The integration of spatial-ecology and animal behaviour in the unpredictable arid zone. A case study with the zebra finch

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Declaration

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.

The protocols to collect morphological measurements and transmitters implant in Zebra Finches used in this thesis were approved by ethics committees at Macquarie University (ARA 2015/017-4).

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Content

General Abstract

Unpredictable environments present several challenges for animals that need to gather information to track ecological fluctuations to ensure access to resources and optimise life-history decisions. Part of the environmental unpredictability is linked to a heterogeneous distribution of resources, both temporally and spatially. Additionally, extreme climatic events (e.g. heatwaves) can prove physiologically and behaviourally challenging. In my thesis I integrated approaches from spatial and behavioural ecology to overcome current difficulties in the study of animal behaviour in the Australian arid environment. I focused research on wild zebra finches (*Taeniopygia guttata*) foraging behaviour. Insight into environmental heterogeneity came from classical vegetation surveys and the most up-to-date freely available remote sensing data, focusing on the spatial distribution of the primary nutritious source for the zebra finch - *Enneapogon* grasses. *Enneapogon* abundance and productivity varied at a local scale, both temporally and spatially, primarily driven by local environmental determinants. This variation was detectable using Sentinel-2A imagery, although with some limitations, validating its use in Australian arid areas, as tool for understanding primary productivity. Furthermore, I demonstrated that in arid landscape, zebra finches have to overcome the challenge of finding food in a patchy environment and cope with extreme climatic conditions. I demonstrated that over two consecutive heatwave events, zebra finch temporal, social and spatial foraging patterns were constrained by the heat. Finally, by experimentally manipulating both food availability and brood size I demonstrated variation in individual foraging behaviour, with some birds using a greater variety of food sources and more persistently checking depleted patches. This behavioural variation in foraging strategy related to reproductive success, providing empirical support for optimal foraging theory. Overall, my results promote the use of a spatial framework for the study of animal behaviour to given valuable insight to the challenges and constraints individuals face in harsh, heterogeneous and unpredictable habitat.

Zusammenfassung

Unvorhersehbar schwankende Umwelten stellen für Lebewesen eine spezielle Herausforderung dar. Die Bewohner solcher Lebensräume müssen laufend Informationen über die Struktur der Landschaft und die wechselnden Bedingungen sammeln um fortwährend ihren Zugang zu Ressourcen zu sichern. Ein Teil der Unvorhersagbarkeit der Umwelt entsteht durch die heterogene Verteilung von Ressourcen, wie Nahrungsquellen, aber auch das Auftreten extremer klimatischer Events, wie Hitzewellen, sind prägende Faktoren. In meiner Doktorarbeit zeige ich auf wie es durch die Integration von Methoden aus der Verhaltensökologie und der räumlichen Ökologie möglich ist einige der derzeitig bestehenden Schwierigkeiten in der Erforschung von tierischem Verhalten in den ariden Bereichen Australiens zu überwinden. Hierbei lege ich einen speziellen Fokus auf das Nahrungssuchverhalten freilebender Zebrafinken (*Taeniopygia guttata*). Dazu kombinierte ich klassische Vegetationsaufnahmen mit den aktuellsten verfügbaren Fernerkundungsdaten („remote sensing“) und legte den Fokus der Untersuchung auf die räumliche Verteilung der primären Nahrungsquelle von Zebrafinken, *Enneapogon* Grasflächen. So konnte ich zeigen, dass die Verfügbarkeit von *Enneapogon* schon in einem sehr kleinen Maßstab sehr stark variiert. Im weiteren konnte ich demonstrieren, dass die Bilder des Sentinel 2A Satelliten, mit einer sehr hohen räumlichen Auflösung, genutzt werden können um verlässlich die räumliche Variation unterschiedlicher Vegetationstypen der ariden Zonen Australiens zu bestimmen, wenngleich es dabei einige Einschränkungen gibt. Zusätzlich analysierte ich das Nahrungssuchverhalten der Zebrafinken im Sommer während zwei aufeinanderfolgender Hitzewellen. Die hohen Temperaturen beschränkten die räumlichen, zeitlichen und sozialen Muster bei der Futtersuche, was darauf hindeutet, dass ein energetischer Konflikt zwischen Nahrungssuche und Thermoregulation besteht. Der erhöhte Aufwand für die Thermoregulation bestätigte sich auch durch die Beobachtung, dass Verhaltensweisen zur Wärmeabfuhr vom Körper mit steigenden Temperaturen zunahmen. In einem weiteren Versuch, bei dem sowohl die Verfügbarkeit von Futter als auch die Brutgrößen in der freilebenden Zebrafinkenpopulation manipuliert wurden, untersuchte ich die Rolle der Beständigkeit mit der Nahrungsstellen besucht wurden. Obwohl die Beständigkeit bei der Nahrungssuche zu einer höheren Anzahl besuchter Nahrungsstellen führte, wirkte sie sich negativ auf den Bruterfolg aus, was empirische Unterstützung für die „optimal foraging“ Theorie darstellt. Insgesamt zeigt die hier vorgestellte Arbeit wie wichtig es ist die räumlichen Rahmenbedingungen in die Untersuchung tierischen Verhaltens miteinzubeziehen um ganzheitlicher untersuchen zu können wie Lebewesen mit den Herausforderungen und Einschränkungen eines harschen, heterogenen, unvorhersehbaren Habitats umgehen.

Chapter One

General Introduction

"Climate plays an important part in determining the average number of species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks. […] The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or distinct species, which subsist on the same kind of food."

Charles Darwin, "On the origin of the species" 1859

Being closely tied to survivorship and fitness, foraging behaviour has been recognized to influence all aspects of individual life-history, from the evolution of communication (e.g. sexual signals, Andersson, 1994; Vehrencamp, 2000; Zahavi, 1975) to the emergence of sociality (Evans et al., 2015; Giraldeau and Caraco, 2000). Studying the economic aspects of foraging revealed that each individual needs to balance its energetic budget between several fundamental activities such as foraging, resting, reproducing and, in some species, rearing offspring (Stephens and Krebs, 1986). This balance depends on the individual current condition and its knowledge on the resource and predation risk distribution and fluctuation across the landscape (Dall and Johnstone, 2002; Stephens and Krebs, 1986). Therefore, the interaction between individuals and environmental structure and temporal variation drive how this energetic trade-off is managed and, consequently, the traits related to foraging context under selection (Dall et al., 2005; Dall and Johnstone, 2002; Stephens and Krebs, 1986).While this interaction has been extensively studied in the wild under predictable environmental fluctuations (Stephens et al., 2007), where the food availability directly depend on few abiotic factors like temperature and rainfall (McNamara and Houston, 2002); in naturally unpredictable conditions little is known. The heterogeneous distribution of resources together with the occasional extreme climatic events make the interaction between environmental condition, food availability and animals' response extremely difficult to predict (Morton et al., 2011; Reynolds et al., 2004). Thus, the traits related to foraging context under selection in unpredictable environments have been limited to theoretical and empirical works in captivity.

The objective of this thesis is to study the foraging behaviour in an unpredictable and harsh environment, and it aims at identifying the environmental constraints which might represent fundamental selective processes that shape the evolution of arid animals' behavioural and physiological adaptations. I believe the best approach to study the proximate and ultimate causation of arid animals' behaviour is to firstly understand the heterogeneity of their landscape structure, characterising the possible challenges. Therefore, before developing hypotheses and testing them experimentally, it is important to focus on the study of the environment *per se*. In consequence, my thesis constitutes a bridge between spatial and behavioural ecology, especially for the study of animal behaviour in arid environment. Combining both theoretical and practical frameworks, I will show how this integrative approach might represent the way to overcome current difficulties in the study of animal behaviour in arid environment, with a special focus on wild zebra finch (*Taeniopygia guttata*) foraging behaviour in the Australian arid environment.

Environmental unpredictability: the Australian arid area

All natural environments share a certain degree of unpredictability, with fluctuations in resource availability and also in internal energetic states and in predation risk (Dall et al., 2005; Dall and

Johnstone, 2002). In order to survive and reproduce, animals need to constantly gather information to anticipate these changes, avoiding dangerous situations and ensuring access to food resources (Dall et al., 2005). Environments where ecological fluctuations (e.g. food resources) are mainly due to changes in climate conditions (e.g. season) are generally referred to as stable, because animals can use indicators (e.g. hours of daylight change, temperature) that reliably predict these changes (McNamara and Houston, 2002). On the other hand, environments where resource availability and other ecological features do not depend on climate alone, they can be called unpredictable, because the signals of changing conditions are not reliable or very limited (Dall et al., 2005; Dall and Johnstone, 2002). Therefore, in unpredictable environments, animals are challenged when gathering information on ecological fluctuations (Dall et al., 2005; Dall and Johnstone, 2002). Furthermore, part of the unpredictability is linked to the occurrence of extreme climatic events (e.g. heatwaves, drought, exceptional rainfall events) that, especially in the current climate change scenario (Ummenhofer and Meehl, 2017), can disturb individuals' energetic states (Wingfield, 2003; Wingfield et al., 2017) and might have catastrophic consequences (e.g. mass mortality, McKechnie and Wolf, 2010). However, investigating how animals cope with environmental unpredictability represent a challenge for researchers, although fundamental to understand the traits under selection. The demanding economical and human resources to conduct long-term ecological surveys *in situ*, together with the limitations of the methodologies to assess large areas and habitat complexity caused research on unpredictable environments to be globally neglected (Greenville et al., 2017).

The Australian arid and semi-arid ecosystem represents one of the largest unpredictable environments of the planet, occupying around 70% of the mainland (Morton et al., 2011; Orians and Milewski, 2007). In this ecosystem, the particularly unpredictable interaction between abiotic factors (e.g. high variability of local rainfall, the heterogeneity of moisture and nutrients in the soil, Morton et al., 2011) and primary productivity, shapes the 'boom and bust' (i.e. extremely fluctuating cycles, Fig .1) population dynamics of a variety of animal species (Morton et al., 2011). Even at a local scale, both annual rainfall and individual rainfall events can be highly variable (Acworth et al., 2016). Furthermore, small rainfall events timed with the phenology of certain plant species can elicit large responses on those species while not greatly affecting others, favouring the heterogeneity of the landscape. On the other hand, heavier precipitation during periods of the year that do not favour the growth of a particular species (e.g. those sensitive to temperature or solar exposition) may not translate into net-productivity (Fernández, 2007; Watson et al., 1997). Additionally, the landscape structure (e.g. topography), the presence of dry creeks, and artificial water sources have been found to affect the soil nutrient composition, the water soil content, and consequently the vegetation response both in type and abundance (James et al., 1999; Morton et al., 2011; Orians and Milewski, 2007). Therefore, it is extremely difficult to make general predictions on rainfall pulses and arid productivity (Reynolds et al., 2004). Nonetheless, tracking the primary productivity variation will allow to predict the fluctuations that determine habitat quality and population dynamics for a variety of consumers (Fernandez et al., 2016). Traditionally, primary productivity variation (i.e. herbivorous and granivorous food availability) was modelled from rainfall and assuming an oversimplified linear relationship between vegetation response and rainfall events (Morton and Davies, 1983; Zann et al., 1995; Zann and Straw, 1984).

To improve our understanding of the way in which animals respond to food availability fluctuations, we need to be able to better quantify local primary productivity, rather than just using the rainfall. Since the 1960s, the idea of using remote sensing tools has been considered a time- and cost- effective solution to overcome limitations in ecological studies (e.g. difficulties in conducted long-term *in situ* researches), especially in extreme environments like deserts (Barrett and Hamilton, 1986; Tueller, 1987). However, remote sensing of (semi-) arid environments remain particularly challenging, because of their clumped nature, the low vegetation cover and the high soil reflectance (Nagendra, 2001; Okin and Roberts, 2004). To date, remote sensing researchers are still working to find the best way to process satellite imageries to represent arid areas, combing the actual vegetation variation measured in the field and satellite data (e.g. Asia: Kang et al., 2018; Africa: Mapfumo et al., 2016; North and Central America: Théau and Weber, 2010; Australia: Chen et al., 2014). Therefore, currently the only way to estimate arid landscape complexity is still through classic vegetation surveys.

A complex environment presents a significant challenge to researchers and even greater ecological challenges for arid adapted organisms (Letnic and Dickman, 2006; Morton et al., 2011). Animals exhibit life-history responses from extreme opportunism to high levels of specialisation (e.g. specialised use of perennial plants; Morton et al., 2011). For example, most of Australian arid zone birds are continuous breeders, so they are able to start breeding whenever the conditions are propitious (Morton et al., 2011). At the same time, species have been found to reproduce and rear offspring avoiding summer months (Duursma et al., 2017), presumably because the extreme temperatures would negatively impact foraging behaviour, adults', chicks' body mass, and ultimately survivorship (Andrew et al., 2018, 2017; McKechnie and Wolf, 2010). Therefore, the unpredictability of food resources of the Australian arid habitat is not the only challenge animals experience. The extreme temperature conditions challenge the physiology of animals that face an energetic trade-off between thermoregulation and other activities, such as foraging and reproduction (du Plessis et al., 2012; Edwards et al., 2015; Funghi et al., 2019). Therefore, studying foraging behaviour in arid environments highlights constraints individuals have to face to survive and which strategies they have developed to cope with extreme conditions. Furthermore, accurately assessing fluctuations of primary productivity in such complex landscape will be pivotal to understand the ecological response of animals that primarily use seeds as food source.

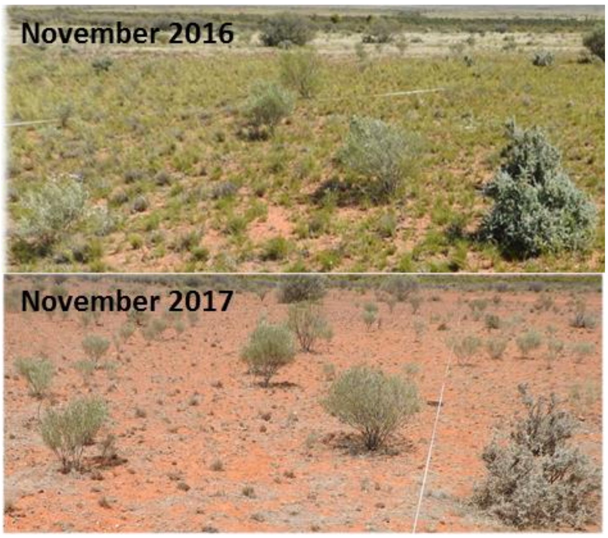

Figure 1 Example of the ‘boom’ (November 2016) and ‘bust’ (November 2017) phases of the primary productivity in an Australian arid area.

Foraging behaviour

The proximate and ultimate causation for the variability in resource-use, especially between conspecifics sharing the same environment, is key to understanding animal evolution (Bolnick et al., 2003; Dall et al., 2012; Darwin, 1859; Stephens and Krebs, 1986; Van Valen, 1965). The optimal foraging model, based on the premise that animals forage in a way which maximises the benefit increasing their energy or reproductive success, has been successfully used in predicting the decision rules used by individuals (Araújo et al., 2011; Stephens and Krebs, 1986). Sampling the landscape for food is an implicit necessity for the optimal foragers (Krebs, 1978). For example, an individual may rely on stable and known food sources, increasing its immediate food intake, or it may instead invest some time in searching for new food sources and return to depleted patches previously experienced as rewarding (Krebs, 1978; Stephens, 1987). Theoretical models predict the optimal balance between food searching and exploitation in stable and unpredictably fluctuating environments, taking into account different levels of predation risk, which can represent a threat influencing preys’ foraging activity in the wild (Dall and Johnstone, 2002; Stephens, 1987). Especially in unpredictable environments, if the risk of starvation or predation is minimal and the possibility of exploiting the food renewal of the tracked patch is high, animals should spend time sampling the landscape, because it will lower the risk of starvation in case of a sudden change of the habitat condition (Dall and Johnstone, 2002). Many empirical studies on a variety of taxa tested whether individuals optimally manage the trade-off between exploration and exploitation of food sources under unpredictable food availability in captivity (insects:Fourcassi and Traniello, 1993; Keasar et al., 2013; fish: Pitcher and Magurran, 1983, birds: Dall and Witter, 1998; Krebs, 1978; mammals:Devenport and Devenport, 1994). However, studies on this topic in the wild are still rare, probably because until recently it was impossible to discriminate between sampling and exploitation of natural patches (Naef-Daenzer, 2000). Recent technological advances may allow to disentangle this discrimination. For example, the use of automated data loggers in a population of mix-species birds (great tits, *Parus major*, blue tits, *Cyanistes caeruleus*, marsh tits, *Poecile palustris*, coal tits, *Periparus ater* and nuthatches, *Sitta europaea*) allowed to understand that individuals in a stable food environment concentrated their sampling effort in the early morning to exploit the best option in the afternoon (Farine and Lang, 2013).

In a changing environment, where food resources are patchy or only temporarily available (e.g. flowers for pollinators, Szigeti et al., 2018 and unpredictable arid habitat, Fryxell et al., 2005), plasticity in searching efficiency may play an important role to enhance individual fitness (Bolnick et al., 2003). In unpredictable and complex environments, ecological generalists that sample and exploit more resources using different parts of a heterogeneous habitat, are expected to be generally favoured because they have more information to cope with changing conditions (Dall and Johnstone, 2002). In such environments, the differences between individuals are expected to be more pronounced and the success of one strategy over others should be directly measured by the reproductive success. However, individual differences in spatial foraging strategies that optimally balance the exploration-exploitation of depleted food resources and their relationship with breeding success in a natually unpredictable environment has rarely been studied.

Study species

The zebra finch (*Taeniopygia guttata*) is a small passerine (10cm, 9-15g) widespread in the Australian arid and semi-arid inland (Zann, 1996). It is a strictly granivorous species (Fig. 2a), as many other estrildid birds (Payne, 2016). Zebra finches' nutritional requirements have been well characterised, with the seeds of dominant grass species (such as *Enneapogon*) making up a considerable portion of their diet (>80%) in the Austral spring, concurring in trigger their reproduction (Morton and Davies, 1983). They are sexually monogamous, and pairs are referred to as 'inseparable' (Zann, 1996). The strength of the pair bond between the male and female is not only long-lasting, but also faithful (Griffith et al., 2010), with low extra-pair copulation and mate guarding (Rossetto et al., 1991). Furthermore, more coordinated couples generally have higher reproductive success (Mariette and Griffith, 2015, 2012a).

While the zebra finch mating pair dynamic are well characterized (Mariette and Griffith, 2015, 2012a), only recently their gregariousness and social dynamics have been investigated in more detail (Alarcón-nieto et al., 2018; Boogert et al., 2014, 2018; Brandl et al., 2019a; Maldonado-Chaparro et al., 2018). Zebra finches can be either nomadic or stationary, depending on the ecological conditions. In favourable conditions, they move in small mono-species, mixed-sex flocks (maximum 20 individuals, Zann 1996, McCowan et al., 2015a, Fig.2c); whereas aggregations of hundreds have been registered during droughts and close to water sources (Immelmann, 1965). Living in such challenging environment, social information is an unreliable predictor of habitat quality (reviewed in Ward and Webster, 2016). Nonetheless, zebra finches showed use of social information by preferentially breeding close to conspecifics and prospecting at conspecifics' nests (Brandl et al., 2018; Mariette and Griffith, 2012b). Recently, it has been suggested that wild zebra finches visit conspecifics' nests to synchronize the breeding with their close neighbours (Brandl et al., 2019b; Brandl et al., 2019c, Mariette and Griffith, 2012b), enhancing the advantages of parents' (and then juveniles') social foraging (Evans et al., 2015). If and how zebra finches gather social information on foraging resources has not been studied yet. However, it has been suggested that some features in zebra finches' landscape, trees on which the birds often aggregate during the day (therefore called 'social trees'), might be used as information centres (McCowan et al., 2015).

The zebra finch is well adapted to unpredictable conditions, both physiologically and behaviourally (Andrew et al., 2017; Perfito, 2016; Zann, 1996). For example, morphological adaptations called 'tip-down' (Fig.2b) allow them to drink efficiently, reducing the duration and the number of visits to water sources (Zann, 1996). Furthermore, the narrow diet based on grass seeds, with birds in most areas specializing in certain species, has been suggested to be adaptive to arid habitats as the high content of carbohydrates in the seeds provide energy and metabolic water (Zann, 1996). Moreover, the seeds produced during climate favourable conditions are abundant and may persist for several months on the ground, especially in dry areas, making arid-adapted grass species the most reliable food source for the zebra finches (Morton and Davies, 1983). The extent of grass seeds variability across the landscape has not been studied yet and therefore the traits under selection related to the zebra finches searching and consuming food remain unknown. However, few studies in the wild found that individuals differ in the amount of food patches (i.e. feeders) visited and their frequency of visitation (Mariette and Griffith, 2013; McCowan et al., 2015a), but their adaptive value still need investigations.

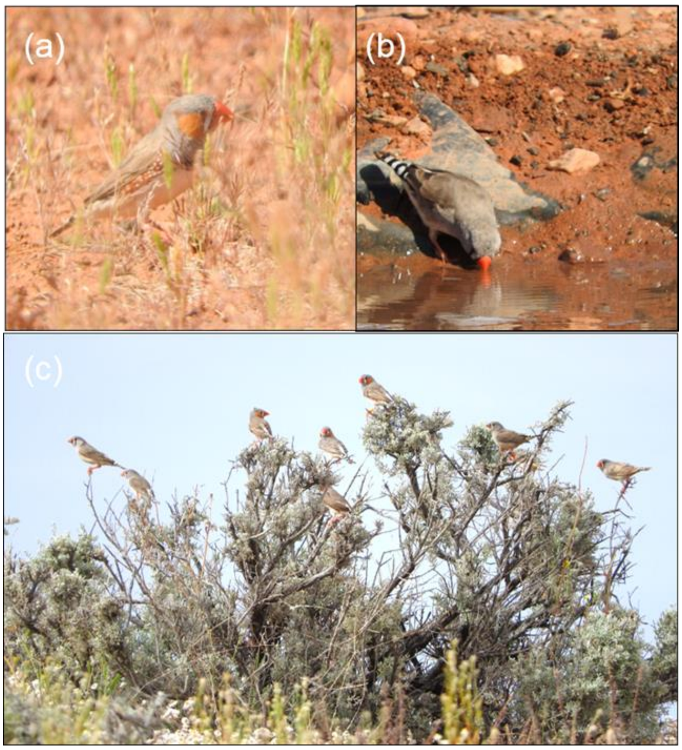

Figure 2 Male zebra finch eating natural grass seeds (a). Female zebra finch ‘tip-down’ drinking (b). Mixed-sex flock of zebra finches (c).

The opportunistic behaviour of zebra finches allows them to reproduce not restricted to a defined period, but rather when the conditions are propitious (e.g. after a rain event). This has concurred to easily domesticate them and breed them in captivity. The zebra finch is one of the most important species used in behaviour, neurobiology and genetics research (Griffith and Buchanan, 2010; Zann, 1996). The majority of this research has been conducted in domesticated zebra finches, which became a supermodel for our scientific understanding (Griffith and Buchanan, 2010). However, the gap between how much the zebra finch contributed to different scientific areas and the scarcity of information about their ecology is striking. Thus, a comprehensive knowledge of wild zebra finches’ behavioural ecology is particularly important, because it might lead to different results and interpretation of studies conducted in captivity (Dall and Griffith, 2014). Additionally, over the past few years the captive zebra finches have also started to become one of the model species in studies on how social behaviour and environment influence individual fitness (Alarcón-nieto et al., 2018; Boogert et al., 2018, 2014; Farine et al., 2015a; Griffith and Buchanan, 2010). Only one recent study has provided a replication of a captive study (Boogert et al., 2014) in the wild, confirming the effect of early-life stress on juveniles’ connectedness within the social network, thus demonstrating that well-designed captive studies can give meaningful insight into the natural social behaviour (Brandl et al., 2019a). Overall, while several aspects of the wild zebra finches’ ecology still need to be investigated, they are a suitable and highly interesting species for the investigation of the evolution of different individual strategies to cope with Australian arid conditions.

Study aims

My thesis consists of four original studies conducted in an Australian arid/ semi-arid area. I characterise the struggles that animals have to face when inhabiting this challenging environment, with a particular focus on wild zebra finches. The broader aim is to provide insight on the complex interaction between environmental unpredictability and animal foraging behaviour integrating classical methods with up-to-date technology and statistical approaches.

Zebra finches are strictly granivorous and base their breeding phenology on primary productivity of Austral spring grasses (Morton and Davies, 1983). However, the variation of grass seeds distribution across the landscape is still unknown. Therefore, the first aim is to understand the fluctuations of seed availability across the zebra finches' landscape and over time, while they were breeding. In **Chapter 2** I describe in detail the phenology of the study site's most dominant grass species: the *Enneapogon* spp. It has already been described as a fundamental requirement representing over 80% of the zebra finches' diet (Morton and Davies, 1983). To characterise the spatial variability of *Enneapogon* grassland at wide and local scale, I set several classical vegetation transects where I performed grass surveys, repeatedly between October 2016 and February 2017.

In **Chapter 3** I propose a method based on remote sensing data, with the aim of studying the primary productivity (i.e. *Enneapogon* grassland) fluctuations at a scale relevant to the individuals in a population and in the challenging arid environment. I match the most up-to-date satellite data freely available (Sentinel-2A, 10m resolution) with another classical vegetation survey (10 x 10 quadrat plots), where I characterise the vegetation association of different vegetation types, *Enneapogon* seed-productivity and the total vegetation cover across the landscape. This method shows that by previously identifying (and geo-locating) patches covered by specific vegetation types (e.g. *Enneapogon*), it is possible to directly track how vegetation respond to abiotic conditions (e.g. rainfall). In this way, the actual condition of a habitat can be estimated at high spatial resolution. This will make it possible to study how animals respond to unpredictable environment, overcoming the complex, interactive and non-linear nature of the relationship between rainfall and vegetation responses (Reynolds et al., 2004).

An absolute definition of extreme conditions cannot exist, because it is the balance between the relative number of predictable and unpredictable events that makes an environment more or less extreme and drives the development of organisms' physiological and behavioural strategies (Wingfield, 2003). In order to understand how environmental constraints may affect individuals' foraging behaviour and ultimately survivorship, in **Chapter 4,** I present a study on foraging activity conducted during the Australian summer and over two consecutive heatwave events. I used RFID (radio-frequency identification) detectors in several artificial feeders (Fig. 3) to follow how RFID-tagged zebra finches' foraging activity changed in response to extreme heat events. I analyse changes in individual activity at a fine temporal scale and the spatial pattern measuring how it varied in relation to the only water source.

Theoretical work predicts that there are two non-mutually exclusive strategies animals may use to cope with unpredictability of food sources: relying on social information, gathered by observing and following conspecifics at foraging location and using inadvertently shared acoustic cues to find food patches; or increasing personal knowledge of the landscape and its fluctuations, avoiding dangerous situations and ensuring access to food resources (Dall et al., 2005; Dall and Johnstone, 2002; Giraldeau and Caraco, 2000; Giraldeau and Dubois, 2008). In **Chapter 5,** I present an experimental study, which aims at understanding the proximate causes of individual differences in resource use across the landscape. In this study, I provided two sets of artificial feeders to a wild (RFID-tagged) zebra finch population and manipulated the food availability in half of the feeders creating a mix of stable and ephemeral food patches. By increasing the quality of food in the ephemeral food sources and by tracking the individuals' use of the ephemeral feeders when they were empty, I test for the presence of individual variability in resource use across the landscape. Furthermore, to fully understand the reproductive pay-off of different spatial foraging patterns, I combined the food manipulation with a brood size manipulation experiment. In this way, I test whether the difference between parents' spatial foraging behaviour predicted their breeding success and, according with the optimal foraging theory, I expect different foraging behaviours to reflect a difference in breeding success of enlarged broods. On the other hand, the reliability of (some, stable) food sources (i.e. stable feeders) should be able to overcome the energetic requirements of the parents with reduced parental load.

Finally, I conclude the thesis in **Chapter 6**, by providing a brief synthesis of the main findings of earlier chapters.

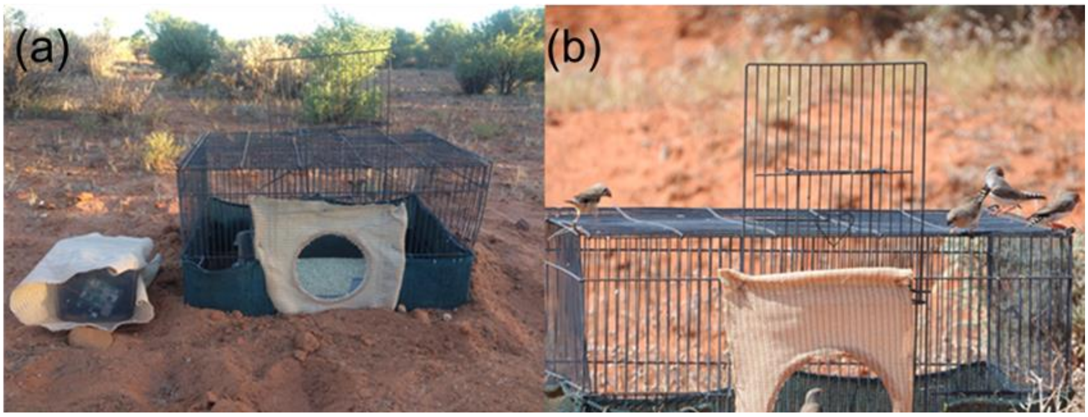

Figure 3 Artificial feeders equipped with seeds in the tray and a round antenna at the entrance connected to an RFID-decoder placed next to the feeder (a). Small flock of zebra finches, composed of males, females and juveniles (with black bill) foraging in the feeder (b).

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Chapter Two

Characterization of spatial and temporal heterogeneity in grass productivity across an Australian arid landscape

Funghi Caterina, Schuett Wiebke, Griffith Simon C.

Abstract

Even though the role of vegetation spatial heterogeneity is generally recognised to determine habitat quality and population dynamics for a variety of consumers, especially for Australian arid areas, little is known about the extent to which it occurs at a local level. Here, we used vegetation surveys to estimate the spatial and temporal heterogeneity of the most dominant grass genus – *Enneapogon* -, which represents the main food source for many animals inhabiting this arid environment. By sampling the landscape at a very local scale, we provide a rare demonstration of spatial and temporal fluctuation in the productivity of *Enneapogon* grassland. Finally, we investigated which environmental factors might influence the complexity that we characterised at the local scale, finding that the interaction between topography and water soil content affected the variability in *Enneapogon* grassland.

Keywords: Australian arid environment, *Enneapogon* grassland, local scale, resource distribution, primary productivity.

Introduction

The Australian arid zone has been recognised as a relatively understudied habitat, although it covers 70% of the Australian mainland (Greenville et al., 2017). One of the major challenges related to studying Australian arid ecology is to understand the abiotic factors (e.g. rainfall, temperature) that shape the heterogeneity in primary productivity across the landscape (Morton et al., 2011). This will allow to predict the fluctuations that determine habitat quality and population dynamics for a variety of consumers (Fernandez et al., 2016). While, for instance, there is a clear link at the broad-scale between the temporally and spatially unpredictable rainfall and primary productivity (Morton et al., 2011; Nano and Pavey, 2013; Reynolds et al., 2004), at a local scale the response of vegetation is likely to be determined by soil water availability (Acworth et al., 2016; Reynolds et al., 2004). The composition of the soil will also affect productivity, and soils in the Australian arid zone are particularly nutrient-poor, with scarcity in both macro (e.g. Phosphorous, Nitrogen) and micro nutrients (e.g. Iron, Zinc, Cobalt; Orians and Milewski, 2007).

A better understanding of local heterogeneity in primary productivity in arid zone landscapes will provide new insights into the challenges faced by secondary consumers as they try to optimise their foraging and breeding behavioural ecology. Thus, understanding the variability of grass distribution across the landscape is a fundamental step for the study of animals that rely on grass seeds to survive and reproduce in arid habitats. Considering the high local variability in rainfall events and the complex, non-linear relationship between rain and primary productivity (Acworth et al., 2016; Reynolds et al., 2004), it would be important to study the grass distribution across the landscape, bypassing the relationship with rainfall, that would be too simplistic, anecdotal and in some cases even misleading (e.g. relating rainfall data collected in an area might be different from the one in study). Australian arid zone animals exhibit life-history responses to the spatial and temporal unpredictability of grass, with adaptions ranging from extreme opportunism to high levels of specialisation (e.g. specialised use of perennial plants; Morton et al., 2011). For example, the summer grasses of the genus *Triodia* (spinifex) represent an Australian biota, unique worldwide, drought-tolerant, perennial and sclerophyllous. It has been demonstrated how several taxa are associated with spinifex, that provides food and shelter (specialized-spinifex-dwelling: *Amytornis* grass-wrens, Christidis et al., 2010; lesser hair-footed dunnart, *Sminthopsis youngsoni*, Haythornthwaite and Dickman, 2006) and, in some cases, even phylogeographical and phylogenetical speciation (e.g. phasmid geckos, *Strophurus* spp., Laver et al., 2017). On the other hand, other species respond to the unpredictable fluctuations showing a dramatic opportunism, developing physiological and behavioural adaptations. For example, zebra finches, *Taeniopygia guttata*, are continuous breeders, and potentially are able to start a breeding cycle whenever the environmental conditions are suitable (Zann, 1996), although they appear to be constrained by the hot summer climate (Duursma et al., 2017). In fact, the diet of the zebra finch has been found to consist of Austral spring grasses and specifically, more than 80% of it consists on *Enneapogon* spp., whose fluctuation has been shown to shape the breeding phenology of zebra finches in southern Australian populations (Morton and Davies, 1983). Therefore, quantyfing the spatial and temporal variability in the primary productivity of *Enneapogon* spp. in the arid landscape will provide insights into the ecological response of zebra finches and other seed-eating animals that primarily use these grasses (e.g. Buckley, 1982; Hoffmann, 2010).

In homogenous, temperate environments, satellite-derived, remote sensing information is commonly used to monitor the synchrony between trophic levels at a scale relevant to individuals and to identify the environmental cues used by animals to time their breeding. Consequently, remote sensing surveys can aim to understand how selection acts on phenological traits (Cole et al., 2015; Durant et al., 2007). On the other hand, in highly heterogeneous arid environments, remote sensing information is currently not a reliable tool to estimate vegetation structure or vegetation types' spatial distribution at a local level (Hamada et al. 2019, Chen et al., 2014; Okin et al., 2001). Actually, the low vegetation cover, their tussock distribution and the high soil reflectance represent a major issue to accurately describe and monitor vegetation cover in arid areas through remote sensing tools (Ren et al. 2018, Nagendra, 2001; Okin and Roberts, 2004). Therefore, in such complex habitat, classical vegetation surveys are still the most reliable way to estimate variability in vegetation distribution.

The role of environmental complexity (i.e. abiotic-biotic relationship between climate, soils and primary productivity) has been demonstrated to influence the habitat quality, population dynamics and, consequently, to alter energy flux input into the trophic web (Fernandez et al., 2016; McNaughton et al., 1989). However, only few studies have quantified spatial heterogeneity (e.g. topography, soil water content, vegetation response) in arid ecosystems (e.g. Alvarez et al., 2011; Augustine, 2003; Watson et al., 1997) and, to our knowledge, none has focused on grass species variability in Australian arid ecosystem. In the present study, we focused on the most dominant grass genus present in a study site in arid Australia, the *Enneapogon* spp. Two sets of survey transects were established across the study site and repeated sampling was performed along four months, between October 2016 and February 2017, covering the transition between a climate-favourable spring (i.e. after winter rainfall events) to extremely hot summer. Additionally, we tested the effect of two environmental factors on the variability of *Enneapogon* seeds abundance: topography and other vegetation cover. The first was estimated through the elevation of each sampled site. Elevation has generally been recognized to influence the vegetation composition affecting soil nutrient composition and solar exposition (e.g. Australia: Morton et al., 2011; Orians and Milewski, 2007; North America: Thompson et al., 2005; Africa: Augustine, 2003). The vegetation cover is related to the vegetation density and thus soil water availability (e.g. Alvarez et al., 2011; James et al., 1999) .We estimated the variability of seeds abundance, the spatial distribution and the characterization of temporal variation of *Enneapogon* grassland in an Australian arid area.

Methods

The study was conducted in Gap Hills, an area located at the northern point of the Fowlers Gap Research Station (31°05′13.1″S, 141°42′17.4″E), New South Wales, Australia. Here, a long-term study established six clusters of nest-boxes in order to monitor the breeding activity of the zebra finches since 2004 (Griffith et al., 2008). A central water dam is surrounded by a dry creek system, dominated by *Acacias* and ephemeral forbs, while further away from the dam the habitat is more open and chenopods shrubs dominate (Griffith et al., 2008). In order to characterize the general grass seed variability (i.e. main food source for the zebra finches, Morton and Davies, 1983; Zann and Straw, 1984) eighteen 50 m transects were established at randomized locations in an area within 2 km of the artificial water dam (hereafter ‘larger-scale set’, maximum distance between transects=2.9 km, mean ± SE=1.4±0.16 km, area= 4.3 km^2). Additionally, another eighteen 50m transects (hereafter ‘smaller-scale set’) were randomly set in order to quantify the grass variation within a smaller spatial scale (maximum distance between transects=1.5 km, mean ± SE=0.64±0.08 km, area=0.9 km^2, Fig.1b), focusing on the area most frequented by the zebra finches during breeding activity (home-range during breeding less than 2 km^2, Zann and Runciman, 1994). Between the 28th October 2016 and 2nd February 2017, along all of the 36 transects, we did a point sample every meter along each transect, and within 10 cm of each of those points we counted the number of *Enneapogon* species (genus level) that had spikelets with

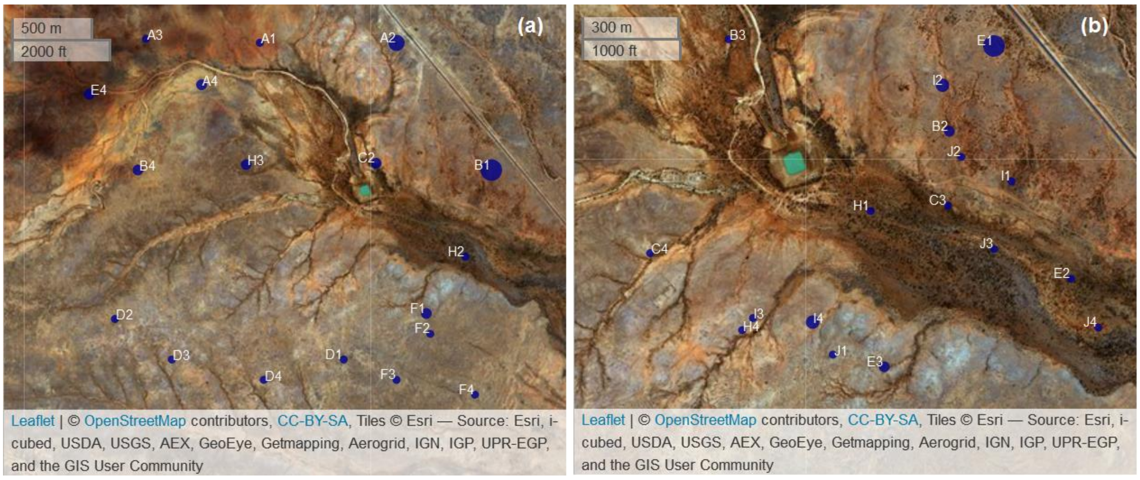

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Figure 1 Map of the spatial distribution of the larger-scale (a) and smaller-scale (b) set of transects across the landscape on Ensri satellite image. The size of the markers are proportional to the number of *Enneapogon*’s spikelets with seeds sampled in October 2016.

fruits (seeds), and those that were without spikelets (vegetative/dead, quiescent, without seeds). Each transect was sampled eight times (Table 1), and averages were calculated for each month and for each transect. Furthermore, during the first sampling event (October) each starting transect point was geo-localized (Garmin GPSMAP 64s, Germany) and used as North-Eastern corner of a 10x10m quadrat. The vegetation cover was estimated for the overall quadrat (i.e. total vegetation cover), the over-storey, under-storey and *Enneapogon* grassland covers. The estimation of competition between *Enneapogon* and other vegetation was calculated as the proportion of the non-*Enneapogon* vegetation cover over the total vegetation cover of each quadrat. The elevation of each transect point was given by the GPS and used to represent the variation in topography.

In order to assess the spatial independence (i.e.: randomness) of the two sets of transects, we calculated the spatial autocorrelation of the (average log-transformed) number of *Enneapogon* spp. with seed for each set of transects separately, using the Moran´s *I* function (two sides) in the ‘ape’ R-package (Paradis and Schliep, 2018). In order to test whether the spatial distribution of *Enneapogon* spp. with seeds was different from homogeneity (i.e. null hypothesis), we run a chi-square test of goodness of fit with the count of spikelets with fruits of the first sample event

Table 1 Time line of transects’ repeated measurements (green) performed between October 2016 and February 2017. The number corresponds to the sampling events

	Oct			November																	December													January							Feb	
	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17 to	7	8	9	10	11	12	13	14	15	16	17	18	19 to	15	16	17	18 to 23	24	25	26 to 31	1	2
Sampling event	1						2							3							4							5						6				7			8	

(October) of the larger- and, separately, the smaller-scale set of transects. We used the October sampling event because the whole vegetation in the study area was at the 'boom' phase of the characteristic 'boom and bust' cycle, as consequence of winter rainfall (Morton et al., 2011)

We tested whether the distribution of *Enneapogon* spp with seed changed accordingly with the sampling events (month, i.e. seasonal effect). A Linear Mixed Model (LMM) was built with the (average log-transformed) number of *Enneapogon* spp with seed of the larger-scale set of transects as response variable, month (as categorical variable) as fixed term and transect ID as random term. We tested whether the distribution of *Enneapogon* spp with seed also changed accordingly with the transect location (transect ID, i.e. spatial component), by calculating the spatial contribution to the total variability of the repeated (seasonal) *Enneapogon* sample. We therefore calculated the repeatability of *Enneapogon* spp with seed at different locations (Nakagawa and Schielzeth, 2010). The adjusted repeatability returns the value of each factor (within-group or 'fixed term' and between-group or 'random term') specified in the model, which correspond to their relative weight on the variance of the dependent variable. It is calculated by the proportion of total variance between-groups (i.e. variance of the random term in the LMM, location) over the total variance (i.e. sum of random term and residual variance in the LMM) and taking into account the effect of the fixed term of the model. Thus, to disentangle to seasonal and spatial effects on our repeated measure sample at different locations, we calculated the portion of variation explained by the location (i.e.: group) and month (i.e. fixed term), we ran the same LMM described with rptR package in R (Stoffel et al., 2018), setting 1000 permutation tests to assess the likelihood of the 95% confidence interval to be significantly different from zero and extracting the variance explained by the fixed effect in the model (i.e. month). The same model was also run for the smaller-scale set of transects. Additionally, separately for the two sets of data, we calculated the spatial component of the variation from a LMM without the month as fixed effect (i.e. un-adjusted repeatability).

We tested whether sample sites also differed in the timing of reaching the maximum number of *Enneapogon* spp. with seeds. Firstly, we counted how many transects reached the maximum number of *Enneapogon* with seeds in each sampling month. Then, we performed a likelihood test (G test) of goodness of fit, corrected for small sample size ("Willing") to test if the maximum number of seeds occurred in a specific sampling month or whether the peak of *Enneapogon* with seeds at each transect was homogenously spread along the sampling time.

Finally, for the smaller-scale set of transects, we tested whether the variation in seeds abundance was related to the elevation and the potential competition with other vegetation. We used a general linear model (LM) with the (log-transformed) number of *Enneapogon* spp with seeds of the first sampling event (October) as the response variable, and elevation, proportion of non-*Enneapogon* cover and their interaction as explanatory variables.

Results

Neither the larger- nor the smaller-scale set of transects were spatially auto-correlated (larger-scale set: observed Moran's I= -0.03, p=0.53, n=18, smaller-scale set: observed Moran's I= -0.01, p=0.28). The spatial distribution of *Enneapogon* spp with seed, counted in October, was not homogenous (larger-scale set: X^2=303.8, p<0.001, n=18, smaller-scale set: X^2=479.6, p<0.001, n=18), confirming the heterogeneity of the spatial distribution of the *Enneapogon* grassland.

A seasonal effect was observed in both the larger-scale (X^2=47.4, p<0.001, n=18, df=4) and smaller-scale set of transects (X^2=52.3, p<0.001, n=18, df=4, Fig. 2 a, b). The proportion of variation in *Enneapogon* spp seeds distribution explained by the location of the transects (i.e. spatial component) was relatively low and only significant (i.e. 95% CI not including 0) for the adjusted repeatability ($R_{spatial}$=0.36 CI=[0.1,0.6], un-adjusted: $R_{spatial}$=0.18, CI=[0,0.4], n=18), meaning that for the wider set of transects, the variation in *Enneapogon* spp seeds abundance was primarily due to seasonal effects ($R_{seasonal}$=0.45 CI=[0.26,0.83]), rather than the spatial distribution. On the other hand, for the smaller-scale transects the spatial component of the variation was greater ($R_{spatial}$=0.57 CI=[0.36,0.75], $R_{seasonal}$=0.34 CI=[0.2,0.7]; un-adjusted: $R_{spatial}$=0.37, CI=[0.1,0.6], n=18), meaning that each location varied consistently over time with

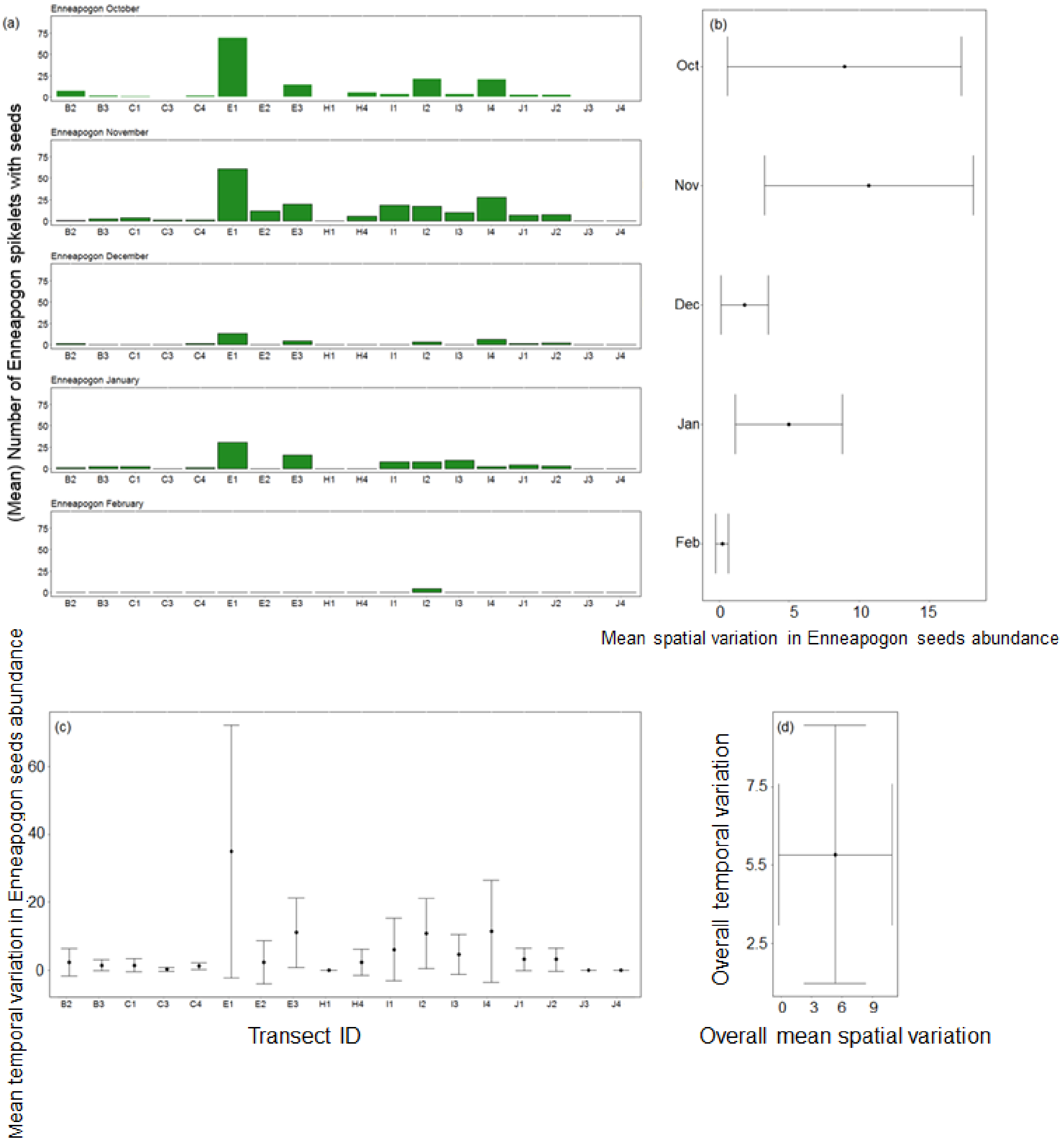

Figure 2 Spatial (a, b, d) and temporal (a, c, d) variation in seeds availability of the smaller-scale set of transects across the landscape and over time. (a) Every histogram represents the (mean) counts of *Enneapogon*'s spikelets with seeds at each sampling month from October 2016 to February 2017. (b) At each sample event (rows), the spatial mean (± 95% Confidence Interval) is shown as mean across transects. (c) The temporal mean (± 95% Confidence Interval) as mean of *Enneapogon* with seeds per transect over time. (d) The overall smaller-scale spatial (horizontal) and temporal (vertical) variation is shown as grand mean of spatial (b) and temporal

57% of the general seasonal variation in *Enneapogon* spp seeds abundance due to the spatial distribution of the transects.

A certain level of synchrony in *Enneapogon* spp seedlings was registered, with the maximum number of spikelets with seeds not occurring homogenously along the sampling time (*G*=39.98, p<0.001, df= 4). Specifically, 50% of the sampled transects (n=36) reached their maximum in November 2016, 20% in October, 8% in January 2017 and in 22% of the sampled transects *Enneapogon* spp was not present (Fig. 3).

The variation in the abundance of *Enneapogon* with seeds was influenced by the (negative) interaction between elevation site and the cover of other species ($F_{3,14}$=10.7, p=0.005, n=18, Fig. 4). That means, that the lower the abundance of other vegetation cover (i.e. low competition), the stronger was the positive effect of elevation on the *Enneapogon* productivity (i.e. number of spikelets with seeds).

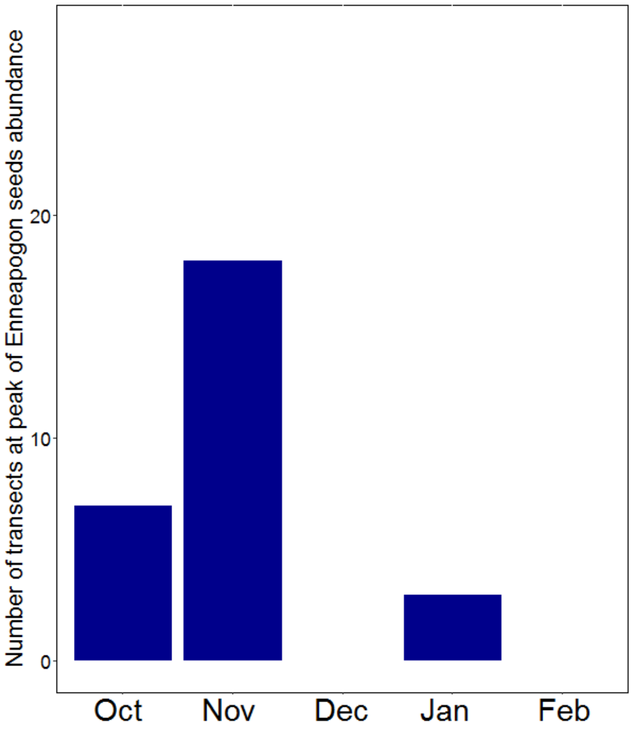

Figure 3 Number of transects (n=36) with the maximum number of *Enneapogon* spikelets with seeds per sampling month.

Discussion

Our data confirmed the landscape complexity characteristic of the Australian arid environment, with respect to productivity in a key grass, whose seeds are an important resource for an iconic granivore (Morton and Davies, 1983; Zann and Straw, 1984). We found the spatial variation in *Enneapogon* abundance to be due to topography and vegetation cover. The temporal (i.e. seasonal) effect on *Enneapogon* grassland abundance was highly significant and that the spatial component was highly important on the smaller scale, explaining almost 60% of the variability. At the wider scale, the spatial component of the variation appeared to be a less important determinant of overall variation, probably because the variation in seeds abundance was less pronounced. Several aspects of the environment might concur to shape the variability we observed. The presence of an artificial water source has been recognized to influence the vegetation composition and abundance (rev. in James et al., 1999). Water dams have been found to increase the soil water content in its immediate surroundings (e.g. 1-2m) and, consequently, the vegetation response. On the other hand, the high turnover of herbivores at points of free

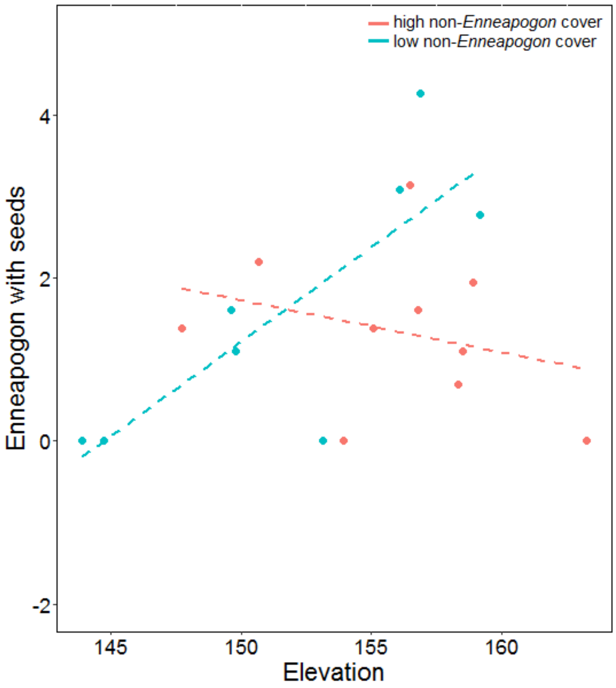

Figure 4 Effect of elevation (in meters) on the (log-transformed) number of *Enneapogon* spikelets with seeds of the smaller scale set of transects. For graphical reasons, the interaction between elevation and non-*Enneapogon* vegetation cover was simplified by categorizing the vegetation cover: the sites with the proportion of non-*Enneapogon* cover higher than the mean (‘high non-*Enneapogon* cover’ > 0.8) are shown in red, while those sites lower than the mean illustrated with green (‘low non-*Enneapogon* cover’ ≤0.8).

available drinking water may have resulted in the selective reduction of the grassland in favour of less palatable vegetation (James et al., 1999). In our study site this effect might be accentuated by the association between the dam and an ephemeral creek system. Dry creek beds increase the soil water content in the area next to it, depending on the depth of the creek, by prolonging the effect of flood after rain events, and triggering a strong vegetation response (Morton et al., 2011).

We estimated the effect of the artificial water dam associated to the creek through the proportion of non-*Enneapogon* vegetation on the total cover, while differences in topography were estimated through the elevation. Elevation has been associated with differences in soil nutrient composition, solar exposition and, consequently, water-soil-recharge and vegetation composition (e.g. Australia: Morton et al., 2011; Orians and Milewski, 2007; North America: Thompson et al., 2005; Africa: Augustine, 2003); although the variation in elevation in these studies is normally more than 100m. However, Australia in general and even more the arid area is the flattest continent (Orians and Milewski, 2007), therefore it is not surprising that minimal changes in elevation concur an influence on the vegetation response at a very local scale. Generally, the interaction we found between vegetation competition and topography might be expected, considering that *Enneapogon* is a minor tussock (around 30 cm height), widespread in arid and semi-arid Australia with short-perennial species (Kakudidi et al., 1988). Thus it is adapted to arid conditions, growing further from the water and responding to winter rains (Foulkes et al., 2014). Actually, our results showed that patches mostly dominated by *Enneapogon* grassland (i.e. highest *Enneapogon* abundance) were linked to higher elevation (i.e. higher soil exposition, more ‘dry’) and a lower proportion of other vegetation.

However, the small scale at which we found the interaction between elevation and (indirectly) water soil content affects vegetation heterogeneity suggests that the Australian arid environment might be an extremely difficult challenge for ecologists searching for a general model that predicts vegetation responses to the abiotic fluctuations (e.g. water soil recharge, rainfall, topography). On the other hand, the extent of the variation found in our study might be encouraging for behavioural ecologists. We demonstrated that the factors which influence the vegetation responses (and food availability) on a wide scale are generally also valid at a very local scale. Therefore, by focusing the ecological surveys effort on a scale relevant to the target species, it will be possible to identify the challenges the animals have to face and their behavioural and physiological responses. In arid areas, the scale relevant to the target species is normally restricted to resource availability, especially during breeding. Thus, having set an appropriate number of vegetation surveys and having monitored their fluctuations, it would be possible to match the spatial and temporal variability in seeds abundance with measurements of habitat selection and individual optimal foraging strategies. Past research on the relationship between rainfall events, grass productivity and animals' breeding activity failed in finding a general pattern, most probably because a correlation does not explain the complex relationship between grass productivity and rain in arid habitat (Morton and Davies, 1983; Zann et al., 1995; Zann and Straw, 1984; Zann 1996). Our results suggest that, for example, it would be possible to directly match the spatial and temporal variability of the zebra finches' main food source at local scale (i.e. *Enneapogon*) with the population breeding phenology. Although it is not always straightforward to determine the scale appropriate for the study species or the most suitable number of surveys to reliably estimate the variability of food availability across the landscape, knowing that spatial variation of grassland distribution occurs at a local scale might be the only feasible way for behavioural ecologists to start understanding arid animals' responses to the habitat, by-passing the interactive non-linear relationship between rainfall and vegetation response.

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Chapter Three

Sentinel 2: an opportunity to integrate remote sensing and behavioural ecology in the arid zone

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Submitted

Abstract

In arid environments, primary productivity is generally low and highly variable both spatially and temporally, depending on a combination of resources not-evenly distributed in space and time (e.g. soil nutrients, water), and both global (e.g. El Niño/ Southern Oscillation, ENSO) and local (i.e. rainfall) parameters. Large scale investigations of the ecological and behavioural consequences of variation in key drivers of primary productivity will provide important new insight into animal ecology in the relatively poorly understood arid environment. Recent progress in remote sensing information analysis and data availability therefore potentially opens up new opportunities to provide insight into ecological and even behavioural studies. In particular the launch of the Sentinel-2A satellites, part of the European Copernicus programme, provides data with a high spatial resolution (10 m per pixel) that is freely available. Here, we aimed to test whether Sentinel 2A imagery were able to accurately assess the spatial and temporal variability of a minor tussock grass (*Enneapogon* spp.) in an Australian arid area. Although very ephemeral, the *Enneapogon* grassland have been identified as a key primary food source to animals in the arid environment, determining the timing and extent of opportunistic episodes of reproduction. We combined field vegetation surveys and Sentinel 2A imagery to test: (1) whether remote sensing data (spectral vegetation indices) can be used to predict the spatial variability of *Enneapogon* seed-productivity and (2) whether this holds over time. We showed that in an arid environment, high spatial resolution satellite-derived vegetation indices provided reliable estimates of vegetation density, both across the landscape and over time. However, we were able to discriminate between vegetation types, and in particular to identify the seed-productivity of *Enneapogon*, only during a climatically-favourable period (i.e. after winter rainfalls) during which this dominant grass reached peak in seed-productivity. During other periods, only the less subtle discrimination of vegetation type and productivity was possible (e.g. barren vs green higher vegetation). Overall, our study highlights to the potential for Sentinel 2 imagery to enable the integration of remote sensing and animal ecology in arid environments, but with some limitations.

Keywords: arid environment, remote sensing, vegetation survey, Sentinel 2A, behavioural ecology.

Introduction

In Australian arid environments, primary productivity is generally low and highly variable both spatially and temporally, being driven by low levels of average rainfall that are typically a-seasonal, with significant rain events exhibiting relatively high variance in scale and timing (Morton et al., 2011; Noy-Meier, 1973). Even at a very local scale both annual rainfall, and the rainfall of individual rainfall events can be very variable (Acworth et al., 2016). As well as presenting ecological challenges for arid adapted organisms (Letnic and Dickman, 2006; Morton et al., 2011), this pattern of rainfall presents a significant challenge to the study of Australian arid zone ecology. For example, in their analysis of 44 years of rainfall data collected over 17 rain gauges across around 380 km^2 of the Fowlers Gap Arid Zone Research Station, Acworth et al. (2016) demonstrate that the rainfall measured in one part of the station is often a poor reflection of that measured in other parts. In a number of representative years, some parts of the station received more than twice as much rainfall as others, despite being less than 20km apart (Acworth et al., 2016). Although at wide scale a large rainfall event tends to have comparable effects across large areas, ecologically, the difference between these levels of rainfall will be profound, and yet studies that explore the response of animals to rainfall typically use rainfall records that were taken at distance from the studied population (Zann et al., 1995; Zann and Straw, 1984), and in many cases are interpolated values between two weather stations that may be hundreds of kilometres from the study area (Crino et al., 2017; Pavey and Nano, 2013). To further confound the problem, the primary productivity on the ground is the result of complex interactions between soils, the water responses of different plant species, climate, season, the total amount and speed at which the rain falls and herbivores' foraging activity (Morton et al., 2011; Nano and Pavey, 2013; Reynolds et al., 2004). For example, rainfall events that are timed with the optimal growth phenology of certain species, can elicit a large response on those, but not on others, promoting great landscape heterogeneity at a small spatial scale, as a result, the link between rainfall and net-productivity of components of the arid zone community is complicated (Fernández, 2007; Watson et al., 1997). Therefore, it is extremely difficult to make generalizations on rainfall pulses and arid productivity (Reynolds et al., 2004).

To improve our understanding of the way in which animals respond to rainfall, we need to be able to better quantify local primary productivity, rather than just using the rainfall itself. Great progress has been made in remote sensing, increasing our ability to study the general response of vegetation to rainfall in remote and arid areas. Data archives have become freely available (e.g.: Landsat by NASA active since 1972, Wulder et al., 2016) and new satellites have been launched, specifically for terrestrial observation as support for land cover change monitoring. For example, the Sentinel 2 satellite, part of the European Copernicus programme, provides data with a high spatial resolution (10 m per pixel) and is freely available (running between 2016 and 2028; Skidmore et al., 2015). In temperate climates, where the relationship between abiotic (e.g.: rainfall, temperature, soil nutrients) and vegetation productivity is more predictable, remote sensing information has been widely integrated into wildlife research, such as the response to plant phenology of both herbivorous (e.g.: mule deer *Odocoileus hemionus,* Hurley et al., 2014) and non-herbivorous birds and mammals (reviewed in: Pettorelli et al., 2011).

Despite this progress, however, the use of remote sensing to address questions in animal ecology in the arid and semi-arid environment remains particularly challenging. Ground cover is often clumped and rather dispersed with a low vegetation cover and a high soil reflectance (Nagendra, 2001; Okin and Roberts, 2004; ; Ren et al. 2018). Specific vegetation properties (e.g.: density, biomass productivity) can be summarized by combining the reflectance of two or more wavelengths (bands, reviewed in: Kalaitzidis et al., 2010; Xue and Su, 2017). Many studies of arid areas have tried to assess the most suitable vegetation indices (e.g. Asia, Kang et al., 2018; Africa, Mapfumo et al., 2016; North and Central America, Théau and Weber, 2010; Australia, Chen et al., 2014), finding that higher spatial resolution better represents the actual situation on the ground; although the use of a single vegetation index to summarize such a complex

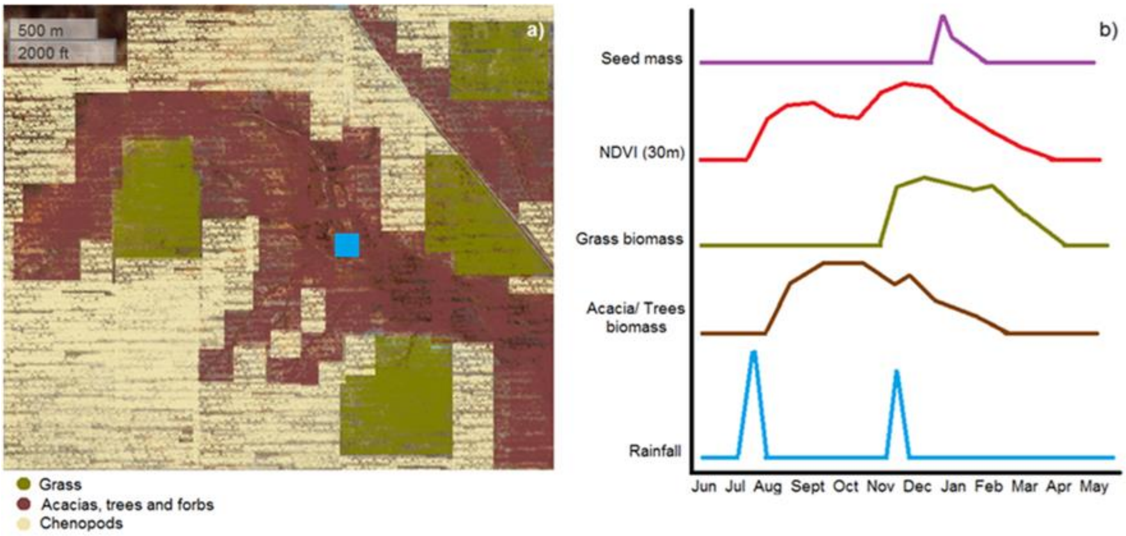


Figure 1 a) Map of the study site showing the main vegetation composition areas (for conceptual purposes only). Brown shading represents the vegetation area mainly composed of *Acacia*, taller trees and forbs. The green shading represents the area mostly composed by summer growing grasses, such as Curly Mitchell grass *Astrebla lappacea*. The light yellow shading illustrates areas dominated by sparse chenopods such as blue and salt bushes and other succulent bushes. Blue square represents the water dam. **b)** The hypothetical response of different components of the community to rainfall events at different times. The rainfall events (blue line) have different effect on vegetation components depending on the time of the year. Here, winter rainfall does not lead to the growth of summer grasses (green line), but it elicits a significant response in *Acacia*-based vegetation. As a result using a general Normalized Difference Vegetation Index (NDVI) response in this area will not provide insight into the growth of components of the system such as grasses, unless we are able to investigate the substructure at a finer resolution, and that lesser components of the vegetation are detectable in the remote sensing signal.

environment is not a reliable tool (Okin and Roberts, 2004; Hamada et al. 2019). In Figure 1 we illustrate, conceptually, the key challenge. Given the patchiness of vegetation in the landscape (Fig.1a), spatial resolution-derived vegetation indices freely available until now (e.g.: Landsat-derived Normalized Difference Vegetation Index, NDVI at 30m resolution, Fig. 1b) may not provide a reliable tool to predict the productivity of some components of the vegetation, such as grasses and grass seeds (green and pink lines in Fig. 1b), because the pixel resolution might not be suitable to represent the heterogeneity of the actual vegetation and the signal may be overwhelmed by more dominant, and perennial components (such as *Acacia* spp., brown line in Fig. 1b). This is important because whilst there may be a general ‘greening response’ to rainfall, it does not necessarily provide evidence of a resource base for a particular guild of animals. For example, the nutritional requirements of the seed-eating zebra finch (*Taeniopygia guttata*) have been well characterised, with the seeds of dominant grass species such as *Enneapogon* spp.

making up a considerable portion of their diet (>80%) in the Austral spring, triggering reproduction (Morton and Davies, 1983). However, these grasses often occur amongst patches of chenopod shrubs that provide little or no nutrition to this granivorous species, and may have a greening response to rainfall, perhaps at other times of the year, that does not support growth of *Enneapogon* spp. Therefore, remotely measured indices that derive from a not optimal spatial resolution for the landscape in study, such as the Landsat-derived Normalised Difference Vegetation Index (Tucker, 1979), may reveal a strong response that may mostly represent the chenopod shrubs, but that may not reflect a response by components of the vegetation, such as seed grasses, that are of relevance to granivorous species.

To date, most of the work on Australian extended arid grassland areas have attempted to relate remote sensing information to areas dominated by perennial, sclerophyllous and tall grass species (Chen et al., 2014). Whilst Australian arid primary productivity is generally considered to be based on perennial, summer grasses like hummock and spinifex (Dickman et al., 2014), these grasses have a peak of productivity in summer. During the Austral spring, when the climate is most amenable for reproduction in many groups of animals such as birds (Duursma et al., 2017), and while the summer grasses are still quiescent, the *Enneapogon* spp. are the most dominant grasses representing the main food source for a variety of animals (Buckley, 1982; Hoffmann, 2010). The *Enneapogon* genus is composed by minor tussocks (around 30 cm height), with 15 short-perennial species present in Australia (i.e.: biannual, Foulkes et al., 2014; Kakudidi et al., 1988). The seed-productivity of *Enneapogon* grassland is commonly represented by a matrix of different *Enneapogon* species (hereafter generally called '*Enneapogon*') that peaks in favourable springs, in response to winter rains, and before the perennieal summer grasses.

By correlating the actual vegetation cover with remotely acquired indices, it may be possible to understand the extent to which a remotely acquired signal is more or less reliable in a specific area, and reflects different components of the plant community (Chen et al., 2014). In this way, testing if the higher spatial resolution of Sentinel 2 imagery is able to accurately assess the primary seed-productivity of *Enneapogon* in the arid landscape, may be pivotal to start understanding the ecological response of seed-eating animals that primarily use these grasses, to different conditions. Here we combined field vegetation surveys and Sentinel 2 imageries that temporally matched the field sampling to directly test: (1) whether remote sensing data (i.e. vegetation indices) can be used to predict the spatial variability of *Enneapogon* seed-productivity and (2) whether this prediction holds over time. The *Enneapogon* spatial distribution was assessed through two main field approaches. The first approach, aimed at directly quantifying *Enneapogon* seed-productivity across the landscape, during October 2016. We compared the reliability of a soil-adjusted and a not-adjusted vegetation indices calculated from Sentinel 2 imageries with 10 m spatial resolution, to predict the variability of *Enneapogon* seed-productivity. The second approach aimed to characterize general vegetation composition of the landscape in the field and to identify areas dominated by different vegetation (i.e. shrub vegetation dominated, *Enneapogon* dominated) and to test the reliability of indices performance along four months (until January 2017) in areas with different vegetation types. Testing whether Sentinel's higher spatial resolution is able to reliably represent actual vegetation heterogeneity in arid areas, across the landscape and over time, even for ephemeral vegetation patches, is a fundamental step for developing a good understanding of the relationship between primary productivity and the ecological responses of animals in such an unpredictable environment.

Methods

Study area and field surveys

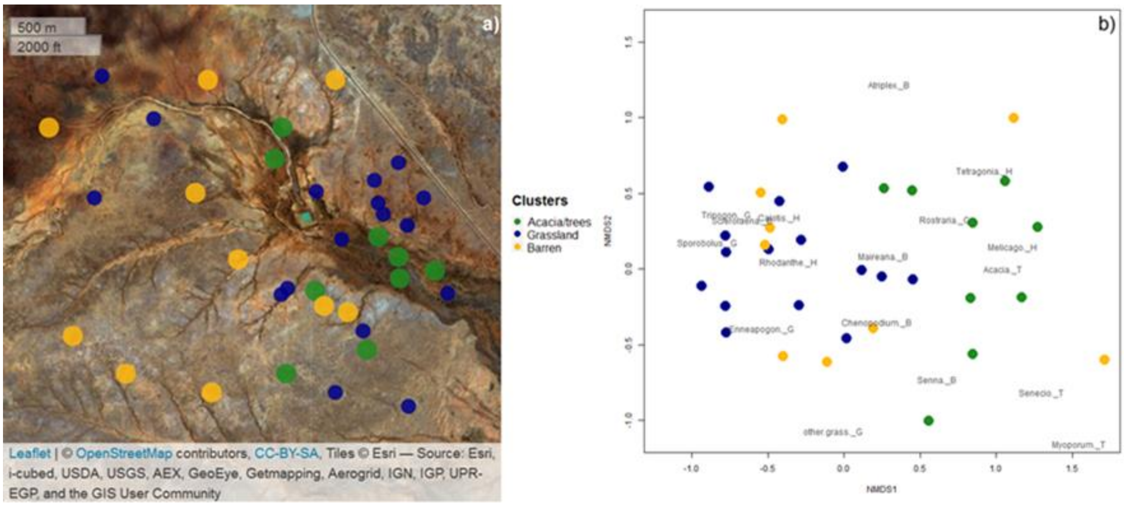
The study was conducted in Gap Hills, an area located in the north of the Fowlers Gap Arid Zone Research Station (31°05′13.1″S, 141°42′17.4″E), New South Wales, Australia. In October 2016, 36 quadrats of 10x10m were established in an area within 2 km of an artificial water dam (Fig. 2a). In each quadrat, we identified all plants at lowest taxonomical level possible (i.e. species or genus). Then, for every identified plant, we estimated the vegetation cover using a modified Braun-Blanquet index (Braun-Blanquet, 1964). We decided to lower the percentage of the original index to adapt it to the semi-arid conditions and to get the most variability at lower coverage (Table 1). We noted the dominant plants of the over-storey, the under-storey and for grasses. The total vegetation cover was estimated by considering the highest vegetation cover between the over-storey, under-storey and grasses (e.g. 3% when the coverage index was ‘2’ and 35% when it was ‘4’).

Table 2 Adaptation of the Braun-Blanquet index to the low vegetation cover in arid areas.

Index value	Original Braun-Blanquet index	Modified Braun-Blanquet index
1	less than 5%	less than 1%
2	5-25%	1-5%
3	25-50%	5-25%
4	50-75%	25-50%
5	more than 75%	50-75%

In order to quantify the variability in seed-productivity of the *Enneapogon* spp. across the landscape, during three weeks, between the 28th October and the 16th November 2016, we performed a 50 m transect along the NE-SW line from the NE corner of every quadrat, once per week. For each transect, every meter, we noted the name of the grass (genus level) and counted the number of spikelets with fruits (seeds, later used to assess productivity) within 10 cm. Additionally, we randomly collected 50 spikelets with seeds of the most dominant grass genus, *Enneapogon*, from different individuals around the transect (and quadrat) area. In this way, the seed-productivity was calculated by estimating the proportion of *Enneapogon* spp. with seeds multiplying it with the average dry weight of one spikelet across the three weeks of sampling ($g*m^{-2} *week^{-1}$, Sartorius BP211D, Wood Dale, Illinois, 0.01mg).

In order to characterize the general vegetation composition of the landscape and identify areas dominated by different vegetation, we used the field based data from our quadrats of October 2016 to estimate the presence of vegetation co-occurrence. We identified the most dominant 19 plant genera and built a matrix of plant genus’s cover across the plots. The cover-plot matrix was combined with the estimation of total cover and *Enneapogon* seed-productivity (‘gower’ method in ‘vegdist’ for ‘vegan’ package in R, Oksanen et al., 2017) to run a cluster analysis which identified two main groups with similar vegetation composition: the *Enneapogon*-



Leaflet | © OpenStreetMap contributors, CC-BY-SA, Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Figure 2 a) The spatial distribution of the 36 quadrat 10x10m surveys on Ensri satellite image, coloured according to the cluster analysis. **b)** Non-metric Multidimensional Scaling (NMDS) visual representation of the vegetation composition (genus of plants identified) and the quadrats surveyed in the three vegetation types considered. Grassland (blue) and *Acacia*/trees (green) vegetation categories were identified through a cluster analysis. The Barren group (yellow) was manually sorted being the total cover estimation less than 10% from the grassland and *Acacia*/trees clusters. Graphical distance represents similarity of the green and blue clusters. The yellow dots, manually sorted, might have belonged to either the green or the blue cluster. The location of the vegetation genus (with name followed by vegetation type) represents their co-occurrence. Vegetation types are indicated with the code: B as "bush", G as "grass", "T" as tree and "H" as herbaceous forb.

based ('grass') and the *Acacia*-based ('green', Table S1). Since we were also interested in barren areas, we manually built a third cluster selecting the 'barren' quadrats, defined by total cover estimation being less than 10% (Fig. 2). Later we used the same clusters to test the suitability of the satellite-derived vegetation indices to discriminate between a subset of vegetation types identified by these clusters.

Satellite Imagery

In order to best match the period of field data collection (*Enneapogon* seeds productivity sampled between 28th October and 16th November 2016) and the satellite-derived indices, we chose the imagery available from Sentinel 2 (Copernicus Earth Observation Program, Thales Alenia Space, ESA, 2015), with cloud free conditions for the study period, which was 29th October 2016. To analyse the temporal changes, from Austral spring 'boom' (October-November) to arid summer (January-February), the imageries selected were: the 18th December 2016 and the 27th January 2017 (0% cloud cover). We excluded data from November, because all imagery had clouds over the study area. Images were projected into the WGS 84/UTM zone 54S coordinates reference system, they were atmospherically corrected (DOS1) and absorption effects were removed from the bands using QGIS (v 2.18.17) pre-processing tool specific for Sentinel (Congedo, 2016). For all images (October, December 2016 and January 2017), we chose to calculate the two vegetation indices that derived from high spatial resolution wavelength and were previously shown to perform well in arid and semi-arid areas, using Landsat imageries (Chen et al., 2014, Table S2). The Modified-Soil-Adjusted Vegetation Index ($MSAVI_2$, , Qi et al., 1994) is adjusted for the reflectance of the exposed soil, whereas the Normalized Difference Vegetation Index (NDVI, Tucker, 1979) is not adjusted. Both of them use the near infrared (NIR, 0.84 µm, band 8) and red wavelengths reflectance (Red, 0.66 µm, band 4). The indices were calculated at native spatial resolution (10 m for $MSAVI_{2,}$ NDVI). We extracted the values of each index at native spatial resolution from the 36 GPS plots/transects points (±5 m, GPSMAP® 64s, Garmin, Olathe, USA), projected into WGS 84/UTM zone 54S coordinates reference system. That means that we obtained the value of $MSAVI_2$ and NDVI for a 10 x 10 m (pixel) square which included the GPS point.

Statistical analysis

Giving the non-linearity of the natural spatial distribution of the vegetation and the spatial autocorrelation of our sampling, we checked the relationship between vegetation indices and biomass data through Generalized Least Squares (GLS) models. We were interested in validation of the remote sensing information by testing the relationship between vegetation indices and field vegetation estimations, therefore, we firstly calculated the amount and direction of the spatial autocorrelation of the variables to be used as dependent variables ($MSAVI_2$, NDVI) using the Moran´s *I* function (two sides) in the ‘ape’ R-package (Paradis and Schliep, 2018). Then, we built GLS linear regression models with $MSAVI_2$ and NDVI, separately, as dependent variables while the total vegetation cover estimation and *Enneapogon* seed-productivity was fitted as explanatory variables. We removed the spatial autocorrelation effects (which would increase type-II-errors), building five additional models changing only the type of autocorrelation structure (exponential, Gaussian, spherical, linear, and rational quadratic, method 'REML') and we selected the simplest model, corrected for spatial autocorrelation, with the lowest AIC (Zuur et al., 2010). Having assessed the simplest model with the appropriate spatial autocorrelation correction, we calculated the root-mean squared deviation (RMSE) for each vegetation index model, to assess the index that fit the data best.

Finally, we tested the performance of the soil-adjusted $MSAVI_2$ and the not-adjusted NDVI in distinguishing between different types of vegetation composition over time. We considered a subset of quadrats belonging to the different clusters that were most representative of the characterization in study, excluding the quadrats with mix vegetation types that might complicate the interpretation of a correct discrimination. Therefore, we subset the five most barren of the 'barren' cluster; the five quadrats from the 'green' cluster composed mainly by *Acacia* and green vegetation and the five composed mainly by dominant grass (i.e. highest *Enneapogon* seed-productivity, Table 2). A series of paired Wilcoxon's signed rank tests was run between different clusters' subset (from clusters previously identified, Fig. 2), separately for each vegetation index and month.

Table 2 Summary of number (N) of quadrats, *Enneapogon* seed-productivity (mean±SD) and total vegetation cover (mean±SD) of the clusters' subset used for the temporal analysis.

	Barren	**Grass**	**Green**
N quadrats	5	5	5
Enneapogon seed-productivity ($g*m^{-2}*week^{-1}$)	0.03±0.03	0.17±0.03	0.001±0.002
Total vegetation cover (%)	2.8±1.1	26±14.4	49.8±26.8

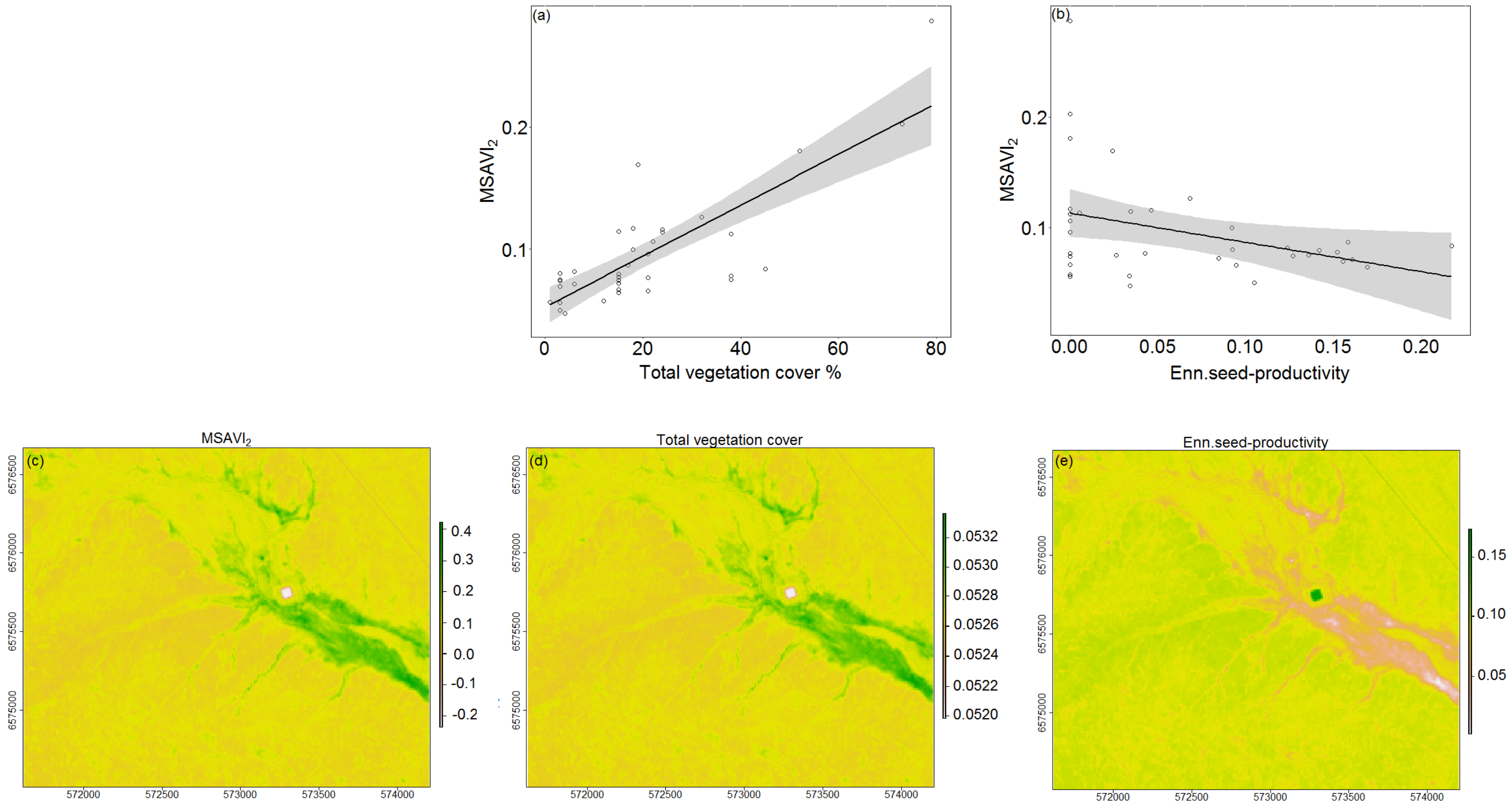


Figure 3 Graphical representation and map of predicted model of the positive relationship between the MSAVI$_2$ and total cover estimation (a and d). The MSAVI$_2$ was negatively related to the seed-productivity of the dominant grass *Enneapogon* (b and e). The map in c) represents the satellite-derived MSAVI$_2$ alone. Spatial analysis performed with data from October 2016.

Results

Both the $MSAVI_2$ and the NDVI were positively spatially autocorrelated ($MSAVI_2$: observed Moran's I= 0.06, P=0.001; NDVI: observed Moran's I= 0.07, P=0.03) and therefore the fitted simple models were corrected for the rational-quadratic spatial autocorrelation error. However, the best fitted models were always the ones without corrections.

The results showed that there was a positive relationship between $MSAVI_2$ (Table 3, Fig. 3a, c, d), the NDVI (Table 3) and the total vegetation cover in October 2016. The model with $MSAVI_2$ as dependent more accurately described the positive relationship with the total vegetation cover estimated in the field, as it had the lowest RMSE ($MSAVI_2$=0.03; NDVI=0.07).

The results showed a negative relationship between $MSAVI_2$ (Table 3, Fig. 3b, d), NDVI (Table 3) and the *Enneapogon* seed-productivity. The model with $MSAVI_2$ as dependent more accurately described the negative relationship with the *Enneapogon* seed-productivity calculated from the field data, as it had the lowest RMSE ($MSAVI_2$=0.04; NDVI=0.10).

The temporal analysis of the clusters' subsets demonstrated that the $MSAVI_2$ distinguished between the three vegetation types in October, when the vegetation was at its peak (Table 4, Fig. 4a), but in December and January, when the temperature started to raise, only the difference between barren and green remained significant, whereas the comparisons between the other vegetation types became indistinguishable (Table 4, Fig. 4b, c).

Table 3 Summary of the simplest GLS models. The dependent and explanatory variables, the test coefficient (t) significance (P) and sample size (N) are specified for each model. Statistically significant values are marked in bold.

Dependent	Explanatory	t	P	N
$MSAVI_2$	Total vegetation cover	7.9	**<0.001**	36
NDVI	Total vegetation cover	7.7	**<0.001**	36
$MSAVI_2$	*Enneapogon* seed-productivity	-2.26	**0.03**	36
NDVI	*Enneapogon* seed-productivity	-2.43	**0.02**	36

The analysis with the soil-unadjusted NDVI revealed a significant difference between barren and green vegetation patches in October, December and in January (Table 4). The differences between green and grass patches also remained from October to January (Table 4). However, the NDVI was able to clearly distinguish between barren and grass patches only in December (Table 4, Fig. 4d-f).

Table 4 Summary of the paired Wilcoxon's signed rank tests. Vegetation index (VI), clusters pairs tested (Pairs), month, coefficient test (Z), significance (P) and sample size are specified for each comparison. Statistically significant values are marked in bold.

VI	Pairs	**Month**	**Z**	**P**	N
MSAVI$_2$	Barren-Grass	October	0.6	**0.03**	10
	Barren-Green		0.7	**0.01**	10
	Green-Grass		0.7	**0.01**	10
	Barren-Grass	December	0.4	0.1	10
	Barren-Green		0.6	**0.02**	10
	Green-Grass		0.4	0.2	10
	Barren-Grass	January	0.4	0.2	10
	Barren-Green		0.6	**0.02**	10
	Green-Grass		0.5	0.06	10
NDVI	Barren-Grass	October	0.5	0.06	10
	Barren-Green		0.7	**0.01**	10
	Green-Grass		0.7	**0.01**	10
	Barren-Grass	December	0.6	**0.03**	10
	Barren-Green		0.7	**0.01**	10
	Green-Grass		0.6	**0.02**	10
	Barren-Grass	January	0.4	0.2	10
	Barren-Green		0.7	**0.01**	10
	Green-Grass		0.7	**0.01**	10

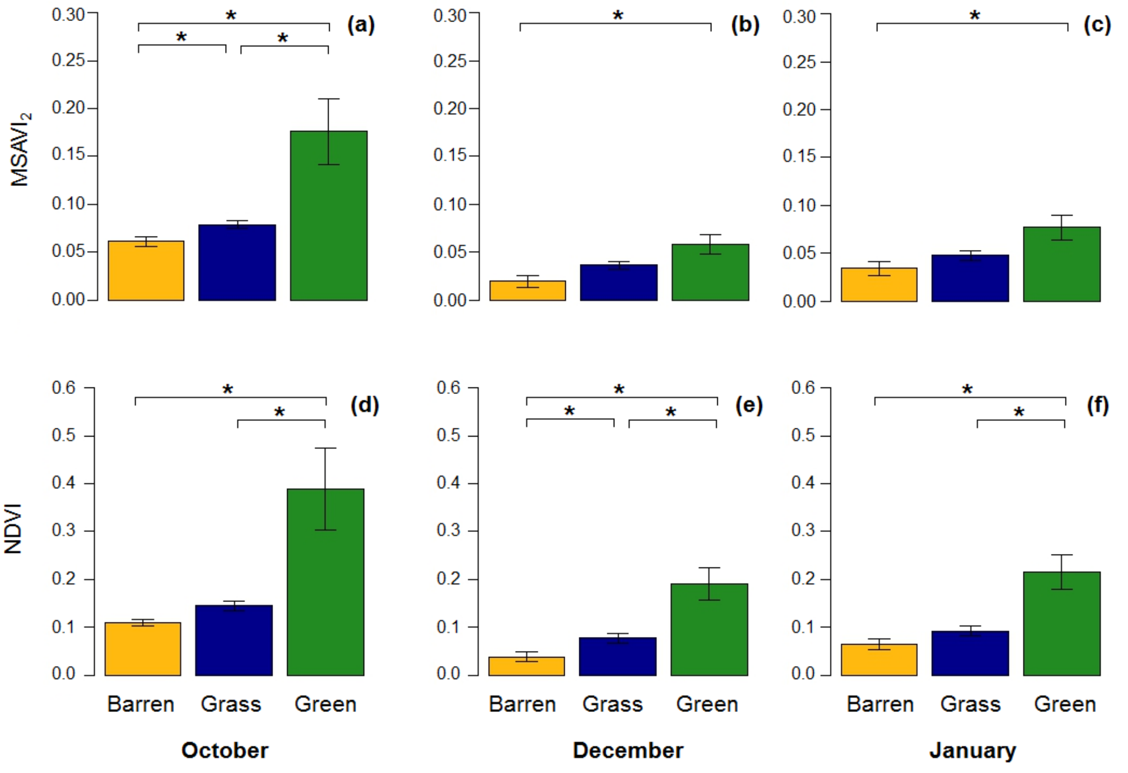


Figure 4 Bar chart with mean ± SE to show the comparison of $MSAVI_2$ (**a-c**) and NDVI (**d-f**) extracted from the subset of the three clusters of quadrats with different vegetation type and density. The comparisons were performed for October 2016, December 2016 and January 2017. Significant differences are marked by * and the analyses performed were Wilcoxon's ranked tests.

Discussion

In the present study, we showed how Sentinel 2 information can be used to estimate habitat condition in a spatially heterogeneous environment, such as the Australian desert and semi-desert. We also showed that, identifying patches of specific vegetation types, the satellite-derived vegetation indices were able to detect their changes along time, although with some limitations. We based the vegetation characterization focusing on a sample period (October 2016), where the whole vegetation in the study area was at the 'boom' phase of the characteristic 'boom and bust' cycle, as consequence of winter rainfall (Morton et al., 2011), and confirmed by being the highest NDVI value since 2010 (Fig. S1).

The total vegetation cover estimated from the field explained both vegetation indices, but the model with $MSAVI_2$ best fit the vegetation cover distribution. This validates the use of

$MSAVI_2$ to assess the density of green, uniform vegetation in arid areas (Nagendra, 2001) and the accuracy of our field estimations. Our results also showed that both vegetation indices were negatively related to the *Enneapogon* seed-productivity, and the model with $MSAVI_2$ was best represented by the field data. This suggests that the dominant grass species is found in different areas to the green, *Acacia* dominated patches (which contribute the main greening response in this habitat), and is associated with succulent shrubs like *Mareana* and *Scleroleana* spp. This negative relationship revealed the utility of mapping *Enneapogon* distribution across the landscape, allowing a careful discrimination between barren and grass areas. The pattern found supported previous studies which explained how the presence of artificial water dam influences the spatial distribution of vegetation types, introducing the effect of selective grazing that favours shrubland over grassland (James et al., 1999). In our field site the water dam is surrounded by a dry-creek system that might further influence the vegetation response found, with the more green vegetation distributed along the water dam and the surrounded creek. Actually, dry creeks have been demonstrated to increase the soil water content in the area next to it, by prolonging the effect of flood after rain events, and triggering a strong vegetation response (Kingsford et al., 1999; Morton et al., 2011). Therefore, it is likely that these environmental structures and their associated effects interact to shape the spatial vegetation variation detected by the Sentinel-derived indices, even at local scales.

The other aim of the present study was to validate the relationship between vegetation indices and vegetation types (*Enneapogon* and total cover) over time. Therefore, we sorted the sampling quadrats into three clusters, and focused on their subset that best characterized the different dominant vegetation kind (or bare soil). Only $MSAVI_2$ was able to distinguish between areas with high *Enneapogon* seed-productivity, bare soil and dense green vegetation in October 2016. The lack of temporal reliability in distinguishing high *Enneapogon* seed-productive areas (in December and January) could be due to the ephemeral nature of the grass in study (e.g. the grass faded), rather than loss of satellite sensitivity signal. Our vegetation indices are designed to detect greenness differences (i.e. wavelengths’ spectra) emitted from the vegetation (Kalaitzidis et al., 2010; Xue and Su, 2017). Therefore, they are expected to be influenced by vegetation phenology. However, the difference between the most stable clusters, the green and barren quadrats, held even when the environmental conditions became more arid (January 2017), despite the reduced power of the analysis at that time due to the reduced sample size of the quadrats' subset. Other remote sensing techniques and indices might be more suitable to detect specific changes in phenology accounting for changes in water, chlorophyll content and plant litter (e.g. Berry and Roderick, 2002; Szabó et al., 2016). However, the scope of our study was to test whether the Sentinel-derived indices, with a higher spatial resolution, were able to discriminate between vegetation types, rather than track the phenology of different vegetation types.

We detected a slight difference in performance between the soil-adjusted $MSAVI_2$ and soil-unadjusted NDVI along time and across clusters, with the NDVI always detecting the difference between green and barren and green and grass patches, while $MSAVI_2$ mainly distinguishing between barren and green patches. Other studies in arid habitats, found that at low vegetation cover (<30%), the unadjusted vegetation index performed better than adjusted one (e.g. Ren and Feng 2014). Additionally, a previous study tested the use of several vegetation indices across the whole Fowlers Gap Research Station, using Landsat TM and intensive ground surveys (six transects of 3 km in 49 sites and 147 3x3m quadrats, Chen et al., 2014) finding that both the MSAVI and NDVI were reliable only in wet conditions. Our results showed that the $MSAVI_2$ and NDVI reliably discriminate between higher vegetation and barren areas over time, but increasing the sample size of the subset of quadrats with different dominant vegetation would provide a better demonstration. Probably, the use of imagery with higher spatial resolution, which matched the sampling areas, was able to overcome the limitations of previous studies based on lower resolution imageries. Furthermore, although the overall size of our study area was much smaller than the area used in all the other studies in the literature, Sentinel's imagery were able to catch the variability across the landscape in great detail, when the vegetation was at its peak. Sentinel's higher spatial resolution has been shown to provide higher accuracy in the retrieval of vegetation phenology of an heterogeneous landscape, like a Dutch barrier island, than medium-resolution sensors (e.g.: MODIS, Vrieling et al., 2018). Sentinel-derived NDVI seems to better reflect soil moisture condition of areas in extreme drought conditions than lower resolution sensor-based

NDVI (West et al., 2018). These results suggest that Sentinel's higher spatial resolution better represents heterogeneous environments such as the arid ones. This is important, because to understand the responses of particular animals to their environmental fluctuations, we need to focus on the relevant patches of vegetation. Some animals, such as kangaroos and others large herbivorous mammals, that can browse on shrubs, although preferentially feed on more palatable grasses (Dawson et al. 2012), may respond to the general greening response detected by the difference between green patches and barren ground, because that will reflect the vegetative status and abundance of shrubs – their food. However, for animals that are strictly granivorous i.e. which dependent solely on the productivity of patches of grass that are detectable only when at peak seed-productivity, as demonstrated here, a challenge remains.

An optimal spatial resolution allows a reliable estimation of the structural characterization of plant association (e.g. species identification), maintaining information on vegetation types and abundance, which relates with spectral heterogeneity (Nagendra, 2001). Thus, whilst in homogenous landscapes (e.g. woodland) a lower spatial resolution may be optimal, more complex and patchy environment (e.g. arid areas) may require a higher spatial resolution to be optimal. For example, to analyse the spatial movement of Topi antelopes (*Damaliscus lunatus*) and vegetation phenology, MODIS images (250 m spatial resolution) revealed a pattern that AVHRR (5 km spatial resolution) did not detect (Bro-Jørgensen et al., 2008). Furthermore, understanding animals' individual variation in habitat use is a key step to reveal their variation in breeding phenology and to test the possible evolutionary responses (rather than individual plasticity) to climate change (Dall et al., 2012; Merilä and Hendry, 2014). For example, a study over 12 years showed a match between the phenology of oak trees across a woodland, with caterpillar availability, and the individual variation in breeding phenology of a population of great (*Parus major*) and blue (*Cyanistes caeruleus*, Cole et al., 2015) tits. This means that it is possible to evaluate the synchrony between trophic levels at a scale relevant to the individuals in a population, identify the environmental cues used by animals to time their breeding and, consequently, to understand how selection act on these phenological traits (Cole et al., 2015; Durant et al., 2007). In this context, our results, showing the Sentinel-derived indices' discrimination of vegetation types, suggest that 10 m may be an optimal resolution to catch some components of landscape variation in arid environment and, at the same time, suitable to study animal responses to environmental phenology at a scale relevant to individuals.

Overall, we showed that the vegetation indices calculated from the highest-resolution freely available satellite are able to provide reliable estimates of both spatial and temporal vegetation density. The fine discrimination between vegetation types (i.e. *Enneapogon*) was accurate only during a climate-favourable period, when the smallest dominant species reach their peak. Less subtle vegetation type discrimination (i.e. barren vs green higher vegetation) held over time, despite spatial heterogeneity and prolonged dry conditions that can reduce the 'green-vegetation' signal, especially in an arid environment. Therefore, by previously identifying patches covered by specific vegetation types, using soil-adjusted Sentinel 2-derived vegetation indices, it is possible to track their responses to abiotic conditions (e.g. rainfall). In this way, the actual condition of a habitat can be estimated at high spatial resolution. Consequently, it would be possible to study how animals respond to unpredictable environment (including local rainfall variability, Acworth et al., 2016) overcoming the complex, interactive and non-linear nature of the "pulse-reserve" relationship between rainfall and vegetation responses which make general predictions impossible (Reynolds et al., 2004). Traditionally, studies that tried to match vegetation and animal breeding cycles are extremely time and effort consuming (both economic and human), and never accurate because based on the oversimplified assumption of a linear relationship between rainfall and primary productivity (Morton and Davies, 1983; Zann et al., 1995; Zann and Straw, 1984). We suggest that the data generated by the Sentinel 2 will provide a reliable estimation of habitat condition (and food availability) over time, with some limitation with respect to some components of the vegetation. Remote sensing of vegetation will enable better long term studies of animal responses to the vegetative conditions in the arid zone.

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Supplementary materials

Table S1 Summary of vegetation composition of the two clusters based on field estimation (each genus cover, *Enneapogon* seed productivity and total vegetation cover), as proportion of occurrence for each plant genus. The vegetation types (Forb, Grass, Shrub and Tree) are also specified.

Plant genus	Cluster Grass	Cluster Green	Type
Acacia	0.14	0.86	Tree
Atriplex	0.33	0.67	Shrub
Calotis	0.95	0.05	Forb
Carrichtera	0.67	0.33	Forb
Chenopodium	0.67	0.33	Shrub
Enneapogon	1.00	0.00	Grass
Erodium	0.67	0.33	Forb
Maireana	0.95	0.05	Shrub
Medicago	0.17	0.83	Forb
Myoporum	0.00	1.00	Tree
other grass	1.00	0.00	Grass
Pimelea	0.67	0.33	Forb
Plantago	1.00	0.00	Forb
Rhodanthe	0.98	0.02	Forb
Rostraria	0.11	0.89	Grass
Sclerolaena	1.00	0.00	Shrub
Senecio	0.14	0.86	Forb
Senna	0.35	0.65	Shrub
Sporobolus	1.00	0.00	Grass
Tetragonia	0.33	0.67	Forb

Table S2 Vegetation indices calculated from Sentinel 2 imageries with relative formulas, native spatial resolution.

Index	Formula	Spatial resolution	Reference
MSAVI$_2$	$\frac{2\rho_{NIR}+1-\sqrt{(2\rho_{NIR}+1)^2-8(\rho_{NIR}-\rho_{red})}}{2}$	10 x 10m	Qi 1994
NDVI	$\frac{\rho_{NIR}-\rho_{red}}{\rho_{NIR}+\rho_{red}}$	10 x 10m	Tucker 1979

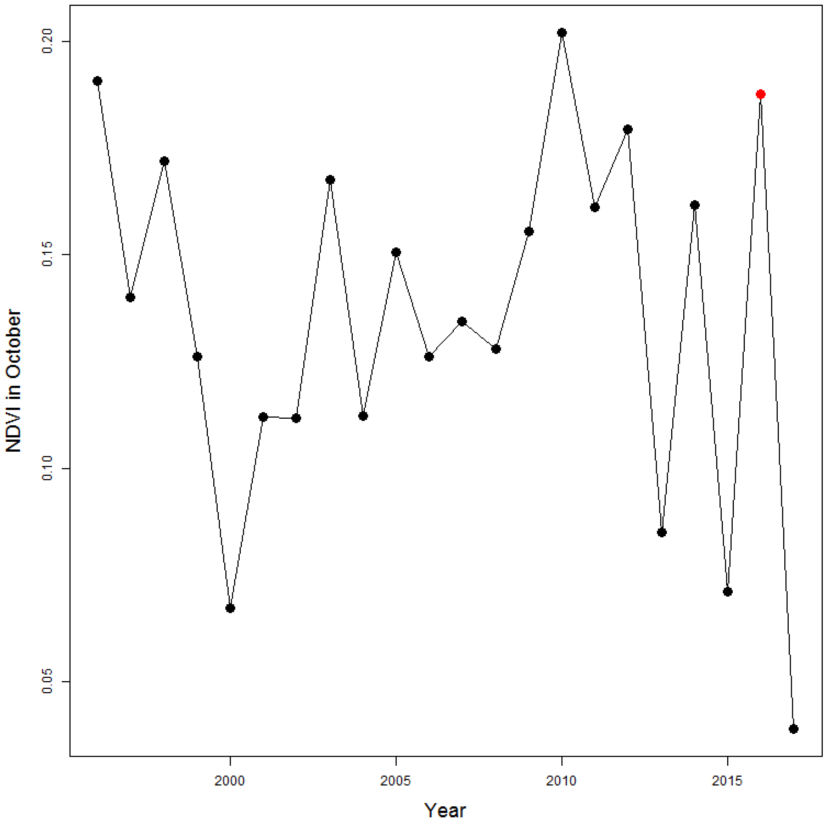

Figure S1 NDVI of October months from 1996 to 2017 (in red October 2016, the period in study) of Gap Hill paddock in Fowlers Gap Research Station, extrapolated by the NDVI maps provided by Australian Bureaux of Meteorology (averaged at 5 km spatial resolution) and processed from Advance Very High Resolution Radiometer (AVHRR, NOAA technology).

Chapter Four

High air temperatures induce temporal, spatial, and social changes in the foraging behaviour of wild zebra finches

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Abstract

Understanding how heatwaves affect organisms is becoming an important issue in animal behaviour, given the changing climate. Exposure to high air temperatures can lead to lethal hyperthermia, when individuals are no longer able to maintain body temperature within their optimal physiological range. Animals will rapidly adjust their behaviour, prioritizing heat dissipation through activities such as drinking and sitting in shade to maintain their body temperature over other activities, such as foraging. Here, we used an automated logging system to consider both the spatial and temporal foraging patterns under a range of different air temperatures at an individual level, in a strictly granivorous species in the wild. We continuously monitored individual foraging activity of wild zebra finches, *Taeniopygia guttata*, a species well adapted to arid conditions, in an Australian arid area across two heatwave events. High air temperatures significantly reduced foraging activity, with the extent of this effect depending on the time of day. They also led to a significant decrease in the number of birds foraging together and to birds spending a higher proportion of their foraging activity close to a water supply. As temperatures exceeded 35°C we saw a significant escalation of heat dissipation behaviour. Our results indicate that extreme air temperatures significantly affected temporal, social and spatial characteristics of zebra finch foraging behaviour and these are likely to adversely reduce an individual’s capacity to forage efficiently, and consequently its food intake in the short term, while also potentially having implications for both reproduction and survival in the long term.

Keywords: arid environment, climate change, foraging, heatwave, heat dissipation behaviour, *Taeniopygia guttata*

Introduction

Understanding how heatwaves affect organisms and ecosystem dynamics is becoming an important question in animal ecology (Ummenhofer and Meehl, 2017). Short-term behavioural decisions and patterns of behaviour are affected by heat (e.g. Levy et al., 2016), and repeated or prolonged exposure to elevated temperature has been demonstrated to have adverse and often long-lasting consequences on both endotherms and ectotherms (reviewed in Grant et al., 2017; Khaliq et al., 2004). Exposure to extreme temperatures can lead to lethal hyperthermia, which occurs when an individual is not able to lose heat faster than it is taken on or produced metabolically (Boyles et al., 2011). Endotherms vary in their heat tolerance, but high tolerances may lead to energetic and physiological costs (Boyles et al., 2011; Jiguet et al., 2006). Small and diurnal animals are particularly affected by repeated exposure to sub-lethal temperatures (Gardner et al., 2016; McKechnie and Wolf, 2010). Endothermic animals react to high temperatures by adjusting their behaviour (e.g. reducing activity, seeking shade) and physiology (e.g. evaporative cooling, vasodilatation) to maintain their body temperature (Wingfield et al., 2017). At a critical air temperature threshold, many mammal and bird species rapidly adjust their behaviour to prioritize heat dissipation behaviour over other behaviours, such as foraging and parental care (du Plessis et al., 2012; Edwards et al., 2015; Levy et al., 2016). In birds, previous studies on thermoregulation and related trade-offs have been based on short and discontinuous focal observations, limited in time and sample size (Carmi-Winkler et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Tieleman and Williams, 2002). Furthermore, while previous studies (cited above) have focused on time budgets spent on foraging and the efficiency of foraging in different conditions in insectivorous and territorial species, there has been no examination of granivorous and non-territorial species and their spatial pattern of movement in hot weather. We may expect very different findings because the former are spatially constrained by their territory, and typically do not drink free-standing water, while the latter are less constrained spatially, and often consume free-standing water regularly, particularly to help alleviate the effects of heat (Smit et al., 2018). Small birds have limited capacity for water storage and a high metabolic rate with high internal heat production (reviewed in Wolf, 2000), with water often being used in evaporative cooling to prevent overheating (Calder, 1964; Calder and King, 1963; Tieleman and Williams, 1999). Therefore, the increasing value of water to small birds as temperatures rise should impose constraints on movement. Specifically, in an arid environment during hot conditions, those granivorous species that depend on water for cooling will face a trade-off between the need to be near a water source and the need to forage in other areas, since the vegetation composition changes around artificial water with a decreased abundance of grass species and increase of woodlands and shrub-lands (James et al., 1999). It is revealing that in the cases of significant avian mortality reported in arid-adapted species, the dead birds were found near water (McKechnie et al., 2012; McKechnie and Wolf, 2010).

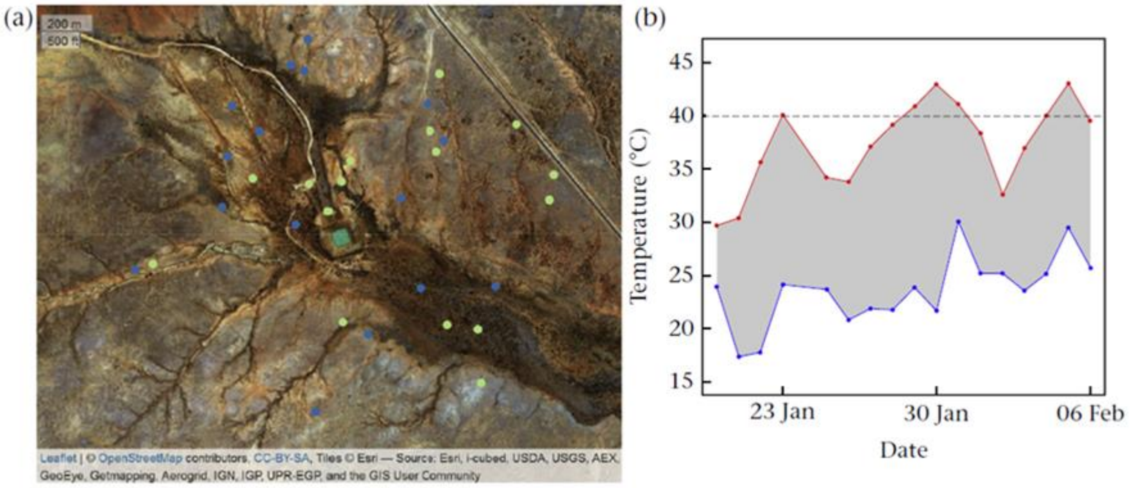
While these mortality events are rare, repeated exposure to sub lethal hot temperatures affects individual fitness in both the short and the long term (du Plessis et al., 2012). A recent analysis of 37 years of data found evidence for carryover physiological costs of short events of extreme conditions in summer and winter that decreased annual survivorship in two Australian passerine species (Gardner et al., 2017). Investigating the relative plasticity of physiological and behavioural traits during short and unpredictable environmental changes (‘perturbation resistance potential’) can help to define when a change should be considered extreme, indicate how the availability of energetic resources will be affected and predict the degree to which a population will be able to resist projected climates in the future (Wingfield et al., 2017). Extreme temperatures are also likely to compromise reproduction through a number of pathways: a recent analysis on the breeding phenology of over 300 Australian bird species found that, in the hot arid areas of inland Australia, birds typically avoid breeding in the summer months, presumably to avoid the extreme heat during this time (Duursma et al., 2017). Reproduction may be compromised by the effect of hot weather on reproductive physiology, such as damage to sperm (e.g. Hurley et al., 2018), but even if reproduction is successful, in hotter conditions the size and mass of offspring are reduced (Andrew et al., 2018, 2017; Cunningham et al., 2013; Gardner et al., 2016).

Although the production of smaller offspring in hot conditions (e.g. Andrew et al., 2017) could be a direct physiological effect of the heat on offspring development, it may also be caused by constrained levels of parental care during extremely hot ambient conditions. To test the idea that foraging ability may be constrained by extreme heat, we monitored the foraging behaviour of individual zebra finches, *Taeniopygia guttata*, in the Australian arid zone during summer, monitoring them at fine timescales over several weeks and across the whole study area. The aim was to investigate how temperature fluctuations influenced hour-by-hour individual patterns of foraging behaviour across two separate heatwaves. Importantly, our approach also permitted the analysis of the spatial distribution of individual foraging behaviour in relation to a water source across a range of air temperatures. Given the importance of water to thermoregulation in the zebra finch (Calder, 1964), we predicted that zebra finches would forage closer to the water source in the hottest conditions to remain close to this important resource. In contrast, when the temperature was not as extreme, the zebra finches were expected to forage more evenly across the landscape, since their natural foraging patches are often further from artificial water sources (James et al., 1999). At the same time, we also conducted an observational study on zebra finch behaviour, relating it with air temperature, to provide some additional context with respect to the point at which birds initiate heat dissipation behaviours.

Methods

Study species

The zebra finch is a small (10 cm, 9–15 g), sexually dimorphic passerine, abundant and widespread across inland Australia. It is strictly granivorous, highly gregarious and described as both resident and nomadic depending on the resources available (Zann, 1996). The study was conducted in Gap Hills (30°56.96'S, 141°46.01'E), an area of approximately 2 km^2, at Fowlers Gap Arid Zone Research Station, New South Wales, Australia. The area is composed of a large patch of scattered shrubs (*Acacia* spp.), around a permanent dam (200 x 150 m) and associated with a mostly dry ephemeral creek system (Mariette and Griffith, 2012a). Here, 230 nest-boxes allow the monitoring of zebra finches' reproduction in a long-term study (Griffith et al., 2008). By the beginning of the current study in January 2017, a total of 158 adult birds were caught using mist-net, feeders and nest-boxes' traps, banded and tagged subcutaneously with passive integrated transponder (PIT) tags (Minichip; Micro Products Australia, Perth, Australia), allowing us to assay their foraging behaviour at monitored feeders as described below.



Leaflet | © OpenStreetMap contributors, CC-BY-SA, Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Figure 1 (a) Spatial distribution of the feeders of the first (green circles) and second trial (blue circles). The green square in the satellite map is the water dam. (b) Daily average minimum (blue) and maximum (red) air temperatures over the study period. The dashed line at 40°C marks the threshold to identify the two heatwaves (as at least 2 days above the line).

Foraging behaviour

Foraging behaviour was measured using artificial feeders at the end of the breeding season, between January and February 2017, when the temperatures are typically hottest, that is, we were studying the birds in a period of the year when recent work suggests that they are less likely to breed because of the heat (Duursma et al., 2017). Feeders were placed randomly within a radius of approximately 800 m of the dam (Fig. 1a), which was the only source of drinking water for the birds within at least 5 km. Each feeder was at least 50 m from the nearest nest-boxes and the dam, at least 2 m from the closest vegetation and with the entrance facing a tree or bush. Feeders consisted of a mesh cage (70 x 40 cm and 50 cm high), partially buried in the ground and open on one side, where the birds could enter the feeder by passing through an antenna (11 cm in diameter). The antenna was linked to a PIT tag reader (RFIDRW-E-232; Priority 1 Design, Melbourne, Australia) and a battery (6 V) that recorded every time a tagged bird passed through the antenna, its unique ID code, the date and time. During the study all the feeders (two trials of 16) were equipped with an antenna and PIT tag reader.

We established 16 feeders on 15 January 2017 (first trial). Feeders were initially provisioned with 120 g of commercial finch seed mixture. After 9 days (i.e. on 24 January) the positions of the 16 feeders were changed (second trial) and they remained there for another 13 days until 7 February. Every 2 days the batteries of the PIT tag readers were changed, and any uneaten seed (commercial finch mix) or seed husks were removed and replaced by 60 g of new seeds. Therefore, feeders were consistently and regularly replenished so that the quantity of food provided was equally distributed across them, once monitoring began. We collected 62306 data records from 158 individual zebra finches foraging in two trials of 16 feeders (32 feeders in total) across 3 weeks. From the reader data, it was not possible to infer the direction of movement through the antenna, but, as previously validated (Mariette et al., 2011), we used a 15 min rule, whereby any two readings within 15 min were assumed to be the same visit to a feeder. We only considered data from adults that visited feeders in both trials and at least 10 times per trial, to exclude individuals that rarely visited the feeders, reducing the sample size to 81 birds. We excluded the days on which the feeders were set up for the first time (15 January), when the feeders were moved for the second trial (24 January) and removed (7 February). Finally, we also excluded the first 4 days of the first trial (16–19 January), when birds were becoming habituated to the feeders and numbers were low (McCowan et al., 2015a), whereas the sample size remained constant throughout the whole of trial 2. Thus, we analysed data from 17 days with varying air temperature conditions (illustrated in Fig. 1b).

Behavioural observations on heat stress

Between 17 January and 26 February 2017, we made behavioural observations to evaluate heat stress at a nearby site, 6.9 km from the Gap Hills dam, known as ‘White Tank’ (31°00.53'S, 141°47.36'E). This work was conducted at this site so as not to disturb the birds’ normal behaviour at Gap Hills during the monitoring study described above. To assess heat-related behaviour in adults, we set up a video camera directed to a small section of a fence (1.5 m wide) located in direct sunlight within a couple of metres from a small but permanent artificial water source (a trough for stock). We analysed individual behaviour during videos of 30 min periods. Although these birds were not individually marked, we recorded any individual perching on the fence as an ‘observation’. Observations ranged from a fraction of a second to 316 s, but visits shorter than 5 s were discarded as we were interested in behaviour in a resting state rather than in a very brief stop between two flights (after discarding <5 s visits: mean ‘resting state’ observation duration ± SD = 19.3 ± 20.4 s, $N_{\text{observations}} = 1454$). After removing two recording periods where no birds visited our focal site, our data consisted of 20 half-hour periods recorded on 19 different days (i.e. one to two periods per day), with the earliest zebra finch visit (observation) made at 0815 and the latest at 1644 hours and the rest relatively evenly spaced over the course of the day. From the videos, during each observation (visit at the water source) we recorded as responses to heat the proportion of time an individual (1) kept its bill open (gasping when breathing, Zann, 1996), (2) held its wings away from its body (lifting the shoulder away from the body to facilitate air flow over the underwing, Zann, 1996), (3) exhibited a ‘spread out’ position when both the wings and the tail were spread and (4) kept its tail fanned when not in a ‘spread out’ position.

Temperature data

We obtained continuous air temperature data (accuracy: 1 min) recorded at the Australian Bureau of Meteorology automated weather station (AWS) based close to the Fowlers Gap homestead, and 16.9 km from Gap Hills and 12.4 km from ‘White Tank’. Since the study locations and the weather station are at similar elevations (Gap Hills: 155.9 m; White Tank: 147.9 m; Fowlers Gap AWS: 181.0 m), and relatively close, we assumed that the temperature recorded here would closely reflect those at the two study sites. Based on long-term climatic data at our field site, we considered a heatwave to be any period when the daily maximum atmospheric temperature exceeded 40°C on 2 or more consecutive days (Hurley et al., 2018).

Ethical note

The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

Data Analysis

Hour by hour temperature and foraging

The detailed temperature data were processed to obtain the average temperature per hour during the recorded zebra finch foraging activity (0600–1959 hours) for all subsequent analyses. A linear mixed-effect model with normal error structure (LMM) was performed to test the relationship between temperature and the hour of the day during the study period. The average temperature per hour was fitted as the dependent variable, the hour of the day as a fixed term and the date as a random term. Using the maximum threshold of 15 min to define independent feeder visits and having reduced the data set as described, we summarized individual foraging activity on an hourly basis as a binary variable (yes/no; feeding occurred/did not occur within a given hour). To understand the relationship between individual foraging behaviour, temperature and time of day, we built a generalized linear mixed model (GLMM) with binominal error distribution and we fitted the binary foraging activity (yes/no) variable as the dependent variable and average temperature per hour, time of day (hour) and their interaction as fixed terms. We included the time of day in the model to account for variables that we did not directly measure but are likely to be related to the time of day and may influence foraging, including both extrinsic (e.g. changes in shade) and intrinsic variables (e.g. diurnal patterns of physiology and nutritional state). Individual ID and date were set as random terms.

Foraging behaviour may be considered a two-step process (Levy et al., 2016), whereby as well as deciding whether or not to forage during a particular period of the day, individuals can also vary the duration of bouts of foraging. To test for the influence of air temperature on the duration of foraging activity, we examined the number of 5 min intervals in which an individual was recorded at each feeder it visited as a proxy for foraging duration. We took this approach because the decoders on the feeders do not record entry and exit of individuals (Mariette et al., 2011; see above). We built a GLMM with Poisson error structure to investigate the probability that an individual was recorded at any feeder during each 5 min period (number of periods summed per hour; i.e. values from 1 to 12 possible), to reflect what proportion of the day each individual was out actively foraging. This foraging duration proxy was the dependent variable, average air temperature per hour, time of day (hour) and their interaction were fixed terms and individual ID, feeder ID and date were random terms.

We also analysed the first and last feeding event per day, as minutes since sunrise and minutes since sunset, respectively. First, we excluded the visits that represent the two tails of the distribution with respect to early and late visits to the feeders, to remove birds that did not visit the feeders at all early in the morning or late in the afternoon. The threshold of exclusion was determined by plotting the bimodal distributions of the first and last feeding events, and removing the outliers from the interquartile range above the third quartile (i.e. first foraging 2 h after sunrise), eliminating 10.6% of first feeding events, and from the interquartile range below the first quartile (i.e. last foraging 3.5 h before sunset), excluding 8.4% of last feeding events. Then, we tested whether the first and last feeding events (in relation to sunrise and sunset) were linked to the temperature at sunrise and sunset, respectively. We ran an LMM with time of first feeding event as the dependent variable, temperature at sunrise as a fixed term and individual ID and date as random terms. The same model was run for the last foraging event and the temperature at sunset.

Temperature and foraging site to water distance

To test the relationship between temperature and foraging activity in relation to the water source (a dam), we calculated the distance to the dam of each feeder visited and built an LMM with this distance as the dependent variable, average temperature per hour, time of day and their interaction as fixed terms and individual ID, feeder ID and date as random terms. To further investigate the effect of air temperature on the zebra finches' spatial distribution in relation to the water source, we first identified the furthest feeders based on their distribution in relation to the dam (average distance to the water ± SD: furthest feeders = 732 ± 52 m, N = 6 x 2 trials; other feeders = 406.7 ± 140.5 m, N = 10 x 2 trials); then, we calculated the proportion of visits to the furthest feeders over the total number of visits per hour. Since the total number of visits changed with time of day (see Results), we excluded the hours with fewer than 10 visits (excluding 35 data points from the total of 237). A GLMM with binomial error structure was built with the proportion of visits to the furthest feeders as the dependent variable, average air temperature per hour, hour of the day and their interaction as fixed terms and date as a random term.

As conditions become hot, individuals may also change the locations at which they feed, placing greater reliance on a single feeder rather than travelling more widely to multiple feeders. Therefore, we built a model on the effect of air temperature on zebra finches' tendency to revisit the same feeder, rather than changing feeders. We calculated the proportion of visits by an individual to its most visited feeder per hour. Thus, we created an index of feeder fidelity that ranged from 0 to 1, with 1 indicating that an individual made all its visits within the given hour to one feeder, and values less than one, indicating that an individual used multiple feeders. A GLMM with binomial error structure was run: the feeder fidelity was fitted as the dependent variable, average air temperature per hour, time of day (hour) and their interaction as fixed terms and individual ID and date as random terms.

We also tested the effect of air temperature on social foraging, by counting zebra finches active at each feeder within 15 min intervals (when at least one zebra finch was present in this period). We built a GLMM with Poisson error structure and the number of birds per feeder during 15 min intervals was set as the dependent variable, average air temperature per hour as a fixed term and feeder ID and unique 15 min periods as random terms.

Temperature and heat amelioration behaviour

To test for a link between temperature and heat amelioration behaviour at 'White Tank' we transformed the data from proportion of time to presence/absence (binomial) of each behaviour per bird observation. For each behaviour we conducted one GLMM with a binomial distribution. The dependent variable was the presence/absence of each behaviour, fixed terms were temperature (average per hour), hour of the day and their interaction and the duration of observation (s) and date were included as random terms.

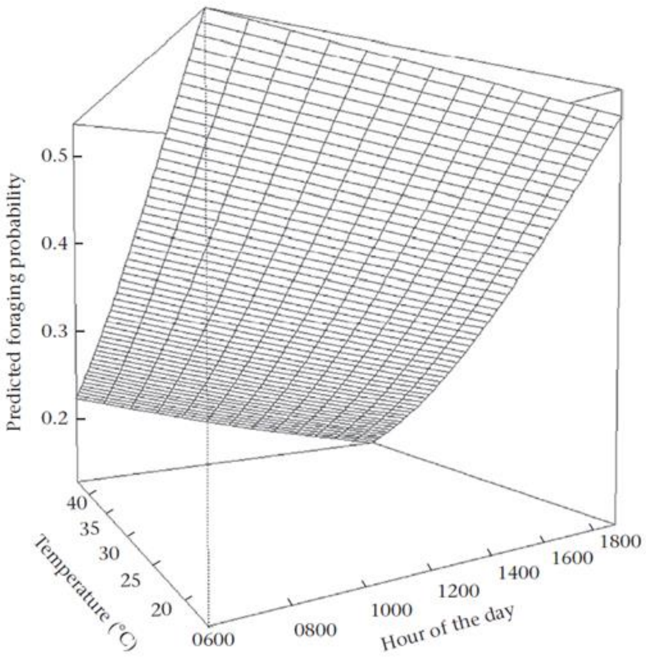


Figure 2 Predicted probability of foraging activity (as individuals' presence at the feeders) as a function of air temperature, hour of the day and their interaction.

Results

Air temperatures (T_a) ranged between 17°C and 44°C during the study period (17 days: 4 days during trial 1 and 13 days during trial 2) and the hours of zebra finch feeder activity (between 0600 and 1959 hours). Temperature generally increased during the day (Table 1). Across the time of monitoring there were two heatwave events: from 29 to 31 January maximum daily temperature was 42–43°C and from 4 to 6 February it ranged between 40.5 and 44°C (Fig. 1b).

A total of 8484 feeder visits by the focal 81 tagged zebra finches (40 females and 41 males) were recorded. The likelihood that an individual was recorded foraging in a particular hour was predicted by temperature, and this depended on the time of day ($N_{observations}$=22032 including the absences of an individual at a respective feeder; Fig. 2, Table 1). At air temperatures of 17°C the predicted probability that an individual was foraging in each hour (across the hours of daylight) ranged between 55.6% and 56.7%, while at temperatures of 40°C the foraging probabilities were much lower with a predicted range between 23.4% and 29.4%. Foraging

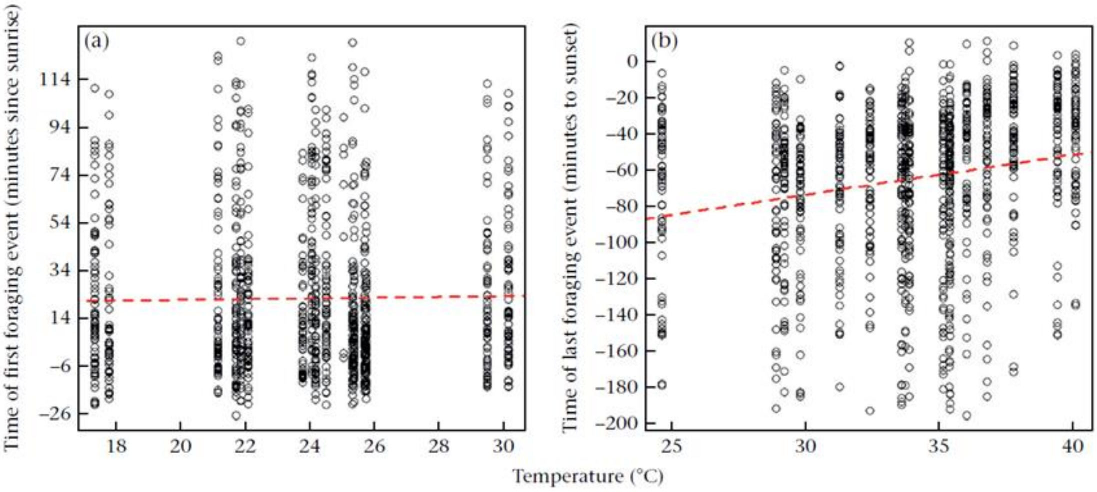


Figure 3 The zebra finches' (a) time of first feeding event (as minutes since sunrise) and (b) time of last feeding event (as minutes to sunset) as a function of air temperature. Note that negative values represent time before (a) sunrise and (b) sunset. The red dashed lines represent the model predicted relationship.

activity was generally lower later in the day with the lowest predicted values (21–26%) at the highest temperatures (Fig. 2). With increasing air temperature, the foraging duration proxy (the sum of presence during 15 min intervals at a feeder per hour) decreased ($N_{\text{observations}}$=8385), independently of time of day and its interaction with temperature (Table 1).

The majority (89.4%) of the tagged individuals foraged for the first time each day between 26 min before sunrise and 2 h after sunrise. The time of the first foraging event, relative to the time of sunrise, was not influenced by temperature at sunrise ($N_{\text{observations}}$ =1201; Fig. 3a, Table 1). The time of an individual’s last foraging event ranged mostly (91.6%) between 3.5 h before sunset and 10 min after sunset. Birds visited the feeders for the last time 2.2 min later in the day with every increase of 1C at sunset ($N_{\text{observations}}$=1232; Fig. 3b, Table 1).

Overall, as air temperatures increased, zebra finches were more active at the feeders closer to the dam ($N_{\text{observations}}$ =8484; Table 1), independently of the time of day and the interaction between time of day and temperature (Table 1). Specifically, the proportion of visits to the feeders furthest to the dam decreased with increasing air temperature ($N_{\text{observations}}$=202; Fig. 4). The predicted proportion of visits to these feeders decreased 0.31–0.98% per 1°C of air temperature, over the birds’ activity period during the day. The time of day had an independent positive effect on the proportion of visits to the furthest feeders from the dam (Table 1).

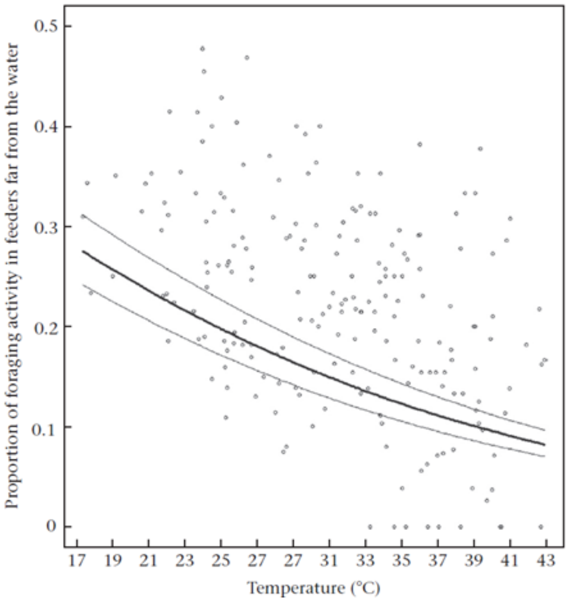


Figure 4 Proportion of visits to the feeders located furthest from the water source in relation to air temperature. The logistic curve and its interval of variation (95% confidence interval) are shown.

The tendency of an individual to forage at the same feeder, measured as feeder fidelity, increased with rising air temperature ($N_{\text{observations}}$=7032; Table 1, Fig. A1) but was independent of the time of day and the interaction between temperature and time of day (Table 1). We also found that the number of birds detected at an individual feeder (i.e. foraging together), within each 15 min interval, was affected by the temperature (Table 1, Fig. 5) decreasing by 50% between 18 and 41°C.

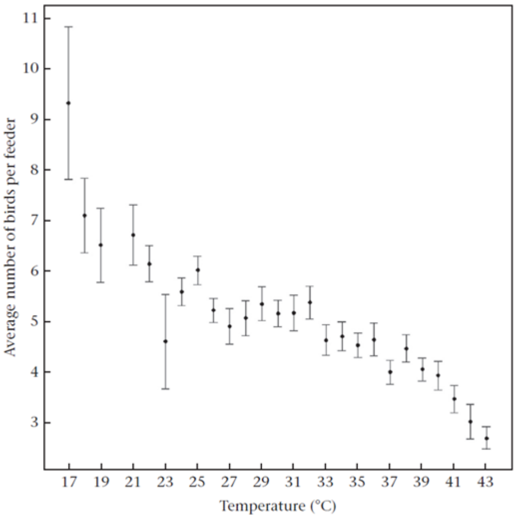


Figure 5 Mean ± SE number of zebra finches per feeder within 15 min intervals in relation to air temperature. Data are summarized to means and SEs per degree Celsius based on raw data for illustrative purposes. Analyses were carried out on average air temperatures per hour (not rounded to the next integer).

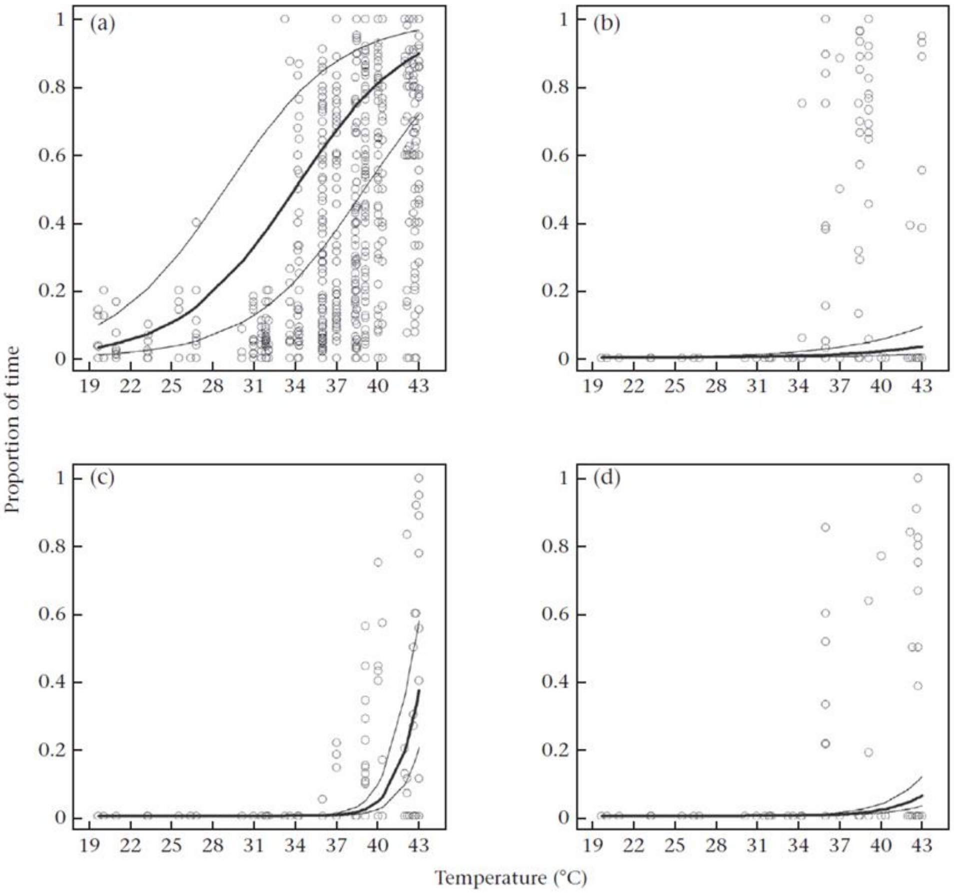


Figure 6 Adult heat stress behaviours (as proportion of time) as a function of temperature. (a) Bill kept open, (b) wings lifted away from body, (c) tail fanned and (d) spread out position. The logistic curves with their intervals of variation (95% confidence interval) represent the probability of showing the behaviour (based on presence/absence of each behaviour in every observation) in relation to temperature. In (a) the likelihood of the behaviour 'bill kept open' occurring is based on a model that does not include the interaction between hour of the day and temperature, to facilitate comparison with the other graphs.

The majority (73.5%, $N_{\text{observations}}$= 1454) of the bird observations on videos occurred between 1100 and 1459 hours at 'White Tank'. The likelihood of the behaviour 'bill kept open' increased with the interaction between temperature and hour of the day (Fig. 6a) and the duration of the observation (Table 1). The behaviour 'wings held away from the body' increased with temperature (Fig. 6b) and duration of the observation (1454), whereas it decreased with the hour of the day (Table 1). The likelihood of the behaviour 'tail kept fanned' and the 'spread out' position, with both tail and wing feathers spread, increased with increasing air temperature (Fig. 6c, d) and with the duration of the observation (Table 1). The proportion of time individuals held their bills open remained low until a slight increase at around T_a=33°C, followed by a steep increase at 35°C and a steady increase up until the highest temperatures at 41–43°C (Fig. 6a).

Similar increases were noted with ‘wings’ at 35°C and ‘tails’ at 39°C (Fig. 6b). The likelihood of individuals keeping their bills open peaked at 87.9% at 41–42°C, ‘wings’ at 10.7% at 38–39°C, ‘tails’ at 17.6% at 42–43°C and ‘spread out’ at 12.7% at 41–42°C (Fig. 6).

Discussion

We analysed the hour-by-hour foraging activity of 81 zebra finches over 17 days across a period of extreme hot weather, in an arid area in Australia, during which 12 days had maximum temperatures over 35°C, and there were two heatwaves, with at least 2 consecutive days over 40°C. We found that increasing air temperature led to a significant reduction in the amount of overall foraging that was observed across the population and in the proportion of time that individuals spent actively foraging. As well as reducing their foraging activity, birds foraged closer to the dam during hot weather. The intensive nature of our monitoring also allowed us to demonstrate a shift in the temporal distribution of foraging behaviour on hot days, with a higher level of foraging closer to dusk, presumably as birds were constrained by the heat from foraging earlier in the day. Both the increasing degree of feeder fidelity and the reduction in the duration of foraging each hour with increasing temperature suggested that the patterns of foraging that we have demonstrated both temporally and spatially were driven by the physiological constraints of foraging in hot conditions and the need to keep cool. This interpretation was also supported by the observed increase in heat dissipation behaviour with increasing temperature. A final important consequence of changes in foraging patterns during hot conditions was that birds foraged in smaller groups as temperature increased, and this may have important consequences for predation, if group foraging helps to reduce the risk of predation in this environment (Sorato et al., 2012).

A negative effect of temperature on bird physiology and behaviour during the hottest parts of the day has been found in other studies, especially in arid environments (Smit et al., 2013; Tieleman and Williams, 2002). The need to prioritize thermoregulation has been shown to be the main constraint in foraging efficiency in a variety of species in extreme temperatures (Carmi-Winkler et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Tieleman and Williams, 2002). However, while our results are consistent with these earlier findings, our temporal and spatial data are more complete and provide important new insights into the relationship between heat and foraging. All these previous studies gathered data as short and discontinuous focal observations of individuals or groups (e.g. 20 min to 2 h per individual), and focused on insectivorous and territorial species, with relatively small numbers of individuals. While this kind of data certainly provides a good estimate of both the level of foraging activity and even foraging efficiency (du Plessis et al., 2012), across different temperatures, none of these earlier studies were able to consider individuals in a temporally complete way. The present study, by using PIT tag system, provided a more comprehensive overview of the effect of high temperature on foraging activity, following a greater number of individuals, consistently, during the entire daily activity range and over several weeks. Although the use of PIT tag technology has been used previously to explore foraging activity related to heat in a small mammal (Levy et al., 2016), our study provides the first evidence for a non-territorial bird species facing an energetic trade-off between the need to stay near water and foraging activity, affecting both temporal and spatial daily patterns of behaviour.

Two important new insights emerged from our more intensive collection of data. First, we found that in addition to being constrained in the amount of foraging activity that was undertaken on hot days, the birds also had a spatially more constrained pattern of foraging behaviour. Different nutritional regimes are expected to reflect differences in resource allocation in trade-off balances (Flatt and Heyland, 2011; Ng'oma et al., 2017), such as that between thermoregulation and foraging behaviour. A recent study examined the difference in the drinking water needs of insectivorous, omnivorous and granivorous species of bird, highlighting the water dependence of the latter compared to other arid avifauna (Smit et al., 2018). While insectivorous and omnivorous species may be less reliant on water during hot periods, it would be interesting to examine the extent to which their movement behaviour changes in response to high temperature. Even though such species will not be constrained by the availability and location of surface water, they will presumably be constrained by the physiological need to reduce activity and the production of metabolic heat, as well as seeking shade and engaging in heat amelioration activity.

We found that individuals' activity increased at feeders closer to the dam (i.e. a source of drinking water) and reduced at the furthest feeders with increasing temperature, independently of the time of day. In our study, food was of the same quality across the range of feeders provided, and birds could therefore access a similar level of resources close to the dam. However, in natural circumstances it is likely that this restricted foraging range would impact their ability to find food efficiently, especially because natural foraging patches are generally further from artificial water sources, where the effect of selective grazing favours shrubland over grasslands (James et al., 1999). Given the similar quality and quantity of food in the different feeders, the shift in pattern relative to the water source suggests that the zebra finches' spatial decision of where to forage is shaped by the air temperature and the availability of water in this arid area. Drinking regularly helps to prevent overheating during the hottest hours of the day (Calder, 1964; Calder and King, 1963). Although the importance of water for thermoregulation is well known and documented (Calder, 1964; Tieleman and Williams, 2002; Zann, 1996), to our knowledge this is the first description of a spatial change in foraging activity in relation to water and induced by high temperature, based on the monitoring of individuals' movement at a fine temporal and spatial scale.

The importance of water and the physiological constraints of heat were further supported by our observations of birds during the hottest periods of the day, and the hottest days, when we encountered zebra finches sitting in small groups near the water. We found that by the time air temperatures reached 35°C, a significant proportion of birds were panting, in line with previous studies (Schleucher, 1993; Zann, 1996), as well as wing spreading or fanning (Eto et al., 2017; O'Connor et al., 2018; Tieleman and Williams, 1999). Above 41°C individuals also exhibited two other behaviours, which we were unable to find any reference to, in a heat dissipation context. Tail fanning, a behaviour previously observed in breeding males during nest searching (Zann, 1996), was performed by both sexes a small proportion of the time, but only at temperatures above 41°C, suggesting it may be used as a further method of either passive or cutaneous evaporative cooling (Gerson et al., 2014), possibly by increasing airflow to the rump of the bird. Furthermore, some individuals adopted an unusual position with the tail fanned and the wings held partially spread out so that they were touching the tail, while the bird sat in a hunched-up position, usually very low on its perch. This position may have acted to increase airflow to both the tail and axillary regions at the same time. Moreover, it may have signified a level of heat stress in individuals.

The second aspect on which our study provided new insight was in relation to the temporal spread of foraging behaviour in relation to extremely hot conditions. While numerous studies have found that the level of foraging is typically reduced in hot periods (Carmi-Winkler et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Tieleman and Williams, 2002), we have been able to examine this in the context of a far longer period of behavioural monitoring. As expected, we found that individuals' foraging activity was influenced by both temperature and time of day, but importantly, on the hottest days the timetable of foraging activity was significantly different, with individuals deferring their foraging activity until significantly later in the afternoon/evening. We believe that this is a sensible behavioural change to enable the birds to avoid foraging earlier in the day when it is hot, given that our feeders probably represented a fairly stable source of food which birds could rely on later in the day. The two peaks of activity predicted by optimal mass regulation theory (Houston et al., 1993) were confirmed in our data, as well as the extreme inactivity during the hottest hours of the day (1100–1600 hours, Fig. A2; Angiletta et al., 2010; McNamara et al., 1994). Therefore, we are reasonably confident that the use of feeders reflects a natural foraging pattern for a passerine bird. In a previous study at the same site during the breeding season (a cooler period of the year) individuals frequented the feeders more constantly throughout the day, with some variation during different phases of the breeding cycle (Mariette et al., 2011). By contrast, a more bimodal distribution of foraging behaviour was found in captive zebra finches in unpredictable food availability conditions, without breeding activity or predation risk (Dall and Witter, 1998). During our study period very few breeding attempts were observed and there was no successful breeding, in line with recent findings showing that arid zone Australian birds typically do not breed in the summer (Duursma et al., 2017). According to theoretical foraging models (Houston et al., 1993), it seems likely that on the hottest days, individuals were refraining from foraging throughout most of the day until it became a little cooler, at which time they needed to forage more intensively to take on food before nightfall. Further studies are required to better investigate how food predictability can change foraging dynamics both during and outside the breeding period.

Our results suggest therefore that while there may be significant drops in foraging behaviour during hot conditions, individuals may significantly alter the timetable of foraging across the day. As such, previous studies that have determined the effect of extreme temperature on foraging activity (e.g. Carmi-Winkler et al., 1987; Edwards et al., 2015; Goldstein, 1984; Ricklefs and Hainsworth, 1968), may have perhaps overestimated the extent to which heat might affect an individual's intake across the whole day. Although we did not examine food intake, our results may suggest that a short period of intense foraging later in the day may, at least partially, provide the opportunity to make up lost foraging during a hot day. The extent to which this is possible will of course depend on the extent to which the day cools in the late afternoon and the foraging pattern of the species. For example, the efficiency of foraging across the day may also co-vary with time for other reasons such as the depth or availability of prey or the light levels (Fernandez-Juricic and Tran, 2007). We did not measure the effect of these extreme heatwaves on the body condition or mass of our birds, and note some of the previous studies have done so (du Plessis et al., 2012; Edwards et al., 2015). This would be a very effective way of determining the short- to medium-term effects of hot conditions on foraging and body condition.

Although we did not measure food intake in this study, it seems likely that the reduced level of foraging activity would be coupled with a reduced food intake, because the birds are always likely to be exposed to a high risk of predation while out foraging, and it is unlikely that they would have increased the rate at which food was processed while at the feeders on hot rather than cool days (i.e. we do not believe the foraging efficiency would change). It would be useful to explore the relationship between air temperature and food intake directly, and ideally account for variation in metabolic rate. However, until such work is done, if we assume that all else is equal, then it seems likely that the reduced foraging activity during high temperatures will constrain successful reproductive activity (when foraging demands on adult birds are typically at their highest level), and potentially also prove physiologically costly if adults are unable to meet their daily nutritional requirements. Again, it would be interesting to examine the extent to which adults lose body condition during sustained periods of high air temperatures and heatwaves in particularly (e.g. du Plessis et al., 2012, Edwards et al., 2015). The negative relationship between high temperatures and foraging activity we have demonstrated could be interpreted as one cause of the low body size of zebra finches that were reared during hot conditions in the field (Andrew et al., 2018, 2017; Cunningham et al., 2013) and the avoidance of breeding in summer for arid species generally in Australia (Duursma et al., 2017).

Overall, our results highlight that hot conditions affect spatial, temporal and social patterns of foraging activity in this non-territorial granivorous species and adds a level of insight into the way in which birds will respond to extreme heat events and to an increasingly hot climate. The effects that we demonstrated using our tracking system have potential downstream effects on body condition, physiology, life history and predation, all of which should be examined in future studies.

Acknowledgments

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Table 1 Summary of all (G)LMMs.

Response variable	Random term	*N*	Variance	Fixed effect	Estimate	SE	X^2 (*df*)	*P*
Air temperature (continuous)	Date	17	12.31	(Intercept)	20.35	1		
	(Residual)		9.35	Hour	0.91	0.04	282.6 (1)	**<0.001**
Foraging activity (binary)	ID	81	0.34	(Intercept)	0.89	0.26		
	Date	17	0.04	Temperature	−0.04	0.01		
				Hour	0.02	0.02		
				Temperature*Hour	−0.001	0	5.13 (1)	**0.02**
Foraging duration proxy (count)	ID	81	0.006	(Intercept)	0.5	0.05		
	Date	17	0.001	Temperature	−0.004	0.001	7.3 (1)	**0.007**
	Feeder ID	32	0.004	Hour	(0.003)	(0.003)	1.06 (1)	0.3
				Temperature*Hour	(<0.001)	(<0.001)	0.1 (1)	0.9
Time of first foraging event (continuous)	ID	81	270.59	(Intercept)	18.76	17.7		
	Date	17	88.64	Temperature at sunrise	0.15	0.73	0.04 (1)	0.83
	(Residual)		681.44					
Time of last foraging event (continuous)	ID	81	463.88	(Intercept)	−140.5	17.7		
	Date	17	53.49	Temperature at sunset	2.22	0.52	12.4 (1)	**<0.001**
	(Residual)		1170.04					
Distance of feeder visited to water (continuous)	ID	81	6.9	(Intercept)	535.2	2.04		
	Date	17	0	Temperature	−<0.001	0.001	3161.7 (1)	**<0.001**
	Feeder ID	32	141.7	Hour	−(<0.001)	(<0.001)	0 (1)	1
	(Residual)		0	Temperature*Hour	−(<0.001)	(<0.001)	0 (1)	1
Proportion of visits to feeders furthest to dam (proportion)	Date	17	0.03	(Intercept)	−0.01	0.17		
				Temperature	−0.06	0.01	32.64 (1)	**<0.001**
				Hour	0.04	0.01	11.15 (1)	**<0.001**
				Temperature*Hour	(−0.002)	(0.001)	2.53 (1)	0.11
Feeder fidelity (proportion)	ID	81	0.27	(Intercept)	0.7	0.2		
	Date	17	0.12	Temperature	0.06	0.007	71.8 (1)	**<0.001**
				Hour	(−0.02)	(0.02)	1.4 (1)	0.23
				Temperature*Hour	(−0.001)	(0.001)	0.7 (1)	0.4
Number of birds around each feeder in 15 min interval (count)	Unique 15 min period	914	0.14	(Intercept)	2.27	0.09		
	Feeder ID	32	0.07	Temperature	−0.03	0.002	124.07 (1)	**<0.001**
Bill open (binary)	Date	19	0.9	(Intercept)	8.32	6.15		
				Duration	0.02	0.004	30.1 (1)	**<0.001**
				Temperature	−0.28	0.19		
				Hour	−1.43	0.5		
				Temperature*Hour	0.04	0.015	5.84 (1)	**0.004**
Wings away (binary)	Date	19	5.56	(Intercept)	−19.73	7.27		
				Duration	0.03	0.006	26.14 (1)	**<0.001**
				Temperature	0.75	0.3	10.88 (1)	**0.013**
				Hour	−1.12	0.53	8.08 (1)	**0.03**
				Temperature*Hour	(−0.13)	(0.14)	1.57 (1)	0.21
Tail fanned (binary)	Date	19	0.65	(Intercept)	−28.48	5.62		
				Duration	0.02	0.01	4.51 (1)	**0.03**
				Temperature	0.63	0.14	30.95 (1)	**<0.001**
				Hour	(0.03)	(0.21)	0.03 (1)	0.87
				Temperature*Hour	(−0.06)	(0.11)	0.37 (1)	0.54
Spread out position (binary)	Date	19	1.2	(Intercept)	−23.68	5.83		
				Duration	0.02	0.01	5.37 (1)	**0.02**
				Temperature	0.48	0.14	26.84 (1)	**<0.001**
				Hour	(−0.14)	(0.3)	0.02 (1)	0.64
				Temperature*Hour	(−0.03)	(0.08)	0.13 (1)	0.72

Response variables, random terms, sample size (N) and variance are specified for each model. Value of fixed effects and SEs are estimates for the variables in a minimal adequate model; values in parentheses represent coefficients and SEs from the model before the term was dropped. Significant P values are highlighted in bold.

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Appendix

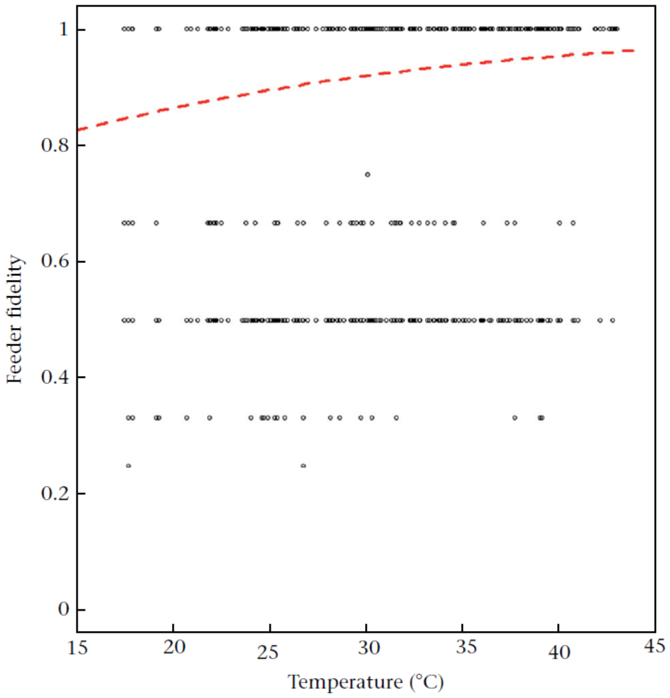


Figure A1 Feeder fidelity, i.e. the proportion of visits of an individual to its most frequented feeder per hour, as a function of air temperature. The red dashed line represents the model predicted relationship.

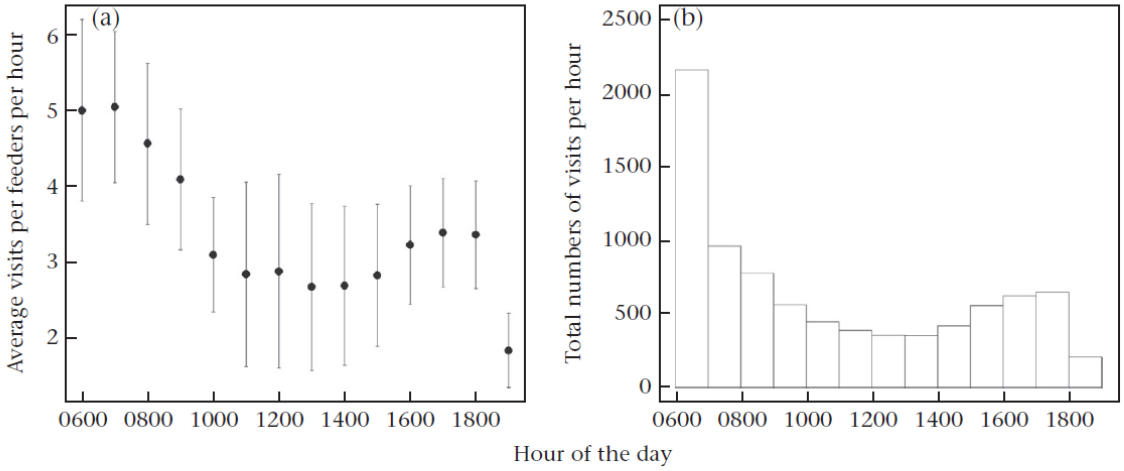


Figure A2 (a) Mean hourly number of visits to the feeders ± SD and (b) total number of visits per hour.

Chapter Five

Persistent sampling increases food patch use, but not reproductive success, in wild zebra finches

Funghi Caterina, Schuett Wiebke, Griffith Simon C.

Photo credit Joseph England

Abstract

Theoretical work predicts that there are two non-mutually exclusive strategies that animals may use to cope with the unpredictability of food sources: relying on social information, by observing and following conspecifics to foraging patches, and by increasing personal knowledge of the landscape and its fluctuations. In a patchy and unpredictable habitat, the latter strategy may also include repeatedly returning to previously profitable patches, even if they are often found to be empty. However, little is known about such persistent checking behaviour, especially in the wild, because tracking foraging movements by individuals over the required period of time is challenging. We were able to address this question using a PIT-tagged wild population of zebra finches (*Taeniopygia guttata*), foraging over an array of feeders in an Australian arid environment. Combining an experiment in which we manipulated food availability simultaneously with a brood size manipulation experiment, we identified individual differences in spatial and temporal foraging patterns and tested their effect on reproductive success. We provided the population with two sets of artificial feeders: one set represented a reliable and stable food source; the other simulated an unpredictable and ephemeral food source that periodically provided higher quality food, but more frequently, provided no food at all. We demonstrated that individuals consistently differed in space use for foraging purpose and that the persistence with which individuals sampled these empty food patches, previously experienced as rewarding, was related to an increase of foraging activity (e.g. number of visits to all the feeders available as an estimation of total food intake) and spatial generalism (also exploiting a greater number of the stable feeders). Differences in the food searching effort of parents predicted the survival rate of enlarged, but not reduced broods. Specifically, the broods of parents that were challenged to rear an enlarged brood, and that sampled empty feeders at a lower rate, had higher survival rate than those of parents that invested more effort in sampling empty patches more persistently. Our results demonstrate that some individuals do adopt quite persistent patch checking behaviour, which co-varies with the use of a wider range of foraging options, than other birds that show a more limited use of the total feeders available and a lack of persistent patch checking behaviour. Although the parameters in our experiment only delivered high quality reward intermittently, presumably under some circumstances the strategy of persistent patch checking would yield dividends.

Keywords: optimal foraging, unpredictability, sampling to keep track, zebra finches, arid environment

Introduction

The variation in the ability of individuals to find food, and optimize their foraging has been a central topic for behavioural ecologists (Bolnick et al., 2003; Dall et al., 2012; Stephens and Krebs, 1986; Van Valen, 1965). A forager can either maximise its immediate food intake, by relying on the patches providing the highest known reward, or, if the risk of starvation is minimal, it may try to optimise the nutritional quality of its food intake by investing time in sampling different food sources or returning to previously depleted patches (i.e. ‘sampling to keep track’, Dall and Johnstone, 2002; Stephens, 1987). The optimal balance between exploration and exploitation of a food patch has been extensively modelled (Dall and Johnstone, 2002; McNamara and Houston, 1985; Stephens, 1987) and tested in captivity (insects: Fourcassi and Traniello, 1993; Keasar et al., 2013; fish: Pitcher and Magurran, 1983, birds: Dall and Johnstone, 2002; Krebs, 1978; mammals: Devenport and Devenport, 1994), but rarely investigated in the wild, due to the difficulties in distinguishing between sampling and exploiting (Naef-Daenzer, 2000). Recent technological advances may allow to make a discrimination between the two. For example, the use of automated data loggers in a population of mix-species birds (great tits, *Parus major*, blue tits, *Cyanistes caeruleus*, marsh tits, *Poecile palustris*, coal tits, *Periparus ater* and nuthatches, *Sitta europaea*) allowed to understand that individuals in a stable food environment concentrated their sampling effort during the early morning to exploit the best option in the afternoon (Farine and Lang, 2013). Most of the theoretical and empirical studies have been focused on the economics of tracking less profitable food patches and little on the return to empty patches, probably because it is considered as the most inefficient strategy (Stephens, 1987), even though under some circumstances such a strategy will pay well. Having gathered information on the location of food sources, individuals may differ in their resource-use efficiencies and specialize (Bolnick et al., 2003; Dall et al., 2012; Van Valen, 1965). This concept, called the ‘individual niche specialization’, has been demonstrated in a variety of taxa, from insects to mammals (reviewed in Araújo et al., 2011), in the context of the variation in diet, but also for spatial foraging patterns (e.g. brook charr, *Salvelinus fontinalis*, Bourke et al., 1997). There has been a recent upsurge in the number of studies focusing on differences in resource-use across the landscape and their relationship with other individual traits e.g. sex, morphology, personality and breeding success (Dall et al., 2012; Patrick and Weimerskirch, 2014; Toscano et al., 2016).

Food availability plays a key role in emerging variability of foraging behaviour (e.g. diet specialization, Araújo et al., 2011; Stephens and Krebs, 1986). When high value food resources are available and predictable, the variability in resource-use within a population (i.e. between individuals) is likely to be due to intrinsic variation in item or food patch preferences (Bolnick et al., 2003; Robinson and Wilson, 1998). In stable environmental conditions, ecological specialists are favoured, as they use few resources more efficiently than generalists (Clavel et al., 2011), maximizing their immediate food intake (Dall and Johnstone, 2002). On the other hand, in a changing environment, where food resources are patchy or only temporarily available (e.g. flowers for pollinators, Szigeti et al., 2018 and unpredictable arid habitat, Fryxell et al., 2005), plasticity in food searching may play an important role in enhancing individual fitness (Bolnick et al., 2003), and ecological generalists, that sample and exploit more resources, are generally favoured (Mettke-Hofmann, 2014).

Australian arid environments are highly unpredictable, characterized by an interactive and non-linear relationship between rainfall and vegetation responses (i.e. ‘pulse-reserve’, Noy-Meier, 1973; Reynolds et al., 2004). Therefore, the low primary productivity results in highly variable food abundance both spatially and temporally, representing an important selective pressure on all animals inhabiting such environments. In these types of environments, animals show a great opportunism (i.e. flexibility) both in reproduction and behaviour (Morton et al., 2011). Experimental manipulation of the predictability of food availability in naturally challenging environments can provide an opportunity to identify individual differences in spatial foraging behaviours (e.g. the number of food resources sampled and exploited), adding insight into their proximate causation (Bolnick et al., 2003).

The zebra finch, *Taeniopygia guttata*, is a gregarious bird widespread in the Australian inland and a model species for behavioural sciences in general (Griffith and Buchanan, 2010). Zebra finches are genetically monogamous and form long-term pair bonds, they are strictly granivorous and forage in non-monopolised grass patches in groups (Zann, 1996). Previous studies in wild zebra finches have shown that individuals differ in food searching behaviour, with some discovering and relying on few food resource patches and others discovering and relying on more (Mariette and Griffith, 2013; McCowan et al., 2015a). In McCowan et al. (2015a), the lack of relationship between reproductive success and individuals' consistent differences in foraging and exploration, suggested that the pay-off for 'sampling to keep track' might be linked to the likelihood of finding higher quality food, rather than quantity alone, as predicted by theoretical models (Giraldeau, 1997; Stephens, 1987). Additionally, the lack of a relationship might also have been due to the fact that the natural variation in brood size (used as a proxy for breeding success in McCowan et al., 2015a) was not strong enough to disentangle whether parents' differences in foraging behaviour predict differences in breeding success.

In the present study, we performed a food manipulation experiment to better understand the proximate causation of differences between individuals in spatial patterns of food resource use. We provided a wild population of zebra finches tagged with passive integrative transponder (PIT)-tags with two sets of artificial feeders. One set represented a reliable and stable food source and the other set represented an unpredictable and ephemeral food source, but with a higher quality food, provided only intermittently. Although seeds are generally found widely dispersed, the unpredictable, ephemeral set of feeders represents a rich patch of seeds, such as those that become trapped in a low depression as they are blown by wind. Such patches are highly unpredictable in time, because they depend on the wind strength, but are more predictable spatially, because they will be driven by fixed landscape structure (e.g. small depressions near habitat in which seed is produced, James et al., 2007). In accordance with theoretical models, we predicted that the number of birds visiting empty feeders decreased the longer they stayed empty, but that some individuals will keep sampling them - persistence (Dall and Johnstone, 2002; Stephens, 1987). Further, we tested whether food searching persistency (i.e. returning to empty patches, 'sampling to keep track') was positively correlated to increasing food intake (when increased quality food became available in these patches) and to a wider use of food sources across the landscape (e.g. exploiting more feeders).

In parallel with the food experiment, we challenged breeding individuals by increasing their parental care load through a brood size manipulation experiment. According to the optimal foraging theory, we expected the use of more stable food resources (i.e. stable artificial feeders) and a higher high-quality food intake to be an important component of energetically challenged parents' fitness rather than the non-challenged ones (Araújo et al., 2011; Stephens and Krebs, 1986). In this way, we expect the individual variation in resource-use to reflect differences in fitness, and the challenged parents with a wider use of the landscape are expected to have higher fitness (measured as nestling survival rate) than challenged ones with a narrower use of the available foraging opportunities in the landscape. On the other hand, for the individuals with reduced broods, we predict the variation in resource-use may not reflect their fitness output, because the reliability of (some, stable) food sources should be able to overcome their energetic requirements. Until now, the relationship between food searching behaviour variability and breeding success has not been directly tested, although theoretical models predicted that in complex environments, the benefit of tracking may not counterbalance the cost of sampling (Stephens, 1987).

Methods

Study site and general procedures

The study was conducted in Gap Hills at Fowlers Gap Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales, Australia. Here, 180 nest-boxes, clustered in six colonies, and an additional 64 boxes scattered in the periphery of the colonies (grouped into three clusters) were established within 1.5 km around a central artificial dam, providing the main water source for birds (Brandl et al., 2019). Between September and December 2017, the breeding activity of the zebra finches was monitored in the nest-boxes and the identity of the breeding parents was assigned by catching them in the nest-boxes with a nest-box trap (as described in Brandl et al., 2019). Adult zebra finches were also caught throughout September and October in artificial feeders and on two days of intensive capture with mist-nets. Each captured zebra finch was banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme), and a PIT-tag was fitted subcutaneously between the wings.

Brood size manipulation

Zebra finches are opportunistic breeders, genetically monogamous with bi-parental care (Zann 1996). The mean (± SD) clutch size is 4.9±1.05 eggs with an incubation period of 11-16 days and a chick rearing period of 17-19 days (Zann 1996). Survival rate in natural nests has been measured in Fowlers Gap as 13% and the clutches or broods failure were due to predation but also parental desertion. In nest boxes the survival rate was measured as on average 58% mostly because the predation was reduced to 2% (Griffith et al. 2008). Between October and November 2017, a brood size manipulation was conducted as described in Brandl et al. (2019). When the nestlings were at day 3 (hatching date=day0), they were swapped between either pairs or triplets of nests, bi-directionally, so that all nests received at least one chick from another brood. For every pair (and one triplet) of nests, we created one (two in the case of the triplet) reduced brood(s) of 2 nestlings (N=19 nests) and one enlarged brood with 5 to 8 nestlings (mean number of chicks: 5.8±0.7 SE, N=18 nests). We estimated the survival rate of each nest by the ratio between the number of nestlings at day 11 and those at day 4, the day after manipulation.

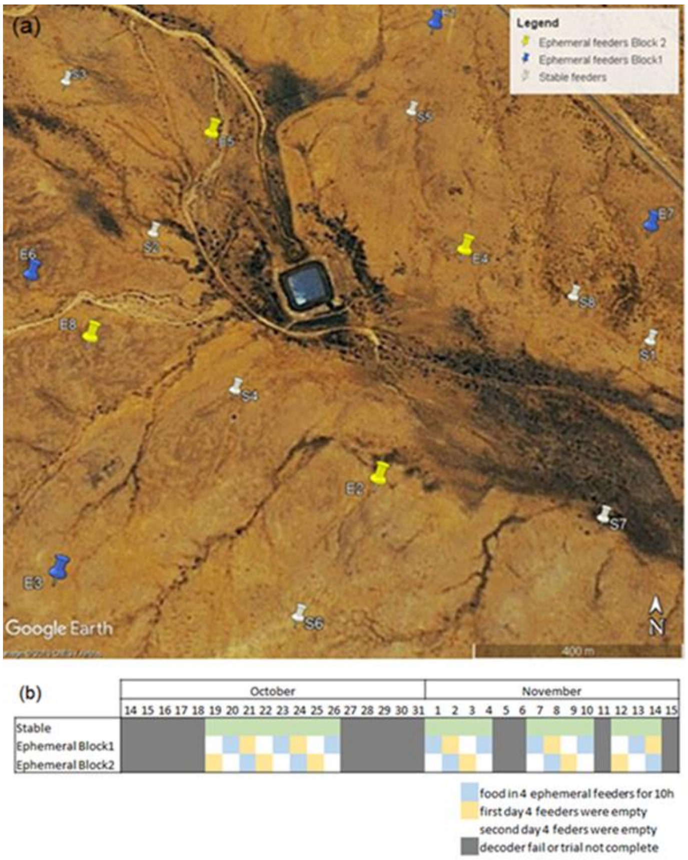


Figure 1 (a) Satellite image (from Google Earth) of the food manipulation set up. In white, marked with S the stable feeders, in blue and yellow, marked in with E, the two blocks of ephemeral feeders. (b) Data availability and food manipulation stages: in grey the days excluded from the analysis, because data from at least one feeder was missing. The stable feeders were filled with a constant amount of food (mix seeds and husks) renewed every day, marked in green. The ephemeral feeders received the food manipulation: in blue "food days", when the ephemeral feeder blocks received high quality food for 10h, in yellow "1st days empty", in white "2nd days empty".

Food manipulation set-up

From early September to December 2017, we provided 16 artificial feeders to the zebra finches, at least 200m from the dam, 180m from each other and 150m from the closest nest-box. The vegetation around the feeders did not vary (Supplementary Table 1). All the artificial feeders used consisted of a wire bird cage (70 x 40 x 50 cm) partially buried in the ground, with shade cloth covering around 20 cm of the cage from the bottom to prevent the seeds to be dispersed by the wind. The feeder door was wired open and fitted with a circular antenna connected to a RFID-decoder which recorded the PIT-tag ID, time and date every time a tagged zebra finch entered the feeder (Funghi et al., 2019).

Between October 14th and November 15th, we conducted the food manipulation experiment. Eight of the 16 feeders were filled with a constant amount of food that was mixed with husks to decrease the quality (500ml=400g seeds and 400ml husks), renewed every day (hereafter 'stable feeders'). The other eight feeders were divided into two blocks of four that did not always hold food (hereafter 'ephemeral feeders'). The first day, ephemeral feeders' block1 were provided with high-quality food (100g seeds mix and 150g of freshly mixed egg and biscuit formula) at sunrise (0600) and emptied after 10h (1600), while the ephemeral feeders block2 remained empty (Fig.1a). The second day, we shifted the order, and the ephemeral feeders block2 were filled with the same amount of high-quality food and the ephemeral feeder block1 remained empty. The third day, all the ephemeral feeders were empty all day long. As a result of this pattern, each day, one ephemeral feeder block received food, followed by two days in which it remained empty (Fig.1b).

Our analyses were dependent on having comprehensive data from all stable and ephemeral feeders simultaneously so that we could monitor all activity that individuals made in a day, knowing where they fed, and also which feeders they did not use. We therefore had to restrict our analyses to those 19 days on which all RFID-decoders at ephemeral and stable feeders were operating and detecting birds with no technical issues (Fig.1b, e.g. excluding 15 days when the decoder of at least one feeder in the array did not collect the data continuously throughout the day either due to battery failure or the use of a corrupted memory card).

Statistical analysis

Individuals' foraging pattern

To investigate an individual's daily foraging behaviour we determined the number of different feeders it used and the number of visits to each feeder to estimate feeder food intake. From the feeder decoder data, it was not possible to infer the direction of movement through the antenna, but, as previously validated (Mariette et al. 2011), we used a 15 minute rule to assess a feeder visit – whereby any two individual PIT readings within 15 minutes were assumed to be part of the same visit of an individual to a feeder (i.e. they will often stay in the vicinity of the feeder and enter and exit the feeder repeatedly during that period). In our data we accounted for individuals that received their PIT-tag part-way through the experiment, or disappeared part-way through (either moving out of the area, dying, or losing their tag) excluding the ‘missing data’. The spatial pattern of stable feeder use was represented by the number of different stable feeders visited per individual. The use of ephemeral feeders was identified by the number of ephemeral feeders visited on the three different days - when food was present; on the 1st empty days; and the 2nd empty day. The use of ephemeral feeders when food is present provides a high pay-off because of the high-quality food and we therefore calculated the individual number of visits to ephemeral feeders at food days as proxy for high quality food intake. Visiting an ephemeral feeder on the 2nd empty day indicates good persistence at checking a food patch, therefore we also calculated the individual number of visits to ephemeral feeders the 2nd empty day. Finally, the general foraging pattern was obtained by the total number of feeders visited (stable and ephemeral) and the total number of visits to (stable and ephemeral) feeders per individual.

We tested whether the difference between individuals in foraging behaviour was consistent along time. We considered the first six days, between the 19th and 24th October 2017, and the last six days of available foraging data, from the 7th to the 14th November 2017. For this analysis, we considered only the individuals who were tagged and foraged in the area using at least one of the feeders during both periods (i.e. including the ‘real zeros’ and excluding the missing values, N=154). For each six days-period we averaged the individuals’ daily number of visits and number of feeders visited along six days at stable feeders. The ephemeral feeders changed their food content at different days in each feeder block along the six-days periods considered. Therefore, we averaged the individuals’ daily number of visits and number of ephemeral feeders visited along the four days per period (i.e. two days per feeders’ block) when the ephemeral feeders were at food renewal day and four days per period (i.e. two days per feeders’ block) when they were at second empty day. Then, we run a repeatability analysis for the variable relative to the stable and ephemeral feeders (i.e. number of visits and number of feeders visited) using GLMM, assigning the Gaussian error structure based on the datatype (i.e. averages) with ‘rptR’ package in R (Stoffel et al. 2018), setting 1000 permutation tests to assess the likelihood of the 95% confidence interval to be significantly different from zero.

We proceeded summarising all foraging variables (repeatable and not, see results) to get the overall individual foraging behaviour on the ephemeral and stable feeders by calculating daily averages (i.e. one value per individual along the whole experimental period). We tested for collinearity between the individual average foraging variables with Spearman’s rank correlations (Supplementary Table 2). The number of feeders visited and number of visits were highly correlated at each set of feeders data considered (i.e. ephemeral feeders food and 2nd empty days, stable and ephemeral feeders together, Supplementary Table 2). We were interested in testing whether the food searching effort (i.e. number of visits to ephemeral feeders the 2nd empty days) affected the high-quality food intake (i.e. number of visits to ephemeral feeders at food days) and the general foraging pattern (i.e. to stable and/or ephemeral feeders). We therefore interpreted as an estimation of total foraging effort the average number of visits to stable and ephemeral feeders, that highly correlated with the average number of total feeders visited and the average number of stable feeders exploited, as an estimation of total foraging effort. For further analysis we considered the variables that were not correlated to any other variable with rho>0.7 (Freckleton 2011): the average number of visits to stable and ephemeral feeders visited (hereafter ‘total foraging effort’), the average number of visits to ephemeral feeders visited at 2nd empty days (hereafter ‘food searching persistency’) and the average number of visits to ephemeral feeders at food days (hereafter ‘high quality food intake’).We tested the relationship between the persistency of visiting empty feeders and the visits to stable feeders and the amount of access to high-quality food intake, in the long-term (i.e. average per individual over the study period). We built two Linear Models (LM) with the total foraging effort and, separately, the high-quality food intake as responses, food searching persistency was set as predictor variable.

Ephemeral feeder use

We tested if the number of birds visiting the ephemeral feeders fluctuated in accordance with the food presence. We characterized the stage of each ephemeral feeder block distinguishing between

’food day‘, ’1st day empty‘ and ’2nd day empty‘. We averaged the number of zebra finches visiting each ephemeral feeder block within a one-hour period (if at least one zebra finch was present), considering the total time of food availability (10h, between 0600 and 1600). We built a General Linear Mixed Effect Model (GLMM) with Gaussian error structure and the average number of birds per ephemeral feeder block per hour as the dependent variable. We included as fixed terms the ephemeral feeder block manipulation stage, hour of the day and their interaction; date and ephemeral feeder block ID were added as random terms. To better understand the significant interaction between hour of the day and ephemeral feeder stage (see Results), we divided the time of the day into two categories of five hours each: 0600-1059 and 1100-1600. We then built a General Linear Mixed Effect Model (GLMM) with Gaussian error structure and the average number of birds per ephemeral feeder block per hour as the dependent variable. We included as fixed terms the ephemeral feeder block manipulation stage, the two time categories and their interaction; date and ephemeral feeder block ID were added as random terms. Significant interactions between categorical variables were tested through a post-hoc comparison ‘phia’ R package (De Rosario-Martinez, 2015).

Foraging behaviour, brood manipulation and breeding success

Breeding activity in the study area started on September 15th when the first egg was laid and continued until November 20th with the last egg laid, therefore most of the breeding activity occurred during the food manipulation experiment. We tested whether different energetic parental load influenced the foraging behaviours of the breeding individuals. Since previous studies showed that the male and female of a breeding pair are highly synchronous in their foraging behaviour, they cannot be considered as independent (Mariette and Griffith, 2012a). We therefore assigned one value per foraging variable per breeding nest. For 21 nests the foraging variables were available for one of the parents, while for 14 pairs the foraging behaviour of both parents was available and thus the average was calculated between the partners to get one value per nest. We built three GLMMs with the parents foraging behaviours (i.e. total foraging effort, high-quality food intake and food searching persistency, separately) as dependent variables, brood manipulation treatment as fixed term and nest-box cluster as random term. Additionally, we tested whether the foraging behaviour predicted the breeding success of the individuals who were breeding during the food manipulation experiment. First, we tested for differences in nest survival rate, in relation to the brood manipulation treatments. We therefore built a GLMM with binomial error structure, using the survival rate (as proportion of chicks which survived at day 11 from day 4, after the manipulation) as dependent, manipulation treatment as fixed term and nest-box cluster as random term. Then, only for enlarged broods, we tested whether the survival rate was predicted by the parents' foraging behaviour, with a GLMM with binomial error structure, survival rate as dependent, parents' foraging behaviour (total foraging effort, high-quality food intake and food searching persistency) as fixed terms, nest box cluster as random term. It was not possible to run the same model with reduced broods because there was no variation between nests (i.e. all nestlings survived).

Table 1- Summary of the repeatability (R) analysis of individuals' foraging behaviours as number (No.) of feeders (fe.) visited and number of visits relative to the stable and ephemeral feeders. The analysis was performed comparing averages calculated for different periods. The confidence interval (CI) at 95% is also provided. The sample size was always 154 birds. The values in bold represent the repeatability considered significant, with CI different from zeros (higher than 0.1).

Foraging behaviour	R	CI	Dates first period	Dates second period
No. visits stable fe.	**0.3**	**0.2,0.45**	19-24 October	08-14 November
No. stable fe.	**0.3**	**0.13,0.42**		
No. visits at food days (ephemeral)	**0.4**	**0.27,0.52**	20-21-23-24 October	08-10-13-14 November
No. fe. at food day (ephemeral)	**0.4**	**0.21,0.5**		
No. visits at 2^{nd} empty day (ephemeral)	0.11	0,0.26	19-20-22-23 October	09-10-12-13 November
No. fe. at 2^{nd} empty day (ephemeral)	0.06	0,0.22		

Results

In the study period, 177 adult zebra finches (92 females and 85 males) foraged in the 16 artificial feeders. Individuals' foraging behaviour related to the stable feeders and ephemeral feeders at food days (i.e. number of visits and of feeders visited, average per individual per period) was repeatable between the first and last experimental week (N_{ID}=154, Table 1). The number of visits and feeders visited related to the ephemeral feeders the 2^{nd} empty days (i.e. average per individual per period), however, were not repeatable across the first and last experimental week (N_{ID}=154, Table 1). On average, individuals visited at least one feeder on 17.3±0.3 days of the 19 days of feeder data being analysed (Fig. S1 a, b). All the birds that remained tagged along the whole experimental period (N_{ID}=154) visited the stable feeders regularly: they visited at least one stable feeder on a minimum of 12 days (Fig. S1a). On average, 160±0.6 birds (i.e. 90% of the tagged population, N_{ID}=177) visited at least one stable feeder per day. 145 zebra finches (i.e. 82% of the tagged population) foraged at the ephemeral feeders at food day at least one time. 93% of the tagged birds that foraged in the ephemeral feeders at food day also sampled them at 1st day empty at least one time. 63% of the tagged population foraged in the ephemeral feeders at 2nd day empty; while 8% visited the ephemeral feeders both on the 2nd empty day and at food renewal day. On average, the zebra finches visited the ephemeral feeders on 6.6±0.3 days of the 19 days of the data used. Specifically, on average, zebra finches visited the ephemeral feeders blocks 3.04±0.18 days of the 13 food days available (Fig. S1c), 2.5±0.12 days of the 11 1st empty days and 1.7±0.12 days of the 14 2nd empty days available (Fig. S1d).

The higher the food searching persistency (i.e. average number of visits to ephemeral feeders visited on the 2nd empty day), the higher was the (average) number of visits to both stable and ephemeral feeders visited (i.e. total foraging effort, $F_{1,175}$=52.3, P<0.001, N=177, Fig.2a) and the higher the high-quality food intake was (i.e. average number of visits to ephemeral feeders at food days, $F_{1,175}$=39.13, P<0.001, N=177, Fig.2b).

The (average) number of birds per feeder block changed over time and differently according to the food manipulation stage, as their interaction was significant (X^2=15.6, P=0.0004, N_{obs}=241). Specifically, when the high quality food was in the feeder block, the number of birds around the ephemeral feeders remained constant along the day (Table 2, Fig. 3). The first day the ephemeral feeders were empty, the zebra finches were in the ephemeral feeders only in the morning, as there was no difference between food days and 1st empty days between 0600 and 1059 (Table 2, Fig. 3). Instead, the number of birds in the ephemeral feeders during the 1st empty

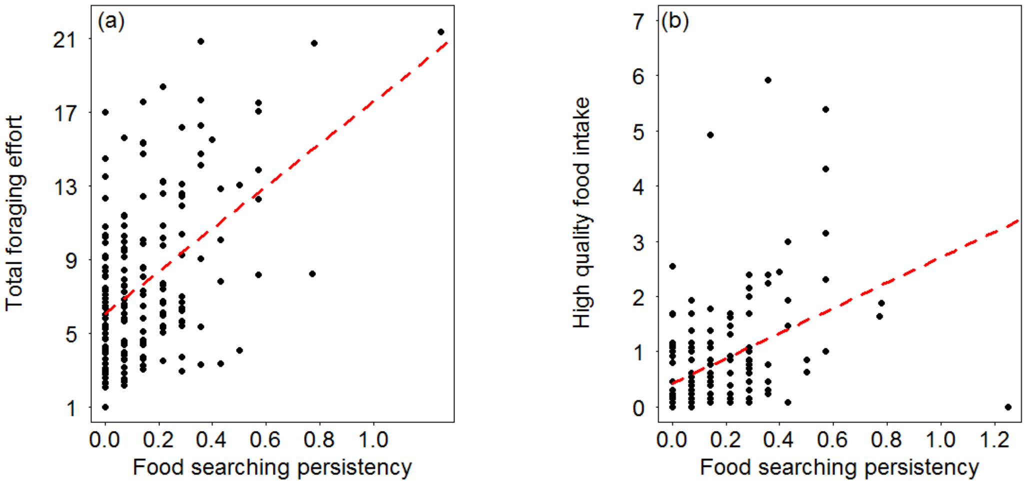


Figure 2 Relationship between food searching persistency (i.e. average number of visits to ephemeral feeders at 2nd empty days) and total foraging effort (i.e. average number of visits to stable and ephemeral feeders) (a) and the high-quality food intake (i.e. average number of visits to ephemeral feeders at food days, (b). Red lines represent model predictions.

days dropped during the second part of the day (1100-1559, Table 2, Fig. 3). The number of zebra finches that kept checking the feeders on the 2nd empty days was lower than those visiting them on food days in both time categories (Table 2, Fig. 3), but some birds kept checking them. The number of birds around the feeders on the 2nd empty days was not significantly different from the

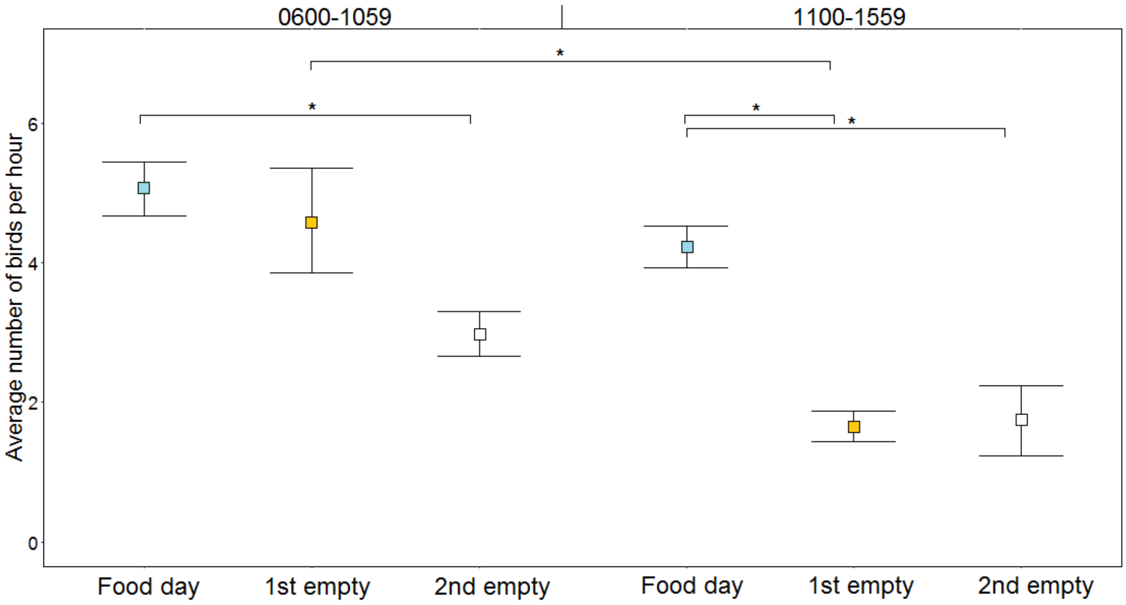
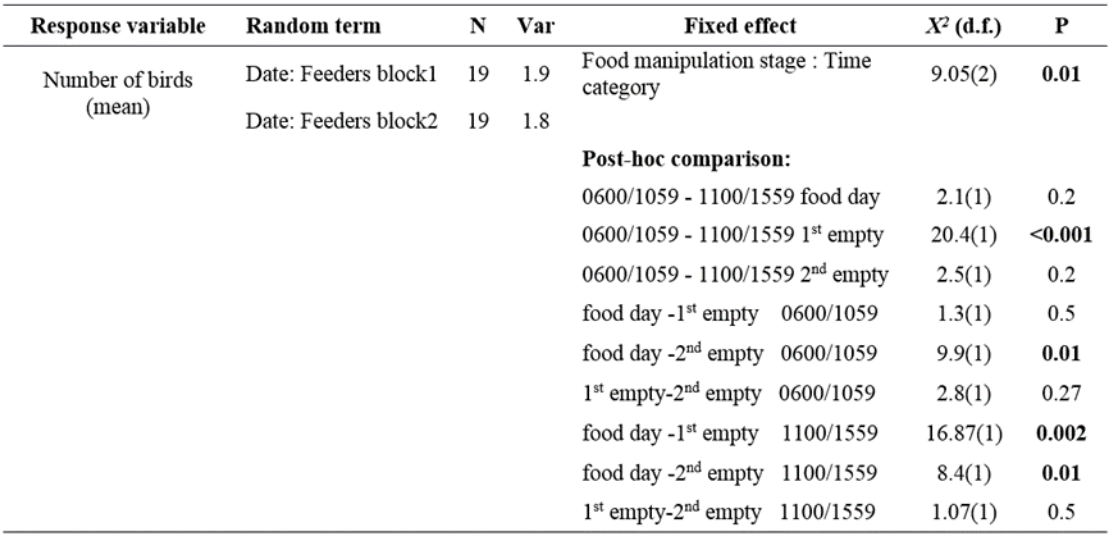


Figure 3 Average number of zebra finches per feeder block per hour as function of the different food manipulation stages. The average number of birds was analysed dividing the hour of the day in two categories: between 0600 and 1059 and between 1100 and 1559, according with the time range of food availability. Significant differences are marked with *.

1st empty days, in both time categories (Table 2, Fig. 3). Therefore, the number of birds visiting the ephemeral feeders decreased the longer they stayed empty (i.e. from food days to 2nd empty days), but some birds kept checking them even on the second empty days (Fig S1).

Table 2 Summary of the GLMM and Post-hoc comparisons testing the effects of food manipulation stage, time categories and their interaction on the number of zebra finches (mean) active in the feeder blocks. Response variable, random term, its sample size (N) and variance, fixed terms, X^2 (degrees of freedom) and P are given. $N_{\text{food days}}$ = 13, $N_{\text{1st empty days}}$ =11, $N_{\text{2nd empty days}}$ =14. Significant effects are marked in bold.



Response variable	Random term	N	Var	Fixed effect	X^2 (d.f.)	P
Number of birds (mean)	Date: Feeders block1	19	1.9	Food manipulation stage : Time category	9.05(2)	**0.01**
	Date: Feeders block2	19	1.8			
				Post-hoc comparison:		
				0600/1059 - 1100/1559 food day	2.1(1)	0.2
				0600/1059 - 1100/1559 1st empty	20.4(1)	**<0.001**
				0600/1059 - 1100/1559 2nd empty	2.5(1)	0.2
				food day -1st empty 0600/1059	1.3(1)	0.5
				food day -2nd empty 0600/1059	9.9(1)	**0.01**
				1st empty-2nd empty 0600/1059	2.8(1)	0.27
				food day -1st empty 1100/1559	16.87(1)	**0.002**
				food day -2nd empty 1100/1559	8.4(1)	**0.01**
				1st empty-2nd empty 1100/1559	1.07(1)	0.5

During the study period, 49 individuals (28 females, 21 males) were foraging in the feeders and breeding in 35 manipulated nest-boxes (17 enlarged, 18 reduced, in two nests the parents were not known). Parents with reduced parental load showed less food searching persistency (N=35, Table 3, Fig. 4a) and less total foraging effort (i.e. average number of visits to stable and ephemeral feeders, N=35, Table 3, Fig. 4b) than the ones with an enlarged parental demand; although they did not differ in high-quality food intake (N=35, Table 3). There was an effect of brood manipulation treatment on survival rate (X^2=5.4, P=0.02, N_{nests}=35). The survival rate was 100% in reduced and 89% in enlarged broods. In the pairs for which broods were experimentally enlarged, parents' foraging behaviour significantly predicted nest survival rate (N_{nests}=17, Table 3). Specifically, the greater the food searching persistency (i.e. average number of visits to feeders at 2nd empty day) the lower the survival rate (Table 3, Fig. 5).

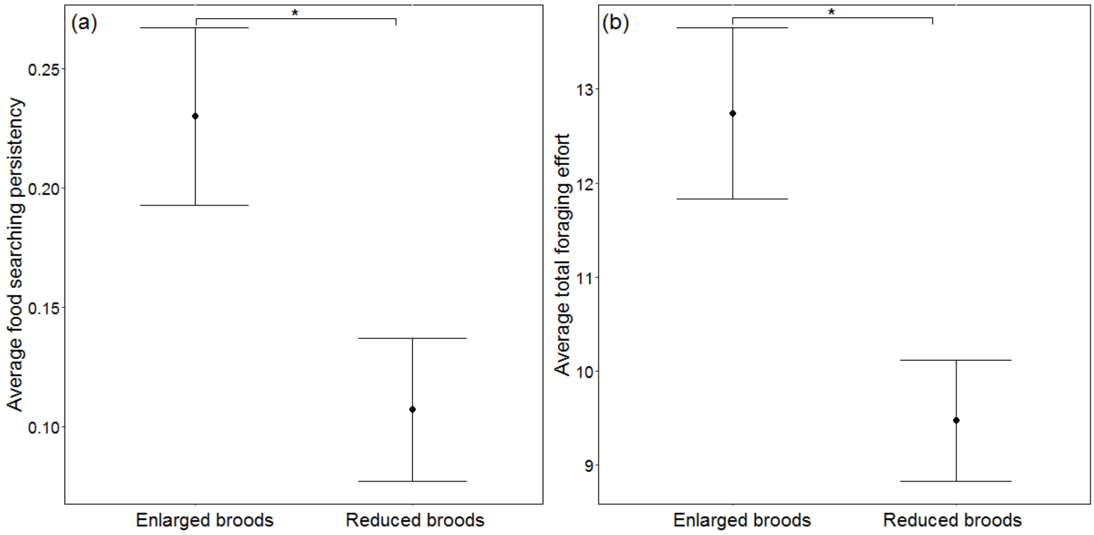


Figure 4 Brood manipulation effect on breeding pairs' food searching persistency (a, mean±SE) and total foraging effort (b, mean±SE). The significant effect is marked with *.

Table 3- Summary of the GLMMs. Response variables, random terms, their sample size (N) and variance (Var) are given. Values of fixed terms and SEs are estimates for the variables in a minimal adequate model; the values in parentheses represent coefficients and SEs from the model before the term was dropped. Significant effects are marked in bold. $N_{\text{breeding pairs}}$=35, $N_{\text{enlarged nests}}$=17

Response variable	Random term	N	Var	Fixed terms	Estimate	S.E.	X^2 (d.f.)	P
Total foraging effort	Nest-box clusters	9	1.96	Treatment			10.2(1)	**0.001**
				Enlarged (Intercept)	12.4	0.9		
				Reduced	-3.5	0.9		
High-quality food intake	Nest-box clusters	9	0.02	Treatment			1.35(1)	0.24
				Enlarged (Intercept)	1.2	0.2		
				Reduced	-0.28	0.24		
Food searching persistency	Nest-box clusters	9	0.003	Treatment			6.5(1)	**0.01**
				Enlarged (Intercept)	0.23	0.03		
				Reduced	-0.12	0.04		
Survival rate (enlarged broods)	Nest-box clusters	7	1.7	Intercept	6.5	1.6		
				Total foraging effort	(0.18)	(0.1)	1.2(1)	0.26
				High-quality food intake	(6.4)	(8.9)	2.9(1)	0.08
				Food searching persistency	-13.26	4.1	18.2(1)	**<0.001**

Discussion

Combining food availability and brood size manipulation experiments in a wild population of zebra finches, we were able to identify differences in foraging patterns and test whether these differences affected the reproductive success of individuals in this arid habitat. First, by

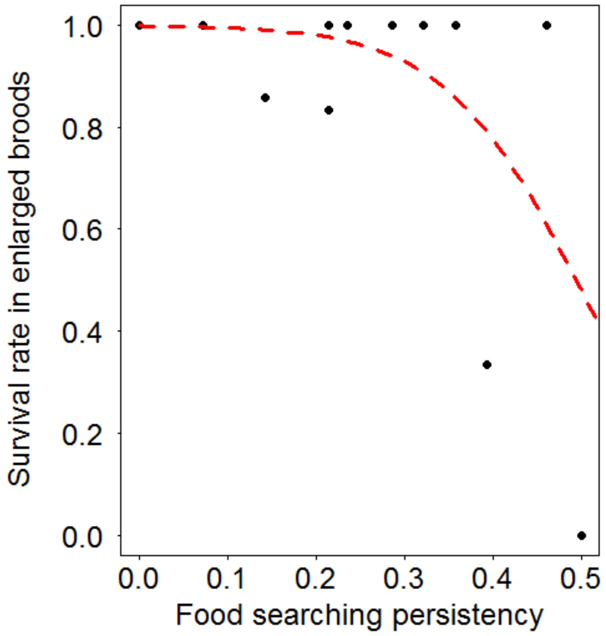


Figure 5 Survival rate of enlarged nests in relation to parents' food searching persistency (i.e. average number visits to ephemeral feeders at 2nd empty days). Please notice that five overlays are present. The line represent the model prediction.

experimentally manipulating the quality and the temporal availability of food in certain feeders, we demonstrated the widespread existence of food searching persistency, with more than half of the tagged population sampling the feeders at 2nd day empty, and having exploited the feeders with food at least once. Only 8% of the monitored individuals always sampled the feeders the 2nd day they were empty having previously experienced them with food. We also showed that the variability between individuals related to the foraging behaviour at stable and ephemeral feeders at food renewal days was repeatable along time. Particularly, the consistent difference in number of feeders visited (both stable and ephemeral at food days) suggested the presence of different strategies of landscape use for foraging porpoise. Recently, research on individual niche specialization, measured as variability in space use, has started to grow and finding individual differences in space use to be widespread for a variety of taxa (Annett and Pierotti 1999; Patrick and Weimerskirch 2014; Patrick et al. 2014; Toscano et al. 2016; Schirmer et al. 2019) increasing our understanding on proximate and ultimate causation of individual differences in resource use. For example, analysing winter mixed flocks of great (*Parus major*) and blue tits (*Cyanistes* *caeruleus*), it was found that consistent differences in number of feeders and visits' duration were related to individual dominance status (Milligan et al. 2017). Our results confirmed previous studies on wild zebra finches which found the presence of individual variability in foraging behaviour in the feeders (Mariette and Griffith 2013; McCowan et al. 2015). Our work also added novel insights into food searching behaviour in the wild, particularly by testing its relationship with landscape use, total food intake and its relationship with reproductive success.

Increasing the sampling effort in food patches previously exploited was positively related to high-quality food intake and to the total foraging effort (i.e. average number of visits to all the feeders). The spatial foraging pattern (i.e. number of ephemeral feeders visited at food days, at 1st and 2nd empty days, the number of stable feeders visited and the total number of feeders visited) was highly correlated to the foraging effort (i.e. number of visits to ephemeral feeders visited at food day, at 1st and 2nd empty days, to the stable and ephemeral feeders respectively, Supplementary Table 2). Therefore, we can interpret the results considering the spatial pattern: sampling different foraging patches provided a better knowledge of the landscape, by increasing the number of overall patches available for use, including the stable ones.

To our knowledge, only one other study has focused on sampling food patches previously exploited in the wild, manipulating the food availability with three different temporal frequencies and food qualities. This study, based on focal observations of one hour sessions, showed that 86% of an ear-tagged population of wild eastern chipmunks (*Tamias striatus*) came back to food patches previously exploited; this behaviour also helped eastern chipmunks to find foraging patches at renewals, while only few returned when the patches were empty and never renewed (Hall et al., 2007).

At the stable feeders, the number of zebra finches active foraging followed the bi-modal peak pattern (Fig. S2) found in previous works (Funghi et al., 2019) and predicted by optimal mass regulation theory (Houston et al., 1993), suggesting the stable feeders use reflects a natural foraging pattern for a passerine bird. On the other hand, our analysis on the fluctuations of zebra finches around the ephemeral feeders in relation to the food presence showed that the food searching activity was mostly concentrated in the earlier part of the day. Specifically the number of zebra finches in the morning did not vary at food renewal day and 1st empty day but it decreased later in the day when there was no food in the feeders. These results are in line with another study on mixed-species flocks of tits in the wild suggesting that birds managed optimally the trade-off between exploration-exploitation of food sources under starvation-predation risks (Farine and Lang, 2013). Unlike the tits studied in a stable food source scenario, that explored for new food patches in the early-morning and exploited the best one the rest of the day (Farine and Lang, 2013), the zebra finches seem to prioritize the exploitation of patches early in the day, when the risk of starvation is higher, especially for small birds in unpredictable food availability situations (Polo and Bautista, 2006). Furthermore, in our study at food renewal days the number of birds around the ephemeral feeders remained steady along the two time categories considered, suggesting that the zebra finches were attracted by conspecifics foraging and supporting the idea that the use of social cues to gather information on food location is an effective way to manage unpredictability (Dall and Griffith, 2014; Dall and Johnstone, 2002; Giraldeau and Caraco, 2000). However, previous studies with zebra finches in the wild (conducted the same year in the same study site) showed that in extreme heat conditions (i.e. during heatwaves in summer) the likelihood to change feeders decreased with increasing air temperature and the same pattern was found for the number of birds around the feeders, suggesting a physiological trade-off between foraging and thermoregulation that might alter both the exploration-exploitation balance and the use of social information in extreme environmental conditions (Funghi et al., 2019).

The number of zebra finches sampling the ephemeral feeders the 2nd empty days was lower than the one at food days and remained low along the day, although some birds kept sampling them. This result, to our knowledge, is the first empirical demonstration in the wild of theoretical models, which predicted that the occurrence of sampling depleted patches (as well as new ones) depends on the energetic state on the individuals: when the risk of starvation is low then it is possible to both track and exploit the food renewal (Dall and Johnstone, 2002). Accordingly, in our study the number of birds around the feeders at 2nd empty days did not present the morning peak of the previous two days (i.e. number of zebra finches at 2nd empty days was lower than the one at food days), suggesting that the 'sampling to keep track' occurred when the risk of starvation was low, and it also related to an increase of the total high-quality food intake, suggesting that it occurred when it is likely to track the food renewal. Our results also showed that the more food persistent individuals, sampling more and more often empty feeders the 2nd empty days, had a wider knowledge of the landscape, increasing the number of visits, the number of overall feeders available (as well as the number of stable feeders). Overall these results support the idea that an individual who better knows the landscape and its fluctuations, also has more options available against unpredictable, complex and harsh environmental conditions (Bolnick et al., 2003; Dall and Johnstone, 2002). Furthermore, although we did not have the information of all the breeding pair bonds, the 'sampling to keep track' (food searching persistency) seems to be an activity conducted by pairs of birds rather than groups, because the average number of birds sampling the 2nd empty days resulted to be around one to two (Fig. 2), suggesting that mating pairs explore and gather information synchronously, as demonstrated in previous work on zebra finches in the wild (Mariette and Griffith, 2013, 2012a; McCowan et al., 2015a) and predicted by theoretical models on information use in poor environmental conditions (Giraldeau and Caraco, 2000).

As expected by individual-based optimal foraging theory (Araújo et al., 2011; Stephens and Krebs, 1986), parents with enlarged parental effort had higher foraging and food searching effort, measured respectively as total number of visits and sampling persistency, than parents with reduced broods. Accordingly, previous studies on wild zebra finches found parents adjusted their foraging behaviour in response to a brood and clutch size manipulation, increasing the synchrony, the number of patches visited and the general foraging activity with increasing brood size (Mariette and Griffith, 2015, 2013, 2012a). However, the extent of intra-individual flexibility in foraging patterns and its relationship with other individual traits remained to be tested and it is likely to provide a more comprehensive view of the variability found here (Dall et al., 2012; Toscano et al., 2016). Furthermore, the foraging behaviour of the parents reflected nestling survival in enlarged, but not in reduced broods. Although sampling empty patches increased the overall food intake, the benefit of tracking did not pay-off the cost of sampling for parents with enlarged broods only. The challenged parents that reduced the cost of sampling empty feeders had higher nest survival rate than challenged ones that spent more time visiting empty feeders. On the other hand, the parents' foraging behaviour of reduced brood did not affect the survival rate, as all their nestlings survived. This supports theoretical work, that predicted the difference between individuals in landscape use and food sampling effort depends on their energetic state (Araújo et al., 2011; Bolnick et al., 2003; Dall and Johnstone, 2002; Stephens and Krebs, 1986). Conceptually, differences in resource use for reproduction might also reflect a difference in parents' metabolism, with the ones who use more lipid reserves, called 'capital breeders', also rely on stored energy; whereas the ones who use more carbohydrates, called 'income breeders' use current intake to overcome the reproductive cost (Jönsson, 1997; Stephens et al., 2009). Although this study did not focus on parents metabolic resources, it would be interesting to investigate whether a relationship between parents' use of the landscape and capital-incoming typology exists, with the hypothesis that 'capital breeders' scan the landscape for food resources while 'income breeders' rely most on the currently known resources available.

Our results suggest that not all parents with enlarged parental load were able to adjust their behaviour reducing the cost of sampling. It might be that one way of optimizing foraging behaviour for the individuals is to invest time in food sampling (related to increasing total food intake in the longer term), increasing their knowledge on landscape fluctuations. While, on the other hand, the survival of the nestlings depends on an immediate food intake (e.g. parents relying on stable food sources). This may potentially generate a conflict of interest in the parents, more pronounced in the ones with enlarged broods, especially considering the unpredictability and harshness of the Australian arid habitat (Davis et al., 1999; Hinde et al., 2010). It has been found that parents optimally adjust clutch and brood size in fluctuating environments (Boyce and Perris, 1987; Clifford and Anderson, 2001), influencing the evolution of nestlings' signalling (Caro et al., 2016). More studies are needed to disentangle the potential conflicts parents have to face in unpredictable and extreme environments like the Australian arid zone.

In conclusion, we provided our population an experimental challenge similar to the one they face in their natural environment, where their food availability fluctuates across time and space. This provided new insights into the foraging patterns birds use to manage unpredictability. Further investigations are now needed, for example monitoring the food searching persistency along a longer time span increasing the food quality at renewal (i.e. limited amount of food in the stable feeders and ad libitum high quality food in the ephemeral), to better understand the adaptive value of differences in food resource use, especially in naturally unpredictable environments.

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Supplementary Materials

Supplementary Table1- Summary of Wilcoxon's sum ranked test (Z) comparing the number of vegetation, grouped at four different height classes and the total coverage estimation, around the stable against the ephemeral feeders within a radius of 5m and 10m.

Vegetation around stable vs ephemeral feeders	**Z**	**p**	**N**
<30cm high around 5m radius	0.1	0.7	16
30-120 cm high around 5m radius	0.2	0.4	16
120-175 cm high around 5m radius	0	1	16
>175 cm high around 5m radius	0.3	0.24	16
Coverage estimation around 5m radius	0.3	0.3	16
<30cm high around 10m radius	0.1	0.64	16
30-120 cm high around 10m radius	20	0.22	16
120-175 cm high around 10m radius	0.3	0.33	16
>175 cm high around 10m radius	0.2	0.21	16
Coverage estimation around 10m radius	0.3	0.2	16

Supplementary Table 2- Spearman's ranked correlation (rho) matrix. Correlation coefficients higher than 0.7 are marked in italics. The variables marked in bold were used for further analysis. All correlation coefficients were associated with P<0.05. All variables are averages per individual (N=177) over the 19 days of data available. 'Number' and 'feeders' are shortened to 'No.' and 'fe.' respectively.

	No. stable fe.	No. fe. at food days (ephemeral)	No. fe. at 1st empty days (ephemeral)	No. fe. at 2nd empty days (ephemeral)	**No. visits at food days (ephemeral)**	**No. visits at 2nd empty days (ephemeral)**	No. total fe.
No. stable fe.	1.000						
No. fe. at food days (ephemeral)	0.596						
No. fe. at 1st empty days (ephemeral)	0.593	0.665					
No. fe. at 2nd empty days (ephemeral)	0.386	0.481	0.439				
No. visits at food days (ephemeral)	0.590	*0.945*	*0.701*	0.497			
No. visits at 2nd empty days (ephemeral)	0.380	0.469	0.441	*0.992*	0.492		
No. total fe.	*0.961*	*0.740*	*0.734*	0.532	*0.730*	0.525	
No. total visits	*0.812*	0.572	0.643	0.357	0.628	0.359	*0.825*

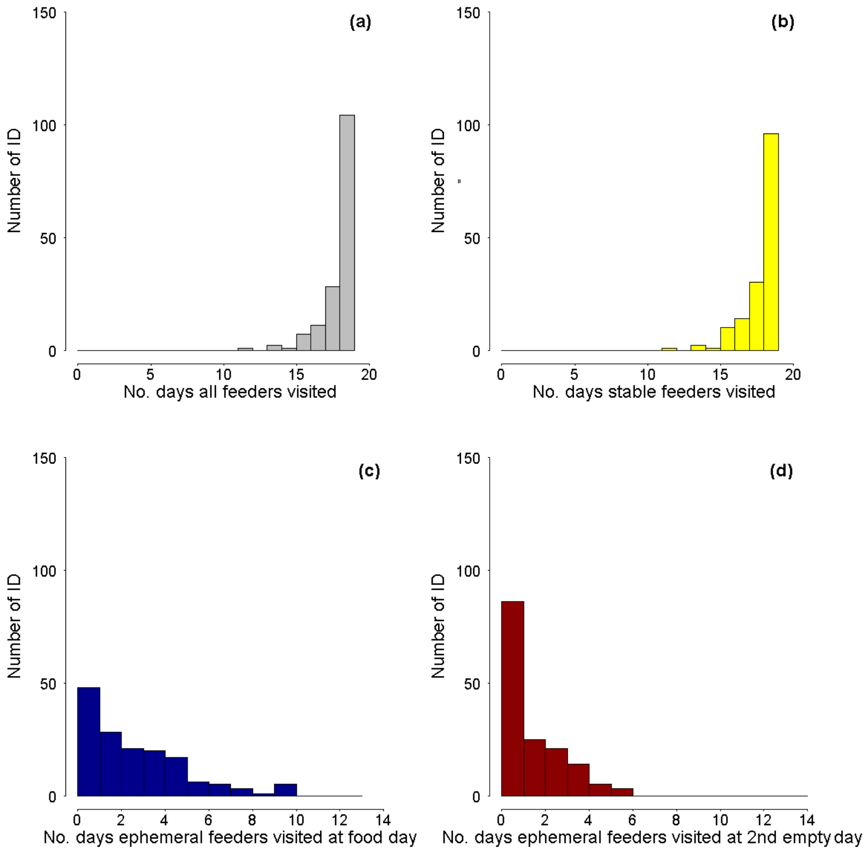

Figure S1 Histograms showing the frequency distribution of the number of days the zebra finches visited a given feeder type. (a) All the feeders 19 available days); (b) the stable feeders (19 available days); (c) the ephemeral feeders at food renewal day (13 available days) and (d) 2^{nd} empty days (14 available days).

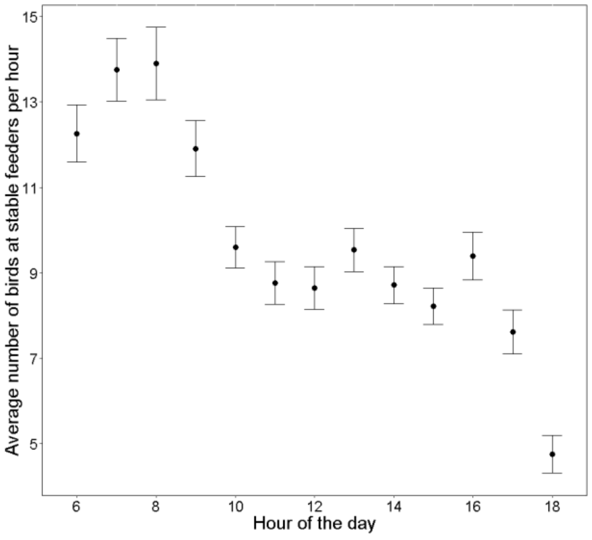

Figure S2 Mean number of zebra finches ± SE active at stable feeders per hour of the day.

Chapter Six

General Discussion

“Have you ever been to Hebel
Where it blows and blows and blows
And barring goats and bottletops.
Nothing ever grows.
The heatwaves in the summer
Make the red plains shine like grass
And there’s seldom any water
And there’s seldom any grass.”

-Anonymous-

-Poem found in the Australian outback, at the historical circle of Hebel, Queensland-

Unpredictable environments represent a challenge both for animals inhabiting it and researchers studying how abiotic fluctuations shape the biotic responses (Greenville et al., 2017). In the Australian arid zone these challenges are emphasized by the peculiar relationship between rainfall events, landscape structure (e.g. topography, water soil content and widespread nutrient-poor soil) and vegetation response (Morton et al., 2011; Orians and Milewski, 2007; Westoby, 1979). In order to start investigating animal responses in such complex environment, several practical issues need to be overcome. First, it is extremely challenging to generate a general model to predict the primary productivity response to rainfall alone in such habitats (Reynolds et al., 2004) and in Australian arid areas in particular (Nano and Pavey, 2013). Therefore, the most feasible way for researchers to start understanding arid animals' responses to their habitat is to bypass the complex relationships between abiotic-biotic factors and find a way to directly predict the primary productivity variation.

In my thesis, I proposed the use of spatial ecology at a scale relevant to the study species as a possible way to overcome this main practical issue and to gain new insights on how animals cope with extreme and unpredictable conditions. Particularly, I focused on wild zebra finches' landscape use in a foraging context during extreme heat conditions and with unpredictable food availability. Hence, the thesis structure reflected two aspects of the challenge of studying Australian arid areas with the integrative use of a spatial ecology framework as basis to disentangle several issues. The first two chapters (Chapter 2 and 3) focused on the challenge represented by the characterization of the heterogeneity of the landscape and the following two (Chapter 4 and 5) on the challenge it represents for the zebra finches' foraging behaviour.

Unpredictable environment: the challenge of heterogeneity

In Chapter 2, by using classic vegetation survey methods, I showed that the spatial distribution of *Enneapogon* grassland, the main food source for a variety of animals, including the zebra finches (Hoffmann, 2010; Morton and Davies, 1983), varied at very local scale. It is well recognized that vegetation spatial heterogeneity determines habitat complexity and quality (Fernandez et al., 2016; McNaughton et al., 1989), but the extent at which it occurs, to my knowledge, was not known in the Australian arid habitat. Knowing that food availability (here: *Enneapogon* seeds abundance) varies at a very local scale is important for studying granivorous species, because it means it would be possible to directly quantify the food availability across the portion of the landscape relevant to the study species that, especially during breeding period in the arid areas, is often constrained by resource availability, such as water and food. Therefore, it would be possible to monitor the primary productivity fluctuations at a scale relevant to the individuals, with a relatively small effort, by setting and monitoring long-term vegetation surveys. Traditionally, animal food availability has been modelled from rainfalls assuming an oversimplified linear relationship between vegetation response and rainfall events (Morton and Davies, 1983; Zann et al., 1995; Zann and Straw, 1984). However, both theoretical and empirical studies demonstrated how complex is the relationship between rainfall and vegetation response in Australian arid areas (Acworth et al., 2016; Orians and Milewski, 2007; Reynolds et al., 2004). Thus, knowing that spatial variation of grassland distribution in Australian arid zone occurs at local scale might be the only effective way for behavioural ecologists to identify the challenges the individuals have to face to cope with environmental structure and fluctuations and start understanding arid animals' responses to the habitat, bypassing the interactive non-linear relationship between rainfall and vegetation response.

While the findings of Chapter 2 suggest the potential of studying environmental fluctuations at local scale, it is not always easy to determine the scale relevant to the study species and it might not be practically achievable to conduct *in situ*, long term research to directly quantify the vegetation response over time and across the landscape (Nguyen et al., 2015; Sparrow et al., 2014). The use of remote sensing frameworks is considered a time- and cost- effective solution to reduce the investment of economical and human resources especially in extreme environments like deserts (Barrett and Hamilton, 1986; Skidmore et al., 2015; Tueller, 1987). In Chapter 3, I therefore tested the use of the most up-to-date and freely available remote sensing information (i.e. the Sentinel-2A satellite as part of the European Copernicus programme) in an Australian arid area.

In homogenous, temperate environments, remote sensing information is commonly used in behavioural ecology to monitor the synchrony of environmental fluctuations, animals' breeding phenology and changes in foraging strategies (Cole et al., 2015; Durant et al., 2007). In heterogeneous, complex environments the use of satellite-derived information is still at a validation phase, because it is complicated by the low and tussock nature of the vegetation cover. These characteristics of the vegetation represent the major issues to reliably measure the actual vegetation cover and type distribution (Nagendra, 2001; Okin and Roberts, 2004).This because the spatial resolution of the satellite images freely available before Sentinel 2A (e.g. 30m of the Landsat satellite) tended to over represent the strongest signal (e.g. greenness or barren soil, Nagendra, 2001; Okin and Roberts, 2004). The main goal of Chapter 3 was to test whether the increased power of a new satellite launched in 2016 (i.e. Sentinel 2A), with a spatial resolution that matched field sampling vegetation surveys (10 m pixel), was able to accurately identify patches of different vegetation types ('grassland', 'green' and 'barren') and reliably follow their temporal fluctuations.

The results of Chapter 3 showed that the Sentinel-derived vegetation indices NDVI and $MSAVI_2$ were able to catch the variability across the landscape in great detail, but only when the vegetation was at its peak. They also confirmed the Chapter 2 results and previous studies, with the *Enneapogon* grassland being more abundant and productive further from the water dam and the creek system (James et al., 1999). From the behavioural ecologists' point of view, the results in Chapter 3 showed that by geo-locating a representative number of patches of certain vegetation types of interest, such as the ones mostly linked with arid animals' food availability, it will be possible to remotely monitor their fluctuations to some degree, at least to identify the spatial variation during their peak. Of course there are some limitations, such as the challenge of defining the most suitable number of patches to have a reliable estimation of the variation in food availability across the landscape. Additionally, it will not always be possible to easily process the Sentinel imageries and obtain the vegetation index and more sophisticated remote sensing skills might be needed, for example to adjust the remote sensing information with atmospheric perturbations (e.g. cloud cover). However, the main results of Chapter 3 strongly suggest that Sentinel 2A has a spatial resolution able to reliably assess vegetation spatial heterogeneity in arid areas. Therefore, it will be possible to finally integrate remote sensing framework into the study of animal ecology in arid environment, but with some caution.

Unpredictable environment: a challenge for foraging zebra finches

The last two chapters (Chapter 4 and 5) focused on how a wild zebra finch population copes with the unpredictable habitat. Part of the unpredictability of the arid areas is linked to the occurrence of extreme climatic events, such as heatwaves, that perturbate individuals energetic state (Wingfield et al., 2017). In Chapter 4 I described how in summer, high air temperature over a period including two heatwave events, affected the zebra finches' spatial, temporal and social aspects of foraging activity. By providing 2 x 16 artificial feeders to a RFID-tagged zebra finches population, 81 adults were intensively monitored while foraging. The results confirmed the pattern found in other studies: with increasing air temperature birds drastically decreased their foraging activity (Carmi-Winkler et al., 1987; du Plessis et al., 2012; Edwards et al., 2015; Tieleman and Williams, 2002), also reducing the foraging group size. Furthermore, the intensive data collection allowed to follow the individuals along the whole temporal range of foraging activity and across a wide landscape area, providing comprehensive temporal and spatial data and consequently important new insights into the relationship between heat and foraging.

By analysing the time of first and last foraging event to the artificial feeders, I showed that the individual zebra finches shifted their temporal distribution of foraging behaviour on hot days to a higher level of foraging closer to dusk. Additionally, zebra finches showed a spatially more constrained pattern of foraging behaviour. Individuals' activity increased at feeders closer to the only water source available in a 5 km range (i.e. water dam) and was reduced at the furthest feeders with increasing temperature, independently of the time of day. Both the increased feeder fidelity and the reduction in the duration of foraging per hour with increasing temperature suggested that the spatial and temporal patterns of foraging were driven by the physiological constraints of foraging in hot conditions and the need to keep cool. This interpretation was also supported by the observed increase in heat dissipation behaviour with increasing temperature. Another important consequence of changes in foraging patterns during hot conditions was that birds foraged in smaller groups as temperature increased, and this may have important consequences for predation, if group foraging helps to reduce the risk of predation in this environment (e.g. Sorato et al., 2012).

Previous studies used RFID-tag technology to explore foraging activity related to heat in a small mammal (Levy et al., 2016), but the study presented in Chapter 4 provided the first evidence of the effects of air temperature on foraging activity of a non-territorial bird species, suggesting that in hot condition the zebra finches face an energetic trade-off between the need to stay near water and the need to fulfil their energetic requirements through foraging, affecting both temporal and spatial daily patterns of behaviour. The effect of high temperature on individuals foraging activity concentrated closer to the water source supported a recent study that found non-territorial granivorous species to be more water dependent than territorial insectivorous ones (Smit et al., 2018). Furthermore, the food provided in the feeders was of the same quality across the landscape, and birds could therefore access a similar level of resources close to the dam. However, in natural circumstances it is likely that this restricted foraging range would impact their ability to find food efficiently, especially because natural foraging patches are generally further from artificial water sources, where the effect of selective grazing favours shrubland over grassland (James et al., 1999, Chapter 2 and Chapter 3).

Although neither foraging efficiency nor food intake were directly measured in Chapter 4 as it was done in other studies (du Plessis et al., 2012; Edwards et al., 2015), the results suggested that a short period of intense foraging later in the day may, at least partially, provide the opportunity to make up for reduced early foraging activity during a hot day. Overall, the study presented in Chapter 4 showed that in extreme air temperatures zebra finches face an energetic trade-off between thermoregulation and foraging activity that significantly affected temporal, social and spatial characteristics of zebra finch foraging behaviour. These aspects are likely to adversely affect an individual’s capacity to forage efficiently and consequently its food intake in the short term. This might constrain levels of parental care during extremely hot ambient conditions, providing a possible explanation for the production of smaller offspring in hot conditions found in the wild (e.g. Andrew et al., 2017) and the avoidance of breeding in summer for arid species generally in Australia (Duursma et al., 2017).

Theoretical work predicts that there are two non-mutually exclusive ways animals may deploy to cope with unpredictability of food sources: relying on social information and increasing their personal knowledge of the landscape (Dall et al., 2005; Dall and Griffith, 2014; Dall and Johnstone, 2002; Giraldeau and Caraco, 2000). In Chapter 5, I explored individual differences in spatial foraging patterns in an unpredictable environment, combining a food availability and a brood size manipulation experiment. The food manipulation experiment altered the quality and temporal food availability in half of feeders ('ephemeral feeders'), while the food of the other half remained stable along the study period ('stable feeders). The food quality of the ephemeral feeders was higher than the one in the stable feeders. The results showed that the persistence with which individuals sampled food patches even when they were depleted (i.e. in the empty ephemeral feeders), but previously experienced as rewarding, was related to increased foraging activity (i.e. number of visits to all the feeders available as estimation of total food intake) and spatial generalism (exploiting also more stable feeders). The optimal balance between exploration (i.e. discovering new food sources) and exploitation of a food patch has been extensively modelled (Dall and Johnstone, 2002; McNamara and Houston, 1985; Stephens, 1987) and has been tested in captivity (insects:Fourcassi and Traniello, 1993; Keasar et al., 2013; fish: Pitcher and Magurran, 1983, birds: Dall and Witter, 1998; Krebs, 1978; mammals: Devenport and Devenport, 1994), but has been rarely investigated in the wild (but see Hall et al., 2007). Actually, the existence of the food searching persistency in the wild is not necessarily expected, because it is also associated with the cost of sampling that may not balance the pay-off of the tracking (Hall et al., 2007; Stephens, 1987). However, the results showed that it was widespread in the population, even taking into account that our measurement of feeder sampling behaviour might have been an underestimation, because the ephemeral feeders were open and the zebra finches could have sampled them flying over the feeders, not passing through the antenna and therefore without being detected. By modifying the feeders, covering them with shade cloth might provide a more exact estimation of the behaviour.

Analysing the fluctuations in number of zebra finches around the ephemeral feeders per hour at different food availability conditions (i.e. food day, 1st and 2nd empty days), it resulted that at days the food was renewed in feeders (after having been empty for two days) the number of birds around the ephemeral feeders remained steady along the day, while at 1st empty days there was a peak of presence in the early morning that dropped after 11:00 a.m. (Fig. 2 of Chapter 5). This suggested that when food was available the zebra finches were attracted by conspecifics foraging, supporting the use of social cues to gather information on food location to manage unpredictability (Dall and Griffith, 2014; Dall and Johnstone, 2002; Giraldeau and Caraco, 2000). However, previous results (Chapter 4) showed that in extreme heat conditions (i.e. during heatwaves in summer) the likelihood to change between feeders decreased with increasing air temperature and the same pattern was found for the number of birds around the feeders, suggesting the presence of a physiological trade-off between foraging and thermoregulation that might alter both the exploration-exploitation balance and the use of social information in extreme environmental conditions (Funghi et al., 2019).

The number of zebra finches around the feeders the 2nd days they were empty did not present the morning activity peak observed on the two previous days (Fig. 2 of Chapter 5), suggesting that sampling the depleted patches occurred when the risk of starvation was low. Furthermore, the food searching persistency was related to an increase in the total high-quality food intake (number of visits to the ephemeral feeders at food days). These results, to my knowledge, are the first empirical demonstration in the wild of the theoretical models, which predicted that the occurrence of sampling depends on the energetic state of the individuals: when the risk of starvation is low it is possible to both track and exploit the food renewal (Dall and Johnstone, 2002). Furthermore, the more food-persistent individuals also increased the number of overall feeders exploited, suggesting that a wider knowledge of the landscape is a strategy used to cope with unpredictability (Dall and Griffith, 2014; Dall and Johnstone, 2002).

The brood size manipulation experiment revealed that, although sampling empty patches increased the overall food intake, the benefit of tracking did not outweigh the cost of sampling for parents with enlarged broods. According to the optimal foraging theory (Araújo et al., 2011; Dall and Johnstone, 2002; Stephens, 1987; Stephens and Krebs, 1986), the challenged parents that reduced the cost of sampling empty feeders had higher nest survival rates than challenged ones that spent more time visiting empty feeders. On the other hand, the parents’ foraging behaviour of reduced broods did not affect the survival rate, as all their nestlings survived. To my knowledge, this is the first experimental evidence that tested the relationship between food searching behaviour variability and breeding success that will deserve further investigation especially in naturally challenging environments.

Both Chapter 4 and 5 showed how powerful the RFID-tracking system can be to study foraging behaviour across the landscape at individual level and at a fine temporal scale. Although it is a technology widely used to study a variety of taxa, its use in unpredictable environments, to my knowledge, is still quite rare. However, by collecting data in high quantity and quality it will be possible to disentangle several aspects of living in challenging habitats. In these two chapters, I provided an example of the way this kind of data can be processed, focusing on how environmental harshness (heatwave) and unpredictability (experimentally altering food availability) affected foraging behaviour at individual level. The same set of data can also be used to study social aspects of foraging through animal social network analysis (Farine and Whitehead, 2015b). An example of a study using the RFID data collected in 2017 to analyse social foraging groups is presented in the Appendix I: focusing on the juveniles which were reared in the enlarged and reduced broods as nestlings, we analysed their behaviour in the artificial feeders. We were able to replicate a previous study conducted in captivity (Boogert et al., 2014), confirming the effect of early-life stress on juveniles' connectedness within the network in the wild (Boogert et al., 2014; Brandl et al., 2019).

Conclusion

The results I presented in my thesis support and promote the use of spatial ecology frameworks towards the study of animal behaviour in arid environments. Following the foraging activity of the zebra finches during two heatwaves and across their habitat allowed to demonstrate that the individuals' foraging activity was spatially constrained to forage closer to the water during the hottest days. This added new insights into the way in which birds will respond to extreme heat events and to an increasingly hot climate, enlighten the role of artificial water sources to mitigate the consequences, although artificial dams have been found to promote plant invaders and landscape degradation (James et al. 1999). Additionally, the use of spatial ecology allowed to directly quantify the variation in food resource distribution across the habitat and to identify and empirically test the challenges this variation may represent for the individuals. Thus, having found that the distribution of food availability of the zebra finches varied at very local scale (*Enneapogon*), it was possible to design an experimental challenge similar to the one the birds have to face in their natural environment. This allowed to add new insights on the foraging patterns birds use to manage unpredictability. Finally, although with some cautions, the validation of Sentinel 2A information will allow future researches to reliably and remotely assess the primary productivity variation at local scale to better understand the interaction between unpredictable environmental condition, food availability and animals' response. In consequence, I hope the works presented, integrating spatial ecology to animal behaviour, will help to improve and inspire new researches in unpredictable environments.

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Appendix I

PROCEEDINGS B

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Research

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Early-life social environment predicts social network position in wild zebra finches

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Early-life experience can fundamentally shape individual life-history trajectories. Previous research has suggested that exposure to stress during development causes differences in social behaviour later in life. In captivity, juvenile zebra finches exposed to elevated corticosterone levels were less socially choosy and more central in their social networks when compared to untreated siblings. These differences extended to other aspects of social life, with 'stress-exposed' juveniles switching social learning strategies and juvenile males less faithfully learning their father's song. However, while this body of research suggests that the impacts of early-life stress could be profound, it remains unknown whether such effects are strong enough to be expressed under natural conditions. Here, we collected data on social associations of zebra finches in the Australian desert after experimentally manipulating brood sizes. Juveniles from enlarged broods experienced heightened sibling competition, and we predicted that they would express similar patterns of social associations to stress-treated birds in the captive study by having more, but less differentiated, relationships. We show striking support for the suggested consequences of developmental stress on social network positions, with our data from the wild replicating the same results in 9 out of 10 predictions previously tested in captivity. Chicks raised in enlarged broods foraged with greater numbers of conspecifics but were less 'choosy' and more central in the social network. Our results confirm that the natural range of variation in early-life experience can be sufficient to predict individuals' social trajectories and support theory highlighting the potential importance of developmental conditions on behaviour.

1. Introduction

The social component of the environment represents a unique aspect among the factors that contribute to differences in fitness. The population-level patterns of social connections that are formed from the interactions among individuals are, thus, of increasing interest. The web of interactions across populations, and where individuals are positioned within this web, is often captured using social network analysis [1,2]. Understanding these social interactions is important on multiple levels. First, most social interactions are often only manifested physically for brief moments, but their consequences can extend well into the future. For example, in primates, rare grooming partners can be important for an individual's survival [3,4], while a vampire bat, *Desmodus rotundus*, donating food to an

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unrelated conspecific can represent a future investment that may be life-saving in case it later goes hungry [5]. Second, the position of individuals within their social environment (i.e. in their social network) can be dependent on both their, and others', social interactions. Indirect, or 'friend of a friend', associations can nevertheless have significant fitness consequences [6,7]. For example, an individual's exposure to disease may not only depend on its own social gregariousness but also on the gregariousness of its associates (see [8]).

Advances in our ability to study and analyse social behaviour [9], especially in the wild, have highlighted the widespread effects of social behaviour on fitness. There is now clear evidence that individuals can exhibit consistent differences in their social network position [10–13], which are resilient to environmental change [14,15] (but see [16]), and that these differences can translate to consequences for fitness [17–21]. For example, being more central in a network has been linked to having access to more information [22], but also being more exposed to disease [23,24]. The overall composition of the social environment can also impact the strength and direction of selection that individuals experience [25,26], with the intensity of interactions among individuals determining the amount of variation in social traits available within versus between populations [27]. Yet, despite over a decade of research on the structure and consequences of animal social networks, little is known about the mechanisms that underlie inter-individual differences in social relationships and network position [28].

Although individuals in a wild population vary extensively in their social behaviour (reviewed in [29]), the ontogenetic sources of that variation remain unclear. A promising area that has recently gained increasing attention is the environmental conditions experienced by individuals during early-life stages. A well-established body of evidence supports the concept that early-life stress exposure increases the probability of social behaviour deficits manifesting later in life across a range of taxa [30–33]. For example, early-life stress increased the probability of psychiatric disorders in humans [30] and had adverse effects on social bonding in prairie voles, *Microtus ochrogaster* [31], and maternal care in rats, *Rattus norvegicus domesticus* [32]. Invertebrates reared in deprived conditions exhibited deficits in social behaviour and cognitive abilities [33], and in the development of behavioural syndromes [34].

Three recent, and complementary, studies on zebra finches [28,35,36] have aimed to comprehensively characterize how the conditions that individuals face during their development can shape different aspects of later social life. All three studies used the same nestlings, from two captive colonies of zebra finches, *Taeniopygia guttata*, that were allocated to two treatments. Approximately half of each brood received physiologically relevant doses of the avian stress hormone corticosterone (stressed juveniles) via pipette feeding, while the other half were handled in the same way, i.e. pipette feeding, but without the active hormone (control juveniles). Once the chicks fledged, the social affiliations among all colony members (including both adults and juveniles) were recorded by detecting the co-membership of individuals fitted with passive integrated transponder (PIT) tags in foraging flocks at feeders using radio frequency identification (RFID) loggers. In the first study, Boogert *et al.* [28] found that stressed juveniles formed less exclusive (or more random) social associations, resulting in a more central network position. Stressed chicks had a higher total number of social associates (higher binary network degree) and were more often located on the shortest path between two other individuals of the network (higher betweenness) [28]. Betweenness reflects how important an individual is as a point of social connection in the overall network [7] and high betweenness can imply an increased tendency of individuals to switch between different groups [28]. The two following studies investigated how early-life stress influenced social learning strategies [35,36]. Evidence suggested that stressed juveniles switched from acquiring novel foraging behaviours from their parents to acquiring them from unrelated adults [36]. Further, stressed juvenile males were less faithful in copying their father's song, although the mechanism there seemed to be linked to variation in association strengths between father and sons [35]. These studies of the zebra finch in captivity have provided some of the best support to date for the importance of the developmental environment on animal social behaviour. They demonstrate how developmentally mediated differences in social behaviour shape social networks and thus can determine the acquisition of skills relating to fitness (song and foraging behaviour). However, while the amenability of the zebra finch as a focus of behavioural research in the laboratory has permitted insightful studies such as those above, an important challenge remained about the extent to which such studies might reflect natural variation in an appropriate ecological context [28].

In the current study, we examine the same question as in the Boogert *et al.* [28] study (described above) in a wild population of zebra finches using a natural source of developmental stress—brood size. We then collected data on foraging associations among individuals (both adults and juveniles, each fitted with a PIT tag) at RFID-equipped feeders located in the surroundings of six breeding colonies. Finally, we conducted the same statistical tests as the original study, thereby producing an almost exact experimental replication, but importantly in a very different context, i.e. using a natural stressor, and in a wild population. Boogert *et al.* [28] called for replication in the wild using brood size as a natural stressor, thus we experimentally increased and decreased the size of broods within the natural range of variation. We predicted that nestlings from enlarged broods would experience higher sibling competition (as shown in the wild by Mariette & Griffith [37]). If the early-life effects on social network position [28] are transferrable to the wild, we expect the juveniles in our study to respond in a similar way to juveniles that were exposed to the corticosterone stress hormones as nestlings in the original study. Thus, we predicted that juveniles from enlarged broods would also be less choosy in their associations, forage with more conspecifics and be more central in the overall social network.

2. Material and methods

(a) Study site

The study was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05′13.1″ S 141°42′17.4″ E), New South Wales, Australia, between September and December 2017. The roughly rectangular area of about 4 km^2 holds a dam with a mostly permanent water body in the centre. We provided 180 wooden nest-boxes arranged in six colonies (mean distance to nearest neighbouring colony $\pm$ s.e. = 413.62 $\pm$ 63.62 m) of 30 boxes each (mean distance to nearest neighbouring nest-box within clusters $\pm$ s.e. = 10.36 $\pm$ 1.98 m; [38]) and an additional 64 boxes scattered in the periphery of the colonies.

(b) Brood size manipulations

Brood manipulations were conducted when nestlings were 3 days old (hatching date = day 0). Nestlings were measured (tarsus length, measured to an accuracy of 0.01 mm), weighed (to an accuracy of 0.2 g) and then swapped between pairs of nests (triplets, if necessary), bi-directionally, i.e. all nests received at least one chick from another brood. In each nest pair, we created a reduced brood with two nestlings ($n = 15$ nests; i.e. low stress) and an enlarged brood with five to eight nestlings (mean number chicks: 6.00 ± 0.18 s.e.; $n = 16$ nests; i.e. high stress). Mean brood size across the study population on day 3 after hatching, before the manipulation, was 3.69 ± 0.13 s.e. chicks. The change in brood size through the manipulation was on average plus 2.13 ± 0.13 s.e. chicks in the enlarged broods and an average decrease of minus 1.95 ± 0.24 s.e. chicks in the reduced broods. The broods in all nests were manipulated, except for five nests where no other nest with nestlings at the same age was available for swapping (juveniles from these nests were included when generating the social networks but not used in the analyses comparing juveniles across treatments). Chicks from these unmanipulated nests were not used because they were naturally mismatched in age compared to others, represented too small a sample size to use as a 'control' group, and because the aim of our study was to replicate the previous results as precisely as possible. A number of studies have previously shown that brood size manipulations can lead to differences in growth rates and body size [37], increased levels of plasma corticosterone [39] and negatively affect the immunocompetence [40] and survival [41] of the offspring raised in enlarged broods in birds. It is also well established that birds optimize their clutch and brood size [42–45], thus, an increase through external manipulation can be expected to cause stress and increase sibling competition. Similar stress responses can be observed, for example, in mammals with large litters [46,47], suggesting that this is a universal mechanism.

(c) Social network data

We collected data on social associations in almost exactly the same way as the Boogert *et al.* [28] study. We caught adults with mist-nets, with walk-in feeder traps and at the nest-boxes when nestlings were between 6 and 11 days old, whereupon we fitted each individual with a uniquely numbered ABBBS metal ring and subcutaneously injected each with a uniquely coded PIT tag (Minichip; Micro Products Australia, Perth, Australia). Nestlings were weighed, measured (tarsus length) and tagged on day 11. For practical reasons, we did not tag all nestlings, but a number proportional to the manipulated brood size (mean proportion of tagged nestlings in small broods: 0.9 ± 0.1 s.e., and in large broods: 0.7 ± 0.1 s.e.). This amounted to a total of 64 nestlings from enlarged broods, 27 from reduced broods and 14 from unmanipulated broods.

We provided 16 feeders (a wire cage of $70 \times 40 \times 50$ cm, see [48]), each fitted with an RFID antenna (*ca* 20 cm diameter) at its entrance, connected to an RFID decoder (RFIDLOG; Priority 1 Design, Melbourne, Australia). These allowed us to detect the presence of individuals as they entered and exited the food source (a very similar design to the original study). Feeders were located in a minimum distance of 200 m from the dam and from each other, minimum 100 m away from the nest-box colonies and within a maximum of 800 m from the relatively central water (dam). The feeders were all refilled daily with commercial finch seed mix from 22 September until 1 October. From 2 October to 6 December, eight of the feeders were kept always filled with food (stable feeders), while the remaining eight feeders were provisioned as an ephemeral food source, as part of another experiment (only half of them filled for 10 h every other day with egg and biscuit formula mixed in with the seeds; all eight feeders were empty every third day). From 7 to 17 December, eight of the feeders were removed and the other eight were filled daily. We used the social association data from all feeders from the entire period, as any co-visitations still represent social associations while foraging, even if no food was present. In terms of breeding, the establishment of the first broods (first egg laid) was on 15 September, and reproduction continued through to the end of the final brood (last egg laid on 20 November).

(d) Statistical analyses

We used the same Gaussian mixture model approach as Boogert *et al.* [28] to infer co-feeding events. This algorithm identifies temporally clustered detections of PIT tags in non-uniform data streams at a given feeder on a given day [49,50]. We combined the data from the feeding events detected across all of the feeders on all days to construct one population-level social network. As with the previous study, associations between individuals, or 'edges', in this social network were calculated using the simple ratio index [51], which represents the probability of observing two individuals in the same event given that at least one was observed. Unlike the original study by Boogert *et al.* [28], we did not create daily networks, as the wild population had a much lower density of social associations given the greater freedom of movement and higher number of potential food sources (see [52] for more details on why replicated, or daily, networks are often required in captive populations). Further, because birds regularly visited multiple feeders spanning different local colonies, we did not create a separate network for each colony as the population-level network was overall well connected (figure 1). The Gaussian mixture model and network construction were done using the *asnipe* package [53,54] in R [55].

We then implemented the same set of 10 analytical tests as performed by Boogert *et al.* [28]. We (1) tested whether mated adults had stronger associations than non-paired adults, and (2) tested whether the association strengths among families were stronger than among non-families (assortativity). The assortativity coefficient is used to describe to which extent individuals are connected with other individuals of a similar phenotype [9,56] (for general definitions of all used social network measures, see [1,7,9]). We also tested whether birds from enlarged broods differed to birds from reduced broods in terms of (3) the size of their foraging groups or (4) the number of foraging groups joined. Having completed these baseline tests, we then investigated the relationship between brood size and social network position. Specifically, we tested whether juveniles from enlarged broods had (5) any difference in weighted degree, (6) a higher unweighted degree, (7) a higher (weighted) betweenness (see definition in Introduction) and (8) any difference in (weighted) eigenvector centrality compared to those juveniles from reduced broods. Unweighted degree is simply the count of the number of connections to distinct individuals, while a weighted degree is the sum of the association strengths (edge weights) that an individual has. Eigenvector centrality captures how well-connected individuals are to individuals with a high degree (here weighted degree as we used a weighted measure of eigenvector centrality). Betweenness and eigenvector centrality both represent measurements of indirect connectedness [8]. We also (9) tested whether juveniles from larger broods had less differentiated relationships (associated more randomly) by calculating the coefficient of variation (CV) of edge weights for each individual. A higher CV suggests that individuals have a mix of both strong and weak connections, whereas a lower CV suggests that individuals associate more equally with all conspecifics. Finally, we (10) tested whether juveniles from larger broods had a weaker association with their parents.

We used the weighted assortment coefficient from the *assortnet* [56,57] package in R to test predictions 1 and 2. We then used linear mixed models to test predictions 3 to 10, fitting the response variable (number of groups, mean size of groups, unweighted degree,

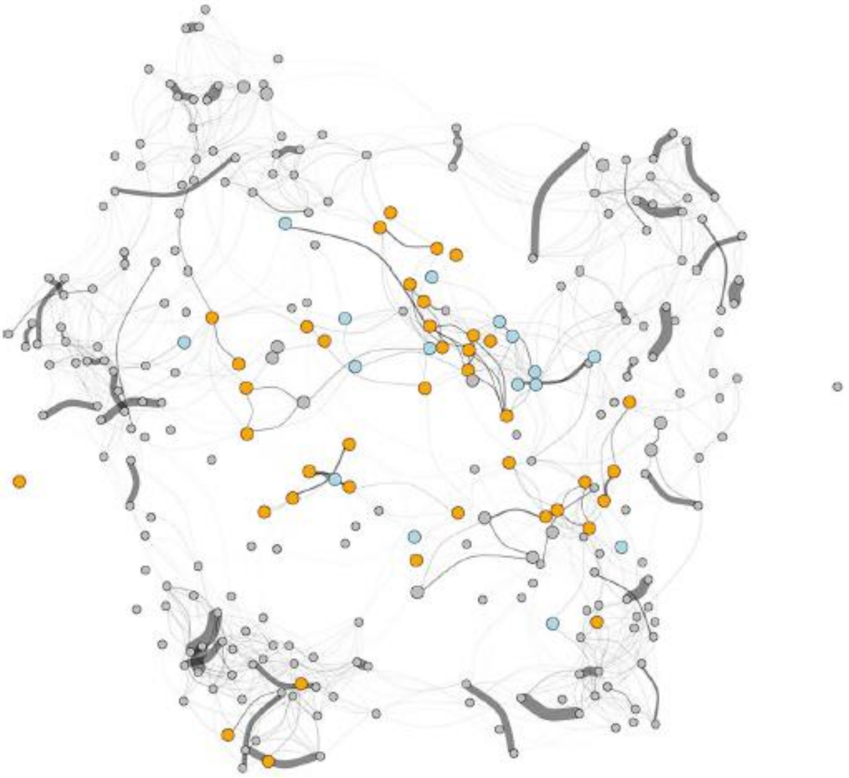

Figure 1. Social network from data collected from a population of wild zebra finches between September and December 2017 at feeders in the Australian desert. Small nodes represent adults, with the many wide edges showing the high association strength between pair-bonded individuals. Large nodes represent juveniles, with juveniles from enlarged broods shown in orange and juveniles from reduced broods shown in blue. Large grey nodes are juveniles not part of the experimental treatment groups. Network is plotted based on each individual's six strongest edges only, although all edges were used in the analyses. The unweighted network plot is provided as the electronic supplementary material, figure S1.

etc.) with treatment being the only predictor, and family and colony fitted as random effects. Because we did not have replicated networks, we did not need to fit time as a fixed effect or individual identity as a random effect. However, because network data are inherently non-independent [58], the significance of each coefficient in each model (herein p_{rand}) was calculated by comparing the observed data to 10 000 coefficients calculated by fitting the same model to permuted versions of our data [59]. As per Boogert *et al.* [28], we used a standard pre-network permutation procedure (originally described by [60], see also [2]), in which pairs of observations of two individuals observed at the same feeder on the same day were swapped between groups. After each swap, we recalculated the network, thus producing 10 000 random networks. Significance was calculated by comparing the observed coefficient value to the distribution of coefficient values from the randomized networks (following [59], see also [61]). For effects that were significant in Boogert *et al.* [28], we used a one-tailed significance test, whereas we used a two-tailed test for effects that were not significant in Boogert *et al.* [28].

Given that birds entered and left the population during the course of the study, our permutation test specifically controlled for any differences in the locations, number of foraging events joined and temporal patterns of presence across individuals in the population. That is, if a chick fledged early in the season, it would have had more opportunity to forage with others. When generating the distribution for the null hypothesis (using pre-network permutations of the data), the observation of that juvenile on a given day could only be swapped with observations of other juveniles on the same day and at the same location. This means that any patterns arising because an individual had more opportunity to forage with more conspecifics (it was present on more days) were maintained in the randomized data (meaning it had an equal opportunity to forage with many conspecifics in the distribution for the null hypothesis). For this reason, the standard errors of the coefficients from the linear models can sometimes be large despite the permutation test generating a significant *p*-value (i.e. because variation among individuals pertaining to their general differences in when and where they were detected are maintained in the permutation test, but contribute towards calculating standard errors).

3. Results

Brood size manipulations had a strong effect on nestling weight. We detected no difference in weight (day 3, weight ~ numerical brood size after swapping: $\beta \pm$ s.e. $= 0.038 \pm 0.042$,

Table 1. Summary of the statistical results, including the predictions based on results from Boogert *et al.* [28]. (Coefficients from linear models (β) are given for juveniles from enlarged broods relative to individuals from reduced broods for the results from the current data. p_{rand} values are calculated by comparing the observed coefficients to a distribution drawn from 10 000 permutations of the data. We used one-tailed tests when the prediction involved a directional effect, and two-tailed tests when no difference was predicted. Complete results tables, including random effects, are provided as tables in the electronic supplementary material (the number is given in the electronic supplementary material, table column).)

test		prediction	observed (coef ± s.e.)	signif.	match	electronic supplementary material, table
1	pair bonds	positive assortment	$r = 0.163 \pm 0.015$	$p_{rand} < 0.001$	yes	—
2	family structure	positive assortment	$r = 0.211 \pm 0.033$	$p_{rand} < 0.001$	yes	—
3	size of foraging groups	no difference	$\beta = -0.160 \pm 0.443$	$p = 0.708$	yes	S5
4	number of foraging groups	no difference	$\beta = 44.36 \pm 61.74$	$p = 0.513$	yes	S6
5	weighted degree	no difference	$\beta = 0.143 \pm 0.411$	$p_{rand} = 0.196$	yes	S7
6	unweighted degree[a]	stressed chicks higher	$\beta = 9.514 \pm 20.301$	$p_{rand} = 0.014$	yes	S8
7	betweenness	stressed chicks higher	$\beta = 218.1 \pm 202.3$	$p_{rand} = 0.049$	yes	S9
8	eigenvector centrality	no difference	$\beta = 0.018 \pm 0.090$	$p_{rand} = 0.280$	yes	S10
9	coefficient of variation of edge weights	stressed chicks lower	$\beta = -0.007 \pm 0.064$	$p_{rand} = 0.001$	yes	S11
10	strength of bonds to parents	stressed chicks weaker	$\beta = 0.000 \pm 0.007$	$p_{rand} = 0.257$	no	S12

[a] See the electronic supplementary material, table S8a for results without connections to family members, which are qualitatively identical.

$t = 0.902$, $p = 0.366$, see the electronic supplementary material, table S1 for full results) or tarsus length (day 3, tarsus length ~ numerical brood size after swapping: $\beta \pm$ s.e. $= 0.064 \pm 0.054$, $t = 1.181$, $p = 0.246$, see the electronic supplementary material, table S2 for full results) among chicks according to their end brood size on the day of manipulation. However, by day 11, every additional nestling in a nest reduced a nestling's weight by 1.6%, or approximately 10% between the smallest and largest manipulated broods (numerical brood size: $\beta \pm$ s.e. $= -0.153 \pm 0.057$, $t = -2.660$, $p = 0.009$, see the electronic supplementary material, table S3 for full results). Nonetheless, we found no effect of brood size manipulations on body size on day 11 (tarsus: $\beta \pm$ s.e. $= -0.018 \pm 0.037$, $t = -0.485$, $p = 0.614$, see the electronic supplementary material, table S4 for full results).

We detected a total of 200 adults, 69 juveniles and 14 individuals of unknown age at the RFID-equipped feeders, from which we constructed the social network ($n = 283$ in total). Of the juveniles, 40 were from experimentally enlarged broods (0.63 of those tagged), 16 were from reduced broods (0.59 of those tagged), eight were from unmanipulated broods (0.57 of those tagged) and five were caught as juveniles from unknown sources (the last two categories were not used in the analyses).

Our data on juveniles from enlarged and reduced broods supported 9 of the 10 predictions made based on Boogert *et al.* [28] (see table 1 for summary results and electronic supplementary material, tables S1–S12 for full results). More specifically, we found our network captured the strong familial structure in the population. The strong connections between paired birds resulted in significant assortment in the social network by pair, while strong within-family links produced significant assortment by family. In both tests of assortment, we found that the network of wild zebra finches was much more strongly assorted than the networks of captive zebra finches (pair bond: $r_{captive} = 0.111$ versus $r_{wild} = 0.163$; family: $r_{captive} = 0.091$ versus $r_{wild} = 0.211$). We found no evidence that birds from enlarged broods differed to birds from reduced broods in the size or number of foraging groups they joined, or in their weighted degree. However, birds from enlarged broods had a significantly higher unweighted degree, meaning that they had foraged with a greater number of conspecifics than birds from smaller broods. Although this might be the effect of living in larger families, the effect size was also significant if we removed each juvenile's connections to its family members. They also had a significantly higher betweenness, suggesting that they were potentially more important in the global connections of individuals across the whole population. We found no significant difference in eigenvector centrality, but birds from enlarged broods had a higher CV, meaning that they had more differentiated relationships. Finally, we found no evidence for a difference in the strength of relationships that juveniles from enlarged broods had with their parents when compared to juveniles from reduced broods. This was the only test where our results did not support the results of Boogert *et al.* [28]. However, we found that the direction (birds from enlarged broods had lower connection strength to their parents) and size ($\beta_{captive} = -0.008$ versus $\beta_{wild} = -0.007$) of the coefficients were very similar to the original study.

4. Discussion

Our data strongly support the prediction that developmental conditions can underlie consistent differences in social network position. The social network of wild zebra finches captured several aspects of social structure that we expected from birds that form lifelong breeding pairs where both parents contribute to the raising of the offspring, and forage together in a coordinated way [37,62]. Associations in the network were significantly assorted by breeding pair, meaning that the density of connections (sum of edges divided by the number of possible edges) between pairs of individuals that bred together was disproportionately higher than expected by chance and also reflected a high degree of assortment by family. In fact, nearly 20% of the total sum of edge weights was between individuals from the same family, despite these representing only 6% of the total possible edges in the network. However, not all families were created equal, and by manipulating the early-life social environment of chicks, through brood size manipulations, we found that being raised in a nest containing more 'siblings' resulted in marked differences in social network position later in life. In particular, juveniles who grew up in experimentally enlarged groups foraged with a greater number of conspecifics, were less 'choosy' and were more central in the overall social network.

The adaptive significance and life-history implications of the position individuals occupy in their social network has received increased attention over the last years. Several studies were able to demonstrate fitness consequences in the wild population linked to network positions. For example, being more central in a social network can lead to improved survival for adults [63] and their offspring [64,65]. Network centrality can also lead to more stable interactions with known individuals, which could facilitate decision-making [13]. The association between network position and its fitness effect is becoming increasingly evident, particularly when it is related to sexual selection, as in the case of the coordinated and cooperative lek display behaviour of male wire-tailed manakins, *Pipra filicauda* [19,66]. A number of studies have found important effects of betweenness, particularly during the juvenile period on fitness. For example, being less 'choosy' and moving more often between social groups (having a higher betweenness score) was shown to increase male reproductive success in wild house finches, *Carpodacus mexicanus* [67], and has been linked to the greater acquisition of social information in flocks of wild songbirds [22]. On the other hand, gregariousness might promote the spread of pathogens [68], with wild house finches that were more central being more likely to acquire a bacterial pathogen, *Mycoplasma gallisepticum* [23]. Generally, social network positions might be viewed as an extended phenotype [18,69,70] which is underlying plasticity and can be closely linked to fitness.

Our replication study found support for 9 of the 10 predictions for the role of developmental conditions on individual network position from the original study conducted on captive zebra finches. The stronger assortment by pair and family we found in the wild zebra finches (compared to captivity) is, in large, expected because the wild birds can spread over a much larger area and had access to a larger number of feeders. These data extend the evidence for the importance of foraging in family groups by zebra finches. In the one test where our results did not support the predictions of Boogert *et al.* [28], i.e. no difference in the relationship of juveniles to parents between enlarged and reduced broods, direction and size of the effects were nevertheless very similar in both studies, which raises the possibility that future studies may find support for this particular prediction. While we could directly compare the coefficients from these three tests (assortment by pair, assortment by family and the relationship of juveniles to their parents), this was unfortunately not possible for the other network metrics. Most network metrics are strongly influenced by the size of the networks, which were different between the captive and wild studies. Thus, the different scale makes a direct comparison of effect sizes challenging [1,6]. However, our results all point towards a tendency for more competition during development to increase gregariousness, which might enable offspring to more quickly reach independence. As already proposed in [28], growing up in adverse conditions may promote a phenotype which might better enable juveniles to disperse quickly from the poor natal nest site.

While there is an inherent preference for novel results in the peer-reviewed publication process [71–73], an increasing number of papers have highlighted the importance of replication in behavioural sciences [74–78]. The value of good replication is perhaps particularly important for those studies that have used a controlled laboratory environment, and less natural manipulation (e.g. directly administering stress hormones), to examine behavioural outcomes. For example, a recent meta-analysis of 23 publications focused on the red-green colour band paradigm in laboratory studies of the zebra finch, concluded that effects were largely irreproducible and that this very well-used experimental paradigm is false [79]. Over the last four decades, numerous studies had suggested that coloured leg bands affected the behaviour, attractiveness, physiology and fitness of zebra finches, with the most pronounced differences being reported between birds wearing either red or green bands (reviewed in [79]). One key hypothesis, that zebra finch males wearing red leg bands are preferred by females over males with green leg bands (presumably because it amplifies the signal of the beak ornamentation) was supported by many studies from different laboratories [80–82], but was rejected by the large-scale meta-analysis [79].

Our current study is a relatively unique example of direct replication of a captive study in the wild (see also studies on personality in zebra finches in the wild and captivity [83,84], and a recent study of sexual coloration in wild guppies [85]). The value of our replicate experiment is enhanced by having used a naturally occurring stressor, here variation in the brood size that juveniles have experienced. This means that we can realistically expect our findings to translate directly to natural situations. Further, although the original study by Boogert *et al.* [28] suggested that the close confines of captivity made it potentially difficult to detect individual differences in some network metrics, such as eigenvector centrality, our data generated almost exactly the same results. This support for the original study suggests that well-designed captive experiments can produce meaningful insights into the natural, free-ranging, social behaviour of zebra finches. Whether this is more broadly applicable or mostly true for zebra finches only (which naturally live and reproduce in small colonies) remains to be determined. Further, the similarity in the design of the data collection (using PIT tag readers that produce large numbers of observations) and analysis between the current and original study, with slight adjustments to the analysis method fitting the respective circumstances (i.e. using daily networks to avoid being swamped by noise for the captive bird data), may have also played a role in producing results that could be so closely replicated (across a number of tests and in effect sizes) in the wild.

There is a clear body of evidence linking differences in early-life developmental conditions to the social behaviour, and resulting social structure [21,28,86,87]. Developmental history could be a key factor underpinning consistent differences in individual behaviour [88–93]. For example, differences in brood size during early life can generate effects that are carried over into the following generations [94]. However, we still know relatively little about why stress appears to programme individuals to be more socially gregarious and less choosy. Captive experiments in which finer details about the directionality of inter-individual interactions can be captured, facilitated by recent innovations in long-term high-resolution tracking individuals [95], could provide new insights into the mechanisms—how do stressed individuals end up being more central and well-connected? A combination of new technology and methods, and additional targeted field studies, will hopefully allow us to determine whether the differences that have been observed are caused by the decisions of the stressed individuals themselves or the behaviour of others towards them.

Ethics. The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

Data accessibility. Raw and processed data, as well as R scripts to replicate the full analysis (from raw PIT tag detections or from the network data) are available to download from: https://dx.doi.org/10.17617/3.1x.

Authors' contributions. All authors contributed to the ideas of this study; H.B.B. and C.F. collected the data; D.F. and H.B. conducted analyses and wrote the initial draft of the manuscript; all other authors provided substantial feedback. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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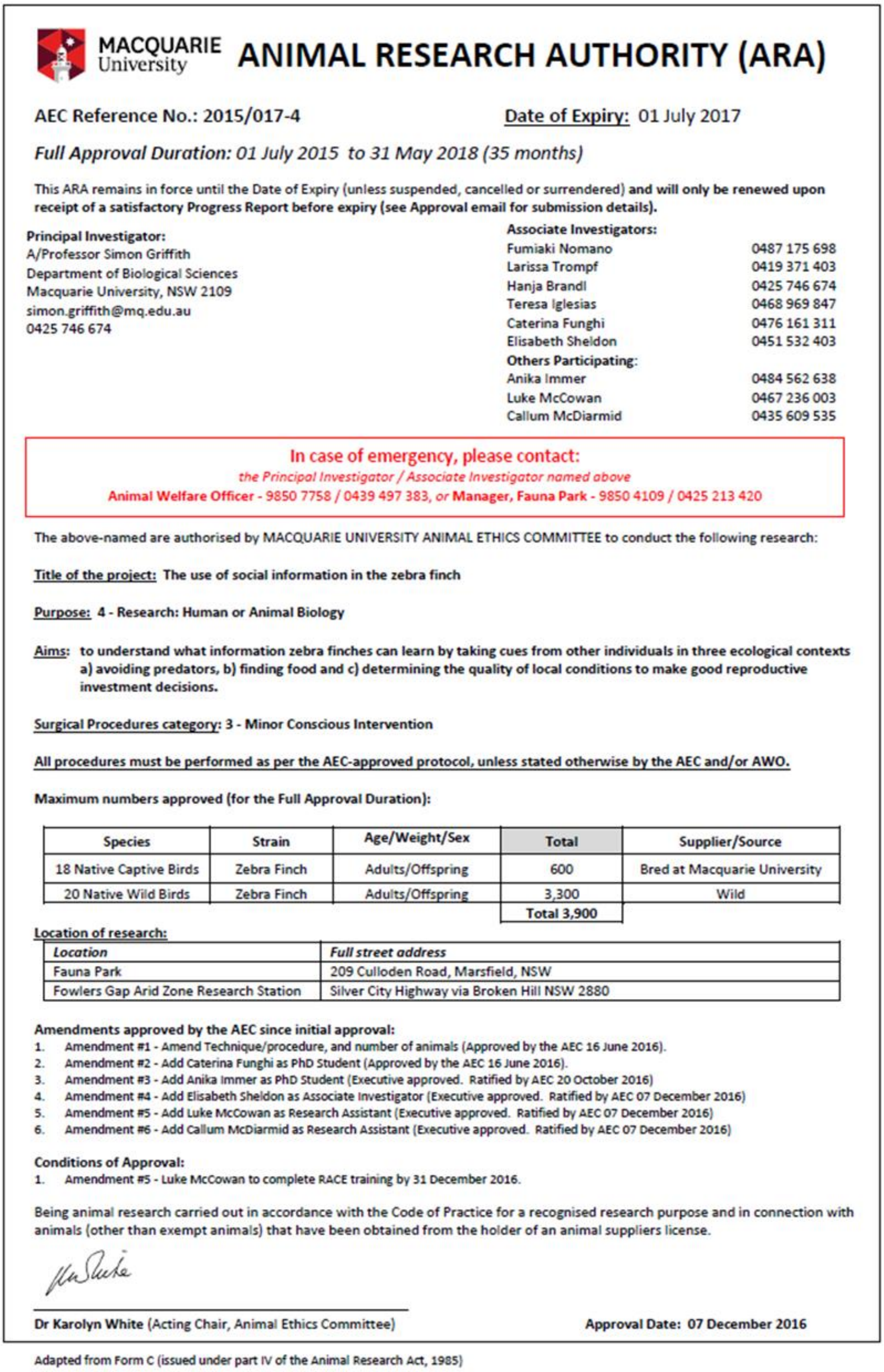
Appendix II

Macquarie University zebra finch ethics approval letter



MACQUARIE University

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2015/017-4 **Date of Expiry:** 01 July 2017

***Full Approval Duration:** 01 July 2015 to 31 May 2018 (35 months)*

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).**

Principal Investigator:
A/Professor Simon Griffith
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Associate Investigators:	
Fumiaki Nomano	0487 175 698
Larissa Trompf	0419 371 403
Hanja Brandl	0425 746 674
Teresa Iglesias	0468 969 847
Caterina Funghi	0476 161 311
Elisabeth Sheldon	0451 532 403
Others Participating:	
Anika Immer	0484 562 638
Luke McCowan	0467 236 003
Callum McDiarmid	0435 609 535

In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above
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: **The use of social information in the zebra finch**

Purpose: **4 - Research: Human or Animal Biology**

Aims: **to understand what information zebra finches can learn by taking cues from other individuals in three ecological contexts a) avoiding predators, b) finding food and c) determining the quality of local conditions to make good reproductive investment decisions.**

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/Weight/Sex	Total	Supplier/Source
18 Native Captive Birds	Zebra Finch	Adults/Offspring	600	Bred at Macquarie University
20 Native Wild Birds	Zebra Finch	Adults/Offspring	3,300	Wild
			Total 3,900	

Location of research:

Location	*Full street address*
Fauna Park	209 Culloden Road, Marsfield, NSW
Fowlers Gap Arid Zone Research Station	Silver City Highway via Broken Hill NSW 2880

Amendments approved by the AEC since initial approval:

1. Amendment #1 - Amend Technique/procedure, and number of animals (Approved by the AEC 16 June 2016).
2. Amendment #2 - Add Caterina Funghi as PhD Student (Approved by the AEC 16 June 2016).
3. Amendment #3 - Add Anika Immer as PhD Student (Executive approved. Ratified by AEC 20 October 2016)
4. Amendment #4 - Add Elisabeth Sheldon as Associate Investigator (Executive approved. Ratified by AEC 07 December 2016)
5. Amendment #5 - Add Luke McCowan as Research Assistant (Executive approved. Ratified by AEC 07 December 2016)
6. Amendment #6 - Add Callum McDiarmid as Research Assistant (Executive approved. Ratified by AEC 07 December 2016)

Conditions of Approval:

1. Amendment #5 - Luke McCowan to complete RACE training by 31 December 2016.

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 license.

Dr Karolyn White (Acting Chair, Animal Ethics Committee) **Approval Date: 07 December 2016**

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

Appendix III

Publications during candidature

Related to the Ph.D. project:

Brandl H. B. , Farine D. R., **Funghi C.**, Schuett W., Griffith S. C. (2019) “Early-life social environment predicts social network position in wild zebra finches” –Proceedings of Royal Society B 286(1897):20182579 DOI: 10.1098/rspb.2018.2579 (Appendix I)

Funghi C., McCowan L. S. C., Schuett W., Griffith S.C. (2019) “High air temperature induce temporal, spatial and social changes in the foraging behaviour of wild zebra finches” –Animal Behaviour 149, 33-43 DOI: 10.1016/j.anbehav.2019.01.004 (Chapter 4)

Unrelated to the Ph.D. project:

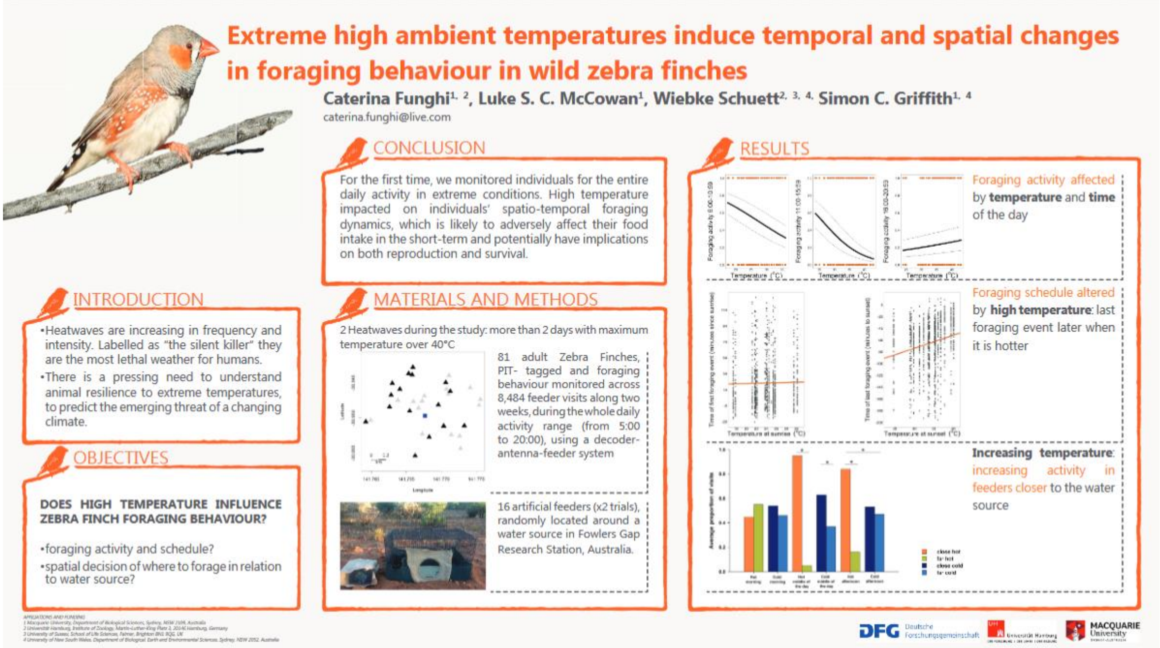
Funghi C., Trigo S., Gomes A. C., Soares M., Cardoso G. C. (2018) “Release from ecological constraint erases sex difference in social ornamentation” – Behavioural Ecology and Sociobiology 72 (4) DOI: 10.1007/s00265-018-2486-6

Appendix IV

List of presentations at international conferences

- **Funghi C**, Schuett W., Griffith S. "Extreme climate events induce foraging activity changes and heat stress behaviour in wild zebra finches"- poster presentation at the 27th International Ornithological Congress, Vancouver 2018, Canada. (Poster, design credit Silvia Paiola)

- **Funghi C**, Schuett W., Griffith S. "Extreme climate events induce foraging activity changes and heat stress behaviour in wild zebra finches"- oral presentation at European Conference of Behavioural Biology, Liverpool 2018, UK. (Talk)



Extreme high ambient temperatures induce temporal and spatial changes in foraging behaviour in wild zebra finches

Caterina Funghi[1, 2], Luke S. C. McCowan[1], Wiebke Schuett[2, 3, 4], Simon C. Griffith[1, 4]

caterina.funghi@live.com

CONCLUSION

For the first time, we monitored individuals for the entire daily activity in extreme conditions. High temperature impacted on individuals' spatio-temporal foraging dynamics, which is likely to adversely affect their food intake in the short-term and potentially have implications on both reproduction and survival.

INTRODUCTION

- Heatwaves are increasing in frequency and intensity. Labelled as "the silent killer" they are the most lethal weather for humans.
- There is a pressing need to understand animal resilience to extreme temperatures, to predict the emerging threat of a changing climate.

OBJECTIVES

DOES HIGH TEMPERATURE INFLUENCE ZEBRA FINCH FORAGING BEHAVIOUR?

- foraging activity and schedule?
- spatial decision of where to forage in relation to water source?

MATERIALS AND METHODS

2 Heatwaves during the study: more than 2 days with maximum temperature over 40°C

81 adult Zebra Finches, PIT- tagged and foraging behaviour monitored across 8,484 feeder visits along two weeks, during the whole daily activity range (from 5:00 to 20:00), using a decoder-antenna-feeder system

16 artificial feeders (x2 trials), randomly located around a water source in Fowlers Gap Research Station, Australia.

RESULTS

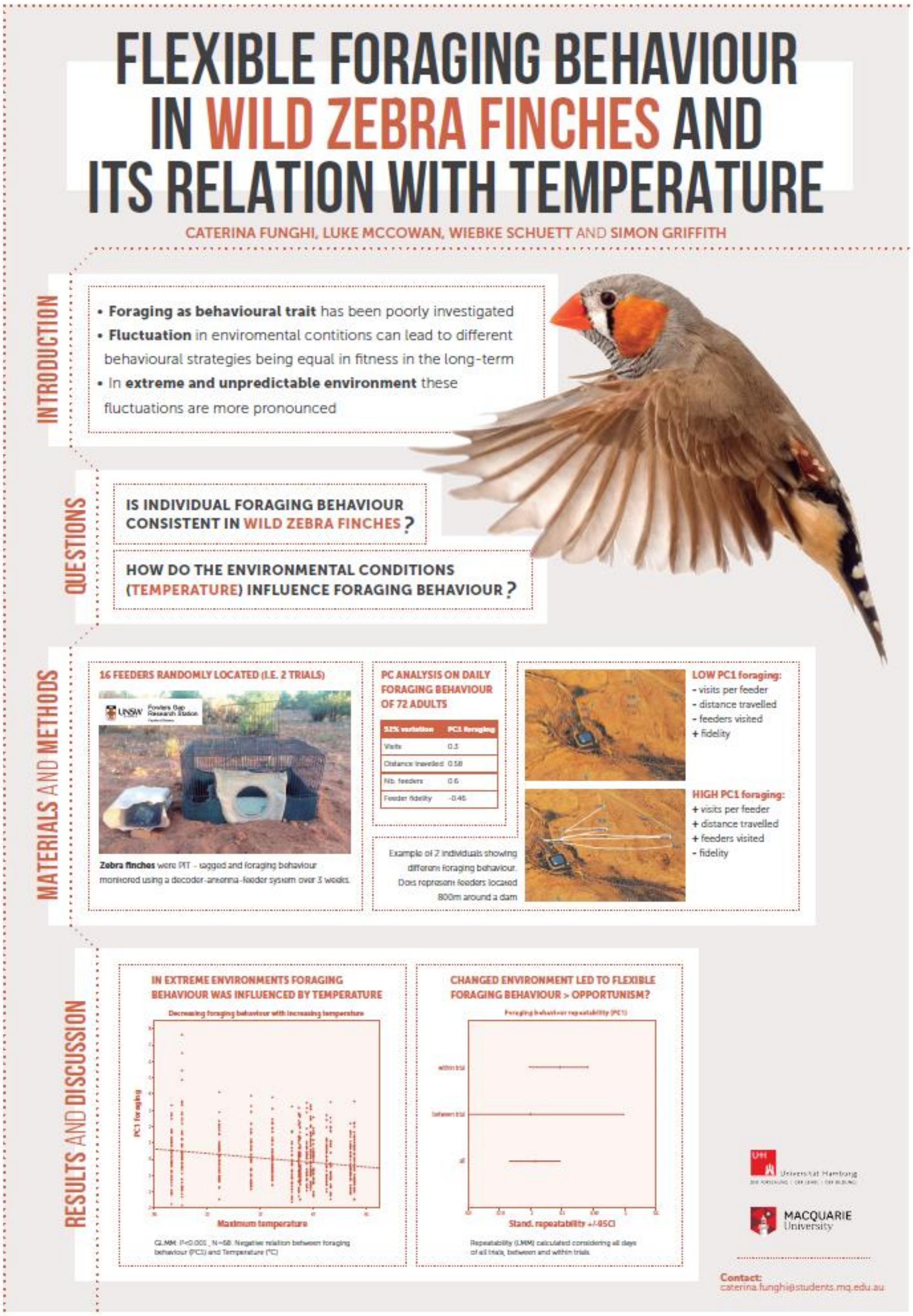
Foraging activity affected by **temperature** and **time** of the day

Foraging schedule altered by **high temperature**: last foraging event later when it is hotter

Increasing temperature: increasing activity in feeders closer to the water source

AFFILIATIONS AND FUNDING
1 Macquarie University, Department of Biological Sciences, Sydney, NSW 2109, Australia
2 Universität Hamburg, Institute of Zoology, Martin-Luther-King Platz 3, 20146 Hamburg, Germany
3 University of Sussex, School of Life Sciences, Falmer, Brighton BN1 9QG, UK
4 University of New South Wales, Department of Biological, Earth and Environmental Sciences, Sydney, NSW 2052, Australia

- **Funghi C**, Schuett W., Griffith S. “Flexible foraging behaviour in wild zebra finches and its relation with temperature”- poster communication at the 35th International Ethological Conference (IEC), Behaviour 2017, Estoril, Portugal. (Poster, design credit Osvaldo Branquinho)



FLEXIBLE FORAGING BEHAVIOUR IN WILD ZEBRA FINCHES AND ITS RELATION WITH TEMPERATURE

CATERINA FUNGHI, LUKE MCCOWAN, WIEBKE SCHUETT AND SIMON GRIFFITH

INTRODUCTION

- **Foraging as behavioural trait** has been poorly investigated
- **Fluctuation** in enviromental contitions can lead to different behavioural strategies being equal in fitness in the long-term
- In **extreme and unpredictable environment** these fluctuations are more pronounced

QUESTIONS

IS INDIVIDUAL FORAGING BEHAVIOUR CONSISTENT IN WILD ZEBRA FINCHES?

HOW DO THE ENVIRONMENTAL CONDITIONS (TEMPERATURE) INFLUENCE FORAGING BEHAVIOUR?

MATERIALS AND METHODS

16 FEEDERS RANDOMLY LOCATED (I.E. 2 TRIALS)

Zebra finches were PIT - tagged and foraging behaviour monitored using a decoder-antenna-feeder system over 3 weeks.

PC ANALYSIS ON DAILY FORAGING BEHAVIOUR OF 72 ADULTS

52% variation	PC1 foraging
Visits	0.5
Distance travelled	0.58
Nb. feeders	0.6
Feeder fidelity	-0.46

Example of 2 individuals showing different foraging behaviour. Dots represent feeders located 800m around a dam

LOW PC1 foraging:
- visits per feeder
- distance travelled
- feeders visited
+ fidelity

HIGH PC1 foraging:
+ visits per feeder
+ distance travelled
+ feeders visited
- fidelity

RESULTS AND DISCUSSION

IN EXTREME ENVIRONMENTS FORAGING BEHAVIOUR WAS INFLUENCED BY TEMPERATURE

GLMM: P<0.001 , N=68. Negative relation between foraging behaviour (PC1) and Temperature (°C)

CHANGED ENVIRONMENT LED TO FLEXIBLE FORAGING BEHAVIOUR > OPPORTUNISM?

Repeatability (LMM) calculated considering all days of all trials, between and within trials

Universität Hamburg
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Contribution Statement

Chapter 1 | General Introduction

I, Caterina Funghi, wrote the general introduction. Wiebke Schuett helped to improve it with comments and edits.

Chapter 2 | Characterization of spatial and temporal heterogeneity in grass productivity across an Australian arid landscape

I collected the field data, analysed the data and wrote the manuscript. Simon Griffith and Wiebke Schuett contributed to the conceptual design and provided feedback on the statistics, structure and wording of the manuscript.

Chapter 3 | Sentinel 2: an opportunity to integrate remote sensing and behavioural ecology in the arid zone

I collected the field data, processed the satellite data and conducted the analysis. Jens Oldeland and Renè Heim supervised the statistical analysis. Simon Griffith and Wiebke Schuett contributed to the conceptual design of the study and of the manuscript. All co-authors commented and edited the manuscript I wrote.

Chapter 4 | High air temperatures induce temporal, spatial and social changes in the foraging behaviour of wild zebra finches

Luke McCowan collected the field data with my collaboration. I analysed the data and wrote the manuscript. Simon Griffith and Wiebke Schuett contributed to the conceptual design of the study and of the manuscript and provided improving comments and editing to the manuscript. Wiebke Schuett supervised the statistical analysis. Two anonymous reviewers gave constructive comments which helped to improve the quality of the manuscript.

Chapter 5 | Persistent sampling increases food patch use, but not reproductive success, in wild zebra finches

This study is based on data collected by me, Hanja Brandl, Camille Delaby, Baptiste Averly, Jannis Liedtke and Olivia Rothberg. I conducted all statistical analysis and wrote the manuscript. Wiebke Schuett and Simon Griffith gave input to the design of the experiments, supervised the statistics and improved the wording of the manuscript.

Chapter 6 | General Discussion

I wrote the general discussion and Wiebke Schuett helped to improve it by commenting and editing.