray in the middle of the cage. The food patches were sieved and the remaining seeds were weighed to obtain GUDs (Brown, 1988). From prior personal observations, birds were exponentially less foraging during the two hours and then ate directly after introduction of ad libitum food.

All three of these experiments involved a new feature in the cage environment, and could been perceived as threatening, or comforting; however, possible neophobic effects could not be discounted initially because these features were new. To address the issue of neophobia we conducted experiments twice with different habituation time. We added the new elements (i) one day prior trials and (ii) one week prior trials. For the experiments with a habituation time of one day, we conducted each trial twice: once with the features on the left and once with the feature on the right of the cage. This allowed us to test both a possible side preference and if the preferences would be repeatable within a bird dyad. Finally, we measured GUDs the day after each trial after removing the features (empty cage). This allowed us to investigate potential carry-over effects: if they foraged more intensively on one side, would the side preference remain after the manipulated difference (feature) has been removed (Figure 2).

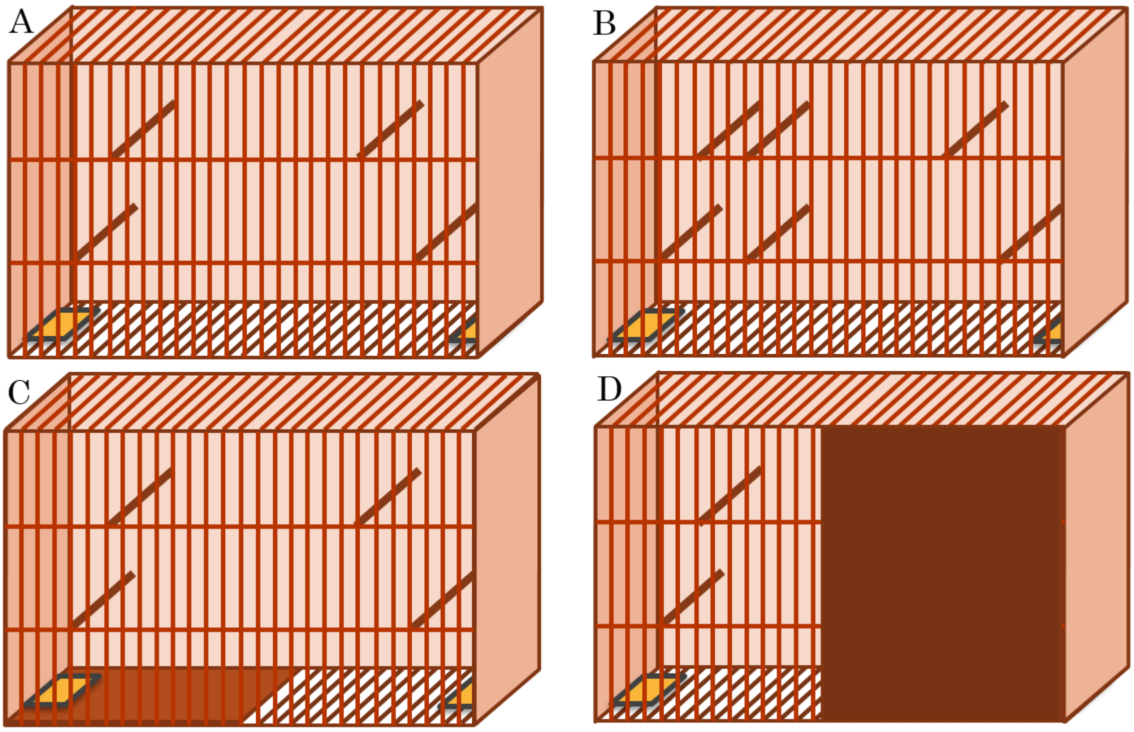

Figure 1. Schematic view of treatments. A Standard; B Four vs two perches; C Paper vs mesh floor; D Uncovered vs covered front.

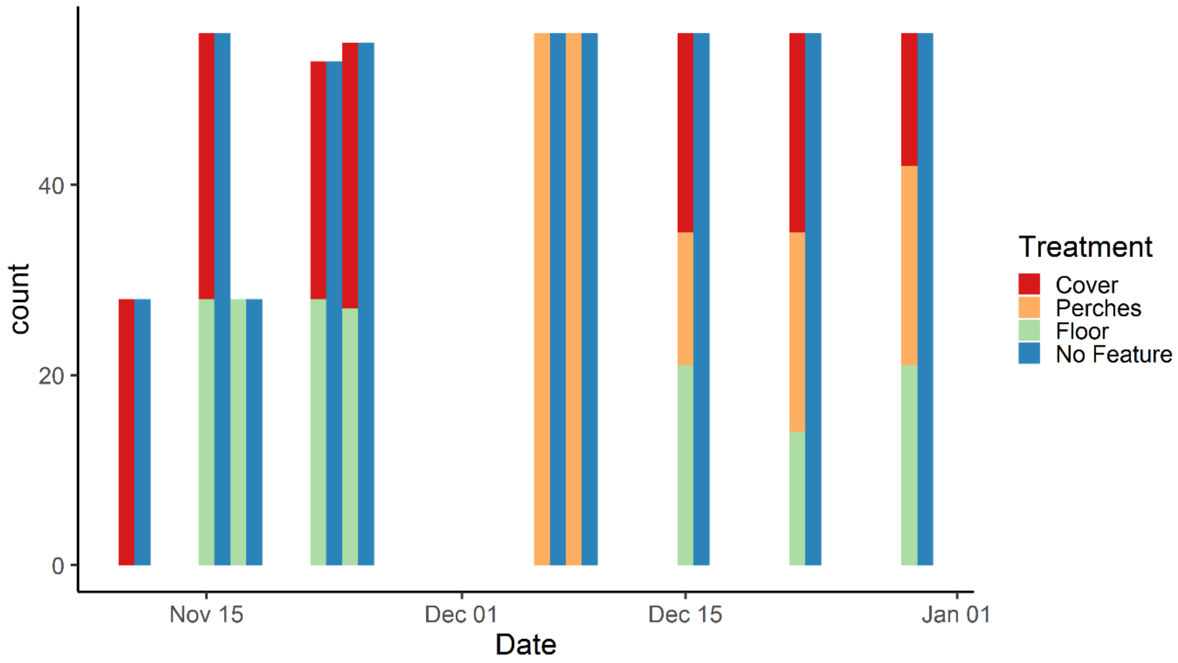

Figure 2. Timeline of experiments. Trials were conducted in 56 cages with added features one day and with the removed features the following day. From December 15, features were added one week before trials. The order of treatments was counterbalanced between pairs except for the four vs two perches treatment with one day of habituation. Inter-treatments intervals were either one or three days for the one day habituations.

Analyses

All analyses were carried out using R statistical software (R Core Team, 2018). In order to detect collinearity among predictor variables, variance inflation factors were calculated with the function 'vif' in the package 'usdm' (Naimi et al., 2014), we used a value of 2 as a conservative cut-off point.

We fitted general linear mixed-models (lme4 package, Bates et al., 2015) with treatment (Covered/UnCovered/Four/Two/Mesh/Paper) in interaction with habituation duration (1 or 5 days). Sex (male/female), strain (wild/domestic), mean weight of paired birds, position of the food (Left/right) and the position of the door (humans/perturbations obligatory came from the room door) were fitted as fixed effects. The date as well as the experimental unit (cage ID on a given day) nested in cage ID were included as random factors. GUD was the response variable. We first fitted the maximal model and then removed each term successively, starting with the highest level interactions. The significance of a term in the model was determined by assessing the change in deviance after removal of that term (LRT). Tukey test ('emmeans', Lenth, 2019) were performed to test the differences between treatments. In order to test repeatability within dyads we used the function ‘icc’ in the package ‘irr’ (Gamer et al., 2019).

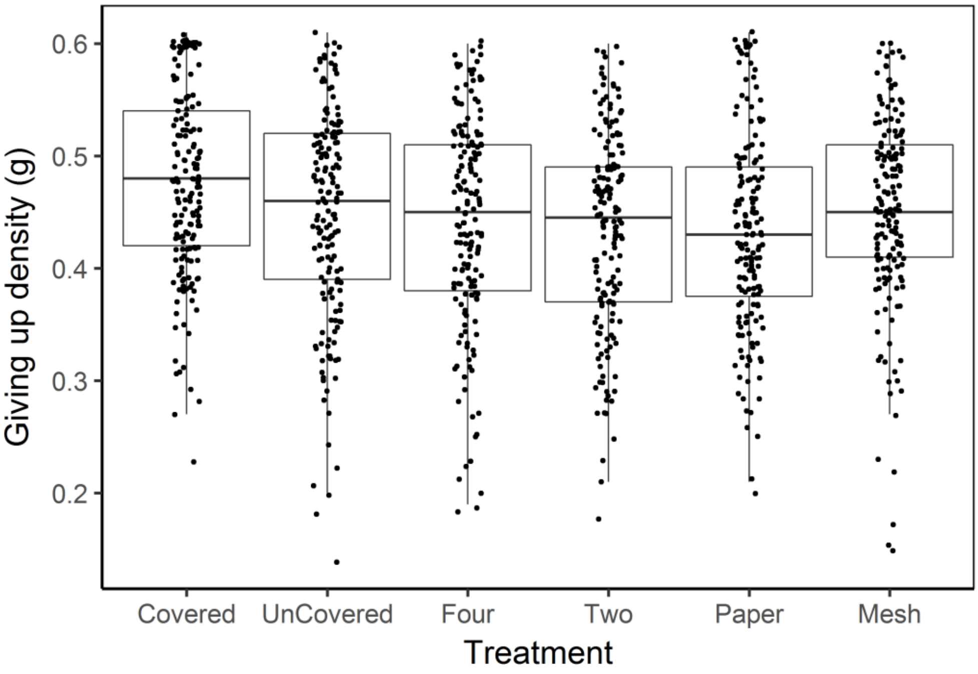

Figure 3. Giving up densities in the different treatments. Food patches behind Cover showed higher GUDs than patches on the Uncovered part of the cage. Treatments were conducted as choices in three separate experiments, each with 2 treatments. Experiment 1: Covered and uncovered (half of the cage was covered and the birds could not see outside). Experiment 2: Four and two (four perches on one half and two on the other half of the cage). Experiment 3: Paper and mesh (half of the cage floor was paper and the other half was a mesh).

Results

We found GUDs to be significantly affected by one of the treatments and by the side of the cage (Table 1, Figure 3). GUDs were 0.013 +- 0.005 lower on the right than on the left of cages (R: 0.443 ± 0.016; L 0.456 ± 0.016; t-ratio $_{df=935}$ = 2.83 p = 0.005). Zebra finches foraged more intensively on the right than on the left of the cage and this was not driven by the position of the cage relative to the direction of potential human threat, here the position of the door, as the door position was on the left for some cages and on the right for others (Table 1). Tukey tests demonstrated that patches behind cover showed higher GUDs than Uncovered patches (0.029 ± 0.008; t.ratio= 3.53; p = 0.006) and relative to papered floor patches (0.028 ± 0.008; t.ratio= 3.33; p = 0.01). The interaction between Treatments and Habituation time on GUD was not significant (Chi-sq = 10.14; Df = 5, p = 0.071, maximal model, Figure 4).

DifGUDs ($GUD_{\text{feature side}}$ -$GUD_{\text{other side}}$) were correlated with the DifGUDs the next day after removal of the features (Pearson correlation, cor=0.15, t_{994}=4.85, p<0.001, Figure 5).

The differences in foraging intensity between the two parts of the cage – reflecting the choice to forage more intensively in presence of one feature - were consistent only for the paper vs mesh floor. The differences in GUDs were consistent within dyads in the treatment with the paper vs mesh floor, both consistent between the trials with habituation of 1 day ($F_{54,54}$=2.15; p=0.003, Figure 6C) and also between the two trials with 1 day of habituation and the trial with habituation of 5 days ($F_{54,108}$=2.23; p<0.001). The differences of GUD within dyads facing the two other experiments were not consistent (Four vs Two perches, 2 first trials: $F_{55,55}$=0.65; p=0.94, Figure 6B; 3 trials: $F_{55,110}$=0.92; p=0.63, Covered vs Uncovered front, 2 first trials: $F_{52,52}$=1.2; p=0.26, Figure 6A; 3 trials: $F_{52,104}$=1.32; p=0.12).

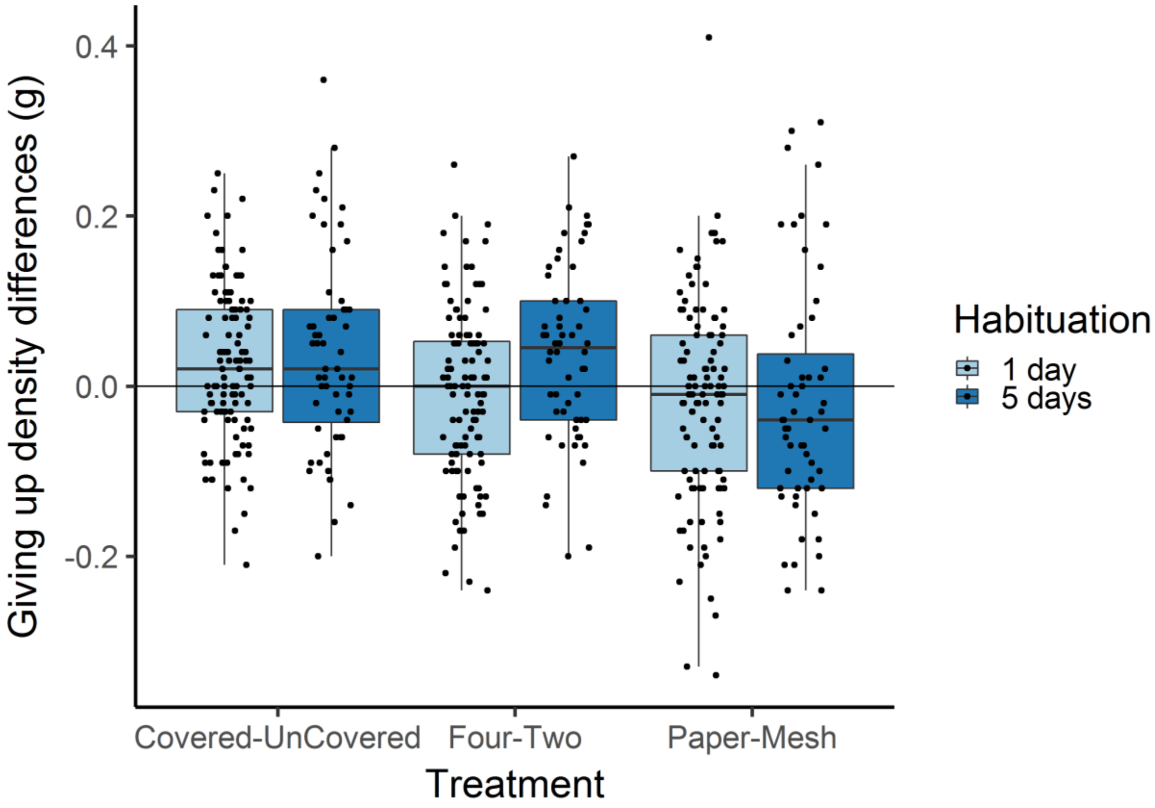

Figure 4. Giving up differences between paired experimental treatments dependent on the number of days birds were habituated with the treatment. Zebra finches ate more on the covered side than on the uncovered side as GUDs behind cover were higher than GUDs on the uncovered side, making the GUD difference positive. The interaction between treatment and habituation time was not significant. Below zero, GUD were lower on the covered side of the cage rather than the uncovered, lower on the side of the cage with four rather than two perches, and lower on the side with the paper rather than the mesh floor.

Parameter	**Df**	**χ^2**	**P value**
Treatment	5	19.93	**0.001**
Food position (L/R)	1	8.01	**0.005**

Table 1. Summary of the minimal adequate linear mixed model fit for testing the effect of treatment on Giving Up Densities. Maximal model: GUD ~ Treatment * Habituation + strain + sex + Weight + Food position + Door position + (1|Cage/ExpUnit) + (1|Date). Minimal adequate model: GUD ~ Treatment + Food position + (1|Cage/ExpUnit) + (1|Date).

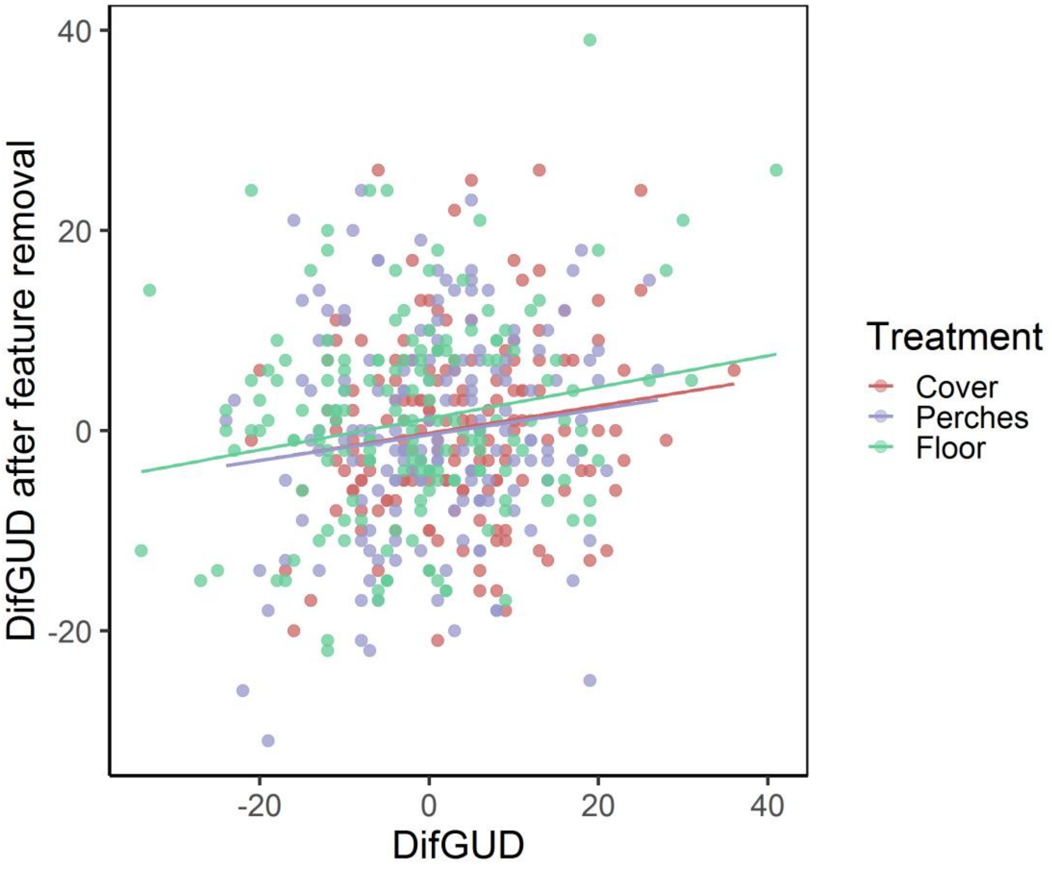

Figure 5. Correlation between the difference of GUD on the side of the treatment and the GUD on the side of a cage (DifGUD) and the same difference after the treatment feature was removed, for the different treatments. Zebra finches ate more on the side of the cage on which they ate more the previous day, even when the feature distinguishing the sides was removed: DifGUDs were correlated with the DifGUDs after removal of features.

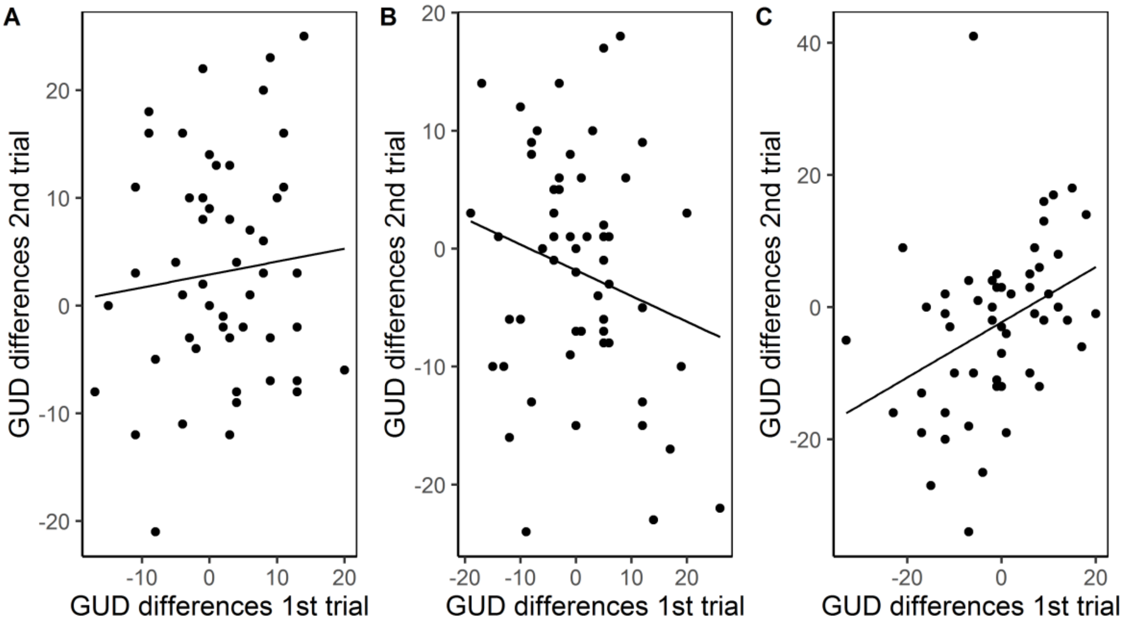

Figure 6. Correlation between GUD differences of the two trials after one day habituation with features. GUD differences (i.e. preference of a cage side related to a feature) were consistent only for the paper-mesh experiment. A Covered-UnCovered; B Four-Two; C Paper-Mesh.

Discussion

We explored if zebra finches foraging intensity were affected by three features: cover on the front cage, additional perches in the cage and paper on the bottom of cages. We found that zebra finches ate more in the uncovered part of their cage. However, additional perches as well as additional paper on the bottom of the cage did not significantly changed zebra finches foraging intensity in our experiments.

GUDs on the covered front half of the cage were higher than the GUDs on the uncovered front half of the cage. This mean that zebra finches forage more intensively in the uncovered part of the cage, corroborating Collins et al. (2008) findings. In laboratory conditions, providing cover does not help zebra finches to feel safer. This contradicts results from wild zebra finches, as they leave higher GUDs further away from vegetation cover (Chapter III) and higher GUDs when their visual fields were limited (Chapter IV). This apparent contradiction can perhaps be explained by the source of risk for the zebra finch. In the wild, zebra finches are at risk in the open as their main predators come from the sky (e.g. bird of prey). In laboratory conditions, humans are taking them by surprise because they are both providing the food and disturbing them by occasionally catching them, which is presumably stressful.

Our study suggests that zebra finches do eat more at the location in which they ate more previously. Foraging where they have foraged previously might be strategic for zebra finches. Foraging site fidelity was found to be more important than previously though in seabirds and were suggested to be common in colonial central-place foragers (Wakefield et al., 2015). Foraging site fidelity confer several advantages to be in familiar spaces, for instance efficient movement and effective escape from predators (reviewed by Piper, 2011).

Although zebra finches foraged less thoroughly behind a cover on average, the magnitude of difference in GUDs in the non-covered, and covered parts of the cage was not individually repeatable. We found personal foraging preferences only for the floor manipulation, as their preferences were correlated with their previous preference.

Zebra finches evolved in unpredictable environments, which makes it harder to disentangle between habituation and natural preferences. Indeed, it might be that instead of having fixed preferences for an environmental feature per se, zebra finches develop preferences for the environmental features that they are used to. It also might be that zebra finches are so flexible that they can accommodate to several different environments without greatly affecting how comfortable they feel to forage. The flexibility/adaptability of the zebra finch is of scientific importance as well, regarding how much we can generalize knowledge from zebra finches to other species.

This study was conducted in cages with same sex pairs. In light of other experiments in different pairing conditions and different group sizes (Chapter VI & VII), we must stress that the present results might be dependent on the group size and the sex of flock mates. The present results might also be dependent on the perceived risk the present zebra finch population was used to, for instance the rate of catching from researchers. Collins et al. (2008) showed that zebra finches' dislike to cover increased with time when repetitively catching them. The result might also be dependent on the location of the food before the period of the trials (here in the front). It would be interesting to repeat the floor experiment with a population used to paper floor, because the zebra finches used in this study were used to mesh floor.

Zebra finches foraged more intensively on the right side of the cages. As cages are set perpendicularly to the room entrance and back to back, we could dismiss the possibility that they forage more intensively close or further away from the entrance door. Moreover, the side distinction was not present during trials without features. This result is difficult to explain. There is some evidence of stronger lateralization (using one side of their body more than the other one) in more challenging contexts in a range of species (Rogers, 2010). As the food patches are beside walls, zebra finches might forage more on one side because they can have a greater visual field on the other side.

The GUD approach relates to perceived risk while foraging, this is an important tool for welfare questions. It is easy to implement in this context as animals are generally kept in single species. Standardizing the amount of food, the amount of sand, the amount of time, the size of the food patches, to generate meaningful GUDs for your study species can be very challenging (Bedoya-Perez et al., 2013). However, once this has been done it can be easily implemented. The GUD framework also allows large sample sizes without direct observation and with minimal investment in materials (sand, seeds, food trays, sieve and balance).

Beyond being a part of the GUD method, giving edible food in inedible substrate could be used to reduce food effectivity in a different way than by reducing the quantity or the quality as D'Eath et al. (2009) suggested in order to decrease health problems. Indeed, the principle of giving animals like finches edible food in inedible substrate is more natural and could improve welfare by acting as an equivalent of enrichment: looking for seeds in the sand is time consuming and natural for zebra finches.

In summary, based on GUDs, zebra finches perceived cover as risky. The number of perches and the ground substrate did not affect their foraging significantly. The GUD framework is an un-invasive and ecologically relevant tool to assess how risky animals perceive their environment. It can be implemented to investigate local environmental variability within the animal enclosure. In other words, the GUD framework helps in drawing a landscape of comfort for a captive animal (Troxell-Smith et al., 2017a,b).

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CHAPTER III

Giving up densities in wild zebra finches: spatial and temporal effects on foraging intensity

Abstract

Both the physical and the social environment can affect foraging decisions. For prey species, distance to vegetation (cover) is likely to affect the perceived risk of foraging in the open. Weather is also an important physical component of the trade off, and can influence the value of food and potentially also the risk of foraging. The local population density of conspecifics will also help to determine the level of risk to an individual. Here, in the zebra finch *Taeniopygia guttata*, we investigated how the intensity of foraging on food patches is determined by weather, distance to vegetation and the distance to the area where a large number of conspecifics aggregate throughout the day. We used the giving up density (GUD) approach to measure the density of food remaining in standardized patches after a fixed period of availability to foraging birds. Zebra finches are extensively studied in captivity, yet little work has been done in the wild where social and weather conditions are more variable and their behavior can be investigated in an ecological context. We presented paired food patches at a distance of one and five meters from bushes - representing cover - along three dry creek lines. The creeks were perpendicular to the area where zebra finches aggregate. Zebra finches foraged more intensively closer to bushes indicating that they feel safer close to vegetation. Zebra finches also foraged more intensively further away from the aggregation area indicating that feel safer to forage away from busy places. Moreover, bush safety increased with increasing distance from the aggregation area when wind was relatively strong indicating that weather, vegetation and social surrounding can interact to affect foraging decisions. Altogether this will help to interpret and direct new research on social prey species.

Keywords: Wild zebra finch; Australian desert; Weather conditions; Giving up density; Social foraging

Introduction

The study of zebra finches in laboratory conditions by dozens of research groups over the past four decades has provided many insights into behavioural ecology (Griffith & Buchanan 2010). However, whilst captivity provides the opportunity to standardise many physical and social parameters, it is also useful to understand the species in its appropriate ecological setting. Zebra finches are passerine birds native to Australia. They are distributed across the arid and semi-arid environments of Australia (Zann, 1996). This environment is highly unpredictable, with patchy and erratic rainfall, and has a strong impact on the food availability (Morton et al., 2011). Zebra finches are commonly described as a gregarious species and generally forage in groups (McCowan et al., 2015; Zann, 1996). They are granivorous and eat almost exclusively grass seeds (Morton and Davies, 1983). The zebra finch is a prey species, they are regularly taken by aerial predators such as butcher birds, and raptors (Zann 1996). The threat of predation is likely to be an important determinant of many aspects of foraging and social behaviour of this species (Dall & Griffith 2014), and yet has rarely been the focus of study (Butler et al., 2017). The risk of predation to an individual is likely to be affected by a number of physical and social parameters.

Weather conditions affect animal behaviour in general (Elkins, 2010). Foraging intensity has been found to be weather dependent, particularly wind and temperature. Zebra finches reduce their foraging activity when air temperatures are high (Funghi et al., 2019). Wind speed could increase the perceived risk in a given food patch in several ways, by: reducing hearing abilities, reducing the ability to distinguish vegetation movement from potential predator movement, impaired flying/escaping capacities. In captivity, zebra finch vigilance behaviour has been shown to be affected by ambient noise (Evans et al., 2018). Foraging rates have been found to be weather-dependent in wintering woodland birds where wind velocity affected foraging intake more at low temperatures (Grubb, 1978). Passerine flocks had a lower tendency to flush to cover at high wind speeds (Carr and Lima, 2010). Wind could indirectly affect predation risk as wind velocity reduces energy expenditure of hovering flight and thereby possibly change hunting techniques of predatory birds, for instance in Hawk (Schnell, 1967), it might thereby increase lethality. Clear predictions regarding the effects of wind were not made *a priori*. For instance, zebra finches could forage more intensively close to bushes in windy conditions as wind might affect their flight. However wind might lead zebra finches to forage more intensively further away from bushes as wind makes the vegetation noisier and in movement.

Perhaps the most obvious local feature of the physical environment that might affect predation risk is the distance to vegetation cover. Zebra finches behaviourally respond by flying away or retreating into vegetation when threatened (Butler et al., 2017). Distance to cover was found to affect perceived risk in many prey species that are depredated by predators attacking in the open (e.g. aerial predators). This is the case for several granivorous rodents and birds (Molokwu at al., 2010, reviewed in Brown and Kotler, 2004). However, crested larks (*Galerida cristata*) in the Negev desert were found to eat more when foraging in the open rather than in bush microhabitats (Brown et al., 1997).

In many prey species, aggregations of conspecifics are an important component of anti-predator behaviour. Aggregation typically decreases the per capita risk of being depredated (dilution effect, Delm, 1990), increased predator detection (many eye hypothesis, Pulliam, 1973), increased opportunities to hide behind conspecifics (Hamilton, 1971), and decreased predator lethality due to the confusion effect (Landeau and Terborgh, 1986). In the Australian semi-desert, larger groups of chestnut-crowned babbler *Pomatostomus ruficeps* encountered more predators but were attacked less than smaller flocks (Sorato et al., 2012).

A very useful method of investigating foraging behaviour at the habitat level is the giving up density (GUD) approach. The GUD is the density of food remaining after foragers stop foraging in a standardised food patch (Brown, 1988). GUD thereby reflects the fitness value of foraging by assaying the foraging returns at which the costs associated with remaining in that food patch exceed the benefits of continuing to forage. The costs include the energy needed to forage, the risk of being eaten by a predator and the opportunity costs of not foraging somewhere more profitable and/or doing something else. Foraging benefits are typically assayed as the net rate at which food is consumed (i.e. the harvest rate). Following pairing design from Brown (1988), we investigated not only variation in GUD among different microhabitats, but also the differences between GUD close to and further away from vegetation (ΔGUD) in any given microhabitat. ΔGUD assays the perceived risk associated with a location as the foraging value of being close to vegetation so that lower delta GUDs indicate higher local predation risk. Pairing patches to assay ΔGUD also controls for variation in local food availability that will influence the lost opportunity costs of foraging at standardised patches. Temperature and cloud cover have been found to affect GUDs in mice (Orrock and Danielson, 2009). We expect metabolic costs to increase at both low and high temperatures in zebra finches, and therefore the costs of moving among patches will likely be higher (decreasing the lost opportunity costs thereby decreasing GUDs). ΔGUD from Nigerian granivorous birds were found to be affected by temperature, and GUDs were lower close to cover possibly due to the lower thermoregulatory costs as they could more easily retreat from the heat (Molokwu et al., 2007). Thermoregulatory costs were also be found in eastern grey squirrels and American crows as GUDs were lower in sunny patches than in patches in the shadow only in winter conditions (Kilpatrick, 2003).

Zebra finches are a prey species and their predators are likely to use “area restricted search” (Tinbergen et al., 1967), whereby they intensify their search once they have located prey. High local densities of zebra finches are therefore likely to attract predators. Even outside breeding season, zebra finches are observed in large flocks gathering around water bodies; we therefore used the distance to the area surrounding the local water body (hereafter aggregation area) as a proxy for bird density. We expect that for these colonial birds, perceived risk would be lower (lower GUD, higher delta GUD) further from such areas of aggregation. GUD has been shown to decline with population density in red-back voles *Myodes gapper*i (Morris and Mukherjee, 2007). Morris (2014) found increasing local densities of meadow voles *Microtus pennsylvanicus* to increase differences in the foraging value of covered and open foraging trays.

Material and Methods

Study area

Data were collected in May 2017 at Gap Hills, Fowlers Gap Arid Zone Research Station, western New South Wales, Australia (31°05' S, 142°42' E). Gap Hills is an open shrub land (*Chenopod spp*.) with patches of *Acacia spp.* trees scattered around a permanent dam (200 X 150 m) and the associated dry creek system (Griffith et al., 2008). This population of zebra finches has been studied over more than a decade, particularly since its establishment in nest boxes (Griffith et al., 2008).

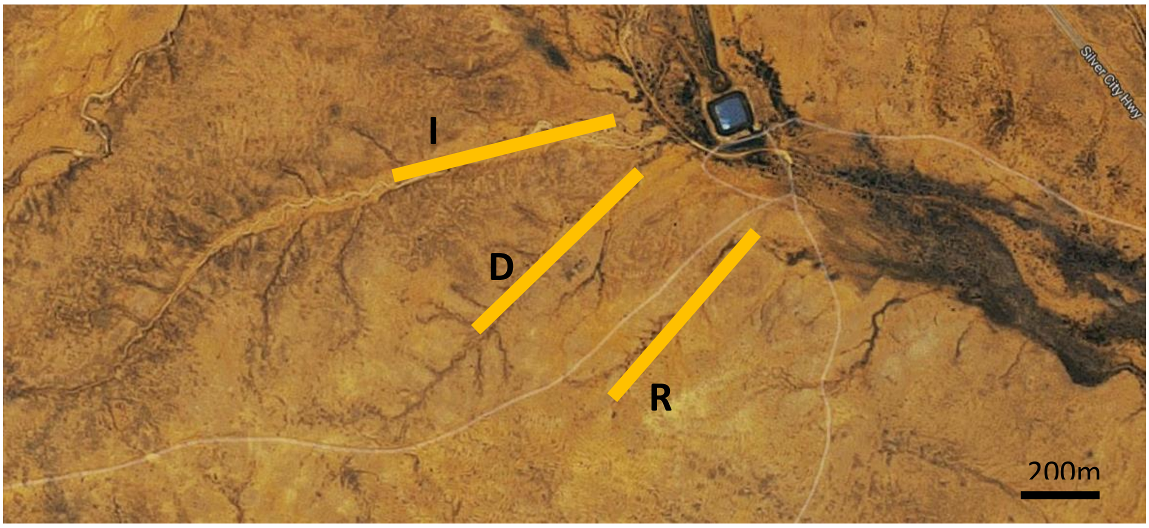

Figure 1. Field site (google maps). Dam (blue), shrubs (green), and transects along dry creeks (3 orange lines).

Giving up densities were measured along 600 meters in 3 different dry creeks (Figure 1). Aluminium trays (16x8x2) were used to hold standardised food patches. The tray mixture was 0.6g of white French millet seeds mixed with 100mL of local sand. Sand was then scattered on the top in order to conceal any visible seeds. Trays were set in pairs along linear transects at one meter and five meters from bushes (small chenopod). Trays at one meter were far enough from bushes to not be shaded during the afternoon. On a trial day, on each of the three creeks, six pairs of trays were set every 100 meters (36 locations in 18 stations). Each day, the starting point to set the first paired trays was at different distances from the aggregation area (roughly every 10 meters, randomly with at least 20 meters distance from day to day). Trials were conducted for 10 days, resulting in GUDs measures every 10m over the three 600m transect. Trials were then replicated at each location (over 10 more days). No trials were performed on one day (18th May) because of rain. The trays were set between 5 and 3.5 hours before sunset. Plastic lids were put on the trays to prevent birds starting feeding before trials. Lids were all taken off within 10 min of setting and GUDs were measured after being left open for 2 hours (3.5 before sunset until 1.5 before sunset). The only instance where data could not be collected was on one creek on one day resulting in a total of 708 food patches.

The weather data were accessed from the Bureau of meteorology for Fowlers Gap AWS (31°09' S, 141°70' E). We used temperature (°C) and wind speed (km/h) at 15:00pm (~3 hours before the sunset).

Analyses

All analyses were carried out in R statistical software (R Core Team, 2018). We fitted linear mixed-effect models (lme4 package, Bates et al., 2014). To investigate the link between GUD and the distance to aggregation area and the weather, we fitted a linear mixed model. The full model was with three 3-way interaction between distance to the aggregation area, temperature and wind speed and the position of the trays within pairs (Bush/away from bush) as fixed effects (Zebra finches could forage more intensively close to the aggregation area when it is hot and windy or when it is cold no matter the wind but eat more further away from the aggregation area when it is hot and not windy). The date, the replicate (each location was assayed twice) nested in the stations (pair of locations) and the stations nested in Creek ID were fitted as random effects. Backwards elimination was used to eliminate superfluous terms, with every reduced model becoming the new full model (LRT, Crawley, 2012). We used the ‘interactions’ package (Long, 2019) to create the interactions plots. We did not fit interaction with the position of the trays within pairs (1m/5m) because we did a second set of analyses with ΔGUD (GUD1m – GUD5m) following the same procedure. The full model was with three 3-way interaction between distance to the aggregation area, temperature and wind speed as fixed effects. The date, the replicate (each location was assayed twice) nested in the stations and the stations nested in Creek ID were fitted as random effects.

Results

During the 20 days of trials, temperature ranged from 17.3 to 26.5°C (mean 21.5) and wind speed ranged from 2 to 22 km/h (mean: 14.7). GUDs ranged from 0.04 to 0.6g (mean: 0.42) and ΔGUD (GUD_{1m} – GUD_{5m}) from -0.36 to 0.24g (mean: -0.038).

GUDs were significantly affected by the distance to the bush and by the distance to aggregation area. GUDs were 0.040 ± 0.005 (Estimate ± standard error) lower at one meter than at five meters away from the bushes (Figure 2, Table 1). GUDs decreased -0.017 ± 0.003 (Estimate ± standard error) with Distance to aggregation area (Figure 3, Table 1). The three-way interaction between Distance to aggregation area, Temperature and Wind speed was not significant (Chi-sq = 3.25, Df = 14, p-value = 0.07). None of the two-way interactions were significant either: Distance to aggregation area and Temperature (Chi-sq = 0.22, Df = 13, p-value = 0.64); Distance to aggregation area and Wind speed (Chi-sq = 0.25, Df = 13, p-value = 0.62); Temperature and Wind speed (Chi-sq = 0.48, Df = 13, p-value = 0.49). GUDs were not significantly affected either by temperature (Chi-sq = 2.25, Df = 10, p-value = 0.13), nor by wind speed (Chi-sq = 0.14, Df = 10, p-value = 0.70).

ΔGUDs decreased significantly with increasing distance from the aggregation area when wind was relatively strong, not on non-windy days (Table 2, Figure 5). ΔGUDs increased significantly with temperature when wind speed was low and decrease when wind speed was high (Table2, Figure 4). For ΔGUD, the three-way interaction between Distance to aggregation area, Temperature and Wind speed was not significant (Chi-sq = 0.03, Df = 12, p-value = 0.86). The two-way interaction between Distance to aggregation area and Temperature was not significant either (Chi-sq = 0.06, Df = 11, p-value = 0.81).

The random effect of date explained a large part of the variance for the GUD models (0.462 ± 0.068, variance ± standard deviation) but very little for the ΔGUD models (0.002 ± 0.004, variance ± standard deviation). GUDs decreased with date.

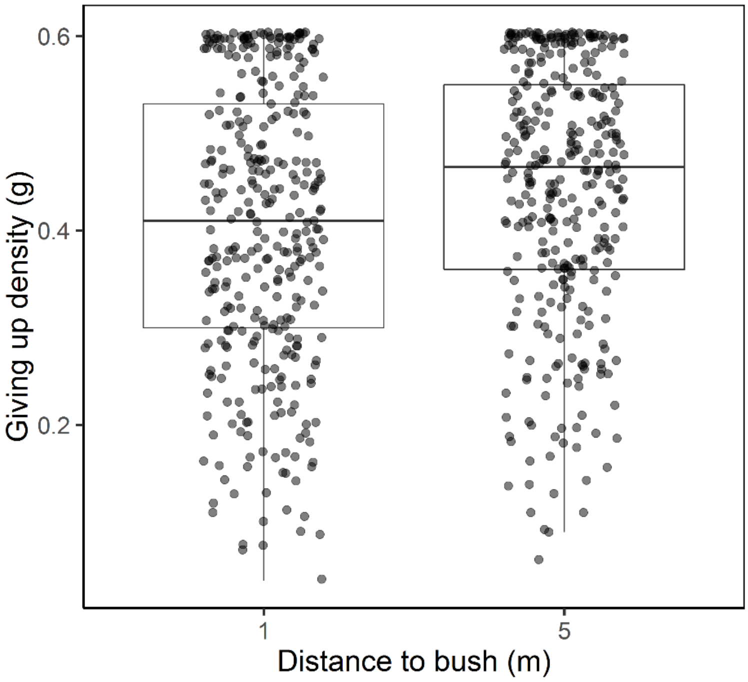

Figure 2. Giving up densities as a function of the distance to the bush, at 1m and 5m away. Zebra finches ate significantly more (GUD lower) closer to the bush, favouring cover proximity.

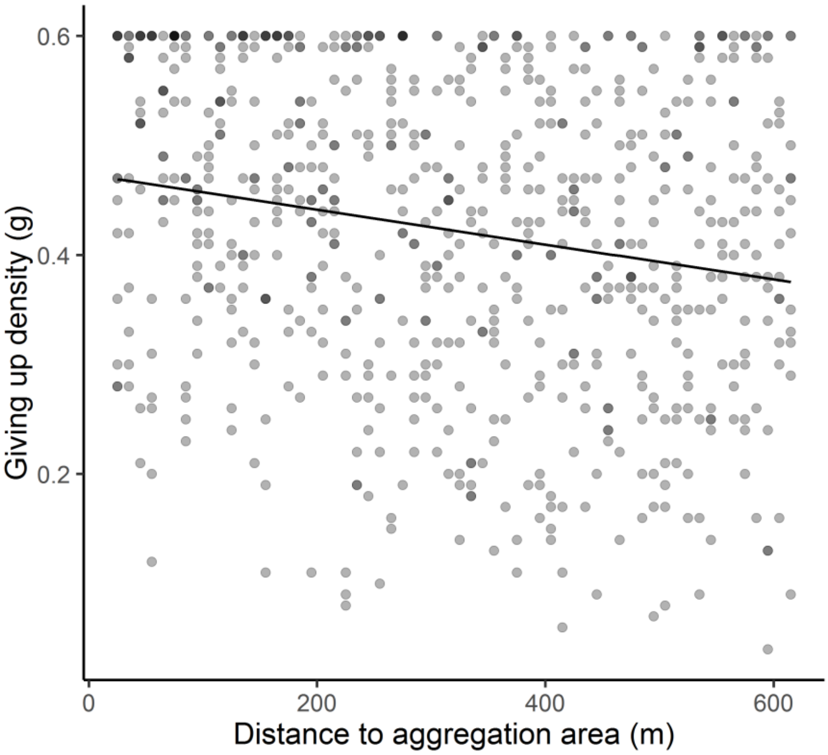

Figure 3. Giving up densities as a function of distance to aggregation area. Zebra finches ate more (lower GUD) further away from the aggregation area. Dark points represent several points overlapping.

Parameter	**Df**	**χ^2**	**P value**
Distance to aggregation area	**10**	**27.03**	**<0.001**
Distance to bush	**10**	**53.84**	**<0.001**

Table 1. Summary of minimal adequate model for the relationship between GUD, distance to aggregation area, distance to bush, temperature and wind speed. Zebra finches had significantly lower GUD (ate more) at a further distance from the aggregation area and closer to cover (bush). Additive model: GUD ~ Distance to aggregation area + Temperature + Wind speed + Distance to bush + (1|Station/Replicate) + (1|Date) + (1|Creek). Maximal model: GUD ~ Distance to aggregation area * Temperature * Wind speed + Distance to bush + (1|Station/Replicate) + (1|Date) + (1|Creek).

Parameter	**Df**	**χ^2**	**P value**
Distance to aggregation area	8	0.94	0.33
Temperature	8	1.05	0.30
Wind speed	8	0.02	0.89
Distance to aggregation area : Wind speed	**10**	**20.65**	**<0.001**
Temperature: Wind speed	**10**	**10.16**	**0.001**

Table 2. Summary of minimal adequate model for the relationship between ΔGUD, distance to aggregation area, temperature and wind speed. The two-way interaction between distance to aggregation area and wind speed significantly explained the variation in ΔGUD. The two-way interaction between temperature and wind speed significantly explained the variation in ΔGUD too. Minimal model: ΔGUD ~ Distance to aggregation area: Wind speed + Temperature: Wind speed + (1|Station) + (1|Date) + (1|Creek). Maximal model: ΔGUD ~ Distance to aggregation area * Temperature * Wind speed + (1|Station) + (1|Date) + (1|Creek).

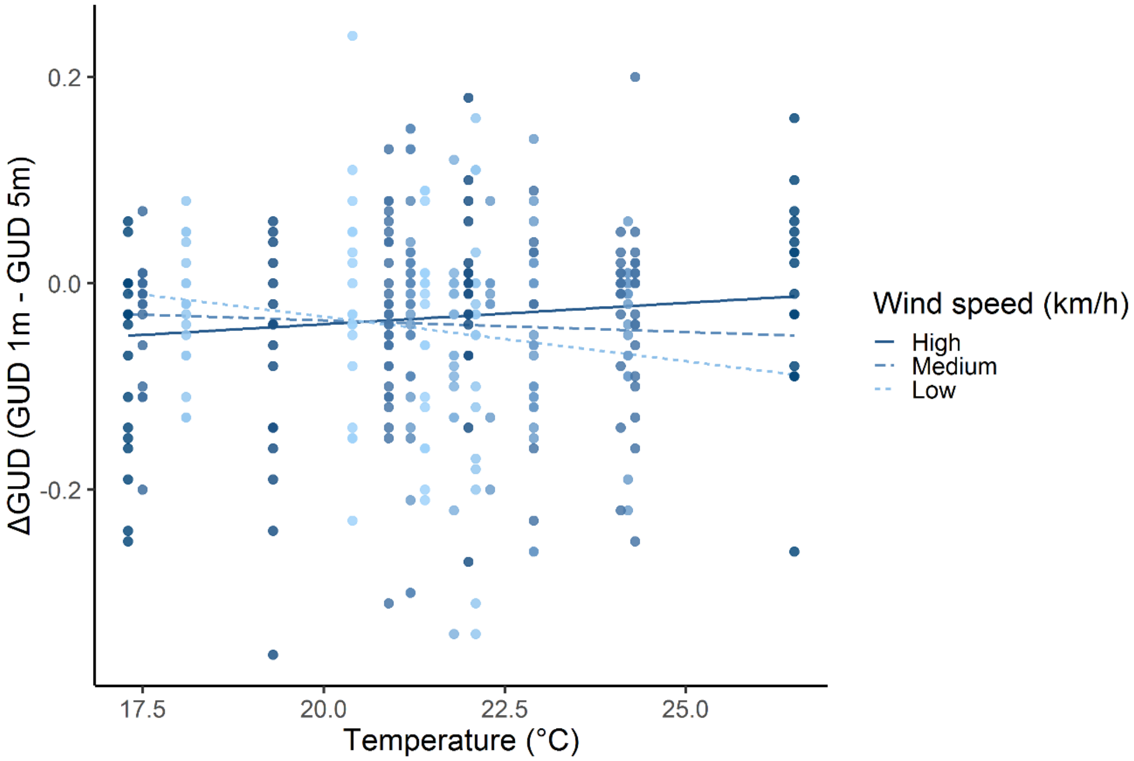

Figure 4. Interaction between temperature and wind on the differences of GUD near and away from vegetation. When the wind speed was low, zebra finches ate increasingly nearer to the bush (ΔGUD negative and decreasing) with increasing temperature. Negative ΔGUD reflect high perceived risk.

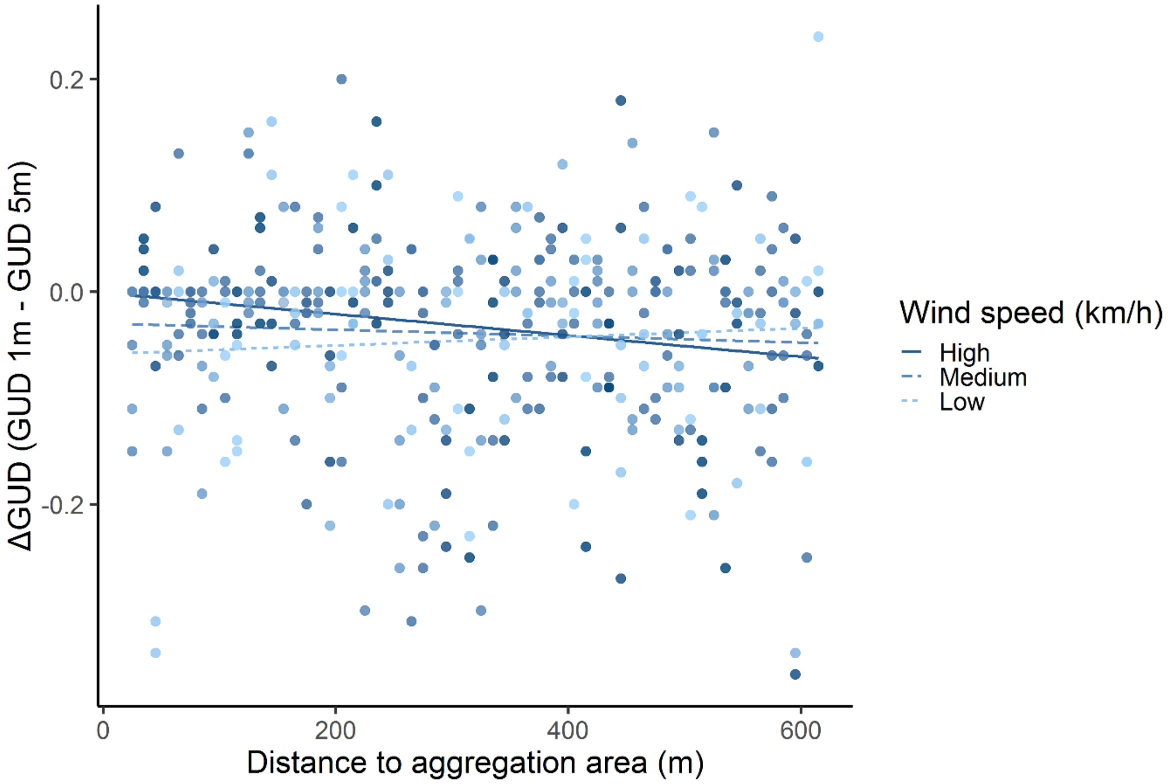

Figure 5. Interaction between distance to aggregation area and wind on the differences of GUD near and away from vegetation. When wind speed was high, zebra finches ate increasingly closer to the bush (ΔGUD negative and decreasing) with increasing distance to the aggregation area. Negative ΔGUD reflect high perceived risk.

Discussion

We were interested in exploring the effects of bush proximity, spatial social aggregation and weather conditions on zebra finches' foraging intensity. Zebra finches ate more close to vegetation as GUD at one meter from bushes were lower than GUD at five meters away from bushes. Food patches at one meter from the bushes were not in the shadow at the time of day the GUDs were measured. These results corroborate the most common result on microhabitat use, although essentially on rodents (Brown and Kotler, 2004) but also in granivorous birds in Nigeria (Molokwu et al., 2010). This also strengthens the idea that zebra finches perceived higher risk from predators in the open (e.g. aerial predators) than from potential ambush predators (e.g. snakes).

Differences of GUDs between one and five meters distance from bushes decreased with increasing distance from the aggregation area when wind was relatively strong, not on non-windy days. On days when the wind speed was low, zebra finches did not changed how much they value bush distance. On windy days, zebra finches foraged more intensively at close proximity to the bush when at long distance to the aggregation area and do not forage much more close to the bush than further away when close to the aggregation area. This suggests that zebra finches value bush proximity less when close to the aggregation area. When not considering weather conditions, differences of GUDs at one and five meters from bushes were not affected by the distance to aggregation area. Although Morris (2014) found a strong influence of population density on relative GUDs in meadow voles *Microtus pennsylvanicus*, Mohr et al. (2003) also found that population density affected GUDs but not relative GUDs in multimammate mice *Mastomys natalensis*.

ΔGUD increased with temperature if the wind was relatively strong. When the temperature is high and the wind speed high, zebra finches do not particularly value the proximity of the bushes (ΔGUD close to zero). However, when the wind is strong but the temperatures are low, they value bush proximity more. This suggests that the predation risk is dependent of the wind and of the temperature in different ways and/or that the zebra finches use different strategies to face risk in different weather conditions. Weather conditions might affect animals energy requirements and thereby influence their GUDs (Molokwu et al., 2011). Also, predators might be more active in warmer temperature and /or use different hunting strategies in different wind conditions, for example in hawks (Schnell, 1967). As zebra finches tend to gather on a bush or a tree before flying down to feed, the temperature might affect the cost of travel to the food patch further away, and the cost of escaping in case they need to. The weather outside the trials time might also have affected GUD, this is partially captured by the variable date. For instance if the weather was not best for foraging in the morning, birds would be hungrier in the afternoon. Or if the birds were attacked on a particular day, it might have affected zebra finches' foraging activities.

Zebra finches left lower GUDs away from the aggregation area. This suggests that zebra finches forage less extensively in busy areas, where the number of conspecifics is larger but also the number of other species, particularly predators is large. Druce et al. (2006) found hyraxes *Procavia capensis* to leave lower GUDs near greatest concentration of individuals. However, the hyraxes' density correlates the density of dens, which are a refuge for hyraxes. Our study system provides a natural disentanglement between distance to refuge and distance to conspecifics aggregation as both are perpendicular. However, the area surrounding the water body that we called aggregation area is characterised by strong vegetation in comparison to the surrounding and this affects food availability. Higher GUDs left near this area might therefore be due to high missed opportunity costs: If the food is more abundant, animals might value food patches less and have higher GUDs (Olsson and Molokwu, 2007) like in Nigerian granivorous birds (Molokwu et al., 2007).

Food patches were paired and this ensured surrounding conditions to be similar regarding local food availability, local environment, local predation pressure and attraction to food patches as birds could detect the shining of the aluminium trays. Zebra finches were often visiting both food patches through switching between them (personal observations). Our results shows that GUDs were strongly affected by date but that ΔGUD were much less affected. Pairing food patches seems to be a good way to take into account spatial and temporal variations that often affect GUDs.

Corroborating the most common result on microhabitat use by desert preys, zebra finches left lower GUDs near the bushes than further away, reflecting distance to bush as distance to safety. Zebra finches left lower GUDs at larger distances to the aggregation area, reflecting the proximity to the aggregation area to be risky. Weather condition affected the relative safety of the bush proximity. Zebra finches are the most widely studied bird in behavioural work in the lab, the insight from this work in natural condition will help to better portray their behaviour and will help guide future work in captivity. Moreover, our results will help better comprehend the behaviour of social prey species.

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CHAPTER IV

The effect of sight lines on the foraging behaviour of zebra finches in the wild

Abstract

Local features of the environment can affect foraging decisions, particularly in prey species that are vulnerable whilst foraging. Close proximity to vegetation can provide refuge, but also reduces the detectability of approaching predators. The effects of visual obstructions have typically been investigated by measuring vigilance behaviour. However, here we used a more integrative approach that provides insights into the perceived costs and benefits of foraging on patches by assaying ‘giving up densities’ (GUD) – the amount of food left in standardised artificial patches. Studying zebra finches in their natural environment, we manipulated sightlines experimentally both through the differential placement of physical barriers and by varying patch elevation. We also manipulated vulnerability using physical structures that increased effective fleeing times, without altering sight lines. Patch elevation did not significantly affect GUDs but GUDs were lower when sight lines were obstructed. This suggests that zebra finches perceive a visual obstruction as safer, possibly because they feel hidden from predators. However, this result was found only in a design where food patches were placed next to each other (combined design, where birds could forage in two nearby trays). This suggests that social specificities of the studied species might have important consequences on how animals perceive risk in their local environment.

Keywords: Predator detectability; Visual fields; Zebra finch; Foraging; Giving up density

Introduction

Local features of the environment can affect foraging decisions. Birds mainly use their vision to gather information on their surroundings. The proximity of refuges affects the potential predation risk, and therefore the value of foraging on a particular patch (e.g. Druce et al. 2006). In many prey species, refuges are created by vegetation cover; however, vegetation can also block sight lines and thereby reduce the detectability of approaching predators. Depending on predation type and antipredator strategies, animals consider vegetation as protective or obstructive. For instance, Allenby's gerbil *Gerbillus andersoni allenbyi* were found to harvest less food when sight lines were horizontally blocked in the presence of foxes and when sight lines were vertically blocked in the presence of owls (Embar et al., 2011).

Previous work has addressed the effects of visual obstruction on measures of vigilance, such as scanning rate, scanning bout length, proportion of time with head up (e.g. Beauchamp, 2015; Lima, 1987). Visual obstructions can both provide cover and prevent detection of approaching predators. For instance, scanning decreased with increasing visual obstruction when the food patch was far from cover in the house sparrow *Passer domesticus* (Lima, 1987). Downy woodpeckers (*Dryobates pubescens*) avoided thick trunks because they obstruct their vision (Lima 1992). Fine-scale spatial variation in vegetative cover was found to affect perceived risk in California ground squirrels *Otospermophilus beecheyi*, with vigilance found to decrease in high vegetative cover and on steep slopes, presumably because prey can more easily detect potential predators (Ortiz et al., 2019). The obstruction of vision by objects in the environment, might also prevent individuals from seeing conspecifics and gain valuable information from their behaviour (Olsson et al 2002). For instance, in Samango monkeys (*Cercopithecus mitus*), staying with the group seemed to be more important than habitat type (Emerson & Brown, 2013).

Whilst vigilance is often used as a proxy of perceived risk, Embar et al. (2011) used a broader framework: the giving up density (GUD) approach, to estimate the perceived riskiness of different patches. GUD offers different insights than vigilance measures, as well as practical advantages. Vigilance measures are time consuming because individuals must be monitored for extended period of time whereas GUDs can be acquired without direct observations of individual animals. GUDs reflect the underlying trade-offs experienced during a foraging event, whereas vigilance is one of the activities performed while foraging (Brown, 1999). Furthermore, vigilance measures, such as the head-down vs head-up dichotomy, is not always accurate and can overlook the effects of detection distance (Fernández-Juricic et al., 2004). The GUD refers to the density of food remaining in a patch when animals cease exploiting that patch (Brown, 1988). Whilst food remains in a patch, one of the major costs of continuing to forage as the density of food declines is the predation risk a prey species is exposed to in that patch. A low GUD indicates that animals were willing to pay such costs for longer and therefore value it more as a productive source of food. GUD were found to be lower in patches with better sight lines in goats *Capra hircus* (Shrader et al., 2008) and in arctic ground squirrels *Urocitellus parryii* (Flower et al., 2019), presumably due to increased predator detectability.

The zebra finch *Taeniopygia guttata* is a prey species extensively studied in captivity (Griffith and Buchanan, 2010). Being a prey species inherently affects the behaviour expressed in daily activities. However, very little is known about anti-predator strategies in wild zebra finches (Butler et al 2017), in captivity, the presence of cover affected zebra finches negatively: caged zebra finches were more disturbed when the experimenter entered the room if their cages were covered (Collins et al., 2008). Caged zebra finches were also found to have higher GUD's on the covered part of the cage in comparison to the uncovered part (Chapter II). Here we investigated if the GUD of wild zebra finches was also negatively affected by a reduction of their visual fields.

We manipulated sightlines through physical obstruction in one experiment and through changes in patch elevation in another. We also manipulated the birds' ability to fly directly out of the patches by using wire, without altering sightlines, in order to disentangle the effect of visual obstruction from that of ease of escape on the GUD.

The risks and benefits of foraging in patches of variable visibility and ease of escape may depend on the presence of conspecifics. Zebra finches are highly social and individuals are rarely found alone (McCowan et al., 2015; Zann, 1996).

An individual could take advantage of the benefits of the group (dilution, many eyes, selfish herd, and/or confusion effects; Hamilton, 1971; Landeau and Terborgh, 1986; Pulliam, 1973) while staying apart from it to avoid competition. To test this hypothesis, we gave zebra finches the choice between foraging simultaneously in two juxtaposed food patches that differed in visibility or ease of escape or in a single, isolated, food patch. We expected zebra finches to forage more intensively in combined food patches as a greater number of individuals could forage at the same time, which increase the perception of safety. We also expected treatments to have less effects on GUDs when food patches were combined as the safety induced by the sight of foraging neighbours would mitigate local environmental differences.

Material and Method

Data were collected in July 2017 at Gap Hills, Fowlers Gap Arid Zone Research Station, Western New South Wales, Australia (31°05' S, 142°42' E). Gap Hills is a patch of *Acacia spp*. trees and chenopod shrubs scattered around a permanent dam (200 X 150 m) and the associated dry creek system. The population of zebra finches breeding in nest boxes in this study site has been monitored for over 10 years (Griffith et al., 2008).

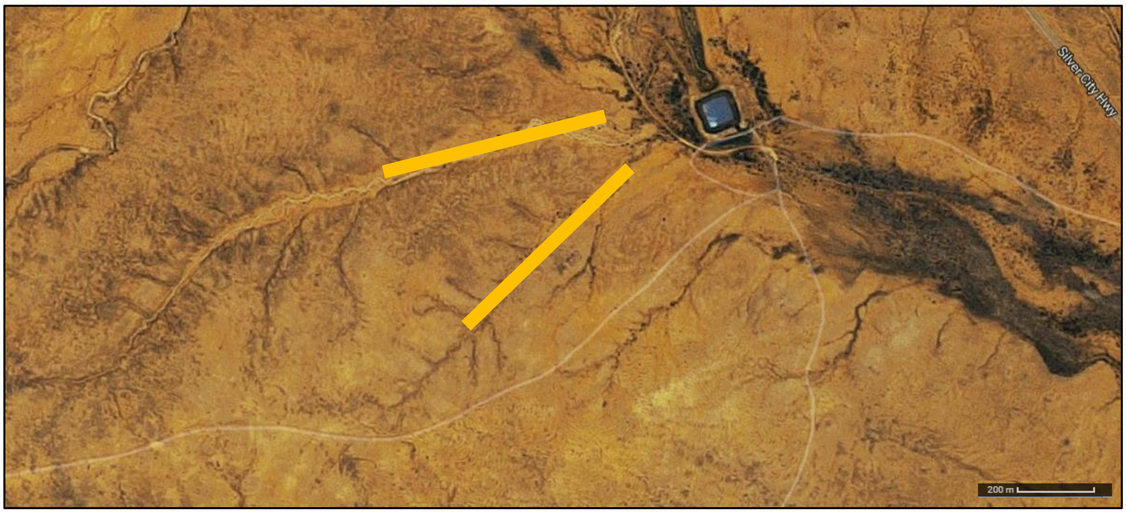

Figure 1. Map of the field site (google maps). Dam (in blue), shrubs (in green), and transects (2 orange lines).

Giving up densities were measured along 700 meter transects on two different dry rivulets, running into the main creek line. Aluminium trays (16x8x2cm) were used to contain ‘foraging patches’. Birds were trained to feed in such trays prior to trials and needed only a couple of days to do so, having previously been used to feeding in arrays of slightly different feeders in this area (e.g. Funghi et al., 2019). The tray mixture was 0.6g of white French millet seeds mixed with 100mL of local sand. A small amount of sand was then scattered on the top to conceal any visible seeds. Trays were placed in pairs at one meter distances from a bush (typically a small *Chenopod (spp.)*, with one meter between them, thereby forming a triangle. Combined trays were set approximatively every 100 meters along the creeks. The trays were set between 5 and 3:30 hours before sunset. Wooden lids were put on the trays to prevent birds starting to feed before trials. Lids were all taken off within 10 min. Zebra finches were able to forage for two hours (3:30 until 1:30 hours before sunset). Food patches were then sieved, and remaining seeds weighed to provide giving up densities. Trials were not conducted on very windy days due to difficulties in standardising the artificial patches i.e. wind would expose seed by blowing off the top layer of sand, and blowing seed off the trays. All three treatments were conducted each trial day but not 1/3 each: as windy days were recurrent and difficult to predict, we prioritized one treatment after another (first mount/depression, then cross/oval and then mesh/frame).

In order to manipulate sight lines when foraging in the trays without changing the visibility of food patches to foraging birds, we used four panels erected in two configurations (Figure 2). In order to obstruct sight lines, panels were placed in an oval around trays with each panel parallel to each side of the tray at a distance of 12.5cm (Figure 2 (A)). To control for the presence of the panels without interfering with sight lines, panels were placed in a cross, perpendicular to each side of the tray; with the centre of the four panels at a distance of 12.5cm from the edges of the food patch (Figure 2 (B)). The visual field for a bird in the tray (middle to corner) was 182° to 187° for the oval configuration and 360° to 276° for the cross. Panels were 15cm high and 15cm wide wire structures, the top 10cm of the panels were covered with baking paper to potentially obstruct zebra finch sight lines while they were foraging on patches, while 5cm gaps were left underneath to allow birds to pass. In this way, sightlines were manipulated with little influence on accessibility through the barriers.

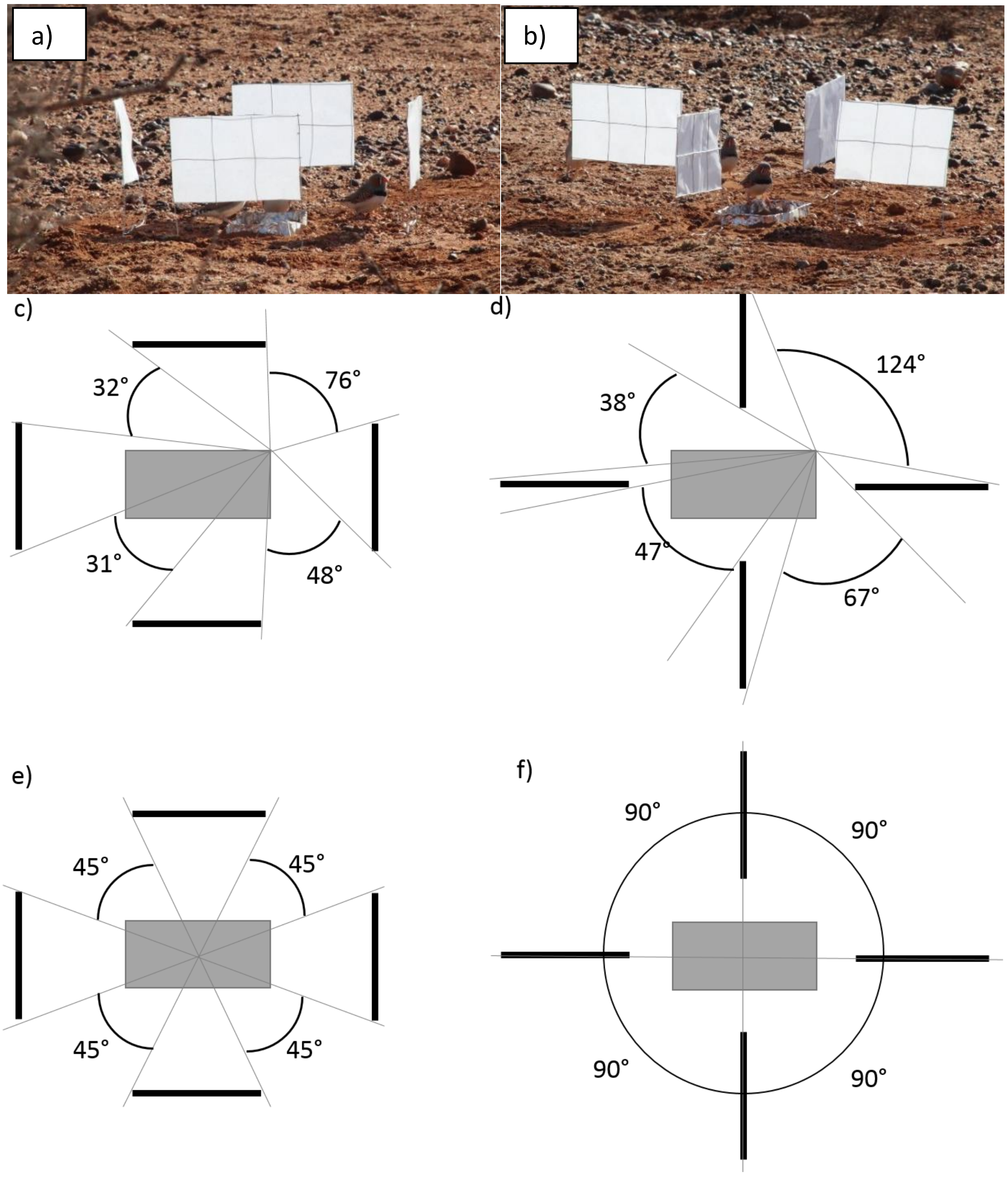

Figure 2. Panels placed in oval to obstruct sight lines (a,c,e) or in a cross to not obstruct sightlines when foraging (b,d,f). Photos: Chi Wei. The visual field for a bird in the tray was 182° in the middle (e) to 187° in the corner (c) for the oval and 360° in the middle (f) to 276° in the corner (d) for cross.

In a second experiment, we manipulated sight lines by elevating or lowering food patches relative to the surrounding environment. These were combined so that the soil removed at one food patch location was used to elevate the other food patch location (triangle setup with one meter between food patches and one meter away from a bush). This ensured that ground colour and texture was similar for the combined food patches. The depression and the mound were

30 x 40cm (~12cm on each of the four sides of the aluminium tray). The heights and depths were approximatively 12cm, which is a bit more than the height of a zebra finch standing up in a vigilant posture (Figure 3).

Figure 3. Schematic representation of the depression and mound manipulation. Food patches were placed in the centre of the depression and on the top of the mound. The centre of the food patches are horizontally at 1m distance from each other, both 1m from a bush.

In a third experiment we manipulated the accessibility to (and escaping from) food patches. We used 5cm mesh chicken wire to build rectangular enclosures (30x40x15cm). The birds could pass through, with a combination of walking/ hopping and/or perching on the mesh, but could not fly directly to/from the patch, as they could not pass through the mesh with open wings. In order not to impede ease of escape yet allow birds to use the structure to perch, we built enclosure frame by removing the internal wire mesh so that birds could fly through. Thus, we controlled for perch availability close to patches.

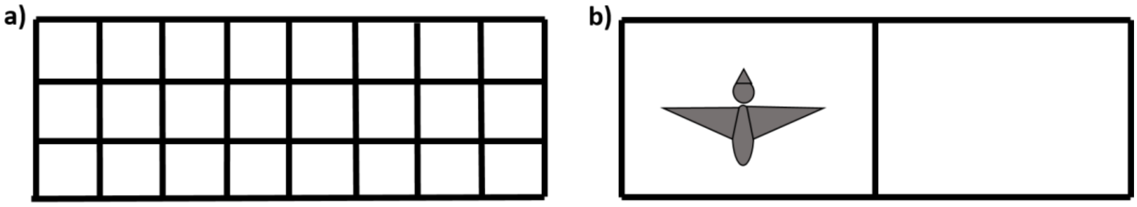

Figure 4. Schematic representation of the enclosures with a) chicken mesh and b) wire frame. Represented are only long sides of the enclosures (40cm). Zebra finches can fly through the frame but not the mesh enclosures. They can only hop through the mesh.

Following preliminary trials where we observed zebra finches hopping between the pair of food patches, we hypothesized that they would behave differently when they can see conspecifics foraging nearby (as it is the case in captivity, chapter V). To test for potential social foraging effects on treatments, for each of the three manipulations (Cross vs Oval, Mound vs Depression, Mesh vs Frame), trials were either combined or non- combined. The two food patches at each location were either set up on the same day (combined) or on different days (non-combined). When combined, birds could forage in one food patch or the other while staying in the vicinity of group members. In order to keep the total number of food patches in the environment constant, on days when non-combined food patches were set up, twice as many locations were used (see Table 1 for an example). Samples sizes are summarised in Table2.

		Day 1	Day 2	Day 3	Day 4
Location 1	Tray A	X		X	
	Tray B	X			X
Location 2	Tray A		X		X
	Tray B		X	X	

Table 1. Example of combined (day1 & 2) and non-combined (day3 & 4) trials. Tray A & B within a single location are the 2 treatments in each experiment. For instance, cross and oval treatments are both set in location 1 on day 1, oval is set on day 3 and cross is set on day 4. The total number of trays set per day remained constant.

Patch combination	Treatment	N, Total	N, Visited patches
Combined	Cross & Oval	23	23
Non-Combined	Cross	37	20
	Oval	38	22
Combined	Mound & Depression	40	31
Non-Combined	Mound	31	24
	Depression	33	18
Combined	Mesh & Frame	10	6
	Mesh	13	6

Non-Combined	Frame	13	7

Table 2. Sample sizes per treatments and food patch combinations.

Analyses

All statistical models were constructed in R (R Core Team, 2018) using the ‘lmer’ function in the package ‘lme4’ v. 1.1–19 (Bates et al., 2015). We plotted our graphs using ggplot2. To determine the influence of our manipulations on GUDs, we conducted three separate linear mixed-effects models. The response variable was the GUD. We included in a two-way interaction the food patch combination (combined /non-combined) and the treatment (Panel in cross/panels in oval or mount/depression or mesh/frame). Location (locations referred to individual bushes and were used for combined and non-combined trays and the same locations were also used for different treatments) nested in Date were random effects.

Results

We found a significant interaction between panel configuration and treatments (Table 3, Figure 5). Giving up densities were lower within ovals than within the cross configuration, but only when the two were non-combined (Figure 5).

Zebra finch patch exploitation was not significantly affected by the elevation of food patches (Table 4, Figure 6). Zebra finches were not significantly affected by the type of the enclosure surrounding the food patch in which they were foraging (Table 5, Figure 7). GUDs were not significantly lower when combined than non-combined (Tables 3, 4 & 5).

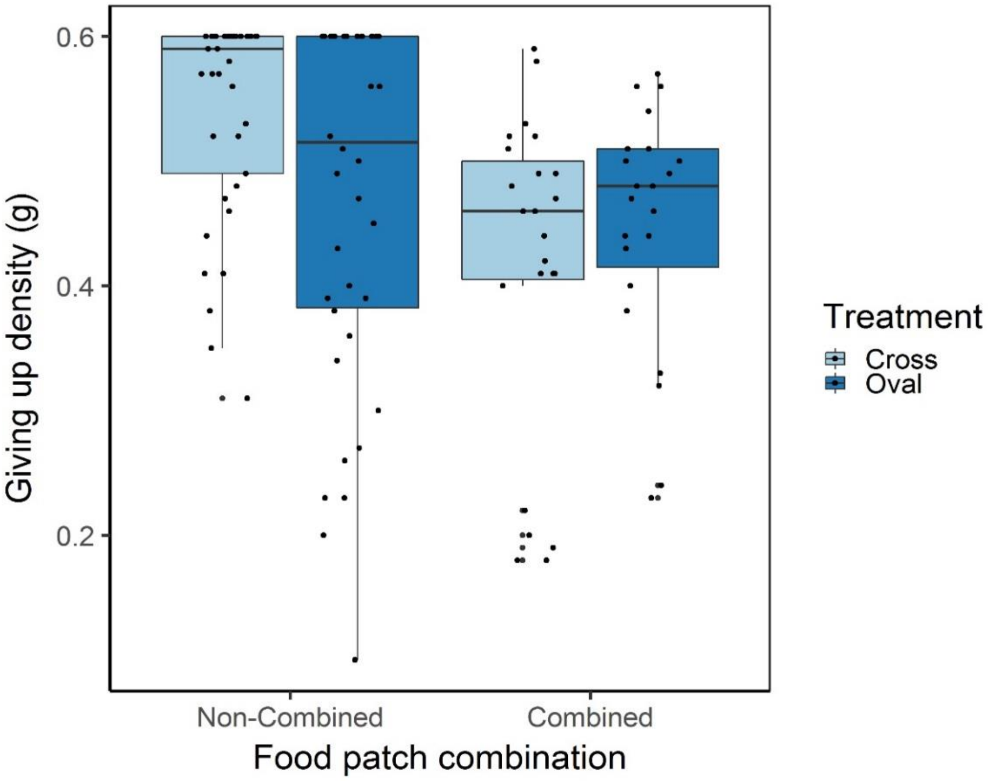

Figure 5. Giving up density as a function of manipulated sight lines and the food patch combination. Zebra finches ate more in the oval configuration when the two configurations were not simultaneously tested. Sight lines were manipulated through panels oriented to form a oval arround the food patch (limiting visual fields) or to form a cross around the food patch (not limiting visual fields). Experiments were done with the treatments set up at each location on the same day (combined) or on different days (non-combined). The middle quartile (lines in the box) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median.

arameter	Df	χ^2	P value
Panel configuration	6	0.61	0.43
Food patch combination	6	0.03	0.86
Panels disposition : Food patch combination	7	12.1	<0.001

Table 3. Summary of linear mixed model fit for testing the relation between GUD, panel disposition and experimental design. Panels were disposed either in oval (obstructing visibility) or in cross (not obstructing visibility). Experiments were done either with the cross and the oval on the same day (combined) or on different days (non-combined). Maximal model: GUD ~ Panels disposition * Food patch combination + (1|Date/Location).

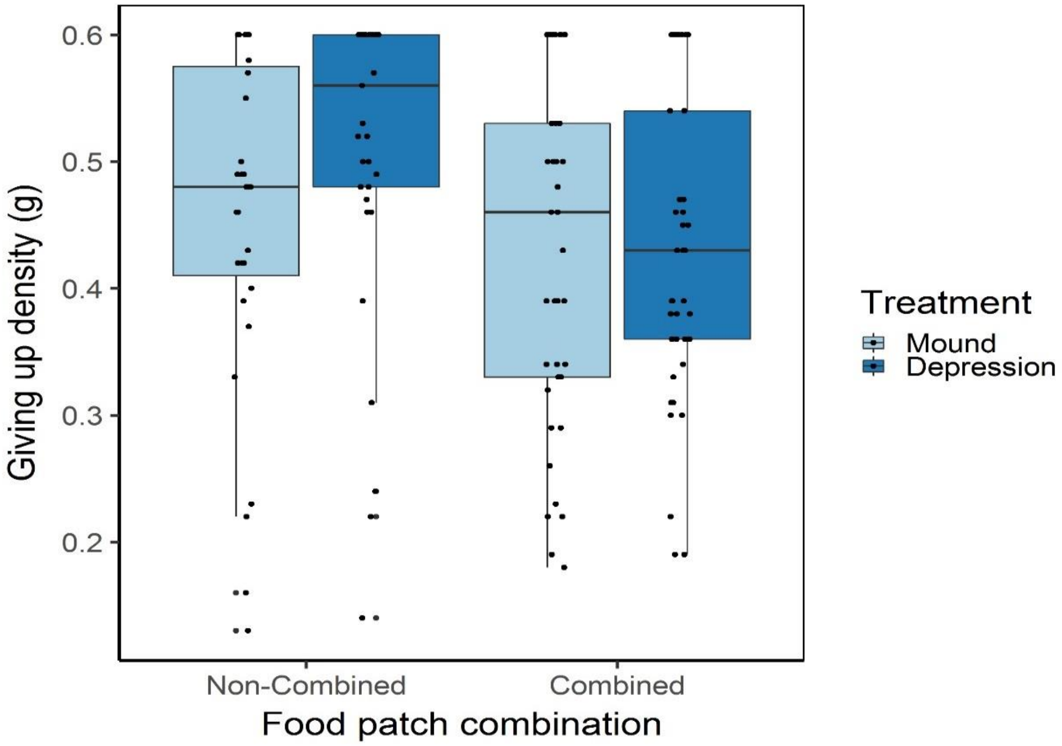

Figure 6. Giving up density as a function of food patch elevation and the food patch combination. Neither the food patch elevation; the food patch combination; or their interaction significantly affected GUDs. Sight lines were manipulated through elevation or depression of the food patch. Experiments were done with the treatments set up at each location on the same day combined) or on different days (non-combined). The middle quartile (lines in the box) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median.

Parameter	Df	χ^2	P value
Food patch elevation	6	0.33	0.56
Food patch combination	6	2.15	0.14
Food patch elevation : Food patch combination	7	2.97	0.09

Table 4. Summary of linear mixed model fit for testing the relation between GUD, food patch elevation and food patch combination. Food patches were located either on the top of a mount (ehancing sight line) or at the bottom of a depression (decreasing sight line). Experiments were done with the food patch on the mount and in the depression either on the same day (combined) or on different days (non-combined). Maximal model: GUD ~ Food patch elevation * Food patch combination + (1|Date/Location).

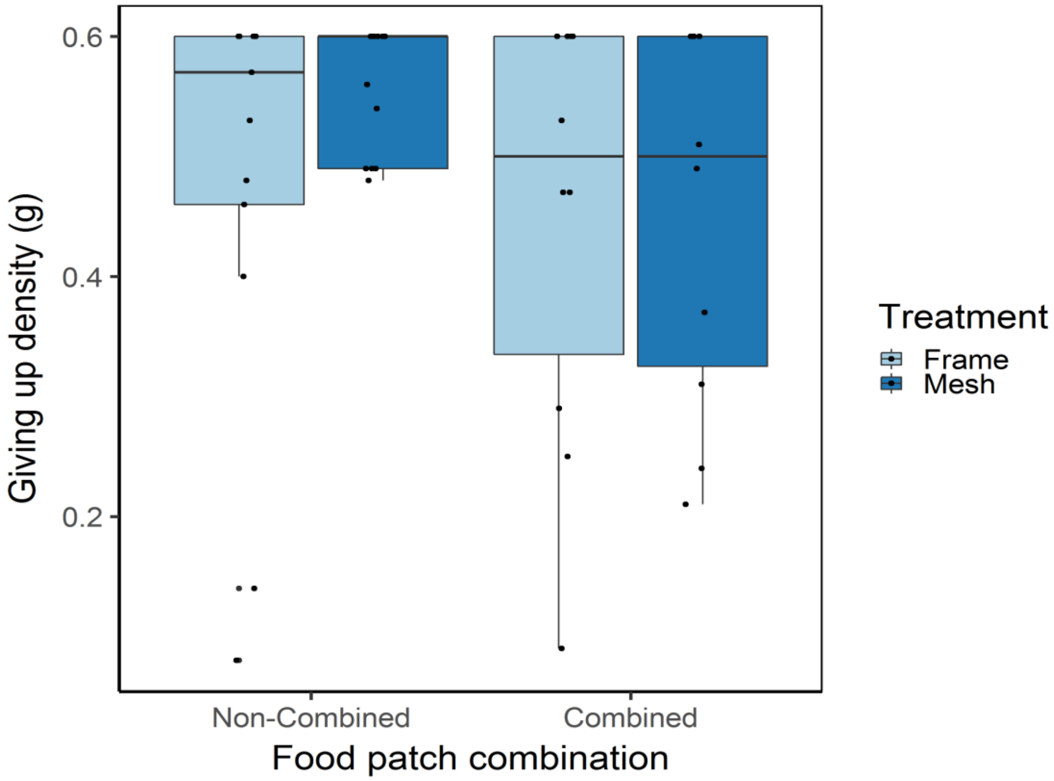

Figure 7. Giving up density as a function of the type of enclosure and the food patch combination. Neither the type of enclosure; the food patch combination; or their interaction significantly affected GUDs. Zebra finches could fly through the frame but not the mesh enclosures and had to hop through. Experiments were done with the treatments set up at each location on the same day (combined) or on different days (non-combined). The middle quartile (lines in the box) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median.

Parameter	**Df**	**χ^2**	**P value**
Enclosure type	6	0.79	0.37
Food patch combination	6	1.40	0.24
Enclosure type: Food patch combination	7	2.02	0.15

Table 5. Summary of linear mixed model fit for testing the relation between GUD, enclosure type and food patch combination. Enclosures were either constituted of 5cm mesh (perch reducing movement) or of the wire frame (perch with less movement reduction). Experiments were done either with the mesh and frame manipulations at each location on the same day (combined) or on different days (non-combined). Maximal model: GUD ~ Enclosure type * Food patch combination + (1|Date/Location).

Discussion

We were interested in exploring how sightlines affected zebra finches' foraging intensity (GUDs). Zebra finches left significantly lower densities of seeds in patches when surrounded by panels blocking their sightlines than when surrounded by panels configured not to do so. This was only true when these configurations were not presented simultaneously at any given location. This suggests that zebra finches view their world as being safer when their sight lines are decreased, perhaps because they value more being hidden than being able to see their potential predators approaching. Similar results on vigilance have been found in house sparrow *Passer domesticus* ; Lima, (1987) showed that birds scanned less in the presence of walls reducing their sight lines than when foraging in the open. Protective cover from a tree placed next to the food was found to reduce vigilance in yellow-eyed juncos *Junco phaeonotus* (Caraco et al., 1980). However, the reduced vigilance was flock size dependent: solitary birds and small flocks reduced vigilance in the presence of the cover, but the decrease was not significant for flocks of 6 or 7 birds (Caraco et al., 1980). Manipulated addition of cover decreased vigilance in snowshoe hares *Lepus americanus* but not their GUDs (Morris and Vijayan, 2018), suggesting that foraging tenacity and vigilance represent different aspects of perceived risk for some animals. Morris and Vijayan (2018) explain the lack of difference of GUDs in the open, with and without presence of cover, by hypothesising that the GUDs were dependent on the distance to refuge rather than on the local cover (which reduced predator detectability). In our study, the bush (refuge) was equidistant to both sightline configuration patches when they were presented together, thus potentially affecting how zebra finches responded behaviourally while foraging (e.g. by increasing vigilance while foraging for longer) without changing how intensively they exploited the patches thereby leaving similar GUDs. This could be explored with further data collection.

Combining the presentation of the trays in pairs seemed to be the best way to account for the majority of the environmentally derived variance in GUD that we were unable to control such as weather and day. One limitation to that approach is that it does also appear to manipulate the immediate social environment at the site of trials. Indeed, we could observe zebra finches going back and forth between paired trays. We know that GUD is affected by the social environment: GUDs decrease with population density in multimammate mice *Mastomys natalensis* (Mohr et al., 2003) and GUDs were affected by foraging group size as solo foragers left higher GUDs than groups of foragers in two rodent species (Carthey and Banks, 2015). We also know this is true for zebra finches as GUDs decrease non-linearly with group sizes from one to six (Chapter VI). The two food patches were only separated by one meter. We know from captive experiments on zebra finches that GUD were not significantly affected by 50cm of distance between conspecifics (Chapter V). Zebra finches could have moved to the less popular food patch of the combined food patches to decrease local competition while remaining close enough to conspecifics to gain group safety. This hypothesis implies that competition decreases at a higher rate with distance to conspecifics than the antipredator benefits of group membership (due to dilution, many eyes, selfish herd, and/or confusion effects; Hamilton, 1971; Landeau and Terborgh, 1986; Pulliam, 1973). For example, in the yellow-bellied marmot (*Marmota flaviventris*), the perception of risk decreased when conspecifics were around (Monclus et al 2015).

Zebra finches were not significantly affected by the elevation of the food patch in which they were foraging. The mound and the depression were higher/deeper than a fully upright zebra finch. Nevertheless, their impacts on the visual fields of the foraging zebra finches may not have been strong enough. The visual field manipulations via the panels were different, as the panels did not interfere with visual fields near the ground. This further suggests their potential predators of zebra finches are more coming from higher (e.g. birds of prey) than from the ground (e.g. snakes, lizards). Even though the interaction between food patch elevation and food patch combination was not significant, GUDs were highest in the depression when non-combined and lowest in the depression when they were combined. Perhaps this can be explained if more birds were present at the same time when patches were combined, and therefore individuals might have felt particularly at risk in the depression when lonelier, due to the decreased sight lines, relative to times when lots of conspecifics were around and could signal danger, whilst the depression may have provided some cover. The depression might thereby be interpreted as protective or obstructive depending on the social context.

Zebra finches were not apparently affected by ease of access to - and escape from - the artificial food patches. They seemed to take longer to approach the food patches when the wire mesh was present (personal observations) but this did not significantly influence giving up densities. They may be more reluctant to feed at first, but once they start foraging they could be foraging more intensively, resulting in equivalent GUDs. Our results do not show that ease of escape from patches does not influence zebra finch foraging behaviour, rather they suggest that the overall costs do not outweigh the benefits more in one situation than in the other. However, the sample size is noticeably smaller than for the 2 other experiments, and the trend goes in a similar direction to the results of the panel experiment: GUDs in combined trays were more similar than those in non-combined trays.

Our study also suggests that the GUD approach could be used to investigate the type of predation pressures that prey are experiencing in spatial contexts through manipulating different aspects of their sight lines. This was previously done on Allenby's gerbil *Gerbillus andersoni allenbyi*, with manipulation of vertical and horizontal sightlines, indicating different predators present different risks: owls from above or foxes along the ground (Embar et al., 2011). GUDs might reflect not only the overall perceived risk, but also how much it varies for different potential threats. Brown (1999) states that in a risky environment, if the vigilance is ineffective, foragers will be less vigilant and in some circumstances, the optimal level of vigilance can be zero. Birds might perceive high risk when in an enclosure, but vigilance might not affect their ability to escape (if they are more vigilant but do not have the time to escape if they see a predator, it would only be an indication of from which predator they have been preyed upon if that occurs). In that case, if they spend less time being vigilant and concentrate on foraging as quickly as they can, a similar GUD would be reached more rapidly. A similar explanation was suggested to explain why Nubian Ibex, *Capra nubiana*, decreased their use of apprehension at farther distance to their refuge (Hochman and Kotler, 2007). On the food patch level, GUD can inform us on the outcomes of decisions, not on how decisions were made.

As there is increasing evidence that GUDs are affected by aspects of sociality, our results suggest caution when designing experiments in which treatments are spatially paired and interpreting their results. As for vigilance, GUDs are affected by risk in a range of ways and risk perception is very important for the ecology of a species, including its population dynamics: type and intensity of predation pressure (Lima and Dill, 1990).

In summary, we found that in one of our experimental contexts, zebra finches perceived a decrease of sightlines as providing a refuge, and reducing the risks of predation whilst foraging. Our failure to find this effect more consistently may have been hindered by the social context that we did not control, thereby altering risk perception through an alternative pathway. Although our results show that zebra finches can perceive obstructions as being more protective than threatening, the variance in their response to visual obstruction and topographic manipulation also show that their physical local environment does not have a major role in how they perceive risk. Our results indicate that zebra finches probably value other cues, such as the immediate social environment, as more important than the physical disposition surrounding a food resource. This would be entirely consistent with the very social nature of the species when nesting and foraging. This should also be of concern when interpreting and designing captive experiments on the zebra finch as a model species and generally on social species.

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CHAPTER V

Zebra finches’ actions rather than presence or numbers affects neighbours’ food patches exploitation intensity

Abstract

The perceived risk of predation within a group often depends on the number of individuals present in the group. It can also depend on inter-individual distances as well as on information available from other individuals. Giving up density methods – that track the resource availability levels at which individuals give up foraging, due to the cost/ benefit ratio of continuing to forage - have extensively been used to investigate perceived risk. The zebra finch is a granivorous bird at great risk of predation, and that lives in varying group sizes. We investigated zebra finch foraging intensity in different sized groups, as a function of the proximity to, and behaviour of neighbouring flocks. Perceived risk was unaffected by the number and proximity of birds nearby. However, zebra finches foraged more intensively in patches near neighbouring birds that were foraging compared to non-foragers. Our results suggest that the behaviour of neighbouring birds may be more important than simply their presence. These results challenge previous studies suggesting that group size was the main factor influencing foraging activities in social species.

Keywords: Giving up density; Foraging; Group size; Neighbouring flocks; Zebra finch; Social foraging

Introduction

There are numerous well-established hypotheses about the effect of group size on foraging. Essentially, group foraging might influence (i) the probability of finding food patches, (ii) the possibility for division of labour to occur (producer-scrounger game), (iii) the safety in numbers and (iv) the possibility of interference between group members. Here, we will focus on the safety in numbers and on some information group members might share. The chance of an individual being depredated decreases as the number of birds in a group increases (dilution effect, Delm, 1990), while the awareness of the group also increases (many eye hypothesis, Pulliam, 1973), as well as the possibility of hiding behind conspecifics (Hamilton, 1971). Also, in a large group, predators can have difficulties perceiving and attacking any particular individual due to the confusion effect (Landeau and Terborgh, 1986). Countering these advantages to individuals of foraging in large groups however, a large group size is potentially more visible and/or noisier, and this may increase detection by predators (Vine, 1973). For instance attack frequency and hunting success from raptors increased with flock size of Chaffinches (*Fringilla coelebs*, Lindström, 1989). Moreover, as the group size increases inter-individual competition and aggression may increase (Beauchamp, 2003) and per capita feeding rates may decrease. As well as determining the influence of overall group size, spatial position within group has been studied in several species with important fitness consequences including for predation risk and feeding competition. Experimental manipulations in brown-headed cowbirds showed that food pecking rates decreased with the distance between neighbours in a foraging group (Fernández-Juricic and Beauchamp, 2007). Vigilance has also been found to decrease with the proximity of the nearest neighbour (Pöysä, 1994). As a result of these well-established positive and negative consequences, grouping behaviour can be complex and context dependent (see Elgar, 1989), and provides important insight into social behaviour in animals.

More than the mere presence of conspecifics, actions – and thereby the information they convey – can affect decisions (ecology of information, Schmidt et al., 2010). Observing conspecifics in order to acquire information is recognized to be important for animals (Dall et al., 2005; Danchin et al., 2004). The foraging rate of conspecifics can influence individuals' decisions to leave a food resource

(Valone, 1989). In geese, a higher proportion of foraging geese models over alert geese models present on a patch was found to attract more geese, irrespective of overall numbers (Drent and Swierstra, 1977). Nine-spined sticklebacks use the feeding rate of conspecifics rather than group size to estimate the quality of a food patch (Coolen et al., 2005).

An important experimental paradigm that has contributed to this area is the giving up density (GUD) approach, which monitors the density of food remaining in standardised food patches when foragers stop exploiting them (Brown, 1988). The rationale is that staying in the patch will incur greater foraging costs than the fitness value of feeding there further, given the density of food left (the marginal harvest rate), and the risk that an individual is exposed to, in that particular context (Brown, 1988). GUD methods have been used in a wide variety of taxa since the paradigm was introduced (Brown, 1988; Bedoya-Perez et al., 2013), and most work has focused on rodents and asocial foragers, (but see Carthey and Banks 2015). Whilst, to our knowledge, no studies have used the GUD approach to explore social behaviour in birds, it has the potential to provide important insight into one of the most widely studied birds – the zebra finch, *Taeniopygia guttata*. They have been very widely studied in the laboratory, where social groups are often artificially constituted in aviaries and cages (Griffith et al., 2017). Zebra finches are endemic to the open habitat of the arid and semi-arid environment within Australia (Zann, 1996). Whilst they are very gregarious, there is some variation in their social behaviour in the wild. Zebra finches will often nest in loose colonies, but many pairs will also choose to nest in very isolated locations hundreds of metres away from the nearest conspecific (Mariette and Griffith, 2012). Furthermore, whilst they do certainly forage in flocks many hundreds strong (Zann, 1996), they are more frequently found in much smaller groups of, on average, 1.71 to 5.25 birds (McCowan et al., 2015).

Group sizes have potentially complex effects on perceived predation risk. Here we investigated if zebra finches forage more intensively in the proximity of large or small groups of conspecifics when not in competition for the resource. In order to disentangle the positive (e.g. dilution, shared vigilance) and the negative (competition) impacts of group foraging, we allow focal birds to forage in the proximity of neighbouring flocks behind a grid. We manipulated the neighbouring flock sizes as well as the focal flock size. By giving focal flocks the choice between two neighbouring flocks of different sizes, we investigated if focal flocks would exploit food patches more thoroughly in the vicinity of a larger neighbouring flock. We also investigated if the neighbouring flock size affected small and larger focal flocks differently. We expected that small focal flocks would perceive less risk near larger neighbouring flocks and that the birds in larger focal flocks would show fewer (if any) differences in perceived risk while foraging near small and large neighbouring flocks. Besides the potential effects of neighbouring flock size, we investigated how the distance to neighbouring flocks influenced the foraging intensity of the focal flocks. Here, we explored if the distance to the neighbouring flocks' food patch influenced the risk perception. We predicted that focal flocks would eat more intensively (lower GUD) next to the neighbouring flocks who had food closer to them. The rationale being that the observation of neighbours being safe at a distance gives less information about one own's safety. Besides the size of the neighbouring flock and the location of their food, we also examined whether the foraging behaviour in neighbouring flocks influences foraging behaviour in the focal flocks. We did this by considering whether zebra finches perceived their environment as being riskier when neighbouring flocks' food was available or not. We predicted that focal flocks would leave lower GUD (feel safer) in the foraging food patch next to the neighbouring flock having food. The rationale being that even though the presence of conspecifics provides information, this information is of lower quality than that provided by the presence of foraging neighbours (i.e. conspecifics that have made the decision that it is safe enough for them to forage).

Material and Methods

Experiments were conducted in January and February 2017 in the animal facilities at Macquarie University, under standardized and baseline climate-controlled conditions (25°C, approx. 50% humidity, 12L : 12D cycle with first light at 7:30am). In our experimental setup, we studied the impact of neighbouring flock sizes, proximity and behaviour on perceived risk without direct competition for the resource. Neighbouring flocks were seen and heard but focal and neighbouring birds could not interact with each other. As zebra finches are social animals, they were not tested alone. Focal birds were the same in the three following experiments and the three experiments were conducted one after the other in the following order.

1) Focal vs neighbouring flock sizes

Group sizes were manipulated for both focal birds and neighbouring flocks. Two or six birds were placed in the focal central cage (61 x 37 x 28 cm). Neighbouring birds were placed in the cages on either side (left and right) of the focal cage, six birds randomly allocated to one side and two birds to the other (Figure 1A, 1B). The neighbouring flocks were all wild-derived zebra finches, and of the same sex as the focal birds. Focal and neighbouring flock cages were divided by mesh allowing visual and acoustic contact. To prevent the transfer of seeds between cages, rectangles of Plexiglas (10x30cm) were fixed on the lower part of the grids. Groups of focal birds were always matched for origin (wild derived or domesticated) and sex: thus we used 9 pairs of domesticated males, 11 pairs of domesticated females, 8 pairs of wild derived males and 10 pairs of wild derived females (N=8 per day, 12 days). They were kept in 4 birds per cage between trials. Focal birds were moved into the experimental cages one-day prior to each trial. They were always paired with the same companion, whether by themselves, with one other pair or with two other pairs.

Trials consisted of 2 hours without any food (8am to 10am) followed by 2 hours with seed and sand mixture which was placed in aluminium trays (16x8x2cm) from 10am to 12am. These food patches were placed on the left and right sides of the focal cage (2 food patch per cage). The mix of seed and sand consisted of 0.6g white French millet seeds mixed with 100mL of construction sand, with a further 25mL of sand on top to conceal any seeds that could be visible. At the end of each trial, the remaining seed and sand mixture was sieved and GUDs for each patch measured as the mass of the remaining seed (Brown, 1988) . Between trials, birds were provided with commercial finch seed ad libitum in a tray in the middle of the cage (with no sand in it).

2) Proximity of neighbouring flocks

The proximity of neighbouring flocks was manipulated by manipulating the positioning of the neighbouring flocks' food trays. In the focal cage, two sand/seeds trays were placed, one on the left and one on the right. In the neighbouring cages, ad libitum food was placed right next to the separation grid in one neighbouring flock cage and at the other end of the other neighbouring cage (53 cm from the focal birds' cage separation). Thus, focal birds had the choice to forage in the dish next to a neighbouring flock's food or 53cm away from the neighbouring flock's food (Figure 1C). Both focal and neighbouring birds were kept in groups of four birds per cage (n=16).

3) Behaviour of neighbouring flocks: foragers vs non-foragers

The behaviour of birds in neighbouring flocks was manipulated by placing ad libitum food in one of the neighbouring cages but not in the other. In the focal cage, two GUD trays were placed, one on the left and one on the right. Focal birds therefore had the option to forage next to neighbouring flocks that had food or neighbouring flocks that did not have food (Figure 1D). For this treatment, we kept the number of birds (focal and neighbouring flocks) constant at 4 birds per cage (n=16).

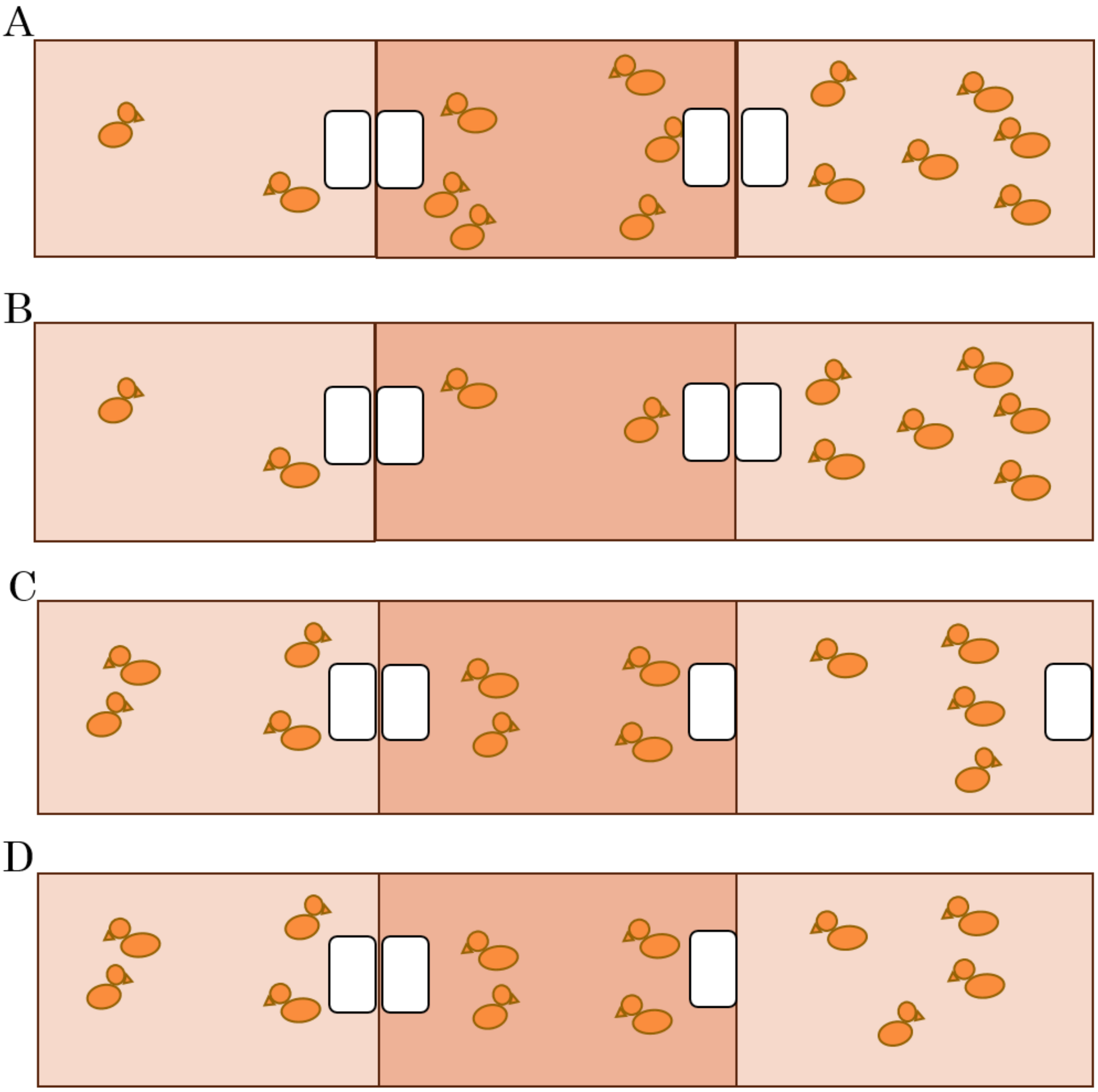

Figure 1. Schematic representation of experimental designs testing the effects of: neighbouring flock sizes for (A) six and (B) two focal birds; (C) neighbour proximity and (D) neighbour food availability. For (C) and (D), four focal birds in the middle were surrounded by four neighbours left and right. In this example the food patch was close on the left and far on the right (C) and present on the left but not on the right (D).

Analyses

All statistical models were coded in R (R Core Team, 2018) using the ‘lmer’ function in the package ‘lme4’ v. 1.1–19 (Bates et al., 2015). Prior to any analyses, variance inflation factors were calculated with the function ‘vif’ in the package ‘usdm’ (Naimi et al., 2014) in order to detect collinearity, we used a value of 2 as a conservative cut-off point.

In order to determine the link between GUD and neighbouring flock size, we fitted linear mixed effect models to the data. The response variable was GUD, the neighbouring flock size (2/6) in interaction with the focal group size (2/6), origin (domestic/wild) and sex (M/F) were fixed effects and the date and the experiment unit (same cage same day) were random effects. We also included individual mass in the models as a fixed effect. However, group mass and the origin (wild or domesticated), were explaining too much of the same variance in the data (VIF > 2). Therefore, we fitted another set of models replacing origin by group mass.

To determine the link between GUD and the proximity of neighbouring flocks, we again fitted linear mixed effect models. The response variable was GUD, the distance of neighbouring food trays (Close/Further), the origin, and the sex were fixed effects and the Cage ID was random effect.

To determine if GUD were explained by the availability of food in neighbouring cages, we again fitted linear mixed effect models. The response variable was GUD, the presence of neighbouring flocks' food (Food/No food), the origin and the sex were fixed effects and the Cage ID was a random effect.

Results

1) Focal vs neighbouring flock sizes

Regardless of whether the focal group was 2 or 6 birds, GUD was not influenced by neighbouring flock size (Interaction between focal group size and neighbouring flock size: Chi-sq = 0.61; Df = 11; p = 0.44). Wild birds left lower GUD than domestic birds and females left significantly lower GUD than males (Table 1, Figure 3 A and B respectively). GUD was significantly lower when 6 birds were in the focal cage than when 2 birds were in that cage (Figure 2, Table 1).

	Parameter	Df	χ^2	P value
Model 1	Focal group size (2/6)	7	78.45	<0.001
	Sex (M/F)	7	20.15	<0.001
	Origin (wild/domestic)	7	20.15	<0.001
Model 2	Focal group size (2/6)	7	77.11	<0.001
	Sex (M/F)	7	8.41	<0.001
	Group mass	7	15.62	<0.001

Table 1. Summary of the minimal adequate linear mixed effect model fit for testing the influence of neighbouring flock size on giving up density. Because the variance inflation factors were above 2 for Origin and Group mass, 2 sets of models were conducted. Maximal model 1: GUD ~ neighbouring flocks size * focal group size + origin + sex + (1|ExpUnit) + (1|Date). Minimal adequate model 1: GUD ~ focal group size + sex + origin + (1|ExpUnit) + (1|Date). Maximal model 2: GUD ~ neighbouring flocks size * focal group size + Group mass + (1|ExpUnit) + (1|Date). Minimal adequate model 2: GUD ~ focal group size + sex + Group mass + (1|ExpUnit) + (1|Date).

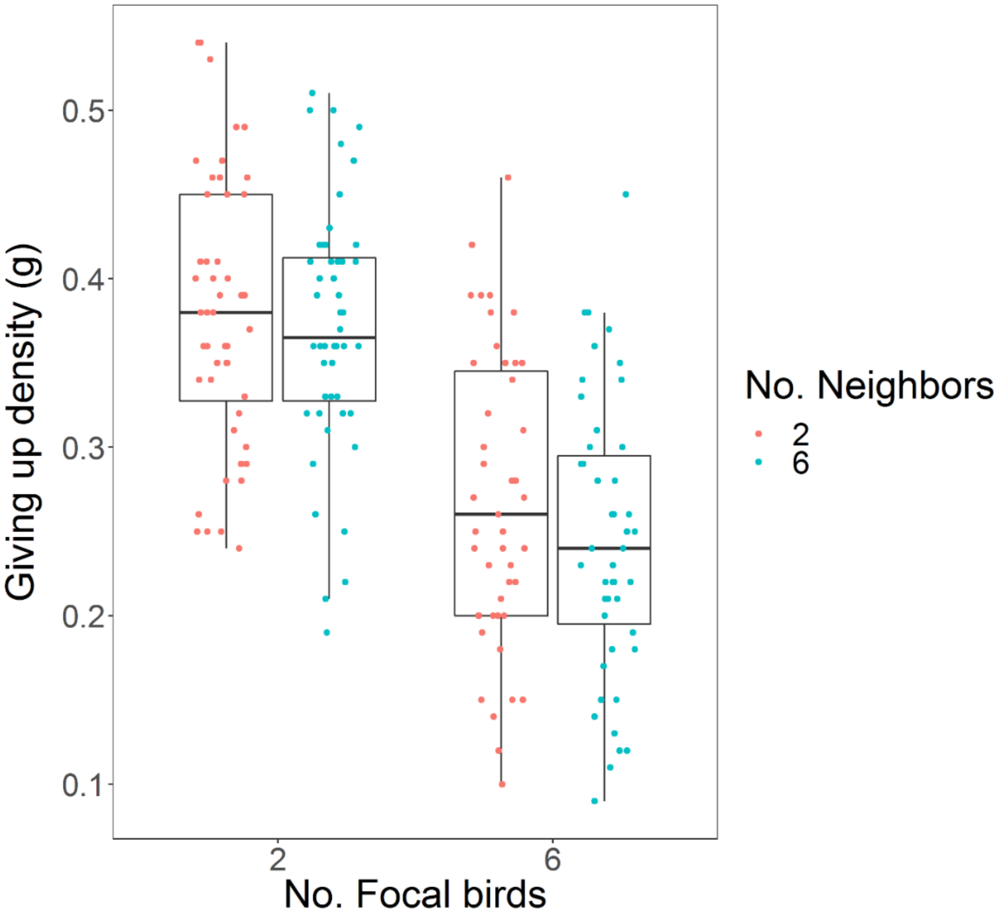

Figure 2. Giving up densities left by focal birds near 2 or 6 neighbours. No significant effects of neighbouring flock size were detected for either 2 or 6 birds.

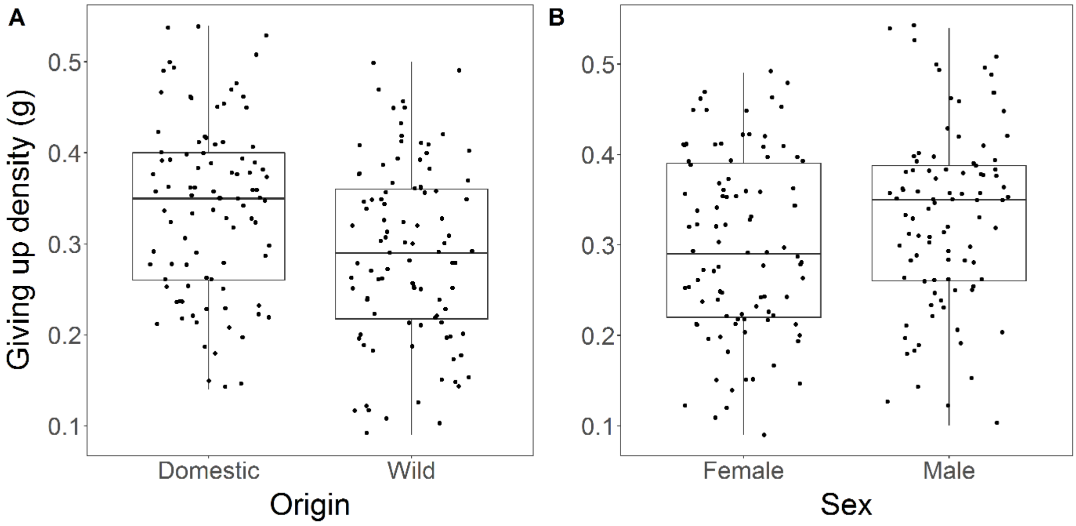

Figure 3. Giving up densities as a function of: (A) origin and (B) sex. GUD was significantly lower for wild birds than for domestic birds. GUD was significantly lower for females than males.

2/3) Proximity and behaviour of neighbouring flocks

The proximity of the neighbouring foragers to the focal foragers did not significantly affect GUDs (Table 2, Figure 4A). However, GUDs were lower near the neighbouring flocks that had access to food than the neighbouring flocks without food (Table 3, Figure 4B). There were no effects of origin nor sex in either of the experiments (Table 2 & 3).

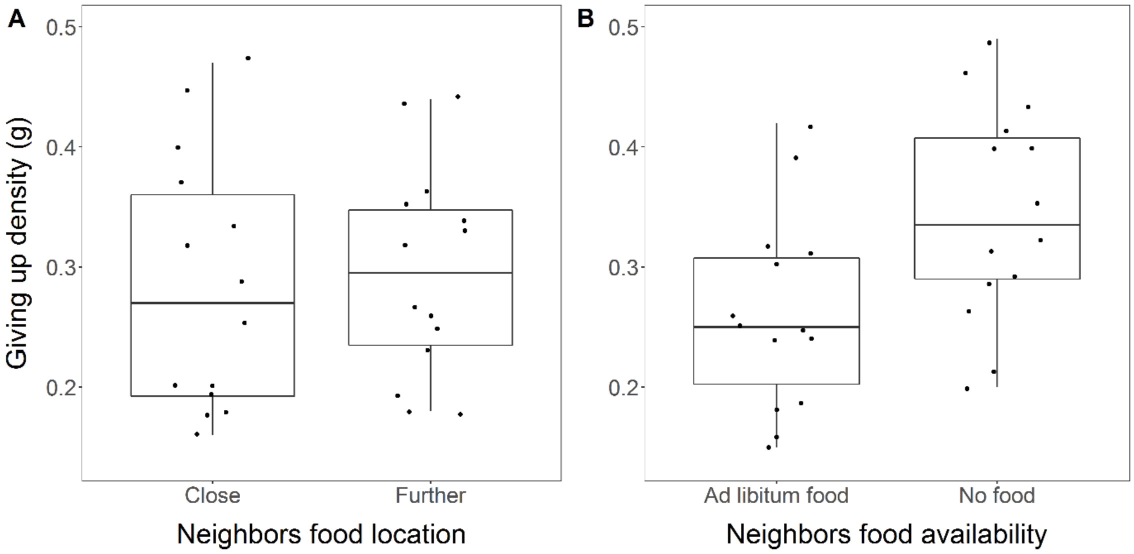

Figure 4. GUDs as a function of: (A) neighbour food location and (B) neighbour food availability. The proximity (3 or 53cm) of the foragers did not significantly affect GUDs. GUDs were lower near the neighbouring flocks that had food in comparison to the neighbouring flocks who did not had food.

Parameter	**Df**	**χ^2**	**P value**
Neighbour food location	6	0.15	0.70
Sex (M/F)	6	1.23	0.27
Origin (wild/domestic)	6	0.34	0.56

Table 2. Summary of the maximal linear mixed effect model fit testing the influence of neighbouring flock food location on giving up density. Maximal model: GUD ~ Neighbour food location + origin + sex + (1|ExpUnit).

Parameter	**Df**	χ^2	**P value**
Neighbour food availability	6	13.01	<0.001
Sex (M/F)	6	0.22	0.64
Origin (wild/domestic)	6	0.47	0.49

Table 3. Summary of the maximal linear mixed effect model fit testing the influence of neighbouring flock food availability on giving up density. Maximal model: GUD ~ Neighbour food availability + origin + sex + (1|ExpUnit).

Discussion

Zebra finches gave up foraging at lower seed densities near neighbouring flocks with food than those without. This suggests that they were more comfortable eating next to neighbouring flocks that were also eating. However, the proximity of neighbouring flocks' food did not affect their foraging intensity, over the distance over which we varied this parameter. Their giving up densities were also not dependent on the neighbouring flock size, with focal birds not feeding more or less intensively near a group of either two or six conspecifics. These results corroborate forager recruitment experiments on Barnacle geese by Drent and Swierstra (1977). In that study, the authors used geese models to manipulate the numbers of individuals as well as the proportion of foraging vs non-foraging individuals. Their results showed that when a high proportion of non-foraging models were present in a foraging area, fewer birds were attracted to that site, irrespective of the total number of individuals. Similar results were found in nine-spined sticklebacks as they use the feeding rate rather than the number of conspecifics to determine food patch quality (Coolen et al., 2005).

The presence of neighbouring birds' food and therefore the presence of foraging neighbouring flocks enhanced foraging by the focal birds. However, the distance of the neighbouring flocks' food patches did not affect GUDs significantly. The distances we used in our experimental setup to investigate neighbouring flock foraging distance might be too short to detect differences. This could be tied to the nature of the predation, if the main threat is coming from the sky (bird of prey), zebra finches might not perceive changes in risk over such short distances. Given that the risk zebra finches perceived was affected by the actions but not the distance of the neighbouring flocks, we can hypothesise that the proximity of neighbouring flocks could be important only if the visibility of the actions (foraging or not) was impaired. Zebra finches may use the fact that birds are foraging nearby as a cue that food is locally abundant and/or there is little risk of predation in the area, thus lowering GUDs (see Fernández-Juricic et al., 2004 for a discussion on information transfer and body posture). Our results corroborate findings that starlings do not alter intake rates as a function of the distance (zero or three meters) to neighbours having better foraging opportunities (Fernández-Juricic and Kacelnik, 2004).

GUDs were lower for wild derived birds than for domestic birds. This means that wild derived birds foraged more intensively (valued food more) than domestic birds. Indeed domestic birds were heavier, however mass explained less variation than the origin of birds, which suggests that there might be other reasons why domestic birds valued food less. The domestication process selected zebra finches able to survive and reproduce in environments where food is unlimited. Therefore, domesticated zebra finches might be prone to patiently wait for better food opportunities to come, whereas wild derived zebra finches would value food more when available, perhaps given the uncertainty of life in the wild versus captivity. However, this is not a general trend as GUDs experiments on domesticated and wild house mouse, *Mus musculus*, found the opposite - domesticated mice had lower GUDs than wild mice (Troxell-Smith et al., 2016)

GUDs were lower for female than male zebra finches. Females foraged more intensively than males; this was not caused by mass differences between the sexes. We did not find sex differences in GUD when birds were in single sex dyads without neighbours (Chapter II). This suggest that females foraged more than males when in presence of groups of conspecifics. Females are learning more from male demonstrators than from female demonstrators while foraging, while males are equivalently influenced by either sex in zebra finches (Katz and Lachlan, 2003). Males were found to be more consistent than females in their behaviour across social and non-social contexts in zebra finches (Schuett and Dall, 2009). Our results suggest that females are relying more than males on social aspects to make foraging decisions.

Flocks of six zebra finches foraged more intensively than flocks of two. This was expected because the initial food mass was equal, if flocks of two and six leave equal GUD, it means that, on average, the flocks of six had three times less food than flocks of two. Therefore, the value of food should be greater for each individual in the flocks of six. Moreover, the competition is higher with more birds.

Zebra finches appear to distinguish between the presence and actions of nearby conspecifics. In the context of a patchy and unpredictable environment like the Australian semi-arid zone (because of the scarce and erratic rainfalls leading to unpredictable primary production, Morton et al., 2011), the presence of conspecifics on the ground is likely to indicate the presence of food. For zebra finches, foraging in groups might be more about the direct information conveyed by conspecifics in this context, than their presence to act as a dilution effect with respect to predation. Foraging in groups can have direct benefits over and above the anti-predator group size effects (many eyes, dilution, confusion, selfish herd). If a conspecific is foraging, it means that this individual made the decision that the trade-offs are such that foraging further in that area is the best strategy. Foraging in groups allows individuals to use conspecific behaviour to estimate the food patch quality (public information, Valone, 1989). Public information is known to influence patch departure: for instance, starlings both forage longer in the presence of successful conspecifics and stop foraging sooner near unsuccessful conspecifics (Fernández-Juricic and Kacelnik, 2004). As discussed in Fernández-Juricic and Kacelnik (2004), we do not know whether the cause of increase foraging near foraging neighbours is due to public information regarding the quality of the food patch or low potential predation risk in the area. Either way, our results suggest that zebra finches inform their foraging decisions by observing conspecifics and choosing to forage near where conspecifics are foraging.

Zebra finches are known to be very sociable, breed in large colonies and can forage in large groups (Zann, 1996). Our study suggests that there is not an intrinsic bias towards larger flock sizes while foraging. Individuals are as likely to associate with a small or large group. What is important is the activity of those potential flock mates, with individuals being sensitive to the behaviour of stimulus birds, and placing greater value on a foraging patch that is near to foraging conspecifics. As zebra finches provide a useful model system for decoding behaviour in social species, our results will guide new research to understand how foraging decisions are established in social species.

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CHAPTER VI

Foraging with conspecifics: group size, group mass and the similarity of group members' masses affect giving up densities in Zebra finches

Abstract

Social foraging is common in many species of animal and there are numerous hypotheses concerning the advantages and disadvantages of it. For instance, an increase of the number of individuals in a location may lead to an increased risk of detection for the whole group but may also lead to a decrease in the per capita risk of being depredated if the group is attacked. Here we investigated if there is an intrinsic preference for group sizes that mitigate net perceived risk in the zebra finch (*Taeniopygia guttata*). We experimentally manipulated group sizes of zebra finches and investigated the effects on the perceived risk, by investigating the giving up density through the amount of food left after foraging events. Our results show that GUD decreased non-linearly with group size of between one to six birds. We also found that individual characteristics, here mass, affect the relationship between perceived risk and group size. Furthermore, the dissimilarity of individual’s mass within a group also affects this relationship. Being in a larger group size does not lower perceived risk if the groups’ individuals are light and/or have dissimilar mass from each other. Our results give insight in the effect of individual characteristics on group foraging in social species.

Keywords: Experimental group sizes; Giving up density, Zebra finch; Mass similarity; Foraging; Aggregation

Introduction

Social foraging is commonly observed across a wide range of animals, and may result from selection for social information sharing, and/or anti-predator strategies (Giraldeau and Caraco, 2018). Foraging in groups has several advantages, one of which is finding resources, with conspecifics providing an indication that there is something of interest (local enhancement, e.g. Pöysä, 1992). Second, individuals considering joining a group can remain in the safety of a refuge and observe the aggregation, gathering social information before deciding (for example accessing the quality of the resource by looking at the proportion of individuals successfully foraging, (e.g. Drent and Swierstra, 1977). Third, while foraging together as a group, individual risk decreases with group size because of the dilution effect (Delm, 1990), many eyes hypothesis (Pulliam, 1973), confusion effect (Landeau and Terborgh, 1986), and “selfish herd” effect (Hamilton, 1971). Fourth, aggregations can also permit a broader behavioural spectrum, for example, as scroungers can opportunistically wait for the seeds to appear on the surface because of conspecifics disturbing the substrate (producer-scrounger games, Giraldeau and Dubois, 2008; Vickery et al., 1991). However, aggregations also entail disadvantages like competition and predator attraction. High densities of prey are likely to attract predators, which will often intensify their search once they have located prey (“area restricted search”, Tinbergen et al., 1967), heightening the risk in such rich aggregations. Overall, social foraging both entail costs and benefits and the balance between those costs and benefits can be affected by the density of the aggregation - the group size. Here we experimentally manipulated group sizes of zebra finches and investigated the effects of that on the perceived risk.

Studies of the effects of group size on perceived risk are mainly focused on observations of behaviours such as vigilance. Here we used a giving up density (GUD) approach. GUD is the density of food remaining in a patch after individuals foraged (Brown, 1988). GUD can be measured using artificial depletable food patches where food items are mixed in an inedible substrate (Brown, 1988). As the density of food decrease every time a food item is eaten, GUD reflects the perceived risk as individuals stop foraging when the cost of continued foraging outweighs the benefits of moving on to another patch, or activity.

GUDs have been found to decrease linearly with population density (reviewed in Morris and Mukherjee, 2007). The GUD framework has essentially been used in solitary species, even largely in species competing for food patches for instance in Allenby’s gerbils (Berger-Tal et al., 2015). Some studies have been investigating density dependence or even aggregation in non-social species (e.g. *Gerbillus andersoni* and *G. pyramidum*, Menezes et al., 2018). However, direct group size effects on GUD have been very little studied. Carthey and Banks (2015) found that group foragers had lower GUDs than solo foragers in two species of Rattus in field experiments.

When introducing GUDs, Brown (1988) suggested that multiple foragers might affect the GUD. Furthermore, individual foragers with different states might also influence GUD (Bedoya-Perez et al., 2013; Brown, 1999). The GUD of a food patch reflects the GUD from the visitor who left the lowest GUD (Brown, 1988). Although GUD often reflects the GUD of the last forager, the last forager could give up before finding a food item. The perceived risk of a patch is an individual assessment and may be related to an individuals’ mass. McNamara and Houston (1990) suggested that fat reserves in birds are a trade-off between starvation and the ease of escape. Individual variation in body mass could affect foraging behaviour as lighter individuals might have a greater relative risk of starvation than of predation: they could thereby generate lower GUD than heavier individuals. This is particularly of importance for small animals which need to eat very often like zebra finches.

Zebra finches *Taeniopygia guttata* are native to the open habitat of the arid and semi-arid environment within Australia (Zann, 1996). Their foraging behaviour is strongly shaped by the fear of predation. They will fly away or retreat in nearby bushes when threatened (Butler et al., 2017). They can be found in flocks of hundreds of individuals (Zann, 1996), although they generally move around and forage in much smaller group sizes, with the most common group size being two (McCowan et al., 2015).

Here we investigated GUD without any manipulation of predation, assuming that going onto the ground to feed per se is perceived as dangerous for a zebra finch. As soon as they feel threatened in captivity, they will take refuge on high perches within the cage (personal observations).

Here, we expected GUD to decease with group size. However, we did not expect a linear relationship as zebra finches are social and are very rarely found alone. Second, we expected individual mass to affect the GUD of the group, heavier birds leaving higher GUDs (we used mass and not body size as we did not measure tarsus length commonly used to calculate skeletal size/mass). Thirdly, we investigated if the similarity of group member's with respect to mass would affect the group GUD, expecting that a larger dissimilarity would create a less safe environment and result in higher GUDs.

Material and Methods

This study was pre-registered. Experiments were carried out at Macquarie University in September and October 2018. A total of 22 birds (11 males, 11 females) were housed indoors in cages measuring 61 x 37 x 28 cm and were kept under standardized, baseline climate-controlled conditions (25□C, approx. 50% humidity, 12L : 12D cycle with first light at 7:30am). Water and grit were provided ad libitum. Cages were arranged in 3 rows of 8 cage units separated by removable dividers (Figure 1). Males and females were housed and tested in sex ratios as close as possible to 0.5. Between trials, flocks of 7 (or 8) birds were housed in 8 cage units, with *ad libitum* commercial finch seed in aluminium trays (16 x 8 x 2 cm) in the middle of the 3rd and 6th cage unit. Birds were weighted before and after the experiment.

Each experimental day entailed the following phases: Each bird was allocated to a group size at 8am (1 time in group size of one, twice in group sizes of 2, …, 6 times in group sizes of 6, within the 22 days). As zebra finch social density can affect their behaviour (Poot et al., 2012), one cage unit per bird was used as the basis of sets of cage units that comprised the group size manipulations (group size of 1 in one cage unit, group sizes of 2 in 2 cage units, etc. to group sizes of 6 in 6 cage units). The sets of cages units were spatially randomised, meaning group sizes were not tied to a particular location in the room. One bird died during the experimental period and was replaced.

The GUD approach was developed in the animals' natural environment (Brown, 1988). Given our closed setup in the laboratory, some aspects of the GUD approach implied specific considerations. One component affecting GUD is the missing opportunity cost (an individual foraging in one patch cannot be foraging at the same time in another patch, which could possibly be of greater value). Here, in a closed setup there is no possibility to forage elsewhere. However, because the trials were conducted in a specific timeframe, GUD still reflects perceived risk. However, the closed system means that the amount of food each individual can eat decrease with the number of birds for a same GUD. In a natural food patch, there is a trade-off between facilitation and competition. Individuals are safer in larger groups however being in larger groups also implies less food per capita. Here, the number of trays constituting the food patch was proportional to the number of birds. Thereby the average food intake per capita for a given GUD was similar in each group size.

Between 8am and 10am, no food was present in the cages. Between 10am and 12pm (noon), the birds were able to forage on our standardised patches: aluminium trays (16x8x2cm) containing a seed and sand (construction sand) mixture. The seed and sand mixture was composed of 0.6g white French millet seeds in 100mL of sand, with 25mL of sand scattered on top to conceal any seed that could be visible (proportions used by Soobramoney and Perrin, 2008). One food tray per bird was placed in the middle of the middle cage unit (or left or right from the middle when paired number of cage units). The total food patch size was thereby proportional to the number of birds. After the trials, food patches were sieved and the remaining seeds weighed to the nearest 0.01g (seed mean weight: 0.005g).

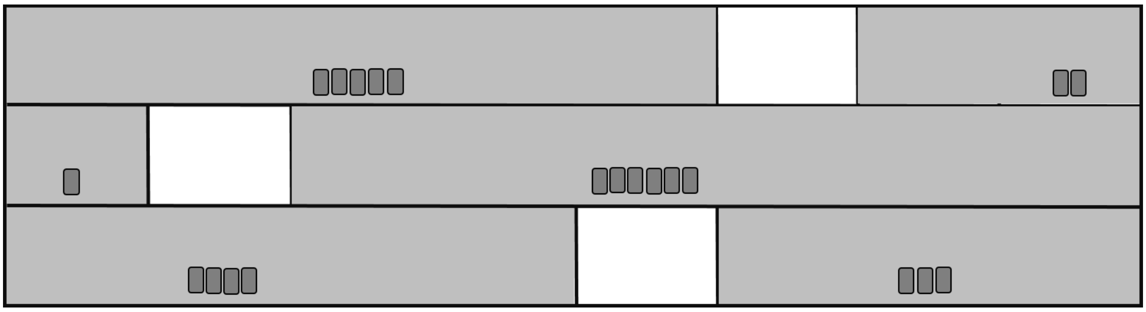

Figure 1. Experimental design for the manipulation of group sizes. Front view of an example of a combined cage unit (left to right and top to bottom: 5 and 2, 1 and 6, 4 and 3). Group sizes were equal to the number of cage units and the number of food trays. The cages in white were not used during trials. The food

patches (dark grey rectangles) were placed in the middle of the combined cage unit.

Analyses

All statistical models were constructed in R (R Core Team, 2018) using the ‘lmer’ function in the package ‘lme4’ v. 1.1–19 (Bates et al., 2015). To determine the relationship between GUD and group sizes, we fitted a linear mixed-effects model to the data. Group GUD was calculated as the mean of the tray GUDs in any given group size configuration (one tray per bird, e.g. six trays for six birds). First, according to the pre-registration, we tested the hypothesis that groups of two will change the theoretical predicted relationship between GUD and group size because of zebra finches’ strong pair bond (prediction: GUD lower for two than for one and three and more). We therefore tested the polynomial level, starting with the polynomial 4. We included the GUD of the group as the response variable, the number of birds in the group as fixed effect and date of trial and bird identity as random effects. As polynomials of 4 and 3 did not explained a significant part of the variance in GUD s than the polynomial 2 but the polynomial 2 explained more than the linear model, we fitted only the polynomial 2 in subsequent analyses. The response variable was group GUD, the fixed effects were included in a 3 way interaction: the group size (polynomial 2), the group’s mean mass (mean of mass before and after the experiments) and the coefficient of variation (standard deviation divided by the mean, $CV=\sigma/\mu$) of the group’s mass. The sex ratio (0: female, 1: male) was a fixed additive effect and the random effects were date of trials and bird identity. We verified model assumptions (plot and qqnorm functions in R). Data visualisation was implemented using the package ‘interactions’ v 1.0.0 (Long, 2019).

Results

We found a significant 3-way interaction between group size, mean weight of groups and CV in group weight (Chi-sq = 11.56; $p < 0.001$; Table 1). Giving up densities decreased linearly with group size for the heavier birds (Figure 2, 3rd panel) if the group members had similar mass (Table 1, Figure 2, 3rd panel, light blue). In contrast, for lighter birds (Figure 2, 1st panel) the GUD-group size relationships were non-linear (they decreased and then increased with group size), particularly when the variation in mass among birds within groups was high

(Table 1, Figure 2, 1st panel, dark blue). GUD was not significantly affected by sex ratio (Chi-sq_{16} = 1.46; $p = 0.23$).

When not taking into account the 3-way interaction, the 2-way interaction between group size and mass indicates that for heavy groups, GUD decreased with group size from one to six. However, for lighter groups, GUD decreased with group sizes from one to four and then increased from four to six (Chi-sq = 36.89; $p < 0.001$; Table 1). The 2-way interaction between group size and mass dissimilarity indicates that GUD decreased with group size from one to six for groups that have similar mass (low CV) and that GUD decreased with group sizes from one to four and then increased from four to six for groups that have dissimilar mass (Chi-sq = 34.51; $p < 0.001$; Table 1). The 2-way interaction between mass and mass CV indicates that for heavy groups, GUD decreased with group size from one to six. However, GUD increased with group mass more for groups with similar mass than for groups with dissimilar mass (Chi-sq = 43.02; $p < 0.001$; Table 1).

When not taking into account the interactions, heavier groups left higher GUDs than lighter groups (Chi-sq = 414.35; $p < 0.001$; Table 1), GUD decreased non linearly with group size (Chi-sq = 587.71; $p < 0.001$; Table 1) and GUD increased with group mass dissimilarity (Chi-sq = 5.81; $p = 0.016$; Table 1).

The individual relationships between GUD and group size are very similar to each other (Figure 3). The heaviest birds, in light blue, have a higher GUD than average within each group size.

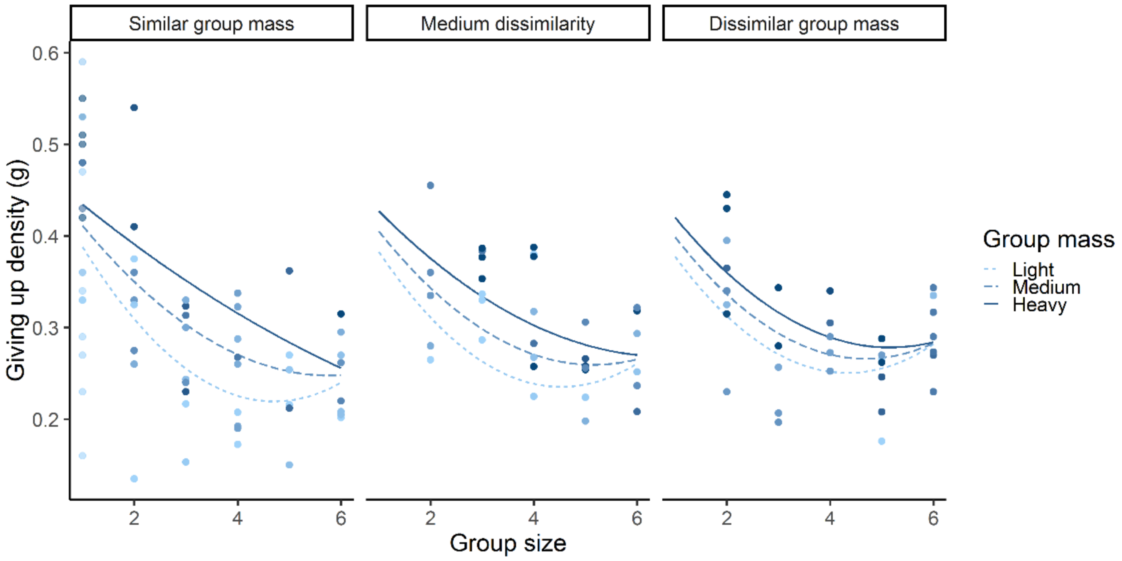

Figure 2. Relation between group GUD, group size, group mean mass and group mass coefficient of variation. The relationship between GUD and group size was dependent on individual mass and on the similarity of mass between group memebers. Group GUDs were calculated as the mean of the tray GUDs in each group size configuration (1 tray per bird, eg. 6 trays for 6 birds). The groups ranged from 1 to 6 zebra finches. Lines represents the predictions of the model. The color of the data points correspond to the color of the lines. The data was devided into tercile for visual purposes (the lowest third of the values, the middle third and the higher third).

Parameter	Df	χ^2	P value
Poly(Group size,2)	9	587.71	<0.001
Group mass mean	9	414.35	<0.001
Group mass CV	9	5.81	0.016
Poly(Group size,2): Group mass mean	11	36.89	<0.001
Poly(Group size,2): Group mass CV	11	34.51	<0.001
Group mass mean : Group mass CV	10	43.02	<0.001
Poly(Group size,2): Group mass mean : Group mass CV	16	11.57	0.003

Table 1. Summary of linear mixed model fit for testing the relation between groups' GUD, group size, group mass mean and group mass CV. GUD was significatively affected by the three-way interaction between group size (polynomial 2), the mean group mass and the coefficient of variance (dissimilarity) of group mass. Group mass is the mean of the mean mass of each bird before and after the experiment. Maximum model: Group GUD ~ poly(Group size, 2) * Group mass mean * Group mass CV + Sex ratio + (1|Bird ID) + (1|Date). Minimum adequate model: Group GUD ~ Group size ^2 * Group mass mean * Group mass CV + (1|Bird ID) + (1|Date).

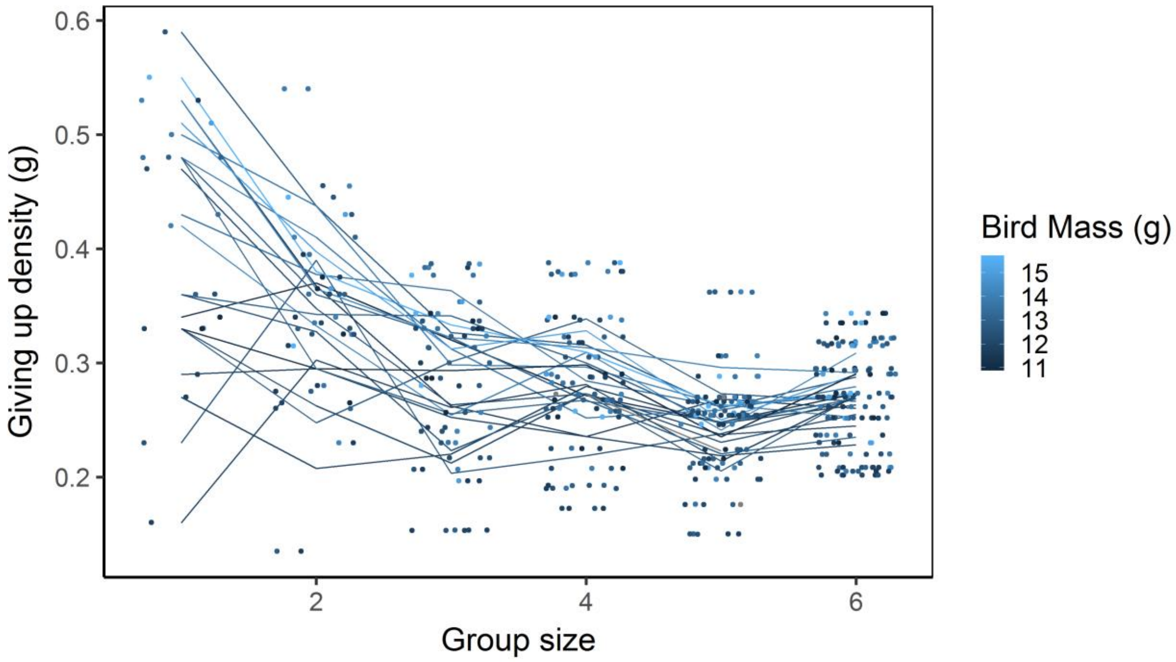

Figure 3. Individual relationship between GUD and group size for every bird (n=22), colour coded for the mass of the bird. Points are representing individual birds for a trial. Lines are built for each bird with the mean GUD for a given group size.

Discussion

We found that in the zebra finch, GUDs decrease with group size. This decrease is linear for groups of similarly heavy individuals. This decrease becomes less linear with the lighter individuals, and as group members have masses that are more dissimilar. When the individuals are most dissimilar in mass, large groups do not have lower GUDs. Large groups do not lower their GUDs when composed by lighter birds either.

The fact that GUD decreases with group size supports previous findings that solo foragers quit sooner in two species of rodents (Carthey and Banks, 2015). Our results further confirm that the presence of conspecifics affects the perceived balance of costs and benefits when individuals are foraging in a patch. Our results also suggest that not only can the number of individuals foraging together affect GUD; the number of individuals in the close surroundings of the patch can affect GUD. Our results suggest that if the most common group size observed in the field is two, this is unlikely to be because zebra finches feel safer at this group size per se. In our experimental design, pairs did not choose each other, and they probably did not have the time to bond in the two hours prior to trials. Zebra finches have strong pair bonds within and outside breeding events. Our results also show an uptick in GUDs with groups of six. Further experiments with groups of seven and eight or even more would help further understand the effects of group sizes on GUD. GUDs might continue to go up and perhaps plateau with larger group sizes. In that case, not being alone (group safety) would not compensate for competition (interference between group members).

The GUD approach provides advantages by allowing a relatively non-intensive assay of behaviour (indirectly), providing large sample sizes easily. Furthermore, it also provides an assay of collective foraging on a patch, rather than a focus on particular individuals. Our results show that the number of individuals potentially foraging in the patch affects GUD. This could be seen as a limitation of the GUD framework when patch quality and social environment might not be easily distinguishable. However, GUD still reflects perceived risk, not only from a location point of view but also from a social point of view. Our study provides further support for the recommendation previously made by Carthey and Banks (2015) to take into account the social environment in both the design and interpretation of studies using GUD as an assay of behaviour. We also suggest a broader possible use of the GUD approach, especially in controlled environments, and not only in solitary species. The GUD approach can easily be implemented to not only investigate predation risk or competition but also social facilitation and group decisions.

Groups made of heavier birds had higher GUDs. Fat levels have been suggested to be a trade-off between the risk of starvation and the risk of predation (McNamara and Houston, 1990). Individual mass might thereby affect the costs and benefits of foraging. A heavy bird should have lower benefits than a lighter bird to build reserves as well as higher predation risk if the heavier birds forage more and that increased foraging on a patch makes flight and escape from a predator less efficient. We also found that the mass similarity of group members affects the relationship between GUD and group size differently for heavier groups than for lighter groups. For heavy groups, GUDs decreased linearly with group size if the mass similarity of the group was high. However, GUDs plateaued at larger group sizes if group members were dissimilar in mass. For light groups, GUDs decreased with group size until groups of four individuals then increased until six. When groups were dissimilar in mass, a group size of more than five was already not lowering GUD anymore. Mass dissimilarity within a group may imply different values of benefits and costs, in other words mass dissimilarity may imply different needs. This suggests that individuals are giving up less quickly when their group members' needs match. Further studies including body size or body condition in the statistical models are needed to explore the generality of these findings.

Our experimental design calls for some consideration regarding the generality of our results. First, in a closed environment, there are no missed opportunity costs of foraging as animals cannot move to forage elsewhere. Second, birds were not free to choose the size of group they foraged in, each bird was restricted to a single group size. Groups were not formed of particularly affiliated individuals. Furthermore, the fact that the length of the cage was proportional to the number of birds in the cage could also affect the perception of risk surrounding the food trays as the cage' walls were further away from the food.

The decline of perceived risk with group size could also be because of the structure of the experimental design. First, the number of cage units equalled the number of birds, influencing how the birds could fly. As birds were often flying from one end to the other end of the cage independently of the length of the cage (personal observation), we cannot exclude the possibility that individuals in larger groups were moving more. This could affect energy requirements and thereby GUDs. Second, the number of food trays in each cage, equalled the number of birds; however, the actual number of birds foraging together is often less than the total number of birds in the cage (personal observation). This could affect the distance between birds foraging together. Individual position within the group is thought to be influencing the effectivity of the foraging (foraging vs vigilance) and the perceived risk (e.g. in primates, Treves, 2000). Treves (2000) suggested that denser groups would theoretically be safer in primates. Consistent with this idea, Pöysä (1994) found that vigilance decreased with the proximity of the nearest neighbour in teal *Anas crecca*.

As the number of birds foraging together might not be the number of birds potentially foraging together, we can wonder if it is the number of potential foraging partners alone that matters or whether it could also be the choice of partners with whom individuals can forage. It can also be that different individuals have different foraging strategies. In larger group sizes, more types can be present and have the potential to forage the different ways. For example, it has been suggested the behavioural diversity of a group with respect to the personalities of the individuals may make the group more effective (Aplin et al., 2014). Furthermore, Keiser & Pruitt (2014) argue that behavioural outcomes commonly attributed to group size might be result of group composition.

Without considering predation pressure increasing with prey number, risk should decrease with group size (e.g. the probability of being preyed upon decreases with the number of other potential preys in case of an attack from a predator, dilution effects, Delm, 1990). However, the access to food also decreases for every individual within the group. Competition could both lead to lower effectivity because of monitoring competitors or the opposite, higher it because they have to be as effective as possible before others eat the seeds they would have been eating if alone. The latter is named ‘scramble competition’ (increase exploitation speed, reduce vigilance) and was found to be experimentally relevant in coots for instance (Randler, 2005).

Zebra finches are found in large groups (Zann, 1996) especially around water holes. However, when resources are more spread than a single water hole, zebra finches are seen in much lower group sizes (McCowan et al., 2015). Our results suggest that zebra finches are not simply in aggregation because of common resources, they actually gain to be in small groups. Zebra finches are a useful model system for understanding group foraging in any social prey species. Our results also reveal that similarity in mass within a group decrease the perceived risk. This opens the question of group formation through similar needs, where groups can be an outcome of individuals having similar trade-offs between benefits and costs.

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CHAPTER VII

Pairing status influences how thoroughly zebra finches exploit food patches

Abstract

Decisions are made through balancing fitness costs and benefits and conspecifics can modulate this trade-off. While foraging, costs include competition for resources and attraction of predation. Benefits include information exchange and per capita risk dilution if the group is attacked by a predator. If individuals gain from each other's fitness, social facilitation can prevail over competition and the exchange of information can be more reliable. Social monogamy is an example of a situation in which two individuals are affected by each other's fitness. Here we investigated if male-female dyads made different foraging decisions than either male-male or female-female dyads. We also investigated if foraging intensity was affected by the time that dyads of male-female had spent together (proxy for pair-bond). We used the giving up density (GUD) approach to measure the intensity with which the different dyads exploited food patches. Our study shows that male-female dyads that spent one or two weeks together (partners) did not exploit patches more thoroughly (leave lower GUDs) than male-female dyads who did not spend time together outside trials (non-partners). We also found that foraging decisions were different when zebra finches were in single-sex dyads than in mix-sex dyads: Single-sex dyads foraged more thoroughly in the back of cages than in the front of cages, whereas mix-sex dyads did not. Our results suggests that at least the sex of the companion in a dyad affects foraging intensity. As the sexual identity of a companion can affect foraging behaviour, this should be of concern when interpreting and designing captive experiments.

Keywords: Pair-bond; Giving up density; Foraging; Zebra finch; Dyads

Introduction

The decision to stay at a food patch to continue foraging is made when the benefits of continuing foraging at that particular location are higher than the costs of staying there. This can be mitigated by conspecifics. Social foraging – two or more individuals concurrently influencing each other's energetic returns (Giraldeau and Caraco, 2018) - can modify benefits and costs. Social foraging affects per capita costs through competition for the same resource. Social foraging can also attract predators, as predators often localise their search once they spot prey (Tinbergen et al., 1967). Benefits of social foraging include information exchange on food patch quality (Templeton and Giraldeau, 1996). Social foraging can also mitigate predation risks (dilution, Delm, 1990; many eyes, Pulliam, 1973; confusion, Landeau and Terborgh, 1986; selfish herd, Hamilton, 1971). Beyond the proximity of conspecifics, partner identity can also affect both costs and benefits of foraging. If individuals gain from each other's fitness, facilitation can prevail over competition and the exchange of information can be more reliable as incentives to misinform decline. Monogamous pair bonds are an example of how individuals can affect each other's fitness (Griffith, 2019; Crino et al., 2017).

Zebra finches, *Taeniopygia guttata*, form strong pair bonds, they are socially and genetically monogamous (Griffith et al., 2010; Zann, 1996). In the wild the most commonly observed group size is two, which is assumed to be a male and female pair moving around together (McCowan et al., 2015). Divorce in zebra finches has negative impact on reproduction (Crino et al., 2017); and separation from a partner has been shown to increase a stress hormone, corticosterone which only returned to baseline levels after reunion with the mate (Remage-Healey et al., 2003). Pair-bond (determined by huddling at least two nights in a row) was found to influence foraging tactics and interindividual spacing (pairs foraged closer) while foraging in zebra finches (Beauchamp, 2000). Zebra finches that were bonded tend to be more synchronised than non-bonded birds when foraging (Caryl, 1976). Templeton et al. (2017) suggested that paired male zebra finches would choose to not compete with their partner for food. In the wild, coordination within mated pairs affects reproductive success positively (Mariette and Griffith, 2015, 2012). Work on zebra finches' response to approaching predator while incubating show that when the partner was perched nearby, the response was quicker (Mainwaring and Griffith, 2013).

Here we investigated whether foraging intensity was affected by the relationship within dyads using the giving up density (GUD) approach. The GUD framework assays the context-specific balance of costs and benefits while foraging on standardised patches (Brown, 1988). GUDs can be measured using depletable food items mixed into a nonedible substrate in a container (Brown, 1988). A forager exploiting such a food patch gets diminishing returns because the more the forager eat the food items, the more the food density decreases and the more difficult it gets for the forager to find new food items. The GUD of a food patch reflects the GUD from the most efficient forager who visited it.

Here we manipulated the time male-female dyads spend together in captivity, thereby generating male-female dyads who spend time together before and in between trials (hereafter: partners) and male-female dyads who did not spend time together outside trials (hereafter: non-partners). We investigated if the density of food left after foraging differed between partners and non-partners. As partners could influence each other fitness, they should not spend time in competition and forage more thoroughly than non-partners, thereby leaving lower GUD. As partners spend more time together, they should facilitate each other even more, we therefore further predicted that difference between the GUD left by partners and non-partners would increase over time, with partners lowering GUD through time and non-partners GUD being constant. Beside the GUD in itself, we investigated whether patch use would be influenced by the opportunity to forage in two distinct food patches, one located at the front and one at the back of the cage. The front of the cage is the only side where something (or someone) can approach them. The front of the cage is where risk can come from but also where it is easiest to detect potential risks. We hypothesise that partners would forage more in the riskier patch (whatever the riskier patch is), causing the difference to be smaller than for non-partners.

Zebra finches are often kept in single sex flocks. Females were found to prefer to forage with a male than with another female (Benskin et al., 2002). Here we compared the foraging intensity of male-female, male-male and female-female dyads. From the food intake perspective, in a context with more than one food patch, equalizing GUDs between patches is the best strategy (Valone and Brown, 1989). In patches differing by perceived risk, the GUD will be left higher in the risky food patch. If foraging with a certain conspecific mitigate the overall risk, the difference between the risky patch and the less risky patch should be affected. We hypothesised that same sex dyads would be more competitive and forage more intensively in the non-risky patch, thereby leaving stronger GUD differences between patches. Alternatively, we expected mix sex dyads to socially facilitate each other and thereby forage more equivalently in both patches.

Material and Methods

Experiments were conducted at Macquarie University in October and November 2018. Eighteen dyads were kept indoors under standardized, baseline climate-controlled conditions (25°C, approx. 50% humidity, 12L : 12D cycle with first light at 7:30). One male was paired with one female in individual cages (61 x 37 x 28 cm). Each cage had a solid metal back and sides but the front, top and bottom were each composed of wire mesh panels. Birds were weighted, then paired and left for six days to acclimatize and bond. Zebra finches bond with a partner in a few days (Silcox and Evans, 1982). Two male-female dyads that were together before the trials and had time to breed together were available from another experiment and experiments were conducted on them in parallel to the 18 dyads. Water and grit were constantly available and commercial finch seeds were available ad libitum during non-testing periods.

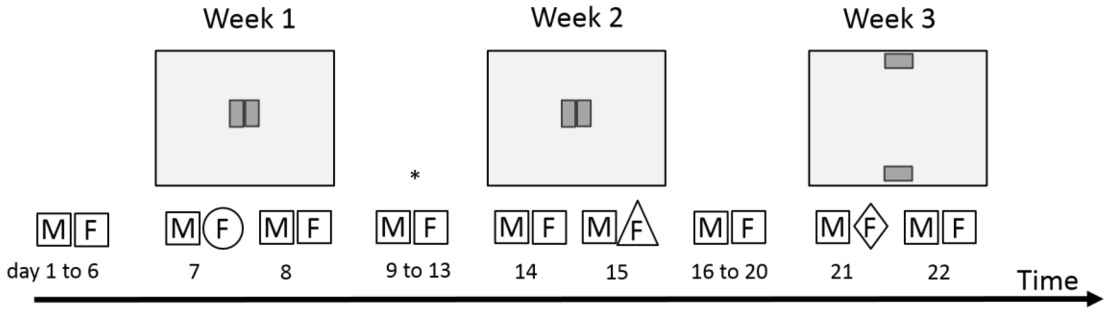

Figure 1. Example timeline of the partners vs non-partners trials. Representations of the top views of the trials: 2 food patches at the middle in the first 2 weeks, then one at the back and one at the front of the cage. Between week 1 and week 2 (day 11,12,13), experiments unrelated to the present study were conducted, as denoted by '*', during which partners stayed together. In this example, the male represented by a square was either with his partner (the female represented by a square) or with different non-partners (females represented by a circle, a triangle and a diamond).

On the first experimental day, half of the dyads were tested with their partners and half were randomly allocated to another member of the opposite sex. On day 8, the birds paired with their partners on day 7 were paired with a non-partner and the ones paired with a non-partner on day 7 were paired with their partner on day 8. Birds remained with their respective partners for 5 more days before being tested a second time. Partners and non-partners were then tested a third time with the difference of the food patches not being both located in the middle but located one in the front and one in the back. Birds were transferred from their holding cages in their respective dyads in the morning just before experiments. No food was present in the cages for two hours then the birds could eat in standardised food patches for two hours. The food patches consisted of aluminium trays (16x8x2cm) filled with 0.6g of French millet seeds in 100mL of sand, with 25 mL of construction sand purred on the top.

Our results regarding the back vs front trials were not consistent with experiments done previously on single-sex dyads as single-sex dyads foraged more intensively in the front than in the back of cages (experiments done parallel to chapter II, 29 male dyads and 27 female dyads). We decided to investigate if birds in 2018 had different preferences than birds in 2016 or if mix-sex dyads and single-sex dyads would make different foraging decisions. We therefore performed back/front experiments again with the same birds in both single-sex and mix-sex dyads (10 male dyads and 10 female dyads).

Analyses

All statistical models were constructed using the 'lme4' package v. 1.1–11 in R. All experiments were in parallel conducted with 2 dyads that were together before ('long paired', used for prior experiments). Analyses were done with and without and as there were no noticeable changes, we present only analyses including them.

1) Partners vs Non-partners

We analysed trials with food patches placed in the middle of the cages and trials with food patches at front and rear of cages separately. To determine the link between GUD in middle food patches (2 patches per cage) and pairing status (partners/non-partners), we fitted a generalized mixed-effects model to the data. The response variable was GUD (per patch). The fixed effects were the pairing status, the time since partners were first put together (1/2weeks), the weight of the dyads and the location of the food patch (left/right). The interaction between pairing status and the time paired was fitted too. The random effects were bird ID and Cage nested in Date.

For the analyses with food patches at the front and at the back we used the differences of GUD between those patches as we are interested in the differences more than in the GUD itself. In order to determine the link between differences of GUD between back and front food patches and pairing treatment, we fitted another generalized mixed-effects model. The response variable was the difference in GUDs between patches within a cage ($\Delta GUD = GUD_{back} - GUD_{front}$). The fixed effects were the pairing treatment (partners/non-partners) and the birds' mass. The random effects were date and bird ID.

2) Mix-sex vs Single-sex dyads

In order to test for the relationship between differences of GUD between back and front food patches and the dyads types, we also conducted a linear model. The response variable was the GUD difference (ΔGUD = GUD back – GUD front).

The fixed effect was the pairing status and year (male & female/2 males 2016/2 females 2016/2 males 2018/2 females 2018). As we did not have reliable mass for birds in 2016, we did not include them in the analyses. Tukey test ('emmeans', Lenth, 2019) were performed to test the differences between treatments.

Results

1) Partners vs Non-Partners

For trials with patches in the middle, GUDs were on average 0.28 (range 0.1 to 0.46). GUDs were overall not significantly influenced by the fact that zebra finches were paired with their partners or with a non-partner (Table 1, Figure 2). GUDs were lower after two weeks than after one week (Table 1, Figure 2).

For trials with patches located at the front and at the back of the cages, GUDs were on average 0.33 (range 0.17 to 0.52) and the differences of GUDs between back and front (GUD_{back}- GUD_{front} = ΔGUD) were on average 0.70 (range -0.18 to 0.29). There were no significant differences in ΔGUDs between partners and non-partners (Figure 3, Table 2).

2) Single vs mix-sex dyads

ΔGUD significantly differed with dyads type ($F_{4,160}$ = 5.408; $p < 0.001$). ΔGUD significantly differed between single and mix-sex dyads but not between sexes nor between experiments conducted at a different time (Table 3). Single sex dyads foraged more intensively at the front of the cages and the mix sex dyads foraged more intensively at the back of the cages (Table 3; Figure 4).

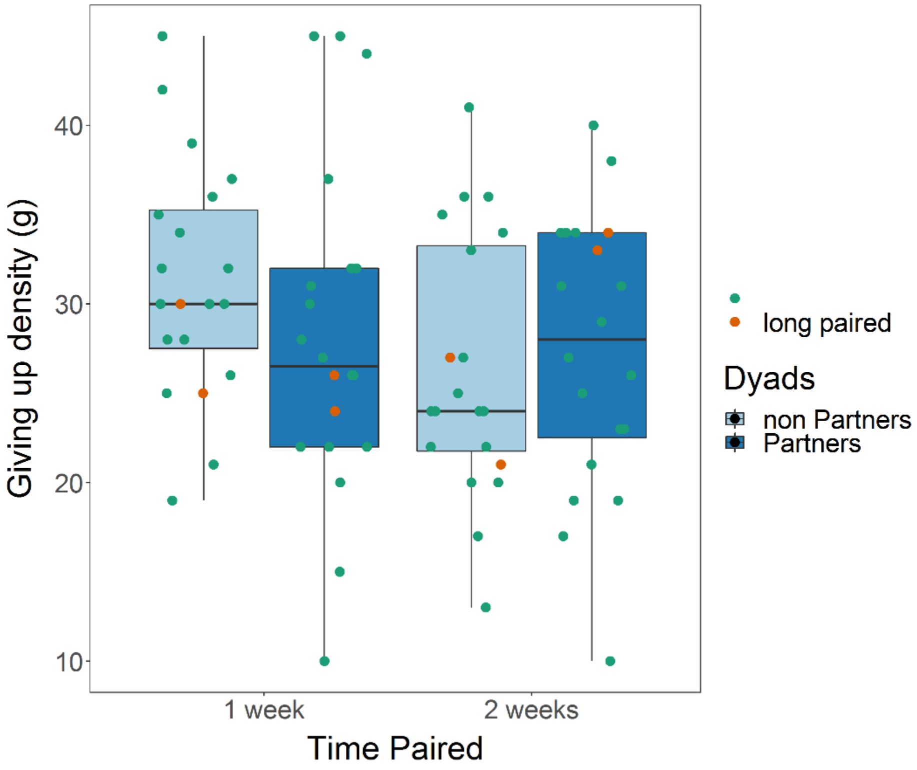

Figure 2. Giving up densities of zebra finches paired with their partner or with a non-partner after 1 week and 2 weeks. The tendency for partners to have lower giving up densities than non-partners in the first week did not continue after two weeks of being together and was not significant overall. The red points correspond to the two male-female dyads which have been together longer than two weeks.

Parameter	**Df**	**χ^2**	**P value**
Bird mass	9	0.002	0.96
Pairing status (partners vs non- partners)	9	1.11	0.29
Food patch location	9	0.96	0.33
Time paired	**9**	**8.91**	**0.003**
Pairing status: Time paired	10	3.65	0.06

Table 1. Summary of linear mixed effects model fit for testing the relationship between GUD, pairing status and time since pairing. GUDs became lower with time. Pairing status were partners or non-partners, time paired was one or two weeks and bird mass was the mean of mass prior and after experiment. Maximal model: GUD ~ pairing status * time paired + mass + (1|Bird ID) + (1|Date/Cage).

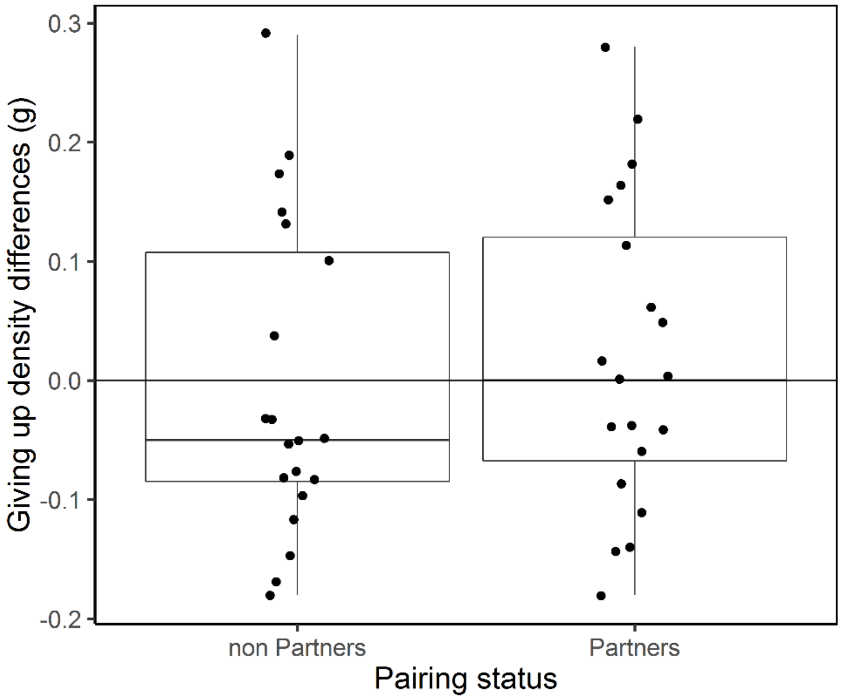

Figure 3. ΔGUD (GUD back – GUD front) for zebra finches paired with their partner or with a non-partner. ΔGUD did not significantly differ between partners and non-partners. Below zero, zebra finches foraged more intensively at the back of the cage.

Parameter	**Df**	**χ^2**	**P value**
Pairing status	6	3.25	0.07
Bird mass	6	0.45	0.50

Table 2. Summary of linear mixed model fit for testing the relation between ΔGUD (GUD back - GUD front) and pairing status (non-Partner, Partner). Maximal model: DifGUD ~ pairing status + Bird mass + (1|BirdID) + (1|Date).

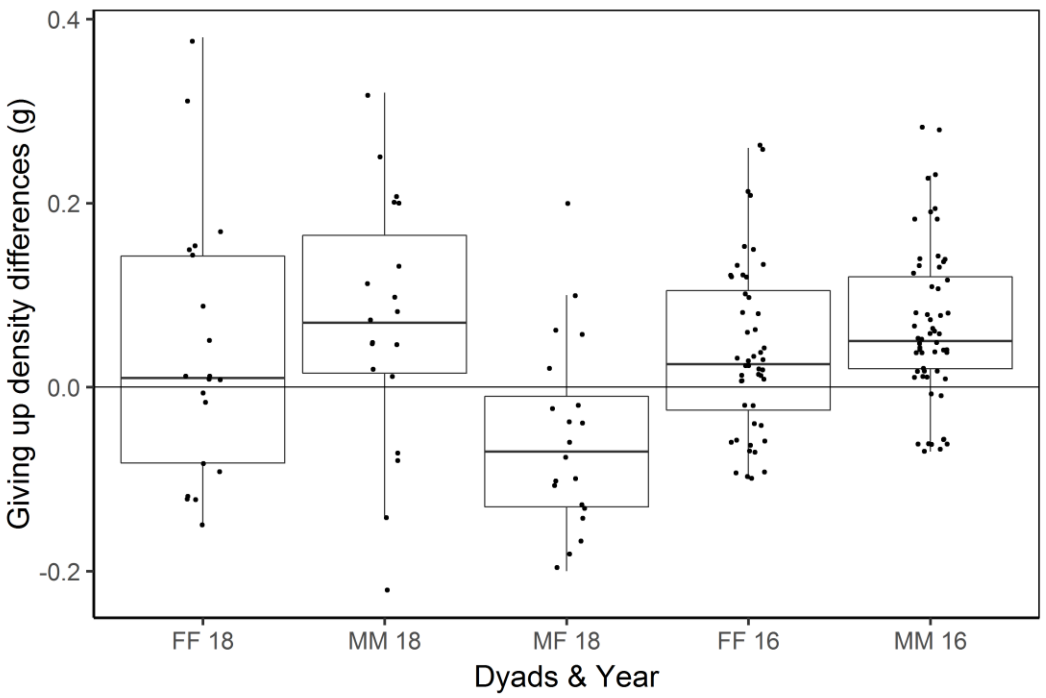

Figure 4. Giving up densities differences between the front and the back of cages for zebra finches in different dyads (2 Males, 2 Females, 1 Male & 1 Female). Single sex dyads foraged more in the front than in the back of the cage and the mix sex dyads foraged more in the back. In 2016, experiments were conducted in single sex dyads only. In 2018, the same experiments were conducted and trials for mixed sex dyads (MF) were added. Above zero, zebra finches foraged more intensively at the front of the cage.

Contrast	Estimate	SE	Df	T ratio	P value
FF 18 – MM 18	-0.03203	0.0334	160	-0.959	0.8730
FF 18 - MF 18	**0.09250**	**0.0330**	**160**	**2.806**	**0.0441**
FF 18 - FF 16	-0.00150	0.0277	160	-0.054	1.0000
FF 18 - MM 16	-0.02805	0.0270	160	-1.038	0.8375
MM 18 – MF 18	**0.12453**	**0.0334**	**160**	**3.729**	**0.0024**
MM 18 – FF 16	0.03053	0.0283	160	1.080	0.8164
MM 18 – MM16	0.00397	0.0276	160	0.144	0.9999
MF 18 – FF 16	**-0.09400**	**0.0277**	**160**	**-3.388**	**0.0078**
MF 18 – MM 16	**-0.12055**	**0.0270**	**160**	**-4.460**	**0.0001**
FF 16 – MM 16	-0.02655	0.0203	160	-1.305	0.6883

Table 3. Summary of the tukey tests (pairwise differences) following the linear mixed model fit for testing the relation between ΔGUD (GUD back - GUD front) and dyads type separated by year (FF 18, MM 18, MF 18, FF 16, MM 16). Single sex dyads foraged more in the front than in the back of the cage in both years and the mix sex dyads foraged more in the back. Maximal model: ΔGUD ~ dyads type separated by year.

Discussion

We were interested in examining the effects of the identity of zebra finches' companionship on their foraging intensity. The foraging intensity was expected to be greater for partners than non-partners, as partners gain from each other's fitness and this should decrease competition between them. However, zebra finches were not foraging more thoroughly with a partner with whom they have spent more time over two weeks preceding the trials. After one week, although not significantly, partners had lower GUD than non-partner dyads. After two weeks, this trend totally disappeared (there was even a tendency for the opposite pattern). In that same week (the three days before the two weeks trials) birds were used for other experiments that were not part of the present study. This could explain the significant lower GUDs in the second week in comparison to the first week, as the overall motivation for food could have been increased. It could also have led to the birds being more familiar with the experimental setups and being less afraid in general. This may have led to a non-response of the paring status (partners vs non-partners). In a more challenging situation with distance between food patches, with one at the front of the cage and one at the back, no significant differences were found either. Not finding differences between partners and non-partners was not expected. Indeed, we expected partners to have their interests more closely aligned and be better coordinated then they should be better able to communicate danger effectively and honestly (Griffith, 2019). Partners might not be important when not in breeding period; there were also no competition for mates nor choice for mates. It might also be that partners were in a different stage of their associations (Caryl, 1976) which might impact their level of coordination generally, and potentially their foraging coordination specifically. Another explanation is that the two hours before the trials plus the two hours trials were already enough to form a bond, and certainly previous work in the species has demonstrated that unpaired singletons will very quickly form new bonds when give the opportunity – usually within 24 hours (e.g. Rutstein et al., 2007). On another hand, competition between non partners can also lead to a decrease in GUD; for instance if the competition (or the time spend interacting with another) is energy demanding.

Single sex dyads foraged more intensively at the front of the cages and the mix sex dyads foraged more at the back of the cages. This suggest that single sex and mix-sexed dyads perceive risk differently. One hypothesis is that birds with a companion from the same sex are foraging in the front even if the front is riskier because they are trying to see, or attract a companion of the opposite sex (which they can hear elsewhere in the room). Same-sex pair bonds can be as strong as opposite sex pair bond in zebra finches (Elie et al., 2011). In our experiments done in 2016, same-sex dyads were together for about two months before the trials. The similarity of the results from 2016 and 2018 further suggest that the results are not just about how long birds were together but with which sex they were together. Zebra finches typically started foraging in the back of cages during trials (personal observation), they ate more (left lower GUDs) near cover (chapter III) and they left lower GUDs when their visual fields were obstructed only when the foraging possibilities were broader in the vicinity (chapter IV). Altogether, our interpretation is that zebra finches feel safer being hidden only when both sexes are foraging together. These intriguing results call for further investigation. More detailed behavioural analyses would be needed to understand why single sex dyads and mix sex dyads perceive risk in their environment differently. Zebra finches are commonly kept in single sex flocks in captivity, with several potential consequences (Griffith et al., 2017; Ruploh et al., 2013). This study suggests another consequence of the construction of single sex groups in captivity. The risk associated with features or local places within their environment is affected by the sexual identity of their companion.

In summary, we did not find evidence that GUDs were affected by the time spent with their partner before trials in zebra finches. We also found evidence that the location of the food patch affected GUDs differently if zebra finches were with a companion from the same or the opposite sex. Our study suggests that, while GUDs were not significantly affected by the individual identity of the foraging companion, GUDs were affected by the sexual identity of the foraging companion. The sex of companions change zebra finches risk perception, this should be of concern when conducting behavioural experiments and overall when considering keeping zebra finches in single sex flocks as it is a potential welfare issue.

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CHAPTER VIII

General Discussion

The aim of this thesis was to gain novel insights into how animal's decisions to keep foraging or to leave a food patch are affected by the environment. I applied a well-known method measuring foraging intensity, the giving-up density or GUD (Bedoya-Perez et al., 2013; Brown, 1988) on a well-studied passerine bird, the zebra finch (Griffith and Buchanan, 2010). In the different chapters of this thesis, I explored how the physical and social aspects of zebra finches' environment affected their foraging decisions in captivity and in the wild.

In chapter II, I conducted experiments on simple physical changes in cages. I showed that GUD could be successfully implemented on captive zebra finches to study welfare. I found that zebra finches were exploiting food patches less thoroughly when located behind a cover. My results also suggest that neither the addition of perches nor the modification of the cage floor (paper or mesh) affect the foraging intensity.

In chapter III, I further investigated how cover proximity affected the GUD of wild zebra finches. Corroborating the most common finding on desert foragers (Brown and Kotler, 2004), zebra finches foraged more intensively close to vegetation. Contrary to the results obtained in chapter II in captivity, Zebra finches foraged more intensively when close to cover in the wild (chapter III). For this reason, I hypothesised that cover can be perceived as a protective or an obstructive element depending on the context.

I therefore examined in chapter IV the effect of sightlines manipulations on the finches' foraging intensity. I found only limited evidence that zebra finches were affected by changes in sightlines, and those results were in contradiction with the ones I obtained previously in captivity: zebra finches in the wild foraged with more intensity when sight lines were reduced.

Particularly through observing zebra finches in the wild, I increasingly doubted that studying their physical environment without being able to control for their social environment could provide much information about their foraging decisions.

Previous studies on wild zebra finches focused on the existence of parallel life history strategies: Some zebra finches are nesting and foraging a few hundreds of meters away than the centre of colonies (Mariette and Griffith, 2012). Mainwaring et al. (2011) found that group size had a negative impact on zebra finches' explorative behaviour. From this body of work emerged the idea that zebra finches were not actively seeking for forming large aggregation, rather they would aggregate because of common needs and their aggregation would be a by-product. In chapter V, I examined whether birds were more attracted to food patches next to large or small groups of conspecifics and found no significant differences. Following findings on geese (Drent and Swierstra, 1977) and fish (Coolen et al., 2005), I hypothesised that neighbours' behaviour would be of greater importance than their number. I found that zebra finches foraged more intensively near neighbouring flocks that had food than next to neighbouring flocks that did not have food.

In chapter VI, I specifically investigated how the group size, from 1 to 6 individuals, and the mass of those individuals, affected foraging intensity. I found that the relationship between GUD and group size was decreasing non-linearly. I also found that groups constituted of heavier birds foraged less intensively than groups of lighter birds. Finally, my results also show that foraging intensity was affected by the similarity of mass between group members. Dissimilar groups foraged less intensively than similar groups. I expected groups of two to be foraging particularly intensively as this is the most common group size observed in the wild (McCowan et al., 2015).

Therefore, in chapter VII, I explored further male-female dyads, hypothesising that pairs would be foraging more intensively after building a bond. I found no significant differences between pairs that spend one or two weeks together and pairs that were together only for the trial period. This could suggest that birds do not forage more intensively after spending more time with their partners or that pairs of zebra finches bond in less than a couple of hours.

GUD Methodology

The GUD technique worked well for zebra finches, both in captivity and in the wild with the same protocol. However, differences in patch food preparation could diminish our ability to compare results between experiments. In the field, the trays' sides were buried into the sand to prevent them from being blown away by the wind. This made any blinding to experimental treatment not practically feasible as the preparation was on site. We tried as much as possible to be aware of the possible bias in being mechanical about the entire process. Regarding lab experiments, trays were prepared before experiments and distributed randomly across treatments. Therefore, the same cages were rarely given the first or the last prepared trays (variance in the way a series of trays were prepared could have been due to my fatigue or me speeding up for instance). In all experiments done in this thesis, I was the only experimenter in charge of preparing, sieving and weighting the tray to increase their consistency, except for field experiment were five observers were in charge of sieving a set of experimental treatment that was randomly assigned to them every day.

Bedoya-Perez et al. (2013) preconize the use of videos to verify which species are foraging. One issue with the use of videos during trials in the wild is that I observed zebra finches to interact with the camera. In the field, videos have been taken during preliminary trials, to check if zebra finches were eating in both paired trays in a same visit, to check if other animals were foraging, etc. In the open area where we conducted experiments for chapter III and chapter IV, we observed only once a pipit. In that open area, zebra finches were habituated to the food patches, often following us while setting up. In instances where zebra finches were not habituated to a location, food patches remained untouched for days. All this strengthens my confidence that the GUDs we collected resulted from foraging zebra finches.

Interplaying of the GUD approach and the zebra finch model

Costs and benefits are important notions that help us better understand the mechanisms involved in decision-making. One limitation of the GUD approach is that it is a single measure of the result of all foraging events in a foraging tray and decisions that does not provide mechanistic insights. Increasing benefits or reducing costs of foraging can both lead to a decrease in GUD. However, benefits and costs are very tied to each other. For instance, the cost associated with predation increases stress level; in turn, stress level increase metabolic activity, leading the benefits of food to become greater. Here we chose to use the GUD approach because we did not intend to show detailed decision-making mechanisms, but rather to investigate variables that generally influence foraging decisions.

The GUD approach can be disorientating at first, as it does not always match with observed behaviours. In captivity, zebra finches start foraging at the back of the cages; however, GUDs are lower at the front. In the field, zebra finches generally start foraging in the unwired enclosure rather than in the wired enclosure and on mounts rather than in depressed patches. However, we found that GUDs did not differ between these conditions.

Experiments were designed to both investigate general trends in GUDs left by zebra finches and investigate individual differences. In captivity, we used repetitive measures on the same individuals to assess repeatability. In the wild, investigating the effect of individual behavioural variations on GUD is less manageable. Yet, it could have important consequences on the interpretation of GUDs results (Bedoya-Perez et al., 2013; Brown, 1999). In the population we used in chap III and IV, the same individuals were likely to forage in several food patches. However, the different creeks are generally used by different birds. Through videos watching for checks before the first lab experiments, some zebra finches got my attention in the way they foraged. Some of them repetitively pecked the edges of the aluminium food tray; I first thought it could be linked to repetitive behaviour caused by distress, as the zebra finches were alone in the cages. However, when I repeated their action on a tray, I realised seeds appeared to the surface as the seeds are less dense than the sand. It could be interesting to investigate if this is an effective foraging technique and if it could be transmitted to observers.

The GUD depends on the most efficient forager who visited the tray (Brown, 1988). If there are individual differences, GUDs will not reflect the GUD of the population considered, but the GUD of the most efficient forager (Bedoya-Perez et al., 2013). Whilst GUD is sometimes argued to be insensitive to the number of foragers that visit a tray because GUD reflect the most efficient one (Hochman and Kotler, 2007), the probability of a forager with greater efficiency should increase with the number of potential foragers. Moreover, the probability of a less effective forager to find a food item after a more efficient forager gave up cannot be zero. This probability should not be zero for any subsequent visit.

Perspectives on zebra finches

Given that the zebra finch is a supermodel (Griffith and Buchanan, 2010), it is surprising that so little is known about their anti-predatory defences. Zebra finches, contrary to other common passerines birds, do not have a flee alarm call and this is not easy to explain (Butler et al., 2017). Zebra finches are also special in the sense they have a strong pair bond. On one recorded video, I could observe two zebra finches staying still on a foraging tray edge for nine minutes. On that day, we did not observe a particular predator in the surrounding. Although we do not know the context, zebra finches staying still for so long seem very unusual. This strengthens the idea that we still know very little about zebra finches' predators and about zebra finches' anti-predatory behaviours. Further studies should therefore concentrate on anti-predatory defences in pairs. Using further the giving up density framework on zebra finches has great potential.

Zebra finches were accessing both food patches before giving up on foraging; they usually went back and forth between food patches. Using large aviaries with larger population would allow us to investigate the choice of flock size throughout the process of foraging in different food patches. Our experiences in cages are constrained by the size of the cage where zebra finches experience no choice of flock size. From my observations in the wild, I hypothesized that zebra finches could first be in larger flocks in order to explore the different food patches and then reduce flock size when returning to previous food patches. In the wild, we observe that zebra finches are foraging on the ground while conspecifics are waiting in a bush nearby. This could be an indication that flock members wait for each other to reach their own GUD before collectively move to another food patch. In other instances with large food patches and dozens of zebra finches, small groups are leaving separately. This could be an indication that zebra finches form foraging groups by similarity in their foraging needs.

Broader perspectives

Although I reported only analyses with temperature and wind speed in chapter III, I also had the data on barometric pressure. There are several reasons why barometric pressure was not included. First, barometric pressure and temperature were giving similar information. But more importantly, we know little on how barometric pressure affects behaviour: the barometric perception is largely unexplored (Bartheld and Giannessi, 2011). Studies have demonstrated that some animals can detect atmospheric pressure changes in their environments, influence foraging decisions or triggering neuropathic pains (insects, McFarlane et al. 2015; bats, Paige, 1995; rats, Mizoguchi et al. 2011;

guinea pigs, Sato et al. 2011). Studies investigating effects of barometric pressure in birds are essentially focusing on large weather changes (i.e. storms). For example, declining pressure stimulated food intake in white-crowned sparrow *Zonotrichia leucophrys* (Breuner et al., 2013). However, they looked at a decrease of 20 hPa over three hours (field data were suggesting that it happens in 13 hours). In our study site, in the 21 days of experiment the range was about 15 hPa. Low pressure tends to mean weather conditions are going to deteriorate. It would make sense that animals would value food more when pressure is low, as a preparation for degrading weather conditions. Animals might respond to changes more than to barometric pressure per se. However, the time frame in which animals integrate this information is not clear, nor how much and how long this change their behaviour. Researchers working on captive animals have different opinions (personal communications) regarding how much animals in captivity can perceive outside atmospheric pressure. Conducting basic research on the effect of barometric pressure on foraging behaviour in the zebra finch might be of interest. Overall, it is puzzling how little we know about the link between animal behaviour and weather conditions. The zebra finch, living in a particularly unpredictable environment, should have all the reasons to use its senses to act according to future weather conditions.

As much as I have been critical about the whole GUD approach and tried to find reason to not trust it, every bit of experiments convinced me of its logic and its relevance. The number of fields it can add theoretical and empirical insights to, soon became very exciting. GUDs can be seen as an integrative measure of whether or not a forager cares about anything/any object that can be manipulated. This is not restricted to animals; plants make foraging decisions through growing roots in particular directions. Soil can be manipulated such that usable items are spread in an unusable matrix. The GUD approach could be used for other activities than foraging: by using the density of something that an individual can use in something that the individual cannot use. One hypothetical example is the use of GUDs in humans in the context of learning intensity, in a situation where subjects are given the choice of challenges in different thematic or different learning methods. If we filled a box with hundreds of paper pieces with only a small portion of the paper pieces having instructions, how much would a student search for new instructions in a box with language challenges in comparison to a box with mathematical challenges? Or between a box with mathematical challenges explained with words and a box with mathematical challenges explained with formulas? We could thereby have quantitative measures of how much more comfortable a student is with a specific thematic in comparison to another. From that, we could investigate how a social surrounding can affect this difference of comfort. This is only one of many examples where thinking in terms of costs and benefits, along with measuring depleatable benefits can help researchers to put prices (a quantitative measure) on things that influence decision-making processes.

Conclusions

We used the GUD approach to investigate physical and social environment of a social passerine, the zebra finch. We illustrated that the array of questions that can be investigated through focusing on the cost/benefits of foraging is large. Many more research topics on behaviour have the potential to be investigated through the GUD approach.

The present work is also a reminder that research can be done with sand, seeds and a balance and that many fundamental questions still have not been answered. Although the theory behind the GUD framework can be overwhelming, the basic understanding of giving up is very intuitive. Putting in place a system including the amount of food, the amount of sand, the amount of time, the time of day and the placement of the food patches can be very challenging (Bedoya-Perez et al., 2013). However, once this is in place, it can be easily implemented and scaled up. We still know surprisingly little on how weather impacts foraging decisions.

In conclusion, this thesis is a first step, a little collection of backgrounds on giving up densities in zebra finches, calling for further investigations. We learned about zebra finches and we learned about giving up densities. While foraging, zebra finches seem to value their social environment more than their physical environment. GUDs are affected by sociality and are particularly valuable tool to investigate decisions making processes in group-foraging species.

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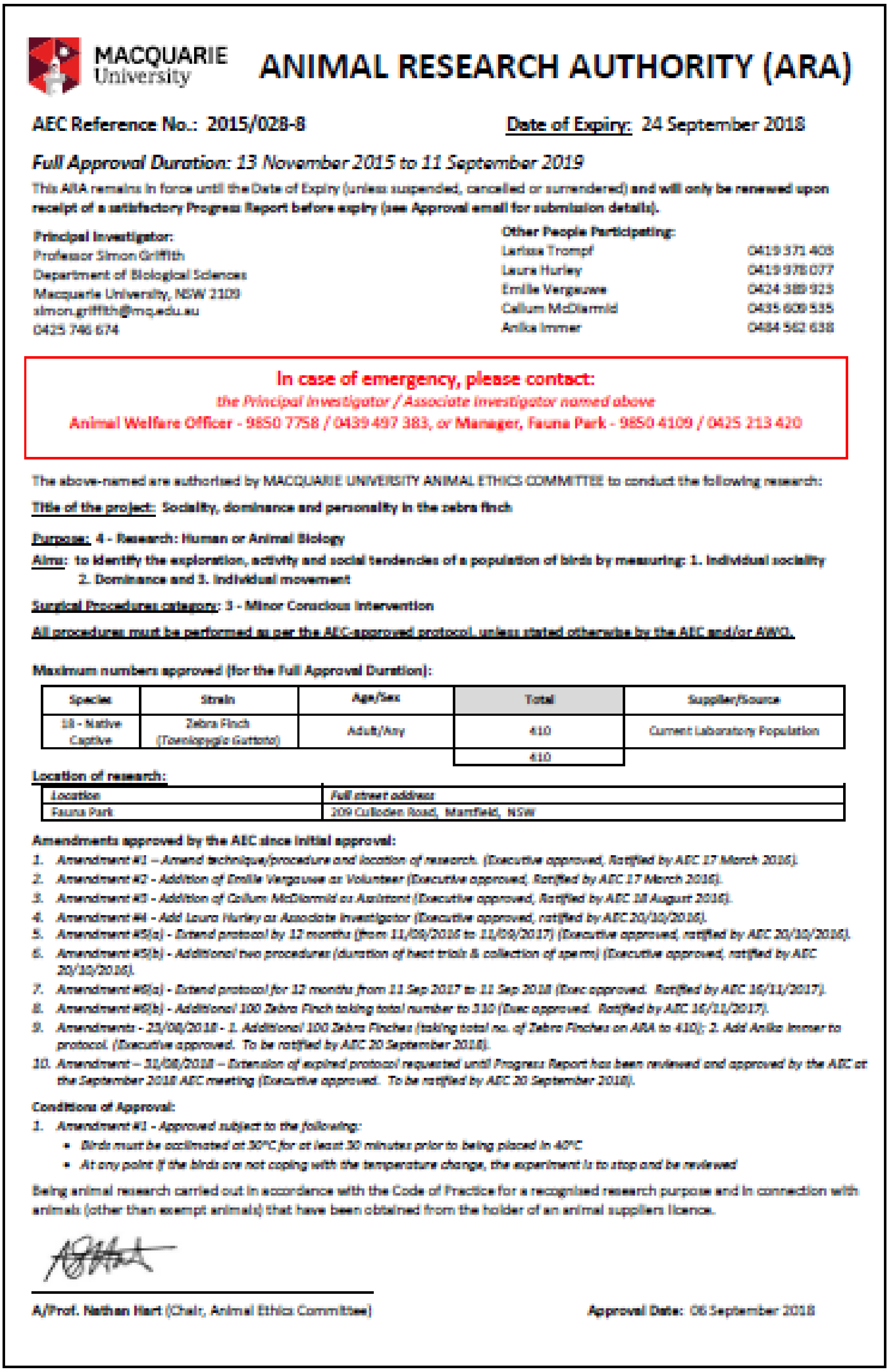

MACQUARIE University

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2015/028-8 **Date of Expiry:** 24 September 2018

Full Approval Duration: 13 November 2015 to 11 September 2019

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) **and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).**

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In case of emergency, please contact:
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Animal Welfare Officer - 9850 7758 / 0439 497 383, *or* Manager, Fauna Park - 9850 4109 / 0425 213 420

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: Sociality, dominance and personality in the zebra finch

Purpose: 4 - Research: Human or Animal Biology

Aims: to identify the exploration, activity and social tendencies of a population of birds by measuring: 1. Individual sociality 2. Dominance and 3. Individual movement

Surgical Procedures category: 3 - Minor Conscious Intervention

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age/Sex	Total	Supplier/Source
18 - Native Captive	Zebra Finch (Taeniopygia Guttata)	Adult/Any	410	Current Laboratory Population
			410	

Location of research:

Location	*Full street address*
Fauna Park	209 Culloden Road, Marsfield, NSW

Amendments approved by the AEC since initial approval:

1. *Amendment #1 – Amend technique/procedure and location of research. (Executive approved, Ratified by AEC 17 March 2016).*
2. *Amendment #2 - Addition of Emilie Vergauwe as Volunteer (Executive approved, Ratified by AEC 17 March 2016).*
3. *Amendment #3 - Addition of Callum McDiarmid as Assistant (Executive approved, Ratified by AEC 18 August 2016).*
4. *Amendment #4 - Add Laura Hurley as Associate Investigator (Executive approved, ratified by AEC 20/10/2016).*
5. *Amendment #5(a) - Extend protocol by 12 months (from 11/09/2016 to 11/09/2017) (Executive approved, ratified by AEC 20/10/2016).*
6. *Amendment #5(b) - Additional two procedures (duration of heat trials & collection of sperm) (Executive approved, ratified by AEC 20/10/2016).*
7. *Amendment #6(a) - Extend protocol for 12 months from 11 Sep 2017 to 11 Sep 2018 (Exec approved. Ratified by AEC 16/11/2017).*
8. *Amendment #6(b) - Additional 100 Zebra Finch taking total number to 310 (Exec approved. Ratified by AEC 16/11/2017).*
9. *Amendments - 23/08/2018 - 1. Additional 100 Zebra Finches (taking total no. of Zebra Finches on ARA to 410); 2. Add Anika Immer to protocol. (Executive approved. To be ratified by AEC 20 September 2018).*
10. *Amendment – 31/08/2018 – Extension of expired protocol requested until Progress Report has been reviewed and approved by the AEC at the September 2018 AEC meeting (Executive approved. To be ratified by AEC 20 September 2018).*

Conditions of Approval:

1. *Amendment #1 - Approved subject to the following:*
    - *Birds must be acclimated at 30°C for at least 30 minutes prior to being placed in 40°C*
    - *At any point if the birds are not coping with the temperature change, the experiment is to stop and be reviewed*

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

A/Prof. Nathan Hart (Chair, Animal Ethics Committee) **Approval Date:** 06 September 2018

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)