Chapter 1. General Introduction

**ADD AN INTRODUCTORY PARAGRAPH TO BRING IN THE GENERAL SUBJECT, OBJECTIVES, AND HOW THIS CHAPTER WILL MOVE**

Sentinel Behaviour

The original definition for sentinel behaviour in animals likely originates from the human definition of a sentinel where a guard keeps watch over other group-members, alerting them of potential dangers or threats. Similarly, animal sentinels take on the role of a “guard” by exhibiting constant vigilance over other group members from a prominent, exposed position and making alarm calls when sources of danger are detected (Bednekoff, 2015; Blumstein, 1999). Observations of sentinel behaviour have very likely been made by naturalists and researchers for centuries but the earliest descriptions of sentinel behaviour in research articles appear in the mid-20th century (REF). Sentinel behaviour has been predominantly researched in avian species, though much research has been done on the behaviour in mammals and even in aquatic species (Bednekoff, 2015). Possibly the most recognizable sentinel species is the meerkat, *Suricata suricatta,* a species whose sentinels stand up on their hind legs to perform sentinel duties (Huels & Stoeger, 2022; Manser, 2018; Rauber et al., 2019; Rauber & Manser, 2021; Santema et al., 2013; Santema & Clutton-Brock, 2013). Studies have also been conducted on sentinel behaviour in certain mongoose and primate species (Bolwig, 1959; Eastcott et al., 2020; Horrocks & Hunte, 1986; Kern & Radford, 2013, 2014, 2018). In avian species, sentinel systems have been described and exhaustively researched in species of *Aphelocoma* (Bednekoff & Woolfenden, 2003, 2006; Fleischer et al., 2003; Hailman et al., 2010; McGowan & Woolfenden, 1989), *Argya* (Edelaar & Wright, 2006; Ostreiher et al., 2021; Ostreiher & Heifetz, 2017, 2019; Wright, Berg, et al., 2001a; Wright, Maklakov, et al., 2001), and *Turdoides* (Gaston, 1977; Rafay et al., 2020). Since this behaviour is not limited to those genera and is shared across several taxa without common ancestry, this behaviour must have evolved when very specific environmental and social conditions were met (Bednekoff, 1997, 2001).

Sentinel behaviour is an effective strategy to help balance a fundamental trade-off between foraging and vigilance (Wright, Berg, et al., 2001b). These two behaviours are generally considered mutually exclusive yet are equally important (Lima & Dill, 1990; Olson et al., 2015). The time spent performing each behaviour must be carefully managed (Lima, 1998; Lima & Dill, 1990). A reduction of vigilance to increase foraging efficiency can result in increased risk of predation. A sentinel’s vigilance can compensate for the individual decrease in vigilance, providing an advantage to species that exhibit this behaviour.

However, the underlying mechanisms for sentinel decision-making are not clear, giving rise to debate over whether this behaviour is selfless or selfish. The former hypothesis was that sentinel behaviour was selfless, where individuals take turns providing benefits to other group members at their expense. Whether through reciprocal altruism (Trivers, 1971) or kin selection (Hamilton, 1964), the individual is self-sacrificing and primarily benefits the group. A more recent hypothesis is that sentinel behaviour could be driven by selfish, state-dependent decisions. The state-dependent model for sentinel decision-making revolves around an individual’s energetic reserves and requirements (Bednekoff, 1997, 2001). Individuals who have sufficient energetic reserves are more inclined to perform sentinel duties if the alternative is foraging without a sentinel, a considerably more dangerous option than being sentinel. Studies on the effects of satiation and body mass on the propensity of an individual to perform sentinel behaviour support this hypothesis (Clutton-Brock et al., 1999; Huels & Stoeger, 2022; Wright, Berg, et al., 2001b; Wright, Maklakov, et al., 2001). These two hypotheses are not mutually exclusive, and sentinel behaviour invariably provides benefits to both the sentinel and other individuals in the group. Moreover, certain individuals in the group could further benefit from sentinel behaviour. Dominant males could be using sentinel behaviour to also gather information about rival groups and defend against intrusion, increasing their sentinel efforts when in the presence of auditory or chemical signals from out-group rivals (Morris-Drake et al., 2019; Walker et al., 2016). Sentinel behaviour could then serve additional purposes apart from the identification of possible threats.

Individuals under the watchful eye of a sentinel receive significant benefits. Other group members could reduce their vigilance and increase their foraging efficiency as vigilance is ensured by the sentinel (Hollén et al., 2008). A sentinel cannot be vigilant in perpetuity and eventually will relinquish the position to perform other behaviours. The coordination of sentinels is therefore crucial to minimize the gaps in coverage and ensure the safety of the group (Bednekoff, 1997, 2001, 2015). The coordination of sentinels has been recognized as the defining feature of sentinel behaviour since adopting an exposed position and making alarm calls are not behaviours exclusive to sentinel behaviour (Bednekoff, 1997, 2015; McGowan & Woolfenden, 1989)..

The decision to perform sentinel behaviour is therefore dependent on an individual’s ability to perform the behaviour (i.e. energetic levels) and the individual’s need for safety (i.e. risk mitigation, threat detection). Individuals must maintain the precarious balance between the two needs while travelling between environments. Different foraging environments can have altered conditions which, in turn, can affect the individual’s decision-making, emphasizing the need to study the behaviour in a variety of contexts.

Urbanization

Urbanization is the shift in the human population towards urban centers, resulting in ever-expanding urban areas and the modification of wide swathes of wildlands. With over 55% of the global human population living in urban areas and a forecasted increase in this percentage in the following decades (UN Department of Economic and Social Affairs, 2018), wildlife will increasingly be affected by the environmental changes made to accommodate human occupation. Species must therefore quickly adapt to minimize fitness losses accrued by foraging in unnatural, anthropogenic environments.

Specialist species are at a disadvantage compared to generalist species if the conditions to which specialists are adapted are no longer present. Since urbanization can cause habitat loss or fragmentation and increases the frequency and severity of anthropogenic disturbances (Isaksson, 2018; Marzluff, 2001), specialist species are often ill-suited for urban spaces, resulting in species extirpation and even extinction. This can be observed in the significant loss of biodiversity caused by the ever-increasing global urbanization (Aronson et al., 2014).

Generalist species are better suited to forage in most conditions than specialist species and even benefit from living and foraging in urban areas (Callaghan et al., 2019; Ducatez et al., 2018). Such species can adapt at many levels, with physiological, morphological, and behavioural adaptations being observed in many species (Isaksson, 2018; Lowry et al., 2013; Marzluff, 2001; Meillère et al., 2015). For example, behavioural adaptations such as the use of anthropogenic structures for nesting, preference for anthropogenic foods, and increased tolerance to human proximity are observed in urbanized species (Isaksson, 2018; Lowry et al., 2013; Marzluff, 2001; Meillère et al., 2015). As a result, urbanized species can increase in abundance in urban areas (Francis & Chadwick, 2012). The abundance of American crows (*Corvus brachyrhynchos*) has been consistently increasing over the years, correlating with an increase in the area and number of cities (Marzluff et al., 2001; Marzluff & Neatherlin, 2006; J. C. Withey & Marzluff, 2009; J. Withey & Marzluff, 2005). Adaptations to urban living have also been observed in this species, such as preferring anthropogenic foods and greatly increased tolerance to human proximity (De León et al., 2019; Gotanda, 2020; Marzluff et al., 2001; J. C. Withey & Marzluff, 2009; J. Withey & Marzluff, 2005).

Urban living can also affects social behaviours. For example, the effectiveness of sentinel behaviour can be reduced in urban areas because of increased anthropogenic noise which makes sentinel calls and signals more difficult to hear (Eastcott et al., 2020; Kern & Radford, 2016). In such scenarios, species increase their individual vigilance despite the presence of a sentinel (Kern & Radford, 2016). Urban areas also have an increased abundance and predictability of food sources (e.g. litter, trash cans, dumpsters) containing highly caloric anthropogenic foods. Individuals could therefore consume more energy more quickly than in wilder, less disturbed areas, resulting in greater body mass and energetic reserves (Schulte-Hostedde et al., 2018; Stofberg et al., 2019). If Bednekoff’s model of state-dependent decision-making holds, individuals should then be able to perform sentinel behaviour earlier, more often and/or for longer (Bednekoff, 1997, 2001). Considering that sentinel behaviour can provide advantages to both antipredator vigilance and foraging efficiency, sentinel species could be better suited to foraging in urban areas, outcompeting non-social and less adapted individuals.

The American crow, *Corvus brachyrhynchos*

American crows are cooperatively breeding corvids that can be found in most North American cities (Marzluff et al., 2001; Marzluff & Neatherlin, 2006). Sentinel behaviour has been described in this species (Maccarone, 1987). Their synurbic and social nature therefore makes them good models to determine if the use of social behaviours, specifically sentinel behaviour, is adaptive in urban areas. By observing the behaviour of foraging American crows in two different urban microenvironments, I could determine how they perceive their environment and adapt their social foraging behaviours. Their use of sentinel behaviour could allow them to forage more effectively and safely than other species, possibly contributing to their success in urban environments.

Research Objectives

In chapter 2, I did a scoping review of the current literature on intrinsic and extrinsic factors affecting sentinel decision-making in terrestrial and avian species. The trends observed in previous studies on these factors were identified in the light of how urbanization could alter an individual’s decision to perform this behaviour. The purpose of this chapter was to help predict and explain the results of the chapter 2’s observational study.

The objective of Chapter 3 was to determine how American crows altered their use of sentinel coverage when foraging in different urban areas. To do this, foraging crows were recorded and the duration of bouts of alert and foraging behaviours were measured. Since these two behaviours are mutually exclusive, they are good metrics to measure how the foragers perceive their environment and use the added vigilance provided by the sentinel. Considering the literature on sentinel in urban centres, the hypothesis was that foragers would spend less time being vigilant in green areas than in commercial areas, as well as in the presence of a sentinel, as the sentinel’s vigilance will be more effective due to increased lines of sight and decreased ambient noise levels.

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