General Introduction

Sentinel Behaviour

It is very hard, see impossible, to find the original definition for sentinel behaviour in animals as it likely originates from the human definition of sentinel, or an individual tasked with watching over other group-members, alert against potential dangers or threats. Similarly, animal sentinels take on the role of a sentinel by exhibiting constant vigilance over other group-members from an prominent, usually exposed, position, and making alarm calls when sources of danger are detected. Observations of sentinel behaviour have very likely been made by naturalists and researchers for centuries, though descriptions of sentinel behaviour in animals started to appear in mid-XXth century research articles, mostly associated with the behaviour of birds. As they are much more visible and considerably louder than their mammal counterparts, sentinel behaviour has been predominantly researched in avian species, though much research has been done on the behaviour in mammal and even in aquatic species. Possibly the most recognizable sentinel species are meerkats, *Suricata suricatta,* a species whose sentinels stand up on their hind legs to perform sentinel duties, though much research has also been done in mongoose and primates. In avian species, sentinel systems have been described and exhaustively researched in species of the *Aphelocoma*, *Argya*, and *Turdoides* genus, although yet again this behaviour is not limited to those genera. It is evident that this behaviour is shared across several taxa and does not follow a common ancestry. This behaviour must have therefore been evolved when very specific environmental and social conditions were met.

Sentinel behaviour could have evolved as an effective strategy to balance a fundamental trade-off between foraging and vigilance. These two behaviours are considered mutually exclusive and must therefore time spent performing each behaviour must be carefully managed. Were one to forgo vigilance, they would expose themselves to an increased risk of predation and threat. The opposite is also true, where one’s excess in vigilance would lead them to increased risk of starvation. It is therefore important to effectively balance these two needs. Effective management of this trade-off can result in an increase in fitness. The use of sentinel behaviour could therefore be an incredible advantage to species that can utilize the behaviour. Yet, the underlying mechanisms for sentinel decision-making are not clear, giving rise to much debate over whether this behaviour is driven by mutual benefits, or by selfish decisions. The former would suggest that individuals perform sentinel duties in a transactional manner, where one ensures the protection of group-members because they will, in turn, receive the benefits of sentinel behaviour when another individual takes its place. This may be due to direct benefits to foraging efficiency and predation risk reduction, or indirect benefits such as by ensuring the survival of other group-members thereby indirectly increasing the likelihood of their survival, but also the likelihood of their genes being passed down. However, this behaviour could be driven by selfish, state-dependent decisions. Originally hypothesized by Bednekoff, this state-dependent model for sentinel decision-making revolves around an individual’s energetic reserves and requirements. Therefore, 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. This has garnered much support from the results of studies performed on the effects of satiation and body mass on the propensity of an individual performing sentinel behaviour. These two hypotheses are however not mutually exclusive, and sentinel behaviour invariably provides benefits to other individuals in the group. Supporting this, studies have shown that dominant males will perform more sentinel behaviour when in the presence of signals from out-group rivals, either auditory or chemical. Sentinel behaviour could then serve additional purposes apart from the identification of possible threats.

Individuals covered by a sentinel receive significant benefits. If a sentinel is present, then other group-members could reduce their individual vigilance and increase their foraging efficiency. The sentinel would incur the cost of a lost foraging opportunity but could recuperate those costs if another sentinel were to replace them. It is therefore crucial that sentinels coordinate their efforts to minimize the “gaps” in coverage and ensure the safety of other group-members. Bednekoff, an important contributor to research on sentinel behaviour, postulated that this coordination of sentinels be the defining feature of sentinel behaviour since adopting an exposed position and making alarm calls are not behaviours exclusive to sentinel behaviour. Though coordination as a defining feature of sentinel behaviour has been used in articles published after Bednekoff’s 1999 article, this is not universally used, resulting in possible misidentification of sentinel behaviour in non-sentinel species.

True sentinel species could therefore be at an advantage over non-sentinel species when foraging in a common environment. Though mixed-species flocks exist, where non-sentinel species forage in the presence of sentinel species and utilize the latter’s sentinel alarm calls, it is important to observe the relative advantages offered by this behaviour. More crucially, the advantages provided by this behaviour could be cumulative or interact with other advantages the species may have. For example, an individual could be better adapted to foraging in a specific environment or on a specific resource, also called a specialist species. Were these specialists to also have a sentinel system, then they could outcompete other species for resources in the conditions to which the species is adapted to.

Urbanization

Unfortunately, these specialist species are at a severe disadvantage in the face of 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. Species must therefore quickly adapt to minimize fitness losses accrued by foraging in unnatural, anthropogenic environments. Specialist species are at a disadvantage when compared to more generalist species if the conditions to which they are adapted to are no longer present. This can be observed in the significant loss of biodiversity caused by the ever-increasing global urbanization. Since urbanization can cause habitat loss or fragmentation, and increases the frequency and severity of anthropogenic disturbances, specialist species are often ill-suited for urban spaces, resulting in species extirpation and even extinction. However, not all species suffer equally. Generalists better suited to forage in most conditions and could even benefit from living and foraging in urban areas. Species could adapt at many levels, with physiological, morphological, and behavioural adaptations being observed in many species. Behavioural adaptations such as the use of anthropogenic structures for nesting, changes in foraging and vigilance behaviours such as preference for anthropogenic foods and increased tolerance to human proximity and disturbances are but some of many adaptations observed in urban-adapted species. As a result, urban-adapted, henceforth referred to as synurbic species, could increase in abundance in urban areas. Synurbic species can be seen in our daily lives, from the squirrels and raccoons eating from our trashcans to the birds that nest on the gutters descending from our roofs. More visible and heard, are the seagulls and crows fighting for food scraps in our parks and parking lots. These two species are great examples of synurbic species as their abundance has consistently increased over the years, correlating with the increase in the size of urban areas. Adaptations to urban living have also been observed in these species, such as preferring anthropogenic foods and greatly increased tolerance to human proximity. This could also extend to social behaviours, including sentinel behaviour. For example, urban areas have factors that could reduce the effectiveness of sentinels, such as by having increased anthropogenic disturbances and noise which make sentinel calls and signals more difficult to hear and understand. In such scenarios, sentinels have adapted the behaviour, sentineling from positions closer to the foraging group. In urban areas, where perching locations are abundant (e.g. lampposts, fences, trees, buildings), this adaptation is facilitated. Urban areas also have an increased abundance and predictability of food sources (e.g. litter, trash cans, dumpsters) containing highly caloric anthropogenic foods which, if Bednekoff’s model holds true, would result in individuals being able to perform sentinel behaviour earlier, more often and/or for longer. Considering that sentinel behaviour can provide advantages to both antipredator vigilance and foraging efficiency, synurbic sentinel species could be better suited to foraging in urban areas, outcompeting non-social and less adapted individuals. There is therefore a need to determine how social species benefit from having adapted social behaviours in urban areas, as these benefits could play a role in the observed increase in abundance of American crows in urban areas. In turn, this could contribute to the loss of biodiversity in and around urban areas, exacerbating an already devastating problem.

The American crow, *Corvus brachyrhynchos*

While seagulls and crows have their similarities, being synurbic generalists that inhabit urban areas, American crows, *Corvus brachyrhynchos*, have much more sophisticated social behaviours than their white-and-grey-feathered counterparts. American crows are a cooperatively breeding species that can be found soaring in the skies and perched on the lampposts of most north American cities. Having a variety of perches to choose from, sentinels are often spotted in the proximity of groups of foraging crows, and a sentinel system has been described in the species. Their synurbic and social nature therefore makes them good models to determine if the use of social behaviours, specifically sentinel behaviour, is adapted in urban areas. If the use of sentinel behaviour is adapted in the species, then foragers could modify their needs for either individual vigilance or foraging efficiency. Were the effectiveness of a sentinel to be impeded by the foraging environment, foragers would need to spend more time being vigilant, reducing the overall time spent foraging. Conversely, the time spent foraging could remain unchanged if sentinel effectiveness is not affected by the foraging environment, with an increase in

Research Objectives

The primary research objectives of this thesis are to determine whether sentinel behaviour can be affected by factors associated with urbanization (Chapter 1) and determine how American crow foragers respond to the presence of a sentinel when foraging in different urban environments (Chapter 2). In chapter 1, I performed a quasi-scoping review on the currently available literature on intrinsic and extrinsic factors affecting sentinel decision-making in terrestrial and avian species. In chapter 2, I investigate the results of an observational study I undertook in summer 2022 to determine how American crows alter their foraging behaviour in the presence of a sentinel, and when foraging in different urban areas. To do this, I recorded foraging crows and measured the duration of bouts of alert and foraging behaviours. Since these two behaviours are mutually exclusive and directly linked with Lima’s theory of a foraging-vigilance trade-off, they are good metrics to measure how the foragers utilize the vigilance provided by the presence of a sentinel. I hypothesize that sentinel decision-making can be affected by urbanization, as it could provide conditions that either facilitate or increase the requirement for a sentinel to be present. In response, foragers are expected to reduce the time spent being vigilant in the presence of a sentinel, regardless of the environment in which they forage in, though the reduction in time spent being vigilant should reflect the relative risk of their foraging environment.

This thesis should, at least, provide some insights into how a sentinel species could respond to having to forage in urban areas. Since not all sentinel species are synurbic, the increased proximity to urban areas could result in an increased frequency of sentinel species interacting with urban environments. Moreover, the results of chapter 2 will help elucidate whether sentinel behaviour.