Foraging under stress: Studies of three neotropical species

Laurie Dufour

Department of Biology
McGill University, Montreal
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Abstract

Animals typically live in ever-changing environments and must assess and respond appropriately to a broad spectrum of risks to maximize their fitness. Understanding how risk modulates foraging behaviour and what role stress plays in decision-making across taxa is essential to better predict the effect of anthropogenic perturbations on wild animals. In this thesis, I explore foraging responses to stress in two species of frugivorous tropical bats (*Carollia perspicillata* and *Artibeus jamaicensis*) and a species of tropical fish, the Trinidadian guppy (*Poecilia reticulata*) using two types of stressors: exposure to artificial light and sleep deprivation. With bats, I also investigate the impact of stress on social learning (learning from others). Since social learning can reduce decision costs in risky situations, I investigated whether social learning was favoured when animals are under higher perceived risk. In Chapter 2, I found no evidence that bats showed different foraging behaviours under environmental (light) and internal (sleep deprivation) stressors. Further, I found no evidence for social learning in control individuals or those exposed to putative stressors, despite previous evidence of social learning of food choices in one of these species. In Chapter 3, I show evidence for light avoidance in guppies, both in space use and foraging behaviour. Taken together, these results demonstrate that animals' responses to stress are variable and likely depend on multiple factors easily overlooked in experimental settings, raising the question of replicability and reproducibility in behavioural experiments. I discuss how methodological differences and cue variability might affect stress coping mechanisms and colour results. Overall, this thesis explores the impacts of stress on foraging behaviour and highlights the importance of conducting replications in varied settings to draw generalisable conclusions.

Résumé

Les animaux vivent généralement dans des environnements en constante évolution et doivent évaluer un large éventail de risques et y répondre de manière appropriée afin de maximiser leur valeur sélective. Il est essentiel de comprendre comment le risque module le comportement de recherche de nourriture et quel rôle joue le stress dans la prise de décision au sein de différents taxons afin de mieux prédire l'effet des perturbations anthropogéniques sur les animaux sauvages. Dans cette thèse, j'explore l’effet du stress sur le comportement de recherche de nourriture chez deux espèces de chauves-souris tropicales frugivores (*Carollia perspicillata* et *Artibeus jamaicensis*) et une espèce de poisson tropical, le guppy de Trinidad (*Poecilia reticulata*), en utilisant deux types de facteurs de stress: l'exposition à la lumière artificielle et la privation de sommeil. Avec les chauves-souris, j'étudie également l'impact du stress sur l'apprentissage social (apprendre des autres). Considérant que l'apprentissage social peut réduire les coûts individuels en situations risquées, j'ai cherché à savoir si l'apprentissage social était favorisé lorsque les animaux sont soumis à un risque perçu plus élevé. Dans le chapitre 2, je n'ai trouvé aucune preuve que les chauves-souris présentaient des comportements de recherche de nourriture différents sous l'effet de facteurs de stress environnementaux (lumière) et internes (privation de sommeil). En outre, je n'ai pas constaté la présence d’apprentissage social chez les individus contrôle ou exposés aux facteurs de stress supposés chez les deux espèces étudiées, malgré des preuves antérieures de l'existence d'un apprentissage social des choix alimentaires chez l'une de ces espèces. Dans le chapitre 3, je montre des preuves de l'évitement de la lumière artificielle chez les guppys, à la fois dans l'utilisation de l'espace et dans le comportement de recherche de nourriture. Dans l'ensemble, ces résultats démontrent que les réponses des animaux au stress sont variables et dépendent probablement de multiples facteurs facilement négligés dans les contextes expérimentaux, ce qui soulève la question de la réplicabilité et de la reproductibilité des expériences comportementales. Je discute de la façon dont les différences méthodologiques et la variabilité des indices sensoriels peuvent affecter les mécanismes d'adaptation au stress et colorer les résultats. Somme toute, cette thèse explore les impacts du stress sur le comportement de recherche de nourriture et souligne l'importance d'effectuer des réplications dans des environnements variés pour tirer des conclusions généralisables.

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Contribution of authors

Chapter 1: General introduction

Laurie Dufour wrote the chapter with guidance and input from Simon M. Reader.

Chapter 2: Social learning in frugivorous bats under two stressors: sleep deprivation and artificial light

Laurie Dufour, Simon M. Reader and Rachel A. Page designed the artificial light studies; Laurie Dufour conducted the artificial light experiments and collected and analysed the data. Alexis Heckley, Hannah Tilley and Rachel A. Page designed the sleep deprivation study. Alexis Heckley and Hannah Tilley conducted the sleep deprivation experiment and collected the data. Laurie Dufour analysed the data and wrote the chapter with input from Simon M. Reader and Rachel A. Page. Other contributors to the conduct of the study are acknowledged within the chapter.

Chapter 3: Foraging under artificial light in Trinidadian guppies (*Poecilia reticulata*)

Laurie Dufour and Simon M. Reader designed the study; Laurie Dufour conducted the experiment and collected data, analysed the data, and wrote the chapter with input from Simon M. Reader. Other contributors to the conduct of the study are acknowledged within the chapter.

Chapter 4: General discussion

Laurie Dufour wrote the chapter with guidance and input from Simon M. Reader.

Chapter 1: General introduction

Foraging behaviours are as diverse as life itself, resulting from animals' need for energy and nutrients to live, grow and reproduce (Brown, 2009). Foragers typically face a fundamental trade-off between maximizing food acquisition and maximising safety, meaning that the optimal strategy will be to tune foraging according to the risks in their environment. Over time, natural environmental stressors such as resource scarcity, competition, and predation have shaped the evolution of species-specific adaptive behaviours (Killen *et al.*, 2013; Lopez *et al.*, 2023;). Recent human-induced environmental changes have introduced new, often unpredictable stressors that disrupt these finely tuned ecological relationships (Hammond *et al.*, 2020). For instance, light pollution (Burt *et al.*, 2023), habitat fragmentation (Debinski & Holt, 2000), human presence (Ditchkoff *et al.*, 2006), and other factors driven by anthropogenic activities can act as perceived threats, influencing both physiological states and behavioural strategies. These stressors can impair essential processes such as foraging and risk assessment, presenting novel challenges for wildlife (Wilson *et al.*, 2020). Understanding how animals respond to these disturbances can shed light on the underlying mechanisms of behavioural flexibility and inform the resilience of species in changing environments. This thesis explores the foraging behaviour of two species of neotropical bats, *Carollia perspicillata* and *Artibeus jamaicensis*, and one species of neotropical fish, *Poecilia reticulata*, in response to perceived risk, including artificial light and sleep deprivation. Furthermore, it examines how these stressors influence social learning processes in bats, offering insight into the potential mitigating role of social interactions on tropical species under environmental change. Social learning - learning from others - allows animals to use cues from conspecifics to access resources at a lesser personal risk and often leads to the adoption of adaptive behaviours that can be culturally transmitted and maintained over time in a given population (Laland, 2008). Through this lens, this research integrates foraging theory with behavioural responses to stress and assesses how animals adapt to rapidly changing environments and the anthropogenic pressures that accompany them.

In this introductory chapter, I provide the foundational context for exploring the foraging behaviour of animals under stress and the effects of stress on social learning. It begins by establishing the broad concepts of animal behaviour, ecological theory, and the adaptive strategies animals use to cope with environmental challenges. It then delves into the role of foraging as a key ecological behaviour and examines how environmental stressors—such as artificial light pollution and sleep deprivation—can alter these foraging strategies. The discussion will expand on how stress influences behavioural processes, including decision-making and risk tolerance, while also considering the impact of stress on social learning mechanisms in animals. Following this, the introduction will highlight the unique ecological context of tropical ecosystems and why bats and fish represent ideal systems for examining these behavioural adaptations. Finally, the rationale for the research will be outlined, focusing on the gaps in knowledge this study addresses, the research objectives, and the significance of this work within a broader ecological and conservation framework. Through this roadmap, the introduction establishes the conceptual and empirical groundwork for the research presented in this thesis.

Ecological behavioural trade-offs

The field of animal behaviour is extremely broad, examining how animals relate to their physical environment and to other organisms, which includes but is not limited to how they find and defend resources, avoid predators, choose mates, reproduce and care for their offspring (Kappeler, 2010; Hunt, 2018). For most animals to be successful, they must be able to sense changes in the external world (e.g. predation pressure, food availability, parasitism) and their internal state (e.g. disease, stress), and respond to this information with appropriate decisions (Manning & Dawkins, 2012). It is impossible to maximize all components of fitness at once and animals must balance their time and energy in specific trade-offs (Stearns, 1989) - for example, time spent reproducing is taken away from foraging, and time spent foraging usually involves higher exposure to predators. Animals will choose when to allocate their time to what activity based, amongst other things, on environmental factors. For instance, wolverines expose themselves to higher predation risks, shown by higher vigilance, by lounging outside on warm days for the thermoregulatory advantages it provides (Glass *et al.*, 2021). Such life history trade-offs are often directly linked to how competitive animals can be under stable and changing ecological conditions (Penk *et al.*, 2016; Sorte & White, 2013). For example, female capital-breeding seed beetles typically live longer when they lay fewer eggs, but this cost of reproduction may only be apparent when food is scarce in the environment because differences in reproductive effort are then significant enough to take over differences in resource acquisition (Messina & Fry, 2003). Many theories and hypotheses aim to explain decision-making and trade-offs in animals. Foraging theory (Stephens & Krebs, 1986) studies how animals seeking resources make decisions and posits that foraging behaviours are regulated by a trade-off between the exploitation of known resources with set values and the exploration of potentially richer novel resources (exploration-exploitation trade-off). To increase their fitness, animals must make the decisions that maximize rewards and limit costs. Individuals can perceive information differently and access resources differently depending on their physiological state and external environmental factors (Real & Caraco, 1986). In optimal foraging theory, the assumption is that all foraging choices should be directed towards an optimal outcome that yields the greatest possible benefit for the individual forager's survival and reproductive success (Smith *et al.*, 1983). This implies that any decision that fails to maximize energy return must be linked to an impediment preventing the forager from making the optimal choice. On the other hand, state and prediction-based theory (SPT) combines the classic trade-offs with regular updating based on past experiences. This way, individuals predict, possibly inaccurately, future food availability and risk from current internal state (e.g. reproductive status, energy) and external conditions (e.g. predator pressure, food abundance) to try and optimize fitness, which allows for interactions with conspecifics and the environment to better inform decisions (Railsback & Harvey, 2013).

Stress and animal behaviour

The concept and term "stress" is at the root of many debates in ecology and evolution, mostly rooted in the intensity of conditions required to call it such (Goldstein & Kopin, 2007). Originally, it referred to any external constraints that limit the rates of resource acquisition, growth or reproduction (Grime, 1989). Some recommend restricting the use of the word stress for situations where environmental demand overcomes the natural regulatory capacity of an organism, ideally including some form of unpredictability and uncontrollability (Koolhaas *et al.*, 2011). Here, we will keep it simple; we know that all individuals must maintain their homeostasis when internal and external adverse forces, stressors, threaten it (Chrousos *et al.*, 1996). As such, stress can occur anytime organisms' homeostasis is threatened or perceived to be so and induces various physiological and behavioural responses (Chrousos, 2009). Stress affects the central nervous system and modulates the activity of multiple systems – for example, in rats, the steroid, catecholamine, peptide and opioid systems. Most importantly, in response to stress, a cascade of neurohumoral events is triggered through the hypothalamo-pituitary-adrenal (HPA/I) axis, which aims to stop the stressed state and re-establish homeostasis (Sutanto & De Kloet, 1994). This axis produces glucocorticoid hormones, corticosterone and cortisol, that regulate the baseline homeostasis related to life events including growth, reproduction and migration (Sapolsky *et al.*, 2000). These hormones are particularly important in food acquisition, appetite peaking when glucocorticoid hormones are at their peak in the circadian cycle (Sapolsky *et al.*, 2000). In stressful situations they take on a new role, becoming responsible for physiological and behavioural responses to unpredictable environmental changes and perturbations (Crespi *et al.*, 2013). Indeed, acute or chronic stress responses are modulated by stress hormones that inhibit or activate the HPA/I axis (Wingfield & Romero, 2001). In most organisms, stress responses can be maladaptive, increasing mortality and decreasing reproduction, or adaptive. The adaptive response is usually caused by acute but short-term stressors that do not lead to a profusion of physiological changes. In that case, facing stress can have beneficial effects (eustress) on individuals, favour survival, and possibly increase resilience and the ability to cope with subsequent stressors (Schreck & Tort, 2016; Suri & Vaidya, 2015). The maladaptive response is on the other hand usually associated with chronic - repeated and long - exposure to stressors and can cause distress, decrease growth, reproduction, learning and predator avoidance and increase susceptibility to diseases (Afonso, 2020; de Kloet *et al.*, 2005). Different types of stressors will also result in varying stress responses. The most self-explanatory are reactive stressors, also called physical stressors, which are direct physiological threats that cause immediate and direct danger to homeostasis and trigger reflexive responses in individuals. More processing is required to respond to anticipatory stressors (or emotional stressors), environmental cues perceived by the organism to be threatening to survival and that need organisms to interpret relevant sensory stimuli through memories of past experiences (Boonstra, 2012). In addition to stressor variability, individuals also show distinct coping strategies to the challenges they face. The first behavioural response to stress, the active response, was first described by Cannon (1915) as a fight-flight response and is defined by territorial control and aggression. Engel and Schmale (1972) offered an alternative called a conservation-withdrawal response, that is characterized instead by immobility and low levels of aggression. We can also think of them as agonistic or avoidant responses, the first seeking to eliminate the stressor and the second aiming to reduce exposure to the threat (Jorquera-Chavez *et al.*, 2019). These strategies are often linked to individual personalities - for example, more proactive and bolder animals show lower glucocorticoid responses than reactive and shy individuals (Cockrem, 2013). Furthermore, stress responses may vary across populations based on the harshness of conditions. For instance, in semipalmated sandpipers (*Calidris pusilla*) individuals in northern sites with harsher climates have lower circulating levels of corticosterone after capture and handling than individuals from milder environments (O'Reilly & Wingfield, 2003). Because stress is often a result of environmental factors and affects individual behaviour, it is likely to play into multiple complex mechanisms such as resource acquisition, foraging efficiency and risk tolerance. Most obvious is that animals may decrease the risk associated with a stressor, by increasing vigilance for example, but in doing so may neglect other essential functions, such as foraging or reproduction. That being the case, animals are expected to balance the length of the stress period and the level of risk it represents against the damage they incur by overlooking fundamental actions to appropriately allocate their time and resources (McNamara & Buchanan, 2005).

Stress, risk and foraging

Optimal foraging theory assumes that animals make foraging decisions (e.g. where, when and on what to feed) that maximize a foraging currency, for example net energy intake, and could not be improved if they used any alternative strategy (Pyke & Starr, 2021). Although criticized for its many assumptions and simplistic model (Pierce & Ollason, 1987; Pyke, 1984), it represents a good baseline to start to investigate the role of stress and risk in foraging behaviours. Broadly, it posits that an animal likely to starve will have the best chance for survival in the most variable situation, while a well-fed animal should edge towards stability (Pyke, 1984). Interestingly, the effects of risk on behaviour seem dependent on how this risk was generated - for instance, when risk arises because of the variability in reward quantity incurred in experimental studies, most animals are risk-averse, but when variability is caused by reward delay, animals are risk-prone (Kacelnik & Bateson, 1996). Predation is arguably the biggest risk most prey species are likely to factor into their foraging decisions. Lima and Bednekoff (1999) developed the risk-allocation hypothesis, which shows that the level of predation risk and the proportion of time the predators are present should affect the trade-off of feeding and vigilance strategies. Specifically, prey should reduce vigilance in safer conditions to gather sufficient resources to be able to reduce foraging rate when exposed to danger, but they might be forced to forage for survival despite high predation risk if that risk is maintained over periods of time long enough for accumulated resources to be depleted.

To manage risk, organisms can change time allocation patterns (change where, when and how long to forage: Brown, 1999) and increase apprehension (for example vigilance: Kotler *et al.*, 2002) behaviours. These coping mechanisms often reduce foraging efficiency by limiting individuals' ability to assess patches and harvest food (Dall *et al.*, 2001). If they must forage in risky areas (for e.g. Berger-Tal *et al.*, 2010), animals typically adopt risk-mitigating behaviours like central place foraging and group foraging (Lima & Dill, 1990). However, foraging decisions are often not as straight-forward as distinguishing high and low predation risk, considering food quality might also be unevenly spread in the landscape - animals might have to choose between low-quality food patches in safe areas, and high-quality food in risky places. This foraging dilemma between food and safety is likely to be modulated by species and individual behavioural and physiological tolerance to risk (McArthur *et al.*, 2014).

Stress hormones most likely alter foragers' perception of risk and shape how individuals experience and respond to potential threats. Predation risk (for e.g. pikas: Yin *et al.*, 2017; mice: Sánchez-González *et al.*, 2018; fish: Archard *et al.*, 2012; hares: Sheriff *et al.*, 2011) has been shown to directly affect stress hormone concentrations in animals. In addition to direct evidence of predator presence, prey species can associate risk with indirect environmental cues, such as open habitats (Powell & Banks, 2004) or the presence of moonlight (Kotler *et al.*, 2010). For instance, gerbils foraged less and showed higher vigilance both under full moons and when predators were present. Moonlight itself was also associated with higher levels of stress hormones, indicating it was most likely perceived as an indicator of predation risk (Juliana *et al.*, 2017). Glucocorticoids can stimulate multiple behaviours, such as feeding, searching and risk assessment, differently depending on context (Dallman, 2007), and are likely to influence foraging behaviours under stress. Wingfield *et al.* (1998) suggested that increased levels of glucocorticoids due to stress can induce an "emergency life history stage" that redirects individual priorities from non-essential activities (for e.g. reproduction) to behaviours allowing individuals to survive the stress. Hormones and stress can thus be critical in allowing animals to trade off food and safety in the appropriate manner as environments change.

Social learning

Living in a group involves both major costs (e.g., competition for food, resources or mates) and benefits (e.g., predator detection, group defence; Krebs & Davies, 1997). One significant benefit is opportunities for the exchange of information among individuals as “close proximity increases the number of opportunities for observation and the rapidity of information procurement” (Lee, 1994; but see Reader & Lefebvre, 2001). Social learning - learning from others - has been shown to influence behaviours across a wide range of taxa, from cetaceans (Rendell & Whitehead, 2001) and fish (Brown & Laland, 2003) to insects (Sherry, 2008) and rodents (Galef, 1996). For instance, the proximity of infant baboons (*Papio cynocephalus*) to foraging adults has been shown to lead to information gathering about food safety through olfactory and visual observation of the foods being eaten (King, 1999). Indeed, group living can be extremely useful to individuals socially learning when, how, and what to feed on (Galef & Giraldeau, 2001) as the ingestion of novel food can be dangerous and relying on information from group members can reduce the risks of harm. In addition to foraging, animals have been shown to learn from others across a range of ecologically important contexts, including mate choice (Danchin *et al.*, 2018), nesting (Vistalli *et al.*, 2023), vocal communication (Janik & Slater, 2000; Szymkowiak, 2024), predator avoidance (Griffin, 2004), movement (Avarguès-Weber & Chittka, 2014) and migration (Jesmer *et al.*, 2018; Mueller *et al.*, 2013). Social learning can be advantageous because it allows individuals to avoid the effort and risks that come with trial-and-error learning. However, it can also be more error-prone than individual learning, leading animals to acquire dangerously outdated information in changing environments (Feldman *et al.*, 1996; Giraldeau *et al.*, 2002; Kameda & Nakanishi, 2002). To balance the advantages of social learning against the risks of its indiscriminate use, individuals should be selective in when and how they rely on social information through various “social learning strategies” (Hoppitt & Laland, 2013; Kendal *et al.*, 2018). For example, starlings are more likely to explore a food patch on their own when it is simple to access but switch to use a demonstrated patch when exploration is more challenging (i.e., they copy others when it is costly to acquire information directly; Templeton & Giraldeau, 1996). Individuals might also discriminate between social learning partners based on age (Galef & Whiskin, 2004), size (Duffy *et al.*, 2009), prior success (Romero-González *et al.*, 2020) or dominance status (Nicol & Pope, 1999). However, little is known about the effect of extrinsic factors, such as environmental conditions, and intrinsic conditions, for example stress levels, on both the efficiency and the likelihood of social learning in the wild.

We know that the environmental conditions during rearing can affect social learning preferences - for instance, minnows raised in high-risk environments showed weaker responses to socially demonstrated predator cues than individuals reared in low-risk conditions (Crane & Ferrari, 2015). Models looking into environmental instability are usually focused on the persistence of social learning across generations, rather than the likelihood of social information use in a single generation. For instance, Boyd and Richerson (1985) concluded that the proportion of social and individual learning will eventually evolve to an equilibrium at which dependence on social learning will be more important when environmental predictability is stronger. Feldman *et al.* (1996) support this idea and show that social learners cannot persist if the environment is too variable. This shows that at a species-scale, social learning should be favoured in stable environments - but what about shorter time scales?

Study species and relevance

The tropics are famously biodiversity-rich, containing 75% of the world's species, including almost all shallow-water corals and over 90% of terrestrial birds (Barlow *et al.*, 2018). Unfortunately, tropical environments also face some of the most important rates of human-induced stressors, notably land-use change, habitat degradation and anthropogenic disturbances (Keenan *et al.*, 2015), which directly threatens the diversity they are home to. It is particularly relevant to study the impact of environmental stressors in places and species likely to experience and suffer from those same stressors, which makes the use of tropical species in this thesis pertinent. In this thesis, I study the impact of artificial light on Seba's short-tailed bats (*Carollia perspicillata*) and Trinidadian guppies (*Poecilia reticulata*), while sleep deprivation is investigated with Jamaican fruit bats (*Artibeus jamaicensis*). Both species of bats are assessed for social learning. Although the impact of light pollution on multiple bat behaviours has been studied (e.g. foraging, commuting, emergence, roosting and breeding behaviours (for review: Stone *et al.*, 2015)), sleep deprivation and the interaction between anthropogenic lighting and social learning have not yet been investigated.

Many tropical bats consume nectar and fruits and are important pollinators and seed dispersers for several hundreds of plant species (Ghanem & Voigt, 2012). Indeed, frugivorous bats are the second most numerous seed-dispersing agent after birds in the Neotropics, where they are particularly important for the dispersal of seeds during the early stages of succession (Medellin & Gaona, 1999; Muscarella & Fleming, 2007). In naturally dark conditions, bats make seed rain essential to regrow deforested habitats and to connect distant forest fragments. As such, they are key species for succession and to maintain plant diversity, even more so in fragmented Neotropical landscapes (Medellin & Gaona, 1999; Muscarella & Fleming, 2007). However, Lewanzik and Voigt (2014) showed that frugivorous bats (*Carollia sowelli*) harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour streetlight than in a dark compartment. Free-ranging bats also neglected to feed on ripe fruits that were experimentally illuminated (Lewanzik & Voigt, 2014). Both of these direct effects of artificial lighting could significantly lower their crucial seed-dispersal ecosystem function by altering flight paths and limiting seed intake. Investigating the impact of light pollution on frugivorous bats' behaviour is thus essential to inform future policy making and strategic planning for the protection of Neotropical habitats. *Carollia perspicillata* provided an appropriate choice for this experiment considering their response to light appears to be reliably negative, showing a distinct reduction in foraging activity (Esbérard, 2007), increase in day roosting (Fleming & Heithaus, 1986) and shorter distance moved to forage (Heithaus & Fleming, 1978) under light. To our knowledge, the effects of sleep deprivation on foraging behaviour have never been investigated in bats. *Artibeus jamaicensis* are highly social, frugivorous and one of the most abundant phyllostomids in the Neotropics (Ortega & Castro-Arellano, 2001), which makes them both feasible to catch and important to study.

Social information is likely to be particularly relevant in bat foraging ecology considering the social nature of bats, and *Carollia perspicillata* are well suited to testing the potential for discriminating the value of social information, as they have explicitly shown socially induced preferences for novel food odours (Ratcliffe & ter Hofstede, 2005). *Artibeus jamaicensis* are also likely to share information about food with one another and have it impact their decisions (Handley *et al.*, 1991). They primarily feed on fig trees, which all ripen at once and within a week of ripeness must be consumed or wasted (Morrison, 1978). This implies that animals consuming this resource must continually seek new food sources, which might make social information particularly valuable (Milton *et al.*, 1982). They also are known to congregate at feeding roosts throughout the night (Ortega & Castro-Arellano, 2001), providing ample opportunities for social information transmission.

The Trinidadian guppy is a tropical freshwater fish that can be found in multiple river systems, with waterfalls dividing the upstream and downstream sections (Magurran, 2005). This geography results in distinct environments inhabited by stable guppy populations (Magurran, 2005) with different characteristics - upstream guppy populations have no significant aquatic predators and downstream populations face high predator risk, which drives the rapid evolution of unique morphological and behavioural traits between wild guppy populations (Reznick *et al.*, 2001). Light environment has been connected to changes in many behaviours in guppies, including courtship (Archard *et al.*, 2009; Chapman *et al.*, 2009; Gamble *et al.*, 2003), shoaling (O'Connor & Krause, 2003), foraging (White *et al.*, 2005) and risk-taking. Notably, guppies chronically exposed to artificial light at night (ALAN) have been shown to emerge quicker from a refuge and spend more time in the more open area of the arena (Kurvers *et al.*, 2018).

Thesis overview

This thesis aims to 1) establish the foraging responses to two distinct stressors, light and sleep deprivation, the first in both the Trinidadian guppy and *Carollia perspicillata*, the second in *Artibeus jamaicensis* and 2) examine the impact of those same stressors on the social learning propensities of the frugivorous bats. In Chapter 2, I found no evidence that bats forage differently under bright artificial light or when sleep deprived. I also surprisingly find an absence of social learning of novel foraging odour cues in both species tested using a well-known paradigm, highlighting the necessity for replication studies in ecology and behaviour. In Chapter 3, I demonstrate light avoidance in foraging and space use for fish given a choice between two zones. Finally, I synthesise and discuss the implications of these findings, as well as propose methodological improvements and future studies (Chapter 4). Overall, the experiments described in my thesis expand our understanding of the influence of stress on foraging behaviour in two widely different tropical systems and highlight the likely highly context-dependent nature of social learning in wild animals.

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Chapter 2: Social learning in frugivorous bats under two stressors: sleep deprivation and artificial light

Dufour, L., Heckley, A., Tilley, H., Reader, S.M. & Page, R. A.

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Abstract

Environmental stressors such as artificial light and sleep deprivation have the potential to disrupt key behaviours in many animals, including social information use and foraging. However, their effects on bats, which often rely on social learning for acquiring information, remain understudied. Here, we investigated whether these two expected stressors influenced social learning and foraging behaviour in two frugivorous bat species. In Experiment 1, we assessed social learning under light and dark conditions, where bats chose between a socially demonstrated food and a novel food after being exposed to the stressor. In Experiment 3, we tested social learning in sleep deprived versus rested bats, with both demonstration and testing occurring under the stressor. Based on the costly information hypothesis, we predicted that stressed bats would rely more heavily on socially demonstrated choices. Surprisingly, we found no evidence of social learning or altered foraging behaviour in response to either stressor. Given the unexpectedly weak response to artificial light in Experiment 1, we conducted a follow-up study (Experiment 2) to assess foraging preferences under three lighting conditions: simulated streetlight (white light), simulated moonlight (green light), and darkness. We predicted reduced foraging in illuminated environments if light functioned as a stressor; however, no significant differences in foraging behaviour were observed. Additionally, the absence of social learning in this study contrasts with previous findings in bats, suggesting that social learning may not be as reliably seen across contexts and species as previously assumed. These results highlight the need for further research into the variability of social learning and the influence of stressors on bat behaviour.

Introduction

Social learning, i.e. learning from other individuals, is often adaptive as it allows individuals to avoid the effort and risks that come with the acquisition of information through trial-and-error learning. However, theoretical work reveals that social learning can be error-prone, leading individuals to acquire dangerously outdated information in changing environments (Giraldeau *et al.*, 2002; Kendal *et al.*, 2005; Laland & Williams, 1998). To balance the advantages of social learning against the risks of its indiscriminate use, individuals should be selective in when and how they rely on social information (Giraldeau *et al.*, 2002; Laland, 2004). This selectivity in the tendency to learn from others can vary within individuals of a species based on personality traits, past associative learning histories, developmental stress and physiological condition (Mesoudi *et al.*, 2016). For instance, studies on rats have shown that maternal deprivation, differences in maternal care and stressed mothers reduce the social learning of food preferences from unfamiliar demonstrators in their offspring (Lévy *et al.*, 2003; Lindeyer *et al.*, 2013; Melo *et al.*, 2006). Additionally, several theoretical models have shown that social learning is more likely to be adaptive when environments are relatively stable, as it increases the probability that others' behaviours will accurately reflect current conditions (Boyd & Richerson, 1988; Feldman *et al.*, 1996) and that copying will lead to the acquisition of useful information (Laland & Plotkin, 1993). In support of these ideas, Galef and Whiskin (2004) found that Norway rats kept either under standard laboratory conditions or in a rapidly changing environment (where subjects were moved daily to new cages and were offered an unfamiliar food for varying durations at different times of day) used social information differently. They found subjects in stable conditions were significantly more attentive to socially acquired information than individuals living in unstable environments. Although this is consistent with rats copying more when the reliability of social information increases, note that social information was not in conflict with personal information, since both flavours offered to the subjects were novel to them (Kendal *et al.*, 2005). That is, other processes than social learning may result in adaptive changes in behaviour (Giraldeau & Lefebvre, 1996), and thus caution is needed in assuming that selective social learning is a product of adaptive specialization.

The “dangerous niche” hypothesis (Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann *et al.*, 2013) posits that prey can reduce the costs associated with ecological uncertainty by increasing their level of caution or vigilance when faced with novel situations (i.e., employ neophobia). Higher levels of spatial and foraging neophobia would reduce costs associated with inappropriate behavioural decisions until they can acquire direct information regarding immediate risks associated with a novel habitat or foraging opportunity (Dall *et al.*, 2005; Mettke-Hofmann *et al.*, 2009). This tendency to lean towards caution in risky novel situations could be translated into a stronger reliance on social information than personal exploration (the “costly information” hypothesis) (Boyd & Richerson, 1985). Previous work in black-capped chickadees has found the rate of social information transmission was higher in rural than urban environments (Jones *et al.*, 2017), supporting the idea that unreliable (risky) food availability might increase reliance on social information (Deygout *et al.*, 2010). Likewise, social information about the environment was found more valuable to individuals in an unpredictable environment in European starlings (Rafacz & Templeton, 2003), which is consistent with the costly hypothesis but could also simply be due to local or stimulus enhancements effects.

High stress levels in animals have often been associated with a decrease in social learning. For instance, Farine *et al*. (2015) found that zebra finches exposed to elevated stress hormones during development relied more on unrelated adults than on their parents to learn a novel foraging task. In this case, developmental stress seems to be used as an environmental cue that promotes the adoption of alternative social learning strategies (Farine *et al.*, 2015). However, this switch from parental to horizontal learning might also be linked to individual differences caused by developmental stress such as developmental rate, adult stress responsiveness (Spencer *et al.*, 2009) or cognitive and social skills (Lupien *et al.*, 2009). Stress can be acute or chronic, leading to different coping responses in animals. These coping responses can be broadly categorised as active (fight or flight), with territorial and aggressive behaviours (Cannon, 1929) or passive (conservation-withdrawal), shown through immobility and avoidance (Engel & Schmale, 1972). Animals’ responses to stress will depend on individuals’ inherent characteristics, such as sex and age, but also on the nature of the stressor itself (Sutanto & de Kloet, 1994). For example, studies in rodents have shown that in the case of acute stressors, a small increase in glucocorticoids (stress hormones produced by the adrenals) enhances hippocampus-mediated learning and memory, while bigger elevations impair those functions (Diamond *et al.*, 1992). This is hypothesised to serve adaptive purposes by increasing vigilance and learning processes during severe challenges (Lupien *et al.*, 2009). In contrast, stress can also have detrimental influences on decision-making by encouraging premature choices, decreasing cognitive flexibility and increasing risk taking (Starcke & Brand, 2012). For example, Sprague-Dawley rats that had gone through early-life chronic stress chose small rewards delivered immediately over larger rewards delivered after a time delay, indicating increased impulsivity that was absent in unstressed individuals (Laguna *et al.*, 2022). Interestingly, the presence of conspecifics can buffer such stress responses in social animals (Kikusui *et al.*, 2006). Humans (Schwarzer & Knoll, 2007) and female monkeys (Brent *et al.*, 2011; Cheney & Seyfarth, 2009) rely on the stability of their social networks to cope with stress. Multiple cues of conspecific presence can lead to stress buffering, including visual (e.g. sheep: da Costa *et al.*, 2004), tactile (e.g. monkeys: Winslow *et al.*, 2003; rats: Latane, 1969) and olfactory (e.g. rats: Ågren *et al.*, 1997; zebrafish: Faustino *et al.*, 2017) cues. Stressors can be exogenous (e.g. weather conditions, predator presence, ectoparasite infestations) or endogenous (e.g. disease, food deprivation, social relationships) stimuli that threaten homeostasis and induce a response to restore it (Chrousos, 2009; Karaer *et al.*, 2023). In this chapter, we were curious to study the influence of two different stressors, one external (light) and the other internal (sleep deprivation), on social learning propensities

Artificial light at night (ALAN) is a consequence of urbanisation and disrupts many light-dependent processes such as reproduction, foraging, sleep and migration across a wide range of taxa (Rich & Longcore, 2013). There is no overarching consensus on the impact of light on behaviour, as it is broad and varies based on animals' life histories, habitat use and circadian rhythms. We do know that exposure to ALAN can increase stress hormone concentrations in captive (Emmer *et al.*, 2018) and wild animals (Ouyang *et al.*, 2015). Laboratory studies based on rodents have shown that only 15 minutes of bright light exposure led to an increase in glucocorticoid hormones (Wilson & Downs, 2015). In addition to physiological work, stress responses in wild animals can be evaluated through changes in behaviour; for example, the nocturnal common spiny mouse decreased activity during nights with ALAN (Rotics *et al.*, 2011). In many cases, the presence of light leads to trade-offs between the ability of an individual to access resources (Foraging Efficiency Hypothesis: Imber, 1975) with the higher perceived predation risk (Predation Risk Hypothesis: Mougeot & Bretagnolle, 2000) to maximise fitness.

Light also regulates, at least in part, the daily sleep-wake patterns of animals (Dijk & Archer, 2009; Fisher *et al.*, 2013). Sleep is a behaviourally inactive state ubiquitous in animals (Vorster & Born, 2015) usually characterized by consecutive periods of resting behaviour, a specific body posture, lower neurological activity, higher arousal thresholds, and homeostatic regulation (Siegel, 2008, 2009). The ability to withstand sleep deprivation depends on species-related natural sleep characteristics like duration and quality (Orzeł-Gryglewska, 2010). These characteristics are often informed by life history traits; for example, large ungulate herbivores have a short, shallow and intermittent sleep, while predators usually sleep long and deeply (Orzeł-Gryglewska, 2010). Sleep-restricted animals typically show negative physiological responses and an increase in circulating levels of stress hormones (Nollet *et al.*, 2020). For instance, mice and rodents experience higher oxidative stress under sleep deprivation (Villafuerte *et al.*, 2015). Various behaviour patterns are also significantly impaired when sleep is restricted, notably decreased alertness (Dinges *et al.*, 1997), neurocognitive functioning (Lowe *et al.*, 2017), learning and memory (Gibson *et al.*, 2010; Karatsoreos *et al.*, 2011). For example, rats that initially showed a strong preference for a socially demonstrated food struggled to recall it after 24 hours of sleep deprivation (Wooden *et al.*, 2014). Altered decision-making has also been associated with sleep deprivation - sleep deprived humans show an increased tendency to abandon rules and adopt a more fluid and exploratory approach to the environment, regardless of the optimality of the behaviour to solve the task (Glass *et al.*, 2011). The presence of light and a sleep restricted state are both likely to affect individuals' presumptions about risk, the first by modifying the environmental context and the second by affecting decision-making processes.

Bats (Chiroptera) are a promising taxon to study the effects of stress on social learning propensities since they are known to be highly sensitive to the effects of environmental change (Jones *et al.*, 2009; Meyer *et al.*, 2016; Struebig *et al.*, 2011) and to routinely learn about novel foods from others (Patriquin & Ratcliffe, 2023; Wright, 2016). Artificial light at night elicits roost abandonment, spatial avoidance and reduces reproductive and foraging success in many bats and can be considered a major stressor to most species (Khan *et al.*, 2020; Russo *et al.*, 2017; Stone *et al.*, 2015). We evaluated the influence of light on social information use in *Carollia perspicillata* (Seba's short-tailed bat), a frugivorous bat whose response to light appears consistently negative, showing a distinct reduction in foraging activity (Esbérard, 2007), increase in day roosting (Fleming & Heithaus, 1986) and shorter distance moved to forage (Heithaus & Fleming, 1978) when exposed to light, most likely due to the higher predation risk such conditions entail (Fenton *et al.*, 1977). Bats of the same genus (*Carollia sowelli*) showed strong responses to ALAN and harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour streetlight than in a dark compartment. Free-ranging *C. sowelli* also neglected to feed on ripe fruits that were experimentally exposed to light (Lewanzik & Voigt, 2014). Little is known about sleep in bats, let alone the possible deleterious effects of sleep deprivation. Previously thought to be "extreme sleepers" (Siegel, 2005), estimated sleep times now suggest considerable interspecific variation partially attributed to size and feeding behaviours (Harding *et al.*, 2022). Sleep quality is thought to be affected by risk perception in bats, with vigilance levels increasing significantly for individuals sleeping at the edge of a roosting colony (Klose *et al.*, 2009). While the effects of sleep loss on alertness (Dinges *et al.*, 1997) and the ability to acquire new information (Hairston *et al.*, 2005) have been well-documented in other animals and highlight its potential influence on social learning, these impacts have yet to be investigated in bats. We chose to study the intersection of sleep restriction and social learning in the Jamaican fruit bat (*Artibeus jamaicensis*), a highly social medium-sized bat and one of the most abundant phyllostomids in the Neotropics (Ortega & Castro-Arellano, 2001).

Here, we examined whether two expected stressors, artificial light and sleep deprivation affected social information use and foraging behaviour in a similar way in two different frugivorous bats. We assessed social learning by providing bats with a choice between a socially demonstrated food and a novel food in a lit or dark environment (Experiment 1) and in sleep deprived or rested bats (Experiment 3). In Experiment 1, demonstration was prior to the expected stressor, while in Experiment 3 demonstration and test were both under the expected stressor. We predicted that the foraging behaviour of subjects under stress - light or sleep restriction - would be altered by those stressors. Previous work has shown that bats exposed to an odour cue from the breath of a conspecific will subsequently prefer that 'demonstrated' flavour when it is offered against an undemonstrated choice, an example of social learning (O'Mara *et al.*, 2014; Ratcliffe & ter Hofstede, 2005). If this was the case, under the costly information hypothesis we anticipated bats would prefer to feed on the social choice. Our results were inconsistent with these predictions, with bats not showing evidence for social learning and not foraging differently under either stressor. Following the unexpectedly weak response observed to the light stimulus in Experiment 1, we set up a repeated measures experiment to assess individuals' foraging behaviour in different light conditions (Experiment 2). We offered bats the chance to feed under white light simulating street lighting, green light simulating moonlight, and dark conditions. We predicted that subjects would forage more readily in naturally dark conditions than in both light conditions if light acted as an effective stressor in this scenario. Once again, we did not find bats foraging behaviour to be significantly changed by the light stimuli.

General methods

We investigated whether frugivorous bats could learn through direct interaction and odour cues to recognize and favour a socially demonstrated flavour. All bats tested were caught by mist-netting or hand netting around Gamboa, Panama. Once the desired species were identified, we sexed them, weighed them, measured their forearms and marked them by hair trimming to allow individual differentiation. Both experiments studying social learning (Experiment 1 and Experiment 3) used the same method, based on Ratcliffe and ter Hofstede (2005) and O'Mara and *al.* (2014). Demonstrator bats were fed approximately 1.5mL of a sugar solution flavoured with novel odours and subsequently left to feed on bananas for an hour. After the demonstrator fed, an individual observer was introduced, and the bats were left to interact. The demonstrator mimics a bat that has returned to the roost after having successfully consumed a novel food. After 30 min, the demonstrator was removed, and the observer was offered a choice for 30 min between dishes placed 30 cm apart that contained 15 g of bananas flavoured with the demonstrator's or an undemonstrated flavour. The dishes were then removed, and the bat was left to rest for an hour. In Experiment 1, bats were either tested in lit or dark conditions to ascertain the influence of light on social learning and foraging behaviour. To assess choice consistency, the same food choice was offered again in the same configuration or in switched locations 1 h after the first trial for a second 30 min test period. In Experiment 3, bats were sleep deprived for 24 h prior to testing or well-rested to evaluate the impact of sleep deprivation on social learning and foraging behaviour. They were only tested once. We filmed the tests and determined first flavour choice, latency to first feeding bout and time spent feeding at each flavour. In Experiment 2, we tested individuals in three different light conditions (green, white, dark) in a larger testing arena to evaluate whether bats forage differently under light in a more naturalistic set up and without social learning interventions. The experiments were video recorded with a Sony Handycam DCR-SR45 on NightShot mode.

From the videos we noted first flavour choice, latency to feed and time spent feeding at each flavour. As bats were held in an outdoor flight cage, they were kept at natural ambient temperature and humidity levels. After experiments were concluded, the animals were released at their capture sites.

Ethical note

All animal-related procedures were approved by the Panama Ministry of the Environment (MiAmbiente permit numbers: SE/AP-13-18 and ARG-278-2022) and the Smithsonian Tropical Research Institute Animal Care and Use Committee (IACUC numbers: 2017-0102-2020 and 2020-0113-2023).

Experiment 1: Social learning and foraging under bright light

Materials and methods

We tested individuals in dark and bright light conditions to evaluate if social information use and foraging behaviour changed under light stimulus. Demonstration was conducted in the dark for all individuals tested.

Subjects

Carollia perspicillata were caught by mist-netting or hand netting at six different locations around Gamboa, Panama. We tested 67 subjects (35 males and 32 females) and used 29 demonstrators in this first experiment. Subjects were housed with their demonstrator bats in mesh cages (60 cm x 37.5 cm x 35.5 cm) to build familiarity over the following day and fed banana chunks on the first night of capture to habituate them to the test diet. We used males as demonstrator bats and both sexes as observers. After this experiment was concluded, seven bats were re-used in Experiment 2 (see Experiment 2, below) and the rest of the animals were released at their capture sites.

Sugar water preparation and choice test

The sugar water solution that flavoured the bananas for the experiments was prepared based on very similar protocols (O'Mara *et al.*, 2014; Ratcliffe & ter Hofstede, 2005) using 20 drops of candy flavour concentrate (LorAnn Oils) to 20g of a 30% (w/w) sugar solution. Using candy flavours to ascertain social information use has been done previously with *Carollia perspicillata* (Ratcliffe & ter Hofstede, 2005) and *Uroderma bilobatum* (O'Mara *et al.*, 2014). To ensure that the bats had no preexisting bias for the experimental flavours, we first conducted pilot trials with nonexperimental bats (n = 4), offering pairwise choices of banana coated with the novel flavours and quantifying choice, time to consumption and amount consumed. One flavour (coffee) was found to be attractive, and two flavours (clove and almond) were found to be distasteful to these bats, but we detected no difference in the attractiveness of the remaining two (ginger and sassafras) that were used in the experiment. Considering all bats in this preliminary bias check only picked a single flavour each test, we assessed preference for a flavour by calculating 'win rate' - how often a flavour was chosen out of all pairs it appeared in. Individuals exposed to these flavoured solutions were kept isolated from naïve bats, and all bats were used only once.

Behaviour testing and scoring

We tested if artificial light influenced the likelihood that an inexperienced individual will eat the same food as a group member following the general methods described above. Half the observers were tested in artificial light (n = 28) and half in the dark (n = 26). Seven bats only made a food choice for one of the two trials and cannot be used to assess individual consistency. We conducted experiments between 7 p.m. and 3 a.m. with supplemental infrared illumination (Wisecomm IR045 LED) with animals that had not been fed since the previous night. An LED light bulb was affixed to the middle of the flight room and turned on when bats were tested in the light. We checked light intensity with a Multi LED Light Meter (HT Instruments, HT309) set up at food level before each test.

We tried to measure the amount of fruit consumed but found the metric to be unusable due to faulty scales. First flavour choice was chosen as the primary metric to evaluate social learning, as 86% of tests (115/134) showed bats only feeding from one feeder and not exploring both.

Bats tested over the first field season (July to August 2022) (n = 21) and the beginning of the second (May to June 2023) (n = 20) were given both tests with the flavours placed on the same side of the cage. We noticed a very high site fidelity once the footage was reviewed which hinted at location bias across trials. When bats are rewarded to return to the same location instead of rewarded for fidelity to a specific odour, they are much more likely to return to the feeders they were trained to recognize by position (Dixon *et al.*, 2023). To verify if the bats in our social learning experiment consistently chose the same flavour because of its odour or its location, we decided to change what side the flavour was presented on between the first and second test for all subsequent bats tested (n = 26) (July to August 2023). Every other design element remained the same.

Statistical analyses were conducted in R version 4.4.1 (R Core Team 2024). Prior to statistical analyses, assumptions of normality and homoscedasticity were verified to ensure the appropriate tests were run. To determine if the proportion of bats that made a social choice differed significantly from chance we used binomial tests. We used a non-parametric Wilcoxon rank-sum test to compare foraging behaviour between stimulus groups (light and dark). To test if stimulus influenced the number of bats that made a food choice and on the number of bats that made the social choice, we used Chi-square tests of independence.

All data and source code for analyses are permanently archived on Borealis at https://doi.org/10.5683/SP3/KWSCDG.

Results and Discussion

Light and foraging behaviour

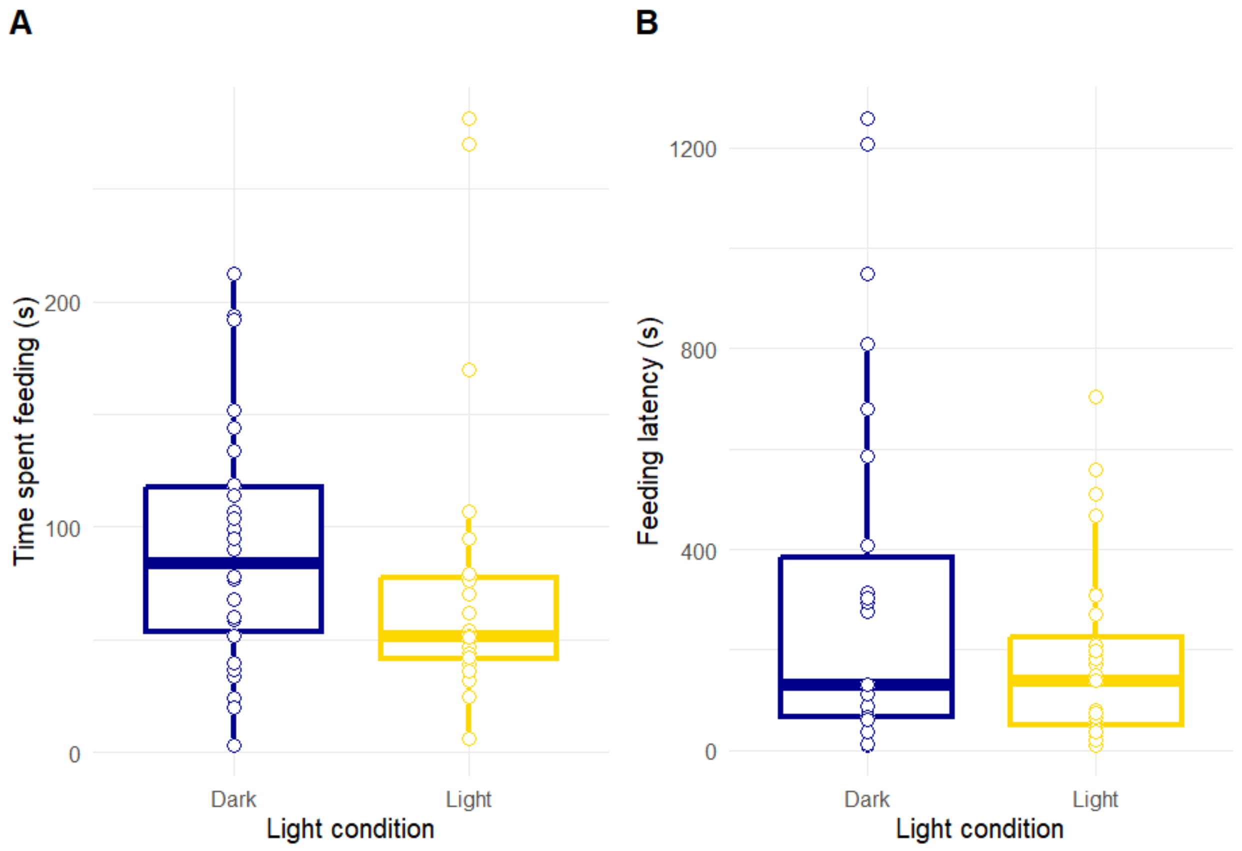

Figure 2.1. Light stimulus had no significant effect on foraging behaviour. *Boxplots' horizontal lines show group medians with whiskers indicating variability in upper and lower quartiles. Points show individuals.* ***A)*** *Bats exposed to light (yellow) (n=28) spend a similar amount of time feeding (s) as bats in the dark (blue) (n=26)* ***B)*** *Bats exposed to light show a similar latency before their first feeding bout (s) as bats tested in the dark. Bats that did not forage are not represented on the graph to aid visualization but are included in the analysis.*

The two foraging measures (time spent feeding and feeding latency) were not significantly different between light treatments (Figure 1; A) W = 618.5, p = 0.47, B) W = 680.5, p = 0.13, respectively). Bats that did not forage (n_{light} = 5, n_{dark} = 8) were included in the analysis with their time spent feeding set at zero and their feeding latency set to the maximum possible latency (1800 seconds). We found no significant difference in the number of bats that did not make a foraging attempt between the dark and light stimuli ($\chi 2(1) = 0.31$, p = 0.58).

Light and social learning

Table 2.1. Light condition had no significant effect on demonstrated food choice*. The table presents the number of bats in the dark and light treatments whose first food approached was the undemonstrated or demonstrated flavour and number of bats that did not feed under the light stimulus and in the dark during the first test of the night.*

Food choice	**Light condition**	
	Dark (n=34)	Light (n=33)
Undemonstrated	15	11
Demonstrated	11	17
No choice	8	5

Amongst the bats that foraged during testing, we did not detect a significant difference in food choice between light conditions ($\chi 2(1) = 1.17$, $p = 0.28$). While marginally more bats under the light stimuli preferred the social choice and a marginally more bats in the dark preferred the undemonstrated choice (Table 1), we found no evidence for social learning in both conditions combined (Binomial test: 28 demonstrated choices out of 54 foraging trials, $p = 0.89$) or in the two conditions analysed separately (Binomial tests: light: 17 demonstrated choices out of 28, $p = 0.34$; dark: 11 demonstrated choices out of 26, $p = 0.55$). These results suggest that the bats have not socially learnt a flavour preference, regardless of the light stimulus.

Flavour location and choice

Table 2.2. Bats were more likely to make the same food choice twice if it remained in the same location than if the food picked first is relocated. *Table presents the number of bats that picked the same food choice for both consecutive tests or that switched their preference if the food choice was moved between tests or not. A total of 15 bats tested were removed from analysis (location changed: 6, location same: 9) as they only made a single food choice or no food choice at all, which makes choice consistency across tests impossible to assess. The asterisk represents the significant difference between bats that moved and stayed stationary when the location of the food was unchanged between tests.*

Food choice	**Flavour location**	
	Changed between tests (n=20)	Stays the same between tests (n=32)
Same both tests	11	26*
Different each test	9	6
Single choice or no choice	6	9

Bats were more likely to make the same food choice across both trials if the location of the food was the same ($\chi2(1) = 4.13$, $p = 0.04$). More than 80% (26/32) of individuals tested consistently picked the same flavour twice when that flavour was placed in the same location both times. Once that flavour was moved, the number of bats making a consistent flavour choice dropped to 55% (11/20), which is not significantly different from chance and does not support the idea of flavour learning and recognition being dissociable from location learning.

Experiment 2: Simulated moonlight, artificial light and foraging behaviour

The light stimulus in the first experiment did not appear to affect the foraging behaviour of the bats tested. To identify whether different light types and experimental setup might yield different foraging responses, we executed this follow-up experiment.

Materials and methods

Subjects

Bats were caught mist-netting or hand netting at six different locations around Gamboa, Panama. We tested 10 bats (5 males, 5 females), 7 of which were used in the previous experiment. All re-used bats were either demonstrators or only exposed to the dark to ensure there was no prior exposure to the light stimulus.

Behaviour testing and scoring

We introduced individual bats into a flight cage (4.8 m x 4.8 m x 2.5 m), with a feeding platform set up in the centre. We placed a plate of 15g of banana chunks on the platform and let the bat feed for 20 minutes, after which it was caught with a hand net and put back in its housing cage. Subjects were tested three nights in a row, once in the dark, once in the same white LED light present in Experiment 1 and once in green light meant to emulate moonlight. Light intensity was measured with a Multi LED Light Meter (HT Instruments, HT309) set up at food level before each test and set to 45 lux in white light and 1.5 lux in green light. The order in which bats were tested across those treatments was balanced and randomised. In addition to first flavour choice, latency to feed and time spent feeding at each flavour, feeding plates were weighed before and after each test to measure the amount of banana consumed.

To assess if different light types led to changed foraging behaviour across repeated measures, we conducted a repeated measures ANOVA using the 'car' library (Fox & Weiberg, 2019) (weight consumed) and its non-parametric equivalent Friedman test for the behaviour metric whose distributions did not meet parametric assumptions (feeding latency and time spent feeding).

Results and Discussion

Light condition and foraging

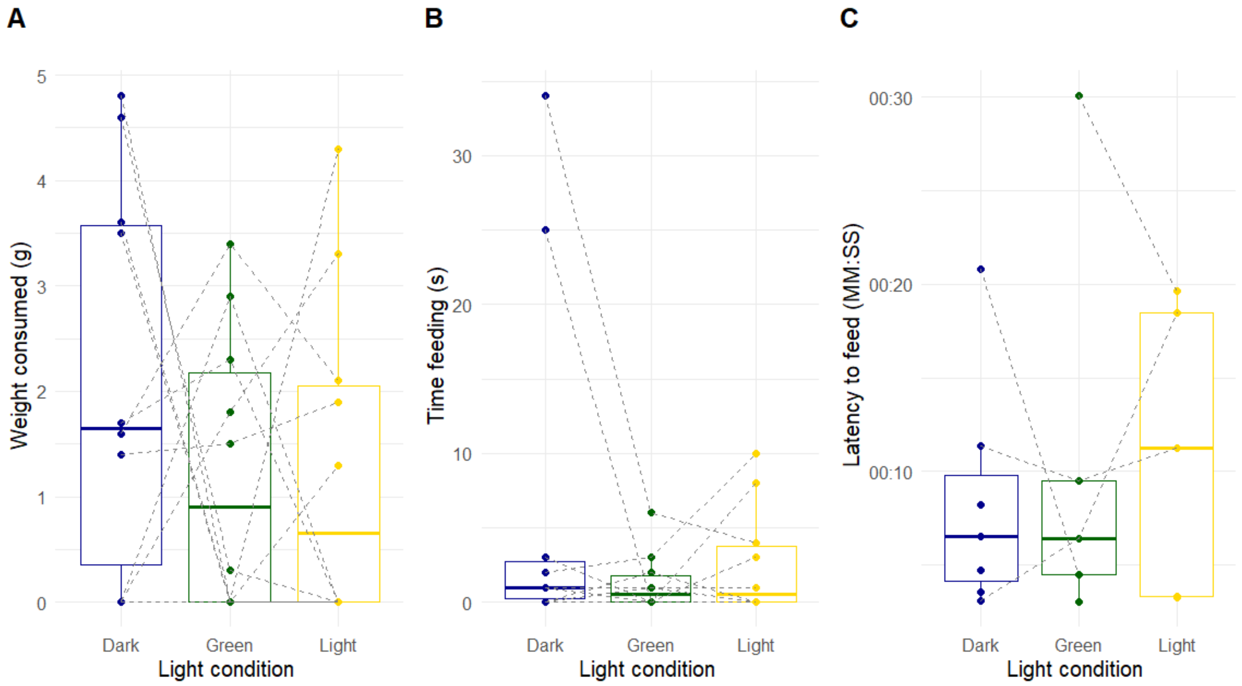

Figure 2.2. Light types do not significantly influence foraging behaviour in a repeated measures experiment. *Boxplots' horizontal lines show group medians with whiskers indicating variability in upper and lower quartiles. Points show individuals tested and dashed lines connect individuals.* ***A)*** *Bats exposed to white and green light ate similar weight of banana (g) as bats in the dark.* ***B)*** *Bats exposed to white and green light spent a similar amount of time feeding (s) as bats in the dark.* ***C)*** *Bats exposed to white and green light show a similar latency before their first feeding bout (s) as bats tested in the dark. Bats that*

did not forage are not represented on the graph as they complicated visualization but are included in the analysis.

The three foraging metrics (weight of food eaten, time spent feeding and feeding latency) were not significantly different between light treatments (Figure 1; A) ANOVA $F(2,18) = 0.799$, p = 0.465, B) $\chi 2(2,10) = 0.77$, p = 0.68 (Friedman), C) $\chi 2(2,10) = 0.19$, p = 0.91 (Friedman)). This suggests that the presence of white artificial light and of simulated moonlight did not affect foraging behaviour in *C. perspicillata*. Bats that did not forage (n = 2) in any condition were included in the analysis with their time spent feeding and weight consumed set at zero and their feeding latency set to the maximum possible latency (1800 seconds). Only two bats made foraging attempts for all three light conditions, the rest fed once or twice. There was no indication that light treatment affected the likelihood of a foraging attempt.

Experiment 3: Sleep deprivation and foraging behaviour

Materials and methods

Overview

We investigated whether frugivorous bats could learn through direct interaction and odour cues to recognize and favour a social flavour. We tested sleep restricted and non sleep restricted individuals to evaluate if social information use and foraging behaviour were affected by sleep restriction. Demonstration was conducted once sleep deprived for the individuals under treatment.

Subjects

Bats were caught by mist-netting or hand-netting at nine different locations around Gamboa, Panama from February through August 2019. We caught a total of 34 adult bats. All bats caught at once were housed together in a large mesh cage to build familiarity over the following day and fed banana chunks on the first night of capture to habituate them to the test diet. When kept for longer than a week, figs, papaya, red apple and occasionally mango were added to their diet to reduce the risk of nutrient deficiencies.

Sugar water preparation and choice test

The bananas in this experiment were flavoured similarly to the bananas in Experiment 1 (see Experiment 1) using 20 drops of ginger or nutmeg LorAnn oils to 20g of a 25% (w/w) sugar-water solution. Ginger and nutmeg were selected as pilot trials with nonexperimental bats (n = 3) showed no preference between the two scents. To evaluate pre-existing bias, we exposed two bats to ginger and one to nutmeg, then offered them both flavours to feed from. There was no difference in weight of banana consumed between the flavours and no impact of pre-exposure. Individuals exposed to these flavoured solutions were kept isolated from naïve bats, and all bats were used only once.

Behaviour testing and scoring

A subset of bats (n = 10) was sleep restricted prior to testing. Sleep restriction ran from 11 a.m. until 5 p.m., during which time a human observer would disturb the bats by gently poking their housing tent at a spot equidistant from all individuals when any individual in the group displayed a sleeping posture or had closed eyes, following sleep criteria established for this species in Heckley and *al*. (2024). They defined sleeping posture as a position in which a bat had wings tucked in, chin tucked up towards the stomach, and eyes fully or partially closed. Each individual was only subject to one day of sleep restriction.

We tested if sleep restriction influenced the likelihood that an inexperienced individual would favour the food eaten by a group member. Bats were tested in a clear plastic-fronted wooden cage (57.2 cm x 37.6 cm x 27 cm), with a mesh top and sides, and cloth backing. Demonstrator bats (n = 10) were removed from their housing cage, fed approximately 2.0 mL of the flavoured sugar solution to ensure consumption, and introduced in the testing cage to feed on bananas for an hour. After feeding, an individual observer (n = 10) was added to the testing cage and the bats were left to interact. This mimics a bat that has returned to the roost after having successfully consumed a novel food. Each demonstrator bat was only used once. After 30 minutes, the demonstrator was removed and the observer was offered a choice for 1 hour between dishes placed 30 cm apart that contained 15 g of bananas with the demonstrator's or a novel flavour.

Results and Discussion

Sleep condition and foraging behaviour

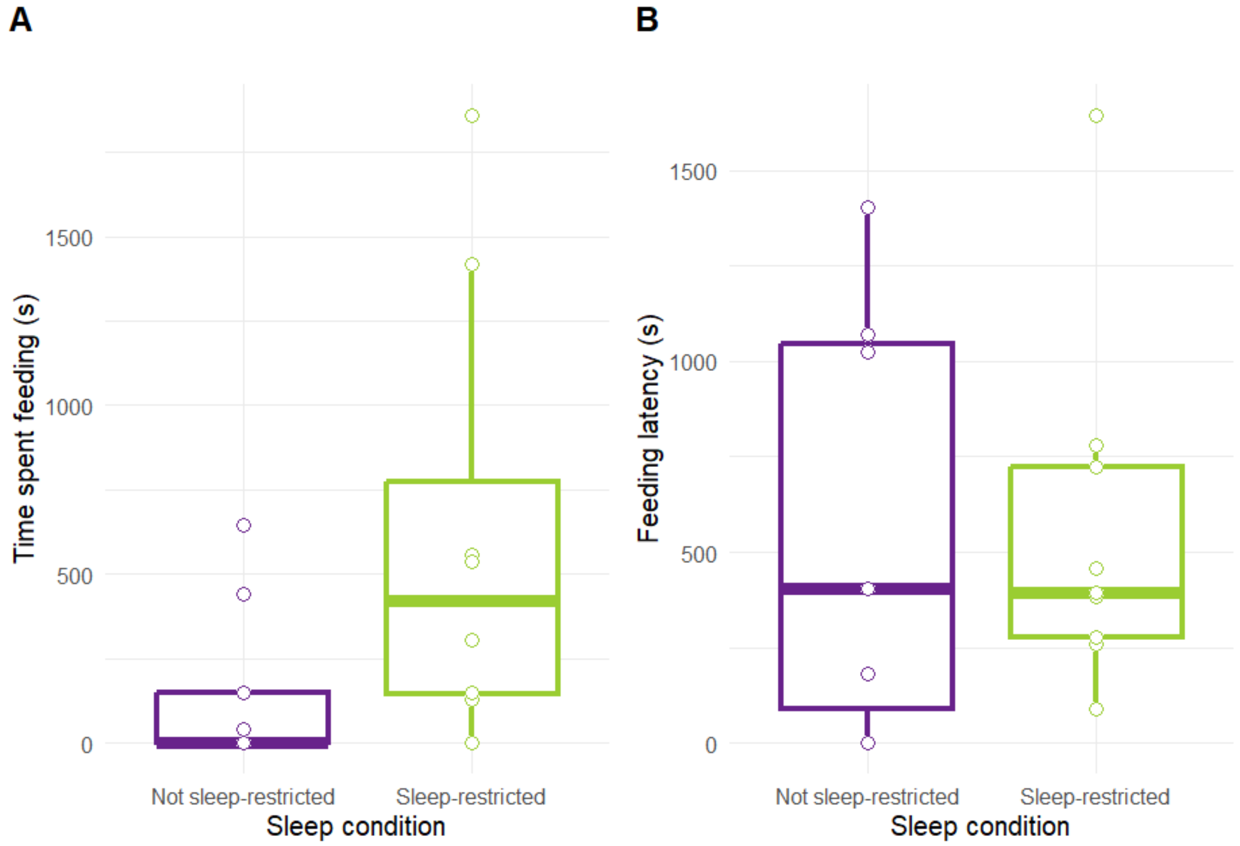

Figure 2.3. Sleep condition had no significant effect on foraging behaviour. *Boxplots' horizontal lines show group medians with whiskers indicating variability in upper and lower quartiles. Points show individuals tested.* ***A)*** *Sleep restricted bats (green) spent a similar amount of time feeding (s) as bats in the dark (purple).* ***B)*** *Sleep restricted bats show a similar latency before their first feeding bout (s) as bats tested in the dark. Bats that did not forage are not represented on the graph as it complicated visual interpretation but are included in the analysis.*

The two foraging measures (time spent feeding and feeding latency) were not significantly different between sleep conditions (Figure 3; A) W = 30, p = 0.12, B) W = 58.5, p = 0.54.). This suggests that sleep deprivation does not affect foraging behaviour in *Artibeus jamaicensis*. Bats that did not forage (n = 5) were included in the analysis with their time spent feeding set at zero and their feeding latency set to the maximum possible latency (1800 seconds).

Sleep condition and social learning

Table 2.3. More rested bats choose the demonstrated food choice, and more sleep restricted bats choose the undemonstrated food choice, but this trend was not significant*. The table indicates the number of rested and sleep restricted bats whose first food approached was the undemonstrated or demonstrated flavour and number of bats that did not feed when rested or sleep restricted.*

Food choice	**Sleep condition**	
	Rested (n=10)	Sleep restricted (n=10)
Undemonstrated	1	6
Demonstrated	5	3
No choice	4	1

We found no significant difference in the number of bats that did not make a foraging attempt between the rested and sleep restricted groups ($\chi 2(1) = 1.07$, $p = 0.30$). Amongst the bats that foraged during testing, we did not detect a significant difference in food choice between sleep conditions ($\chi 2(1) = 1.88$, $p = 0.17$). We found no evidence for social learning in both conditions combined (Binomial test: 8 demonstrated choices out of 15 trials, $p = 1$) or in the two conditions analysed separately (Binomial tests: sleep restricted: 3 demonstrated choices out of 6, $p = 1$; rested: 5 demonstrated choices out of 6, $p = 0.21$). These results suggest that the bats have not socially learnt a flavour preference, regardless of sleep status.

Figure 4 summarises social learning results for Experiment 1 and 3 together, illustrating the lack of evidence for social learning in both studies.

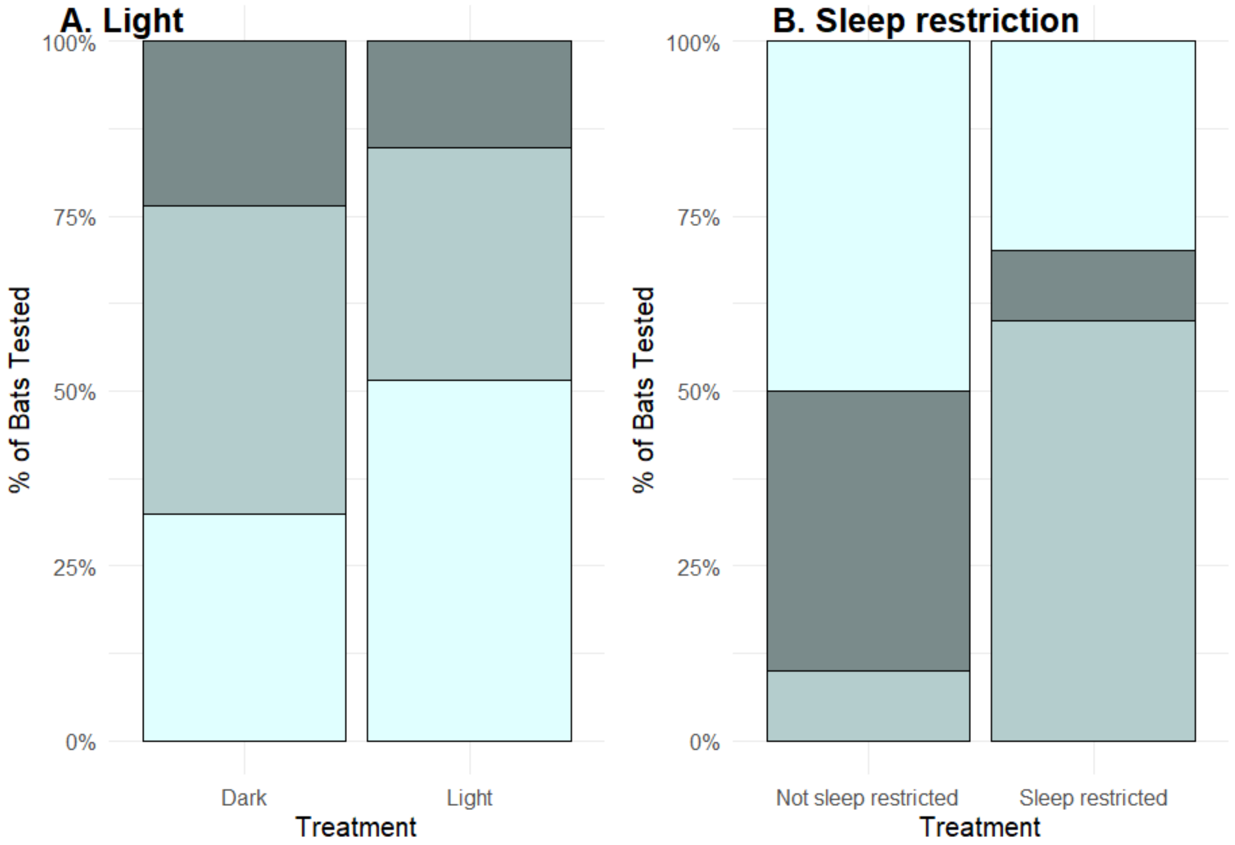

Figure 2.4. Absence of evidence for social learning in both experiments. *Across all bats tested in both social learning experiments (light and sleep restriction), we found no clear evidence that bats preferred demonstrated flavours over undemonstrated ones.* ***A)*** *Percentage of bats tested in the light experiment and* ***B)*** *Percentage of bats tested in the sleep restriction experiment. The proportion of bats that first approached the undemonstrated flavour are shown in middle blue, the ones that approached the demonstrated flavour are in pale blue and the proportion of bats that did not feed for each experiment is shown in dark blue.*

General discussion

We found no evidence in two studies for social learning of a food preference in *C. perspicillata* and *A. jamaicensis*. That is, we detected no influence of social demonstration on foraging choices, both in bats exposed to a stressor (light or sleep deprivation) and in bats not exposed to these stressors. Despite past literature showing aversion to light stimulus in *Carollia*, we found no evidence that foraging behaviour was affected by artificial light at night (ALAN), both in the social learning test (Experiment 1) and the follow-up light treatment test (Experiment 2). Sleep deprivation also did not have a significant effect on foraging behaviour (Experiment 3). Our results were consistent with recent evidence that bats rely more on spatial cues than odour cues to inform foraging decisions (Dixon *et al.*, 2023), as they were much more likely to return to the same location twice whether the odour cue was the same or not than to 'follow' an odour that had moved after a first successful foraging bout.

Social learning in bats is fairly well established (for reviews, see Kohles & Dechmann, 2024; Patriquin & Ratcliffe, 2023; Vernes & Wilkinson, 2020), experimental work showing a wide variety of species from predators (Page & Ryan, 2006), to insect-eaters (Wright *et al.*, 2011) using social information to inform foraging behaviours, roost-finding (Furmankiewicz *et al.*, 2011; Ruczynski *et al.*, 2007) and vocal learning (Boughman, 1998; Knörnschild *et al.*, 2012). For example, *Trachops cirrhosus* famously eavesdrops on mating calls to locate prey and can discriminate what calls indicate safe foraging opportunities (Page & Ryan, 2005). Although they usually ignore cane toad calls, as they are too big to handle and toxic when ingested, they have been shown to learn to associate those calls with safe food once given the chance to observe trained conspecifics respond to them (Page & Ryan, 2006). Through social learning, *T. cirrhosis* can avoid costly mistakes when uncertain about personal information or novel foods (Patriquin & Ratcliffe, 2023). Most of the bat social learning literature is focused on the social transmission of various foraging cues, with bats learning from others when uncertain about where to find food and when learning to identify a food through trial-and-error is costly (Patriquin & Ratcliffe, 2023), but only three studies have investigated social learning with the social transmission of food preference paradigm used here (Christiano, 2024; O'Mara et. *al.*, 2014; Ratcliffe & ter Hofstede, 2005). When given a choice between two novel flavours, *C. perspicillata* (Ratcliffe & ter Hofstede, 2005) and *Uroderma bilobatum* (O'Mara *et al.*, 2014) ate more of one flavoured food if they had previously interacted with a conspecific demonstrator that had eaten food of the same flavour. When uncertain, bats may therefore use cues from conspecifics to identify which local fruits are likely safe to eat. Contrastingly, Christiano (2024) failed to find evidence of social learning in *A. jamaicensis*. The social transmission of food preference (STFP) paradigm is a test of olfactory memory first developed in the 1970's and since then implemented extensively with rats and mice (Clark *et al.*, 2002; Galef & Wigmore, 1983; Valsecchi & Galef, 1989). Following this protocol, observer rats typically prefer whichever food their demonstrator has eaten (see for review Galef, 2012). This protocol has been used to assess the influence of multiple factors such as familiarity (Galef & Whiskin, 2008), dominance status (Awazu & Fujita, 2000) and stress levels (Choleris *et al.*, 2013) on the social transmission of information in rats and mice. Other social, omnivorous and opportunistic foragers such as dwarf hamsters and dogs tested with the STFP paradigm were able to learn flavour preferences from each other and ate significantly more of the food consumed by the demonstrator (Lupfer *et al.*, 2003; Lupfer-Johnson & Ross, 2007). Although STFP has demonstrated social preferences in many studies, some social animals did not present the same result (e.g. spotted hyenas: Kubina, 2014) and social learning performance can be sensitive to early developmental experience (e.g. maternal care: Lindeyer *et al.*, 2013).

The absence of social learning in the current study contributes to the growing evidence that social learning might be species and context-dependent in frugivorous bats. Although our approaches were comparable, specific methodological differences might explain our diverging results from O'Mara *et al.* (2014) and Ratcliffe and ter Hofstede (2005). Ratcliffe and ter Hofstede (2005) used *Carollia perspicillata* from a mixed species colony kept under semi-naturalistic captive conditions at the Biodôme de Montréal (Québec, Canada), while our bats were caught by mist-netting or hand netting in the forest in Gamboa (Panama). Captive animals experience different ontogenetic social and physical environments than free-ranging animals (McCune *et al.*, 2019). In this case, captivity is characterized by milder and more predictable environmental conditions such as an absence of predation risk and high food availability. Social learning has been predicted to reduce the ability of individuals to discover alternative food sources when food sources are unreliable (Sasaki *et al.*, 2016) and the benefits of social spatial information have been shown to increase with environmental stability (Schürch & Grüter, 2014). Experimental work with food-caching chickadees supports this hypothesis, finding the contribution of social learning in novel food discovery significantly lower in less predictable and harsher environments (high elevation) than milder ones (low elevation) (Heinen *et al.*, 2021). Similarly to this, it is possible that free-ranging animals habitually experiencing harsher environments favour less reliance on social learning than captive animals. Captive bats might also be more likely to experience chronic stress through human perturbations or high population densities than free-ranging animals (Widmaier & Kunz, 1993), which might affect social learning tendencies. In mice, the injection of a stress hormone (corticosterone) facilitated the social transmission of food preferences (Choleris *et al.*, 2013). It is possible that captive bats' stress baseline was higher, which could have facilitated social learning. That being said, if stress were an important factor here, we would expect the bats we tested under stressors to show a social learning response, which was not the case.

The captive experiment (Ratcliffe & ter Hofstede, 2005) also guaranteed bats were chosen from the same colony and were likely to have pre-existing experience and familiarity with each other that cannot be verified easily with wild caught animals. O'Mara *et al.* controlled for prior familiarity as well with their wild-caught bats by testing all animals with individuals from their home roosts. It is possible that *Carollia* show a bias to socially learn from familiar individuals, argued to be advantageous as it provides reliable information from the same foraging environment (Barta & Giraldeau, 2001; Beauchamp & Giraldeau, 1996; Laland, 2004). However, previous work in frugivorous bats has shown the opposite, with higher foraging in subjects from food demonstrated by unfamiliar bats than by roostmates, which does not support the familiarity hypothesis (Ramakers *et al.*, 2016). The main other methodological difference between our study and the 2014 O'Mara *et al.* paper is the species of bat they tested, *Uroderma bilobatum*. All three species (*U. bilobatum*, *C. perspicillata* and *A. jamaicensis*) have similar foraging ecology and return to their roosts after foraging, which makes them all susceptible to use roosts as information centres and good models for this experimental setup. However, *U. bilobatum* are significantly smaller than both *C. perspicillata* and *A. jamaicensis* and known for their sensitivity to handling. They are also the only ones to engage in tent-making behaviour by modifying leaves to roost in them (Barbour, 1932; Kunz, 1982). The construction of a tent requires a large time investment and reduces time spent foraging (Rodríguez-Herrera *et al.*, 2011). This trait might naturally encourage these bats to rely on social information more readily as a strategy to reduce time wasted in risky personal investigation when already under shorter time constraints than other species. Our findings suggest that social learning may depend on cues tied to specific prior experiences, a particular context, or associated costs to facilitate the acquisition and application of information (Kendal *et al.*, 2005; van Bergen *et al.*, 2004).

We also did not detect a difference in foraging behaviour between bats tested in our social experiment in the dark and in the light (Experiment 1) as well as in bats tested in dark, green and white light conditions (Experiment 2). Assuming that feeding bats experience significant predation risk at night, we expected them to respond with a drop in activity under bright nocturnal conditions as an antipredator measure if their predators perform better in brighter light (e.g. owls: Kotler *et* *al.*, 1991). Bat predators are presumed to be owls, birds, raptors, snakes and mammals (Gillette & Kimbrough, 1970; Sparks *et al.*, 2000), but little is certain on the extent of predation risk in bats and what factors might enhance it. It is believed that most bat predators are opportunistic and focus on roost-emergence and other contexts when bats can be found in high densities (Mikula *et al.*, 2024). Most fruit-eating bats show moonlight avoidance through altered flight paths, decreased overall activity and later roost emergence, which is recurrently suggested to be caused by heightened perceived predation risk under brighter conditions (Lima & O'Keefe, 2013). Even within this feeding guild, these behaviours are still species and context dependent. For instance, work on the impact of light on *A. jamaicensis* behaviour found urban bats more sensitive to moonlight than rural bats, and counterintuitively rural bats more sensitive to artificial light than urban bats (Sealey *et al.*, 2024). In *C. perspicillata*, moonlight has shown a strong negative effect on activity levels (Esbérard, 2007; Fleming & Heithaus, 1986) and moving distance (Heithaus & Fleming, 1978). However, very few studies have tested the susceptibility of frugivorous bats to artificial light. High illuminance can increase the abundance of insect prey (Davies *et al.*, 2012) which might be advantageous for insectivorous bats, but has no apparent benefits for frugivorous bats. Experiments with both captive and free-flying frugivorous *Carollia sowelli* showed reduced foraging success under brightly lit conditions compared to low lit conditions (Lewanzik & Voigt, 2014). We did not find evidence of light avoidance, measured by time spent feeding and feeding latency, in *C. perspicillata* in this study. Previous work suggests their main response to light stress is active escape behaviour (Lewanzik & Voigt, 2014). Avoiding risky areas is a common coping strategy that minimises environmental risks (Blanchard *et al.*, 2011). The exploratory strategy adopted then represents a trade-off between the benefits (access to a food source) and the potential risks (predation) (Lima, 1985). It is likely that light is a context-dependent stressor and that we did not detect a stress response because bats under illumination could not avoid the stressor, which prevented behavioural adaptation. For example, a study in stressed rats found they stopped avoiding an area previously associated with stress when a refuge was present (Nemati *et al.*, 2013), showing context-dependent flexibility in behaviour. Here, bats were not offered the chance to trade-off safety and foraging - they were forced to be under the light whether they foraged or not, which might have rendered the stressor null. That being said, our follow-up experiment tested bats in an open space that did allow for active avoidance behaviours which were not seen. Moreover, bats are highly mobile and sensitive to handling (Korine *et al.*, 2023). For instance, handling of small flying foxes (*Pteropus hypomelanus*) bats for 15 minutes was associated with elevated steroid levels (Widmaier & Kunz, 1993). As such, it is possible that stress related to light was not detected because baseline stress associated with handling and experimental setup was already high and confounded the effect of treatments.

Bats did not use social information more or forage differently when sleep deprived. Past animal studies have reported that sleep deprivation leads to impaired hippocampal memory and increases anxiety levels (Fernandes-Santos *et al.*, 2012). These changes are explained by the fact that the hippocampus is highly sensitive to the effects of sleep deprivation. For example, rats that reliably showed preference for a socially demonstrated food saw that preference disappear if they were sleep deprived for 24 hours and re-offered the same choice, highlighting the role of sleep in memory consolidation (Wooden *et al.*, 2014). Accordingly, sleep deprivation damages hippocampal-dependent learning and we expected sleep deprived bats to retain social information less. In humans, sleep deprivation has repeatedly shown higher exploration (defined as a willingness to try new strategies) and lower exploitation (reliance on previous knowledge) in foraging tasks, whether that exploration was beneficial or not (Glass *et al.*, 2011). We did not observe a difference between rested and sleep deprived bats, which might imply that sleep deprivation does not affect social learning in this species. However, since the expected basal social learning could not be observed, it is hard to determine why the treatment was not impactful. It is also possible that bats deprived of sleep for longer time periods would have shown a stronger response in learning ability.

Our experimental setup might not have allowed us to detect social learning because of the propensity of our bats to develop location bias when offered with a binary choice. In our first social learning experiment, more than 80% of individuals tested picked the same flavour twice when that flavour was placed in the same location both times. If the flavour picked first was moved, the number of bats making a consistent flavour choice dropped to 55%, which indicates that odour learning and recognition is less important than location recognition to inform foraging success. A recent study comparing the value of spatial, odour and noise cues in the foraging decisions of *A. jamaicensis* found the spatial aspect to be most important (Dixon *et al*., 2023). Similar work with *C. perspicillata* found the same pattern, with bats choosing to eat again at feeders based on proximity to the original location rather than scent or shape (Carter *et al.*, 2010). Other studies delve deeper into why animals might favour location over cues of other sensory modalities (for e.g. see discussion in Dixon *et al.*, 2023). Here, we will mention that when individuals learn locations, it involves an amalgamation of cues that can be perceived with multiple senses (e.g. echolocation, vision, smell) and are supported by many indicators (e.g. egocentric, geometric or landmark cues) (Gibbs *et al.*, 2007). This is likely to make them more salient to individuals in general than cues based on a singular sense. Absolute location may also be the most reliable cue for animals that frequently return to a spatially predictable resource, such as frugivores that return to the same trees to feed each night. It is interesting that we find the same pattern here, despite odour cues being supported as reliable through social information. Although our bats clearly relied on spatial cues most when foraging twice, Ratcliffe and ter Hofstede's work did not see this happen, with bats following odour over spatial cues. Indeed, bats were offered the choice between the demonstrated diet and the undemonstrated one over four consecutive nights. Ratcliffe and ter Hofstede (2005) switched the positions of the diets between days and calculated the intake of the demonstrators' diet as the total amount of food eaten by the end of the experiment. If their bats showed the same location preference over odour cues as our study and the work stated above, they would not have detected social learning by averaging days with differing locations.

Our study aimed to evaluate if social information use would vary under two different assumed stressors, light and sleep deprivation. We did not detect social learning in control conditions, despite following protocols using odour on breath as the social foraging cue that had previously found evidence for social learning (O'Mara *et al.*, 2014; Ramakers *et al.*, 2016; Ratcliffe & ter Hofstede, 2005). This made it difficult to evaluate the relevance of the applied stressors on behaviour, although our results suggest light and sleep deprivation might not have an impact in foraging behaviour. Despite prior work suggesting light and sleep deprivation would likely be significant stressors, the lack of response observed here indicates they might not operate as expected. Considering we only assessed this through behavioural responses, if this experiment were to be repeated it would be especially interesting to monitor bats' corticosteroid levels to assess physiological responses to our "stressors". Furthermore, our results indicate that social learning may be less consistently employed than frequently assumed. Instead, the expression of social learning seems dependent on multiple factors, for example requiring a specific combination of cues and experience to lead to the acquisition and use of information. Knowing that spatial cues are particularly salient in food choice in bats, we suggest future iterations of this experiment develop methods to test odour preferences independently from location. This raises the question of result generalizability and supports the implementation of measures like the STRANGE framework to highlight possible biases in studies that might limit reproducibility (Webster & Rutz, 2020).

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Linking statement to Chapter 3

In Chapter 2, I explored how artificial light and sleep deprivation influence the foraging behaviour of frugivorous bats. I demonstrated that the species I tested did not respond to artificial light or sleep deprivation, adding to the body of evidence of species-specific sensitivities to stressors. Having investigated how artificial light affects the behaviour of nocturnal animals, in Chapter 3, I turned to a diurnal aquatic species, the Trinidadian guppy, to examine how artificial light influences foraging behaviour and space use. Chapter 3 investigates whether guppies avoid illuminated areas, the potential trade-offs between predation risk and foraging in illuminated environments, and the broader implications of artificial light on prey behaviour and predator-prey dynamics.

Chapter 3: Foraging under artificial light in Trinidadian guppies (*Poecilia reticulata*)

Dufour, L. & Reader, S.M.

Abstract

Artificial light is an increasingly pervasive environmental stressor that can significantly alter animal behaviour. In this study, we investigated how artificial light intensity influences the foraging behaviour of guppies (*Poecilia reticulata*). When presented with a choice between brightly lit and dimly lit zones, guppies were slower to enter the brightly lit area, with the majority preferring the dimly lit zone. These findings suggest that even moderate levels of artificial light can elicit avoidance behaviour, likely driven by a higher perceived predation risk under increased visibility. Our results align with previous research across taxa, demonstrating that light intensity affects foraging decisions in species ranging from invertebrates to mammals. Despite theoretical expectations that male guppies would show stronger antipredator responses due to their bright coloration, we found no significant sex-based differences in foraging behaviour under varying light conditions. This highlights the complex trade-offs between predation risk and the energetic demands of foraging. Furthermore, while light avoidance may serve as an anti-predator strategy, guppies entered well-lit zones occasionally, suggesting trade-off with foraging and exploratory motivation. Our study emphasizes the ecological impact of artificial lighting, suggesting that even mild artificial illuminance can disrupt natural behaviours. These findings underscore the need for further research into how anthropogenic light affects prey populations across different environmental contexts.

Introduction

Natural biotic and abiotic cues essential to vital aspects of animal behaviour such as foraging, reproduction and predator avoidance can be altered by anthropogenic perturbations and lead to maladaptive behaviour patterns. Shifts in natural light conditions due to human activities have received increasing recent attention from the scientific communities as they represent a significant threat for both terrestrial and marine ecosystems (Davies & Smyth, 2018; Gaston *et al.*, 2013; Hölker *et al.*, 2010; Sanders & Gaston, 2018). For instance, coastal developments, fishing vessels and oil platforms all contribute to the alteration of visual cues used by marine animals by adding artificial light to the underwater environment (Nagelkerken *et al.*, 2019). This can directly modify the foraging actions of exposed individuals and enhance mortality rates by increasing visibility to nocturnal predators (Davies *et al.*, 2014). While some natural impacts on the visual environment such as turbidity (suspended sediments), light spectra and artificial light at night (ALAN) are relatively well studied (e.g. Fox *et al.*, 2024; Kranz *et al.*, 2018; Marangoni *et al.*, 2022; Nuñez *et al.*, 2021; Sanders *et al.*, 2021; Swanbrow, Becker & Gabor, 2012; Utne-Palm, 2002; Webster *et al.*, 2007), less well known is the impact of artificial light on foraging behaviour during daytime.

Low light limits the ability of animals to gather visual information and has been shown to affect habitat use and foraging in multiple systems. Both prey and predators that use visual cues to forage successfully are likely to benefit from higher light levels to find food sources, but prey animals might have to balance this advantage with an increase in vigilance behaviours due to increased predation risk (Cerri, 1983). For instance, house finches (Fernández-Juricic & Tran, 2007) and bats (Lewanzik & Voigt, 2014) tested under bright light reduced their number of foraging attempts. Deer studied throughout the day showed different choices in habitat use as light levels changed, which suggests their visual perception drives their movement behaviours and decision-making (Newman *et al.*, 2023). When investigated, the effect of light is often directly connected to photoperiod patterns and the importance of activity timing; prey are diurnal or nocturnal and can benefit by reducing their activity when their predators are awake (Lang *et al.*, 2006). Because light levels are partially responsible for the regulation of photoperiodic activities (Kumar & Rani, 1999), it is often difficult to tease their roles apart. When exposed to artificial light at night or moonlight, many nocturnal species from all taxa show lower foraging rates often associated to heightened predation risk (e.g. nocturnal gerbils: Kotler *et al.*, 1994; inshore mollusc: Manríquez *et al.*, 2021;

Leach's Storm-petrel: Miles *et al.*, 2013; bats: Lewanzik & Voigt, 2014; etc.). Prey's ability to avoid visual predators and visual predators' ability to detect prey depend on the preys' capacity to hide and the predators' aptness to distinguish the prey against intricate backgrounds of varied shapes, colours and patterns (Troscianko *et al.*, 2009). Changes in illuminance can affect these skills by altering colour perception and contrast sensitivity, thus making individuals more or less noticeable (Endler, 1993; Endler & Thery, 1996). This is most obvious in polymorphic species; for example, in polymorphic raptors, dark-morphs showed decreased foraging in brighter light levels and a preference for more enclosed habitats that was not observed in light-morphs, which suggests that individual detectability under different light conditions is key to the maintenance of those morphs (Tate & Amar, 2017). In general, behavioural changes associated with light levels are often thought to be adaptive responses to perceived heightened predation risk. However, this hypothesis relies heavily on predators using sight-focused hunting strategies, which is not always the case and must be considered when discussing preys' perception of predation risk under light.

Amongst aquatic animals, cephalopods and vertebrates have eyes with a lens that can focus an image on the retina, which allows them to gather information about the light environment such as intensity, temporal change and spatial distribution (Cronin *et al.*, 1988). Visibility underwater is affected by target size, transparency, contrast and light attenuation (Johnsen, 2014). Direct artificial light has been shown to increase the abundance of large predatory fish and small shoaling fish in estuary systems, which could lead to top-down regulation of fish populations by concentrating prey and improving visual foraging performance in predators (Becker *et al.*, 2013). That said, phototaxis - the movement of an organism in response to light - varies across species, with some attracted and others repulsed by the presence of light, which influences the relationship described above across different predator-prey systems. Prey might also factor in light intensity and visibility to find optimal foraging zones. For instance, three-spined sticklebacks took longer to locate food and ate less food once they reached it in turbid water than in clear water (Chamberlain & Ioannou, 2019). In fact, responses to changes in visibility might take many forms depending on individual physiological and ontogenic qualities. Notably, turbidity can have positive or negative effects on prey detection depending on several factors (Abrahams & Kattenfeld, 1997; Ortega *et al.*, 2020; Utne-Palm, 2002) – turbidity can be beneficial and attract individuals in species with short visual fields like larval fish, but detrimental and lead to avoidance in adult piscivore fish with better vision (Utne-Palm, 2002). Individuals might also be able to compensate for lacking visibility by relying more heavily on other cues, such as chemical cues (e.g. damselfish, Leahy *et al.*, 2011), or social cues (e.g. damselfish, Manassa *et al.*, 2013) to detect predators.

Guppies (*Poecilia reticulata*) provide a valuable system for studies of aquatic behaviour (Magurran, 2005), and multiple aspects of their response to light have been examined. Most abundant is the evidence for changes in courtship behaviour following light exposure - males court less (Endler, 1987) and choose sigmoidal displays over sneak copulation under bright light (Chapman *et al.*, 2009), suggesting they compensate for poor visual cues by adjusting mating strategies. Mate choice was also found to vary based on different exposures to the light spectrum - females were more responsive to male courtship and males were less likely to engage in sneak attempts under midday woodland shade light than early morning/late afternoon light and midday forest shade (Gamble *et al.*, 2003). Moreover, a study investigating light variation in natural streams found light intensity and the proportion of ultraviolet light negatively correlated to display rates. Additional laboratory work highlighted the causality of this relationship and showed males displaying more at lower light levels, leaving more time for females to choose mates but reducing their ability to visually distinguish them (Archard *et al.*, 2009). Most of previous work indicates a strong influence of light on mate choice and highlights the propensity of guppies to use visual cues in decision-making. Less is known on the role of vision in behaviours unrelated to mate choice. Individuals exposed to bright artificial light at night (ALAN) for 10 weeks showed an increase in risk-taking behaviour by emerging quicker from a refuge and spending relatively more time in the open area of the testing apparatus (Kurvers *et al.*, 2018). Guppies exposed to light or dark environments for 2 weeks foraged better in the light regardless of their exposure treatment. After 4 weeks, they performed better in the environment they had been maintained in, suggesting they are capable of adapting foraging behaviours to different light conditions given enough time. That being said, foraging remained most successful when olfactory cues were paired with vision, even for the successful dark foragers, indicating preference for visual cues remained unchanged under dark conditions (Kimbell *et al.*, 2019). To our knowledge, no study has looked at the effect of light on foraging behaviour with no preliminary exposure to treatments and not in conflict with their natural photoperiod.

In this study, we aimed to evaluate if a short-term exposure to bright artificial light affected foraging and space use in guppies. To do so, we provided fish with a choice between two feeders located in a bright and a dim environment. We predicted that fish would forage less and spend less time on the bright side of the tank. Our results were consistent with these predictions, with fish showing light avoidance behaviours in foraging and space occupation.

Materials and methods

Overview

We examined whether bright artificial light affected foraging behaviour and habitat use in guppies. We assessed light avoidance and foraging behaviour by comparing subjects' foraging time and latency to feed in dark and light zones.

Subjects and housing tank

We used adult female (n = 17) and male (n = 17) laboratory bred wild-type Trinidadian guppies, gifted by the Rodd Laboratory (University of Toronto, Canada). The fish were descendants of guppies captured from a tributary of the Paria river in Trinidad in 2008, supplemented with guppies from the same location in 2016 (the "Houde" tributary; Trinidad National Grid System: PS 896 886). Their capture site is considered a low-predation locality (Houde, 1997; Li *et al.*, 2022; Magurran, 2005). Subjects had never been used in prior experiments and had no experience with the experimental setup. Subjects were socially housed in groups of four including two fish of each sex in a 9.5 L (40.0 x 26 x 21 cm, water depth 12 cm) tank on a 12L:12D photoperiod. The sides of the housing tanks were blacked out with dark contact paper to ensure the light levels in the tank were dimmed to 75 ± 10 lux to habituate the fish to the light level they would experience during testing. Light level was measured with the light meter of the Photone app (2024 Lightray Innovation GmbH, version 3.5.5) by placing the front facing camera level and centre at water level in the zone of interest. Fish were fed flake food once daily (TetraMin Tropical Flakes, Tetra, Germany) until the start of testing, after which they were only fed during testing to encourage feeding motivation. All tanks were maintained at 25 ± 1 ºC using a submersible aquarium heater and contained a filter, plastic plants, terracotta shelter and gravel substrate.

Testing apparatus

The 60 L experimental tanks (76 x 33 x 31.5 cm) were divided in three equal sections of 25 x 31.5 cm by two opaque corrugated plastic partitions. The three zones will be referred to as 1) starting, 2) dark and 3) light. Two circular feeders (ø = 6 cm) were half submerged at opposite ends of the tank in the dark zone and the light zone. The sides of the tank were blacked out with dark contact paper to control the outside light input. An LED light array (Lumahawk, LMX-LD500AVL, Nadel Enterprises, Canada) was placed over each feeder, 45 cm above the water surface, with one lit up each testing trial. The lit side was randomly chosen for each fish and balanced across all fish. The unlit light provided a control stimulus to ensure responses were to light and not an object above the water. The room lights were lowered until 75 ± 10 lux registered above water level with the light meter app before the LED lights were turned on. The bottom of the tank was covered in white contact paper to help fish detection and tracking in the behaviour coding software. A Raspberry pi camera (Raspberry Pi 4 Model B) was placed 45 cm above the middle of the testing tank to record fish behaviour. Two identical testing tanks were used so multiple fish could be tested and trained simultaneously. Each fish was always tested and trained in the same tank to limit tank influence on the results.

Behaviour testing and scoring

Each fish experienced 1) 8 habituation days, 2) 4 training trials and 3) 1 testing trial. For all three phases, the room lights were lowered until 75 ± 10 lux registered at water level and a pinch of mixed flakes (TetraMin Tropical Flakes, Tetra, Germany) and a preferred food, freeze-dried bloodworm (Blood Worms, Nutrafin, Taiwan) was added to each feeder. Subjects were then introduced to a glass cylinder (ø = 8 cm) set in the middle of the test tank and given 1 minute to habituate. The cylinder was lifted and the subject had 10 minutes to explore the tank and its feeders. In the first 2 days of the 1) habituation phase, the partitions splitting the tank in three zones were resting above water level to allow the fish to explore the tank unimpeded. They were lowered by 2 cm every other subsequent day until they were 8 cm deep, leaving a 5 cm gap for fish to swim through while limiting light diffusion throughout the tank. 2) Once the partitions reached the depth of testing, the fish were recorded for 4 days with no lights turned on to gather control data. In the 3) testing phase, one of the LED light panels above the ends of the tank was lit up to its maximum capacity so the light at water level registered at 2100 ± 200 lux in the “light” zone and 75 ± 10 lux in the “dark” zone. Reeve *et al.* (2014) used light levels ranging from 0.2 lux (to mimic dawn) to 121.9 lux (to imitate midday sun) to assess the influence of light on guppy reproductive behaviours experimentally and showed significant behavioural differences. A study assessing light levels in Trinidadian streams found average light intensities to vary from 1871.2 to 2175.2 µmoles m -2 s -1 across streams with natural vegetation cover, which converts roughly to above 100 000 lux using Thimijan and Heins’ (1983) conversion (Heatherly, 2012). The average light intensity our laboratory-reared fish are exposed to is approximately 500 lux. Thus, our bright light was considerably milder than the natural maximum experienced in the wild but was considerably brighter than the usual laboratory lighting that had been experienced by the fish and higher than other experiments studying the effect of light on guppy behaviour. Brightness was also limited by the maximum capacity of the cameras to pick up on fish movement in both the dark and bright zones despite high contrast. An experimenter recorded the latency to enter and time spent in the dark and light zones and their respective feeders from the recorded video using Ethovision software (Noldus, EthoVision XT, version 11.5.1026).

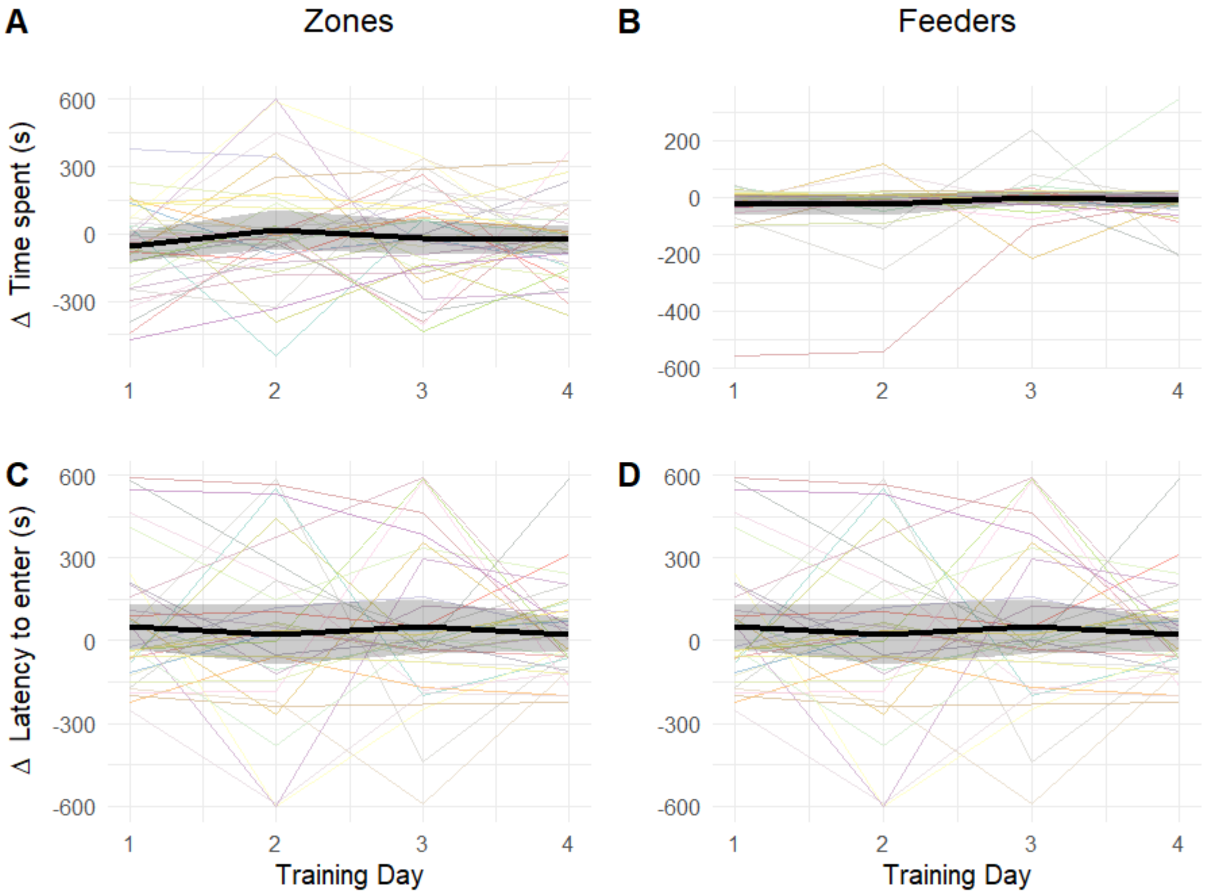

Figure 3.1. Difference in time spent and latency to enter left and right zones over the four training days. *The first row shows the time spent preferentially in the left zone (A) and feeder (B). A positive value indicates more time spent on the left than on the right. The second row shows the difference in latency to enter the left zone (C) and feeder (D) over the right. Each color represents a different individual. The connected dots show the same individual across the training phase. The thick black line shows the average across all individuals, which is centered around zero, and the grey shaded zone its 95% confidence interval. There were no discernable patterns of increased or decreased time spent or latency to enter zones across the training phase. Fish spent 38-45% of their time on the left side, 42-51% of their time on the right side, 3-5% of their time in the left feeder and 5-8% of their time in the right feeder over the 4 training days.*

For many fishes, maximum risk due to predation naturally occurs at the highest light intensities and light intensity can be used as a cue for predator avoidance (Endler, 1987). We predicted that fish would alter their space use and foraging behaviour in bright artificial light as an antipredator response. We calculated our first variable of interest, the amount of time spent preferentially in one zone, by subtracting the time (in seconds) each fish spent foraging in the left zone by the time they spent foraging in the right zone. We did the same for the duration of time spent in the feeder located in the left zone compared to the feeder in the right zone. A positive difference score indicates more time spent in the left zone or feeder, while a negative value signifies more time spent in the right zone or feeder. We used the same method to calculate the latency to enter the left zone over the right zone and the left feeder over the right feeder. We set a maximum latency of 600 seconds for each fish that had not entered a zone by the end of the recording period. A difference latency score of 600 thus indicates the fish never entered the left feeder but entered the right feeder immediately, while -600 means it never entered the right feeder but entered the left feeder immediately. This difference measure allows us to simultaneously visualize both the effects of our manipulation and any side preference.

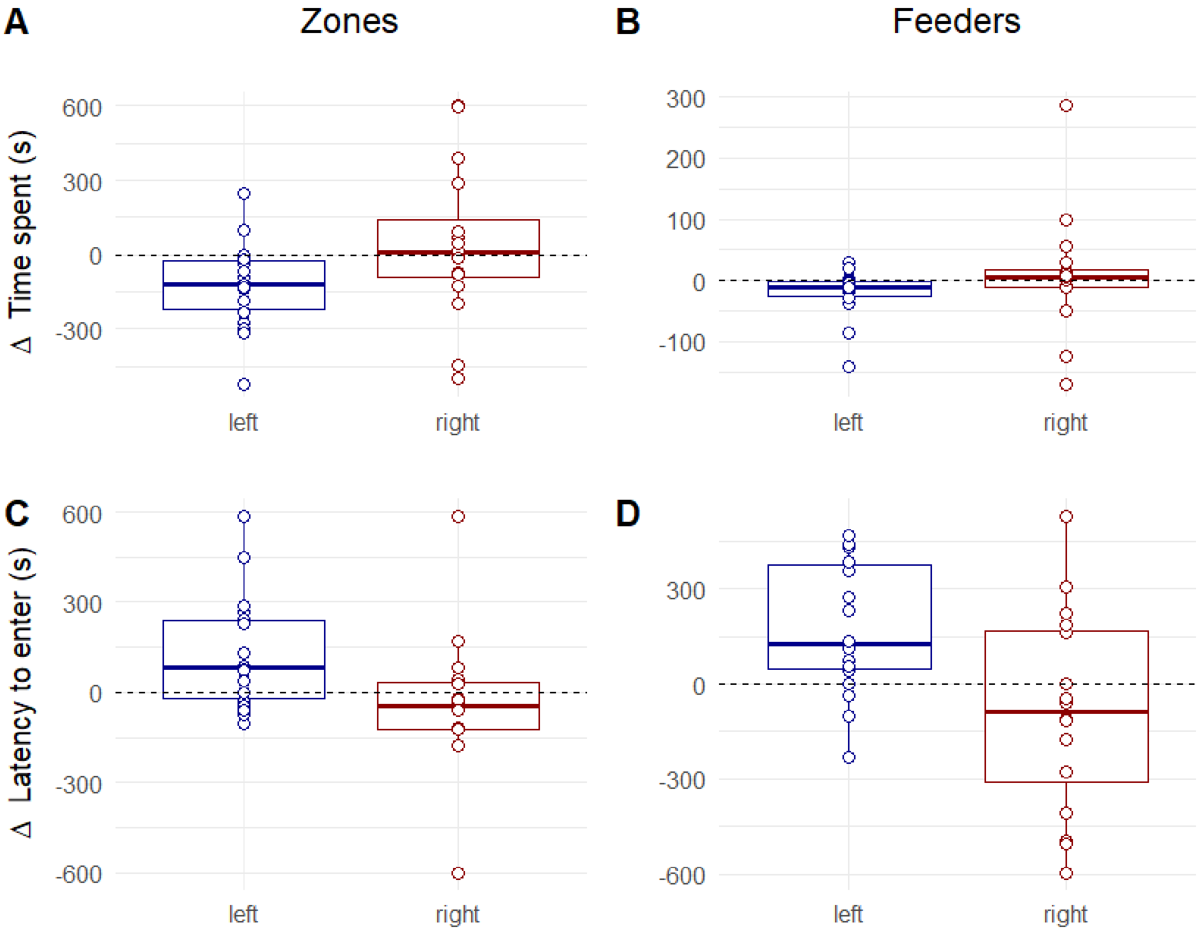

Figure 3.2. Difference score of time spent (s) and latency to enter the left and right zones and feeders*.* *The first row shows the time spent preferentially in the left zone (A) and feeder (B). A positive value indicates more time spent on the left than on the right. The second row shows the difference in latency to enter the left zone (C) and feeder (D) over the right. Blue indicates light was turned on the left side of the tank and red light turned on the right side of the tank. Positive values for blue boxplots and negative values for red boxplots indicate preference for the light side.*

Statistical analyses

All statistical analyses were performed using R version 4.4.1 (R Core Team 2024) and the packages ggplot2 (Wickham, 2016) and lme4 (Bates *et al.*, 2015). We used linear models to compare space use and foraging behaviour between light conditions. Prior to statistical analyses, assumptions of homoscedasticity and normality were verified by plotting model residuals as scale-location and Q-

Q plots, respectively. Assumptions were not met for the analysis of the differences scores of the latency to enter feeders and we thus used the nonparametric Wilcoxon signed rank test instead. We ran individual linear models for each behavioural metric to investigate how space use varied as a factor of light stimulus, sex and body mass. Individuals' weight was measured the day after testing by adding fish to water and calculating the difference on a scale. Since females are larger than males, mass was transformed to the standard deviation of mass from the mean body mass of each sex before analysis to avoid a confound between sex and mass. We included the interaction between sex and light treatment as well as mass and light treatment to the model using the time spent in zones as a response variable. We also included the tank in which the fish were tested as a random variable. We looked at count data as well through Chi-square tests to evaluate the proportion of fish that spent more time on one side of the tank.

All data and source code for analyses are permanently archived on Borealis at https://doi.org/10.5683/SP3/KWSCDG.

Results

Training phase

There were no discernible patterns of increased or decreased time spent or latency to enter zones or feeders over the training phase where both feeders were under identical dim lighting (Figure 3.1). For space use, this indicates no strong pre-existing preference for or against one side of the tank. For feeder use, this shows no change in motivation to feed in the testing apparatus through increased experience that might make it difficult to discern a change in foraging behaviour once light conditions are altered.

Testing phase

Light and space use

Fish took significantly longer to enter a zone when there was light in that zone (LMER: $t_{30} = -2.34$, $p = 0.03$) (Figure 3.2C). They also spent less time in the light zone, but not significantly so (LMER: $t_{28} = 1.62$, $p = 0.1$) (Figure 3.2A). We additionally observed a significant interaction between the time spent on the lit side and the relative size of individuals ($t_{28} = 2.05$, $p = 0.04$), with bigger individuals spending more time in the dark than smaller ones but did not see a relationship between space use and individual sex ($t_{28} = -0.16$, $p = 0.9$). Looking at count data, we see that significantly more fish spent more time in the dark zone ($\chi 2(1) = 5.76$, $p = 0.02$) and took less time to enter the dark zone than the light ($\chi 2(1) = 5.76$, $p = 0.02$).

Light and foraging behaviour

Fish took significantly longer to enter a feeder when it was illuminated (LMER: $t_{30} = -2.34$, $p = 0.03$) (Figure 3.2D). They also generally spent less time feeding in lit feeders, although not significantly so ($W = 87.5$, $p = 0.05$) (Figure 3.2B). Looking at count data, we see that significantly more fish spend more time in dark feeders ($\chi 2(1) = 5.76$, $p = 0.02$) and were faster to enter the dark feeder than the light feeder ($\chi 2(1) = 9.52$, $p = 0.002$).

Discussion

We found that artificial light affected foraging behaviour: when given the choice between a brightly lit and dimly lit feeder, fish were slower to enter the brightly lit zone and feeder, and more fish spent the majority of their time in the dimly lit zone and feeder. Considering our light condition was artificial and did not represent the extremes in light intensity fish would experience in the wild, these results show that relatively mild illuminance in a limited area can change foraging behaviour in guppies. This supports the hypothesis that fish engage in avoidance behaviours in brighter light environments, most likely due to the perceived higher predation risk under such conditions.

Our results are consistent with other work showing that light intensity can affect foraging behaviours across a vast number of species ranging from Australian garden orb-web spiders *Eriophora biapicata* (Willmott *et al.*, 2019) to beach mice *Peromyscus polionotus leucocephalus* (Bird *et al.*, 2004). See for example work on great tits *Parus major L.* (Kacelnik, 1979), Mongolian five-toed jerboas *Allactaga sibirica* (Zhang *et al.*, 2020), house finches *Carpodacus mexicanus* (Fernández-Juricic & Tran, 2007), kangaroo rats *Dipodomys stephensi* (Shier *et al.*, 2020) and southern elephant seals *Mirounga leonina* (Guinet *et al.*, 2014). The same pattern is echoed in many fish systems (e.g. perch *Perca fluviatilis* (Diehl, 1988), Eurasian perch *Perca fluviatilis* (Czarnecka *et al.*, 2019), yellow perch *Perca flavescans* (Richmond *et al.*, 2004), largemouth bass *Micropterus salmoides* (McMahon & Holanov, 1995), reef fishes (Rickel & Genin, 2005) and Atlantic Salmon *Salmo salar* (Fraser & Metcalfe, 1997)). To our knowledge, guppies' direct foraging responses to light intensity, also known as illuminance, has never been studied until now. Research in Trinidad shows that guppies are benthic feeders, opportunistically eating mostly algae, organic debris and benthic invertebrates (Dussault & Kramer, 1981, that forage in the daytime (although note that Fraser et al. (2004) has shown that guppies can continue foraging at nighttime in the absence of nocturnal predators). Light-manipulation experiments also reveal that foraging rate is reduced by the removal of long wavelengths of light (White *et al.*, 2005) and that guppies exposed to low light for four weeks can adapt to feeding in the dark (Kimbell *et al.*, 2019), which indicates changing light conditions can affect foraging behaviour. Importantly, other behaviours to foraging (e.g. courtship: Endler, 1987) have been shown to be reduced in guppies under bright light. Such changes in behavioural activities under high illuminance are most often argued to be a functional response to reduce predation risk but could also be linked to stress or visual impairment.

Many species of diurnal visually hunting predators feed on guppies in Trinidad, the most studied being killifish (*Rivulus hartii*), cichlids (pike cichlids *Crenicichla spp.* and blue acara cichlids *Aequidens pulcher*), and characins (*Astyanax bimaculatus* and *Hemibrycon taeniurus*) (Haskins *et al.,* 1961; Liley & Seghers, 1975; Seghers, 1973). These predators often rely on visual cues enhanced by light to locate prey - for instance, the blue acara cichlid fish attacks and captures more brightly coloured than dull male guppies, likely due to their higher visibility (Godin & McDonough, 2003). Our results suggest that bright artificial light can act as a cue of increased predation risk, leading guppies to steer clear of well-lit environments as an anti-predator response. However, guppies did typically enter the illuminated zone as well as the dark zone. This suggests a certain level of flexibility in response level and vigilance over time. In 1992, Sih presented a similar scenario, where prey hidden inside refugia could not observe predators and could not determine whether predators were absent or whether they were present but undetectable. Remaining hidden indefinitely would lead to missed foraging opportunities, eventually forcing prey to emerge to prevent starvation. The study found that prey were more likely to leave refuges when they were hungrier, had greater body size offering protection, or when more time had passed since a predator was last detected. This could point to a cost-benefit trade-off, where the act of foraging (even in light) outweighs the costs of the perceived risk. Considering the fish in our study were not fed outside of this testing trial, it is possible that food was attractive enough to encourage individuals to spend longer periods of time in lit environments than they would have had they been well-fed. Indeed, prey exposed to high levels of risk tend to resort to bold behavioural tactics (i.e. higher risk taking) to meet daily foraging needs (Brown *et al.*, 2005). For instance, the European sea bass (*Dicentrachus labrax*) shows increased risk-taking tactics following periods of food deprivation (Killen *et al.*, 2012). Likewise, guppies reared under conditions of unpredictable foraging opportunities were consistently bolder than those reared under stable food conditions (Chapman *et al.*, 2010). In our study, relatively little feeding was observed, suggesting that exploration of the zones might have been a motivator alongside foraging.

In addition to the risk of predation, it is possible that fish in our study responded to bright light as a physiological stressor. Artificial lighting can act as a source of stress for many fish species, as it may signal environmental instability or interfere with their sensory systems, leading them to prefer darker areas (Brüning *et al.*, 2015). One of the most common indicators of stress in fish is cortisol, a hormone that plays a key role in energy metabolism and as such can affect foraging. Cortisol levels in fish often follow a circadian rhythm, though the specifics vary by species, season, and environmental factors (Wendelaar Bonga, 1997). For example, in goldfish (*Carassius auratus*), cortisol levels are synchronized with the photoperiod, peaking around the onset of light and reaching their lowest levels at light offset (Noeske & Spieler, 1983). Interestingly, in some salmonid species, cortisol peaks have been observed during the dark phase of the photoperiod and were also associated with feeding times (Laidley & Leatherland, 1988; Pickering & Pottinger, 1983). These findings underscore the complexity of cortisol regulation and its sensitivity to environmental cues such as light exposure (Brüning *et al.*, 2015). In guppies, higher cortisol levels have been linked to individuals with lifetime exposure to predator cues as well as populations with evolutionary history with predators (Fischer *et al.*, 2014). Importantly, in 2015, Kolluru *et al.* tested guppies under high and low light and found no influence of light level on stress hormones. This suggests that light may act as a stressor largely through impacts on perceived predation risk and be particularly impactful when guppies must trade predator avoidance against other behaviour patterns.

Most surprising of all results was perhaps the lack of differences in male and female responses. Much of the literature shows male guppies are more susceptible to predation risk when light conditions increase because of their bright colouring than females (Godin & McDonough, 2003; O'Neill *et al.*, 2019). Knowing this, we would have expected males to show stronger antipredator responses under artificial light to limit predators' visual advantage. Although male guppies do not seem to have different foraging responses to light than females here, they do show changes in courtship behaviour that hints at evident reproductive trade-offs (Archard *et al.*, 2009; Chapman *et al.*, 2009; Gamble *et al.*, 2003). While bright light increases predation risk, the need to forage might override that risk, especially if food is scarce or energy demands are high. Males often invest more energy in activities like courtship and maintaining their bright coloration (Abrahams, 1993; Santostefano *et al.*, 2019). These needs may limit changes in foraging under conditions of increased risk. Furthermore, the males' tendency to reduce conspicuous courtship under bright light may be more specific to reducing movement patterns that attract predators, whereas foraging may involve subtler movements that they perceive as less risky. Males, despite their vulnerability, may not have been able to afford reducing foraging activity to the same extent as they reduce conspicuous behaviours like courtship displays. Indeed, when given the choice between foraging and courtship, male guppies make state-dependent decisions, prioritizing building sufficient energy reserves before investing time and energy in courtship (Abrahams, 1993). Our findings suggest that foraging might not carry the same trade-off with predation risk as courtship does, at least under the conditions of this experiment. Exploring how food availability, prior experience, or the presence of predation cues might alter this behaviour could provide further insights.

Finally, the effectiveness of light avoidance as an anti-predator strategy likely depends on the visual system and foraging behaviour of the specific predator. A study on the foraging efficiency of *Crenicichla* (cichlids) and *Hoplias* (wolf fish) under turbid conditions—where visibility is limited—provides insight into this. The study found that *Crenicichla* were significantly negatively affected by reduced visibility, while *Hoplias* were not. The most likely explanation is that *Hoplias* are nocturnal predators with adaptations for foraging in low-light conditions, while *Crenicichla*, being diurnal predators, lack these adaptations (Ehlman *et al.*, 2020). This suggests that if light avoidance is an anti-predator behaviour, it would likely be most effective against visual diurnal predators, but much less so against nocturnal predators. Our results must also be interpreted cautiously considering the variability in predators and predation-risk of different guppy populations. Indeed, Trinidadian guppies live in rivers that have upstream and downstream sections separated by waterfalls that limit the dispersal of predators (Reznick *et al.*, 2001). This has been associated with downstream populations facing high predation risk but enjoying low competition for food and upstream populations experiencing low predation risk and high competition for food (Magurran, 2005). Most importantly, upstream fish most likely encounter Hart's rivulus (*Rivulus hartii*) and predatory freshwater prawns whereas downstream guppies can expect bigger and more numerous predators such as *Hoplias*, *Crenichichla, Chichlasoma* and *Airus* (Liley & Seghers, 1975; Templeton & Shriner, 2004). If light avoidance is primarily a response to heightened predation risk, the visual sensitivity of the most prevalent predators in a stream will affect the response to light of the prey in that stream. Interestingly, the brightness and the brightness contrast of individuals were found to be more conspicuous to the weaker upstream predator (*Riuulus hartii*) than to larger visual predators (pike cichlid, *Crenicichla alta*) and have a smaller effect where predation is stronger (Endler, 1991). As we only tested a single population, we can only speculate on expected population differences.

This study provides evidence that even in the presence of accessible food, guppies may prioritize avoiding environmental indicators of risk over foraging. This reflects how survival priorities may trump food-seeking under unnatural environmental stressors. This finding also suggests that artificial light might disrupt natural behaviours in guppies and other fish, highlighting how urbanization, artificial lighting, or habitat modification can influence ecological behaviour.

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Chapter 4: General discussion

My thesis investigated the behavioural responses of two distinct neotropical study systems—bats and guppies—to stressors, artificial light and sleep deprivation, to better understand some of the factors that shape foraging behaviour and decision-making. In Chapter 2, I examined whether bats altered their foraging behaviour under artificial light or sleep deprivation and whether they demonstrated social learning of novel foods. Contrary to previous findings, my results showed no evidence for social learning of food preferences in frugivorous bats, nor did they forage differently when they were exposed to light or sleep deprived. This raises questions on how stressful my chosen "stressors" might have been, and how context-dependent social learning might be. Tackling context dependence is a major challenge in ecology and essential for enhancing our understanding and predictive capabilities. Context dependence, also known as contingency, occurs when relationships shift depending on the specific conditions (or context) in which they are observed (for e.g. Chamberlain *et al.*, 2014; Hoare *et al.*, 2004; Miguel *et al.*, 2018; Tanner & Adler, 2009). Amongst other factors, context variability can refer to differences in biotic or abiotic factors, spatial or temporal scales, or observational methods (Catford *et al.*, 2022). In Chapter 3, I explored the effects of artificial light on the foraging behaviour and space use of guppies. I found that guppies exhibited slower entry into illuminated zones and feeders, consistent with broader findings linking artificial light at night (ALAN) to heightened risk perception in most visually guided prey species. Together, these results reveal striking differences in behavioural responses across taxa and highlight the importance of context and species-specific traits in shaping responses to environmental stressors and social learning tendencies.

In this discussion, I explore how these findings contribute to our understanding of behavioural plasticity, with a focus on the challenges of reproducibility and replicability in behavioural research. I consider how species-specific sensory systems and ecological niches influence study outcomes, with particular attention to the context-dependent nature of social learning in bats and sensitivity to light intensity in guppies. I also discuss the broader implications of these results for understanding variability in responses to anthropogenic changes, emphasizing the need to test assumptions about behavioural responses across diverse taxa and conditions. Finally, I highlight the importance of reproducibility as a tool for identifying general patterns in behavioural ecology, offering suggestions for future studies to refine our understanding of how animals respond to environmental anthropogenic stressors in an increasingly human-dominated world.

Reproducibility in behavioural studies across taxa

Reproducibility is a cornerstone of science (see for e.g. Cassey & Blackburn, 2006; National Academies of Sciences, Engineering, and Medicine, 2019; Voelkl *et al.*, 2020) and particularly useful in ecology to uncover general patterns in animal behaviour. However, it remains a challenging goal due to the inherent variability across species and contexts (Voelkl *et al.*, 2020). My thesis highlights these challenges by comparing the responses of bats and guppies to artificial light. While previous studies have shown that *Carollia* alter their foraging behaviours in the presence of light (Esbérard, 2007; Heithaus & Fleming, 1978) and can learn socially in certain contexts (Ratcliffe & ter Hofstede, 2005), my results did not replicate these findings. In contrast, guppies exhibited behavioural changes consistent with broader literature on artificial light at night (ALAN), such as delayed foraging under brighter light conditions (e.g. McMunn *et al.*, 2019; Shier *et al.*, 2020). These contrasting outcomes underscore the complexity of studying behaviour across taxa and highlight how even slight variations in experimental setups or ecological relevance may influence whether findings are replicable.

For bats, several factors may explain the differences between my results and those of earlier studies (see discussion, Chapter 2 for more details). Variability in the individuals tested, light intensities used, time of night or the size of the testing area could all have altered how artificial light influenced foraging. Similarly, the lack of social learning in my experiments could reflect the lower salience of the cues presented or context-specific constraints that limited the expression of this behaviour. It is also important to mention bats are wonderful but difficult animals to work with, most species requiring exhaustive and lengthy sampling to catch enough individuals to study confidently. The other study investigating social learning in *Carollia perspicillata* only tested 8 individuals from a single captive population (Ratcliffe & ter Hofstede, 2005), a sample that may limit the generalizations that can be drawn from the results. In guppies, however, behavioural responses to artificial light were fairly robust and aligned with general findings on risk perception and predator avoidance in visually guided species. This suggests that while some taxa may show more consistent responses to environmental stressors, others exhibit greater variability based on contextual or ecological factors. Overall, model systems with high numbers of studies on a single species investigating multiple aspects of behaviour, such as guppies, lend themselves much better to generalisations and assumptions regarding behavioural responses than diverse and lesser studied taxa like bats. Together, these findings emphasize the need for reproducibility studies to test behavioural plasticity across multiple species and conditions to refine our understanding of when and why behaviours diverge.

Contextual variables and behavioural variability

Context-dependent factors play a significant role in shaping the replicability of behavioural responses. Environmental stressors, such as artificial light, may carry different ecological relevance depending on species' sensory systems, life histories, experience, and habitats. For guppies, a species susceptible to visual predation, artificial light seems to directly shift the balance of foraging with predation risk, resulting in delayed entry into illuminated zones and feeders (see Chapter 3). These behavioural changes are for the most part consistent with ALAN research on fish and other diurnal animals, where increased light exposure heightens perceived risk (for an interesting synthesis in fish, see Bassi *et al.*, 2022). Notably, however, the response we observed is completely different from Kurvers *et al.* (2018) who assessed chronic changes in activity level in guppies exposed to 10 weeks of ALAN (either bright at 5,000 lux or dim at 0.5 lux) and did not observe differences in activity level compared with fish kept on a normal light-dark cycle. Additionally, the behavioural response of individuals may depend on specific experimental conditions, such as light intensity, duration of exposure, and the presence of conspecifics or predators. For example, the swimming speed of juvenile rudd (*Scardinius erythrophthalmus*) was higher under halogen light (5.4 lux) compared with high pressure sodium (8.2 lux), while not differing from metal halide (7.1 lux), perhaps due to visual differences across those conditions (Tałanda *et al.*, 2018). Minute changes in location can also lead to vastly different results in a single study - for instance, ALAN increased rainbow trout density in the right river of a stream system but not the left one (Nelson *et al.*, 2022). In bats, artificial light may not always carry the same ecological salience. Many bats rely on echolocation for navigation and prey detection, which may reduce their dependence on visual cues, although this varies significantly across species based on foraging modality (Boonman *et al.*, 2013). Besides, artificial light can have variable effects depending on whether it attracts prey, such as insects, or creates a perceived risk by mimicking predator activity (see Rowse *et al.*, 2016 and Stone *et al.*, 2015 for detailed reviews). For instance, 18 out of 25 neotropical insectivorous bat species were observed foraging around streetlights in

Panama (Jung & Kalko, 2010), most likely because they can increase their foraging efficiency thanks to the high and predictable insect densities present there (Rydell, 2006). Contrastingly, Lewanzik and Voigt (2014) found that the frugivorous Sowell's short-tailed bat *Carollia sowelli*, harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour streetlight than in a dark compartment, and free-ranging bats neglected ripe fruits that were experimentally illuminated, most likely due to increased perceived predation risk. The trade-off is thus completely different between foraging modes, but also between preferred hunting grounds: open-space foragers and forest-dwelling species tend to show different responses to light (Rowse *et al.*, 2016). These contextual variables and species-specific responses make it challenging to generalize behavioural responses across taxa or experimental settings and essential to account for when predicting likely responses.

The differing outcomes in my studies demonstrate the importance of carefully considering contextual factors in behavioural experiments. Behavioural traits are labile and can change over short periods of time in response to changes in internal and external stimuli (Wolak *et al.*, 2012). This is what makes them hugely interesting to study, but also comes with a slew of challenges, because high lability implies that individual differences seen at one point in time might not be observed again even under highly controlled conditions (Biro & Stamps, 2015). For example, bats may only exhibit behavioural changes under specific light intensities or in habitats where prey availability is directly affected by artificial light. Similarly, social learning in bats may occur more readily in captive contexts, where animals are more likely to be familiar with one another and experience more frequent human disturbances, or when the social cues are highly salient. Guppies, on the other hand, demonstrated consistent sensitivity to artificial light, suggesting that their responses are more readily reproducible in controlled environments. By acknowledging the role of context in shaping behavioural variability, researchers can design studies that better account for ecological relevance, leading to more reliable and interpretable results. If small experimental differences can have a significant impact on results, the question is raised of the relevance of those results to nature. That is, if behaviours are only performed in extremely controlled environments under specific circumstances, their ecological relevance may be small and should be transparently reported.

Reproducibility as a tool for understanding variability

My findings underscore the value of reproducibility not just as a means of confirming prior results, but as a tool for understanding the variability in behavioural responses across taxa and contexts. The differences in responses between bats and guppies to artificial light highlight the need for reproducibility studies to address when and why behaviours diverge. For example, the variation between studies in bats suggests that behavioural responses may be variable and context-dependent experimental designs that explicitly address this complexity will be valuable, for example comparing subpopulations or sampling locations. By combining species-dependent and context-dependent perspectives, reproducibility efforts can move beyond confirming findings to uncovering the mechanisms that drive behavioural variability.

Experimental animal research often holds as the gold standard rigorous standardization to try and remove all the variability described above that might lead to differing results. I believe this might often be impossible despite all best intentions and efforts, especially when working with wild animals in fairly natural conditions. A growing body of evidence supports this perspective, showing poor reproducibility of research findings across virtually all disciplines (e.g. psychology: Open Science Collaboration, 2015; drug testing: Begley & Ellis, 2012; biology modelling: Tiwari *et al.*, 2021; behavioural neuroscience: Loss *et al.*, 2021; ecology and evolution: Fidler *et al.*, 2017). Recently, alternative approaches have started to emerge to better deal with and address the diversity of living things and what they respond to. Amongst promising propositions is the idea to systematically heterogenize study samples and conditions by actively incorporating biological variation into study design (Voelkl *et al.*, 2020).

In behavioural ecology, reproducibility can also help refine conservation strategies by identifying taxa or contexts that are particularly sensitive to anthropogenic stressors. For instance, the sensitivity of guppies to artificial light underscores the potential ecological consequences of ALAN for visually guided species, particularly those in aquatic ecosystems. In contrast, bats' robustness to artificial light in my study supports other evidence that their responses may depend on specific ecological contexts, such as prey availability or predation risk. Recognizing these differences is critical for developing targeted conservation strategies that account for the unique traits and vulnerabilities of each species. Overall, reproducibility in behavioural studies is not about eliminating variability but about embracing it as a source of insight into the diversity of life and its responses to a changing world.

General summary and conclusions

This thesis explored the context-dependent and species-specific behavioural responses of bats and guppies to environmental stressors, with a focus on artificial light and, in the case of bats, sleep deprivation and social learning. My findings provide new insights into the variability of behavioural plasticity across taxa and highlight the importance of testing assumptions about general patterns of response to anthropogenic changes.

In Chapter 2, I investigated whether bats altered their foraging behaviour under artificial light or sleep deprivation and whether they demonstrated social learning of novel foods. My results revealed no measurable changes in foraging behaviour under artificial light or after sleep deprivation. Additionally, bats did not demonstrate social learning, suggesting that the ability to learn socially may vary across contexts, species, or experimental conditions. These findings underscore the complexity of studying social learning and behavioural plasticity in highly mobile, ecologically diverse taxa like bats. They challenge the generalizability of previous conclusions, emphasizing the need to account for context-specific factors such as habitat, experimental design, and the ecological relevance of the stressor.

In Chapter 3, I explored the effects of artificial light on the foraging behaviour and space use of guppies. Unlike bats, guppies exhibited clear behavioural changes under artificial light, taking longer to enter zones and feeders with bright illumination. These results align with broader findings that artificial light at night (ALAN) influences risk perception and space use in diurnal and visually guided species. However, my findings also highlighted species-specific sensitivity to light intensity, with guppies responding to even moderate artificial light levels by altering their foraging behaviour. This sensitivity may reflect the ecological and evolutionary pressures faced by guppies in their natural habitats, where predation risk and habitat structure are key factors shaping behaviour.

Together, the results of my two chapters reveal striking differences in behavioural responses across taxa, highlighting the context- and species-dependent nature of responses to environmental stressors. Assumptions about the universality of behavioural responses must be tested rigorously across multiple species and contexts. These findings contribute to the growing body of research emphasizing the importance of variability and plasticity in evolutionary and behavioural ecology (Fox *et al.*, 2019).

The implications of this thesis extend beyond the specific taxa studied, offering insights into the broader challenges of reproducibility and replicability in behavioural research. My findings underscore the importance of considering species-specific sensory and ecological adaptations, as well as the experimental conditions under which behaviours are tested. Artificial light, as a pervasive anthropogenic stressor, has diverse effects on behaviour that are shaped by the ecological and sensory worlds of different organisms. Testing these effects across a range of taxa and contexts is crucial for identifying general patterns and for predicting the impacts of anthropogenic changes on biodiversity. Overall, this thesis highlights the necessity of a comparative and context-aware approach to behavioural research. By examining two contrasting systems—bats and guppies—under similar environmental stressors, this work contributes to a deeper understanding of the complexity of behavioural responses and suggests future studies aimed at untangling the interplay between environmental stressors, species-specific traits, and context-dependent behaviours.

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