**General Introduction**

There are two essential needs that all individuals must effectively balance in nature: the need to eat, and the need to not be eaten. This trade-off is important when discussing foraging and vigilance behaviours in any species. If an individual forgoes vigilance in favor of greater foraging efficiency, it leaves itself exposed to increased predation risk which can have profound negative impacts on its survival. If the same individual were to prioritize vigilance over foraging, the decreased foraging efficiency can negatively affect its fitness. Individuals must therefore carefully balance the time spent performing both foraging and vigilance behaviours. Group foraging can decrease individual vigilance by virtue of the increased likelihood of at least one individual being vigilant at a time (Lima 1995). Some species coordinate their vigilance, ensuring that at least one individual is always vigilant. Coordination is inherently more costly but provides greater safety for foragers. One example of a coordination of vigilance in animals is sentinel behaviour, the topic of my thesis.

**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 alerting other group members when sources of danger are detected (Blumstein 1999, Bednekoff 2015). 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 (Dharmakumarsinhji 1954). 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-using species is the meerkat, *Suricata suricatta,* a species whose sentinels stand up on their hind legs to perform sentinel duties (Santema and Clutton-Brock 2013, Santema et al. 2013, Manser 2018, Rauber et al. 2019, Rauber and Manser 2021, Huels and Stoeger 2022). Studies have also been conducted on sentinel behaviour in certain mongoose and primate species (Bolwig 1959, Horrocks and Hunte 1986, Kern and Radford 2013, 2014, 2018, Eastcott et al. 2020). In avian species, sentinel systems have been described and exhaustively researched in species of *Aphelocoma* (scrub jays, Bednekoff & Woolfenden, 2003, 2006; Fleischer et al., 2003; Hailman et al., 2010; McGowan & Woolfenden, 1989), *Argya* (babblers and thrushes, Edelaar & Wright, 2006; Ostreiher et al., 2021; Ostreiher & Heifetz, 2017, 2019; Wright, Berg, et al., 2001a; Wright, Maklakov, et al., 2001), and *Turdoides* (jungle babblers, 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 et al. 2001b). These two behaviours are generally considered mutually exclusive yet are equally important (Lima and Dill 1990, Olson et al. 2015). The time spent performing each behaviour must be carefully managed (Lima and Dill 1990, Lima 1998). 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. Sentinel behaviour was originally hypothesized to be a selfless behaviour, 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, Wright et al. 2001c, 2001b, Huels and Stoeger 2022). 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 (Walker et al. 2016, Morris-Drake et al. 2019). 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 alerting group members are not behaviours exclusive to sentinel behaviour (McGowan and Woolfenden 1989, Bednekoff 1997, 2015).

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 maximize their fitness when 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 (Marzluff 2001, Isaksson 2018), 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 urban-living than specialist species and can benefit from urban areas (Ducatez et al. 2018, Callaghan et al. 2019). Physiological, morphological, and behavioural adaptations have been observed in many urbanized species, and are expected to improve a species' ability to exploit urban advantages (Marzluff 2001, Lowry et al. 2013, Meillère et al. 2015, Isaksson 2018). 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 (Marzluff 2001, Withey and Marzluff 2005, 2009, Lowry et al. 2013, Meillère et al. 2015, Isaksson 2018, De León et al. 2019, Gotanda 2020). As a result, urbanized species can increase in abundance in urban areas (Francis and Chadwick 2012). An example of an urbanized species is the American crow (*Corvus brachyrhynchos*), whose abundance has increased with increasing urbanization (Benmazouz et al. 2021).

Urban living can also affect 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 (Kern and Radford 2016, Eastcott et al. 2020). In such scenarios, species increase their individual vigilance despite the presence of a sentinel (Kern and Radford 2016). Urban areas also have an increased abundance and predictability of anthropogenic food sources such as litter, trash cans, and dumpsters. 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-using 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 and 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 seek to shed light on their perception of their environment and how they 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 conducted a scoping review of the current literature on intrinsic and extrinsic factors affecting sentinel decision-making in terrestrial and avian species. The purpose of this chapter was to help predict and explain the results of my observational study in chapter 3. 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 sentinels 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 in green areas such as the many parks and trails of St. Catharines, Ontario.

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