**General Discussion**

**Thesis summary**

The objectives of my thesis were to investigate in the urban American crow (1) how sentinel behaviour could be affected by both intrinsic and extrinsic factors, and (2) observe changes in behaviour in response to the presence or absence of a sentinel. Sentinel behaviour, where individuals take watch over other group members in a coordinated manner, is an essential tool for the reduction of predation risk (Bednekoff 2015). The behaviour could be even more useful in human-altered environments where wildlife must navigate novel challenges and adapt to their surroundings. By observing changes in social behaviours and understanding the underlying mechanisms behind behavioural decisions, we could gain a better understanding of how these behaviours have evolved, and how they could continue to evolve in the future.

Chapter 2 identified several intrinsic and extrinsic factors that can influence sentinel behaviour across several different species. Intrinsic factors (i.e. internal) such as sex, maturity, body mass, and satiation were found to affect the likelihood of performing sentinel behaviour. Males generally performed more sentinel behaviour than females (Yasukawa et al. 1992, Wright et al. 2001, Bednekoff and Woolfenden 2003, Arbon et al. 2020), possibly due to differences in energetic investment between the sexes. Older and more experienced individuals also sentineled more than younger individuals (Zacharias and Mathew 1998, Bednekoff and Woolfenden 2006, Kern et al. 2016, Rauber and Manser 2021), likely because their greater experience with threats made them more effective sentinels. Satiation and body mass were also found to influence sentinel behaviour, with heavier and more satiated individuals more likely to sentinel (Bednekoff and Woolfenden 2003, 2006, Arbon et al. 2020, Ostreiher et al. 2021). The effects of intrinsic factors can be explained through the state-dependent model for sentinel behaviour, where the core motivators are the energetic reserves and the need for safety (Bednekoff 1997, 2001, 2015).

Extrinsic factors (i.e. external or social) such as dominance, group size, and risk also played significant roles in shaping sentinel behaviour. Dominant individuals, usually males, were observed to sentinel more than subordinates (Wright et al. 2001, Walker et al. 2016, Ostreiher and Heifetz 2017, 2019, Houslay et al. 2021), possibly due to their greater access to resources and additional benefits received from sentinel behaviour. Group size predictably influenced sentinel behaviour, with larger groups showing decreased individual sentinel behaviour but increased group-level sentinel behaviour (Yasukawa and Cockburn 2009, Hailman et al. 2010, Arbon et al. 2020, Houslay et al. 2021). Increased risk, whether from predators (Yasukawa et al. 1992, Sorato et al. 2012, Arbon et al. 2020), outgroup rivals (Walker et al. 2016, Morris-Drake et al. 2019), or the presence of pups (Santema and Clutton-Brock 2013), also led to increased sentinel behaviour. Overall, the review highlighted the complex interplay of intrinsic and extrinsic factors in shaping sentinel behaviour across terrestrial vertebrate species.

The factors identified in the scoping review generally aligned with the findings of chapter 3. There were no differences in the presence of a sentinel caused by generalized environment suggesting that environmental and energetic factors were equal throughout the different environments within an urban area, but more research is needed. The absence of effects of disturbance frequency and group size were surprising and could be due to differences in the types of disturbances and increased availability of food in urban settings.

My empirical study focused on investigating how the presence of a sentinel and the generalized environment affected the behaviour of foraging American crows. Unexpectedly, I found that sentinel presence had very few significant effects on forager behaviour, apart from significantly increasing the duration of all behaviours. This was contrary to my initial prediction where the presence of a sentinel would decrease individual vigilance in foragers. Sentinel coverage could have had more subtle effects on foraging behaviours, potentially allowing group members to forage over a wider area without suffering an increased risk of predation (Hollén et al. 2008). In contrast, the generalized environment had a significant effect on forager behaviour. Crows in green areas exhibited longer bouts of foraging behaviour and more transitions from the vulnerable to the alert state compared to those in commercial areas. This could be because green areas are perceived as less safe, possibly because they need to spend more time being vulnerable looking for food, or the increased presence of urban predators like the red-tailed hawk (Morrison et al. 2016). The significant interactions between the effects of generalized environments and sentinel presence sheds light on how adaptable American crow behaviours can be and highlights their ability to succeed in urban environments.

The foraging environment could therefore influence sentinel behaviour in both the sentinel but also the response of foragers to the sentinel. Drawing from both the scoping review and the empirical study on American crows, we can infer the key effects of the generalized environment on sentinel behaviour. The availability and distribution of food resources can impact the propensity of individuals to perform sentinel behaviour (Bednekoff and Woolfenden 2003, Arbon et al. 2020). Litter, usually a highly concentrated patch of food, can be easier to locate and take less time to forage on than resources found in tall grasses. Small invertebrates such as beetles, grubs, and caterpillars are examples of the more natural foods crows forage on, which are of greater nutritional value than most anthropogenic foods yet can take more time to forage on. The increased risk from spending more time being vulnerable can result in individuals choosing to sentinel more often, though this was not observed in our study. Anthropogenic foods found throughout urban areas are also more calorically dense than more natural foods, potentially increasing the energetic reserves of individuals (Auman et al. 2008), and allowing urban individuals to sentinel more than their rural counterparts.

The frequency and types of disturbances could also alter the need to rely on sentinels. In commercial areas, foragers could encounter more vehicular disturbances than in green areas where the odds of encountering a raptor are higher. The presence of a raptor could trigger a more urgent antipredator response than a vehicle, to which crows could be much more tolerant towards despite the increased frequency of encounters (Mukherjee et al. 2013). High-risk microenvironments in urban areas could lead to increased sentinel behaviour as individuals prioritize vigilance to reduce the risk of predation. In contrast, lower predation risk environments could result in a reduced need for sentinel behaviour as individuals feel safer and allocate more time to foraging.

Truly understanding the decision-making underpinning sentinel behaviour requires a holistic approach that considers a very wide range of individual and environmental factors. Determining how these factors interact and play a role in shaping the trade-offs associated with sentinel behaviour should be of particular interest to future studies. Furthermore, studying sentinel behaviour in urbanized species such as the American crow can provide unique insights into how animals perceive and respond to human-altered landscapes and can lead to a better understanding of how sentinel behaviour contributes to the success of these species.

Despite the insights gained from our empirical study, I should acknowledge some of the limitations of the empirical study. One limitation is the relatively small sample size of crows observed, which could have limited the statistical power of our analyses. A larger sample size would have allowed a better examination of the factors influencing forager and sentinel behaviour. Collecting observations from a wider diversity of microenvironments could also help reveal more subtle environmental effects at play. Our study was conducted in St. Catharines, Ontario which is known for its 1000 acres of parks, gardens and trails and is aptly named “The Garden City”. This could limit the generalizability of our findings to other populations of crows in different cities with fewer green spaces. Factors such as local food availability, predator presence, and the distribution of green spaces can also vary widely between cities. Therefore, caution should be exercised when extrapolating these results to other populations or environments.

**Future Studies**

Our empirical study revealed significant effects of different urban areas on the behaviours of American crows, yet the specific elements in each environment that caused this response are require further study. Considering how diverse urban areas can be, we should continue studying the behaviour of species in urban areas, paying particular attention to how these species behave within different environments. We looked at differences in behaviour in two environments that are very different from one another, commercial and green spaces, but there are many other environments that we did not look at. Residential areas can have less overall impermeable surfaces than commercial areas, but greater vehicular disturbances than in green spaces. Future studies should sample over a greater breadth of urbanization and make a more comprehensive evaluation of each environment to better disentangle the effects of various environmental parameters on the behaviour of urban species. Additionally, researchers could consider conducting a long-term study to observe sentinel behaviour and forager responses over an extended period. This could allow the identification of temporal effects on the behaviour. Future studies could also sample populations from different cities to help improve the generalizability of my findings. The discovery of differences in sentinel behaviour between populations from different cities would be interesting and analysis of the causes of such differences could be fruitful in furthering our understanding of how social behaviours change in urban settings. These avenues for future research could help better our understanding of the effects of human settlement on the behaviour of wildlife and might serve in mitigating these effects.

**Concluding statements**

The main findings from the scoping review and empirical study shed light on the factors influencing sentinel behaviour in urban environments, particularly in American crows. The scoping review identified a range of intrinsic and extrinsic factors that can affect sentinel behaviour, including group size, predation risk, and resource distribution.

The findings of this thesis can have several implications for understanding sentinel behaviour and its effect on forager behaviour. The scoping review suggested that sentinel behaviour decision-making is complex and revolves around individual motivators such as energetic reserves and requirements for safety. The findings of my empirical study reinforce the importance of considering environmental factors affecting the behaviour of urban social species. While this study provides valuable insights, it also raises new questions and challenges that warrant further investigation and reemphasizes the need for further research to explore the effects of urbanization on the social behaviour of urban-adapted species, and its contribution to the success of these species. Overall, these results contribute to the growing literature on the effects of urbanization on the behaviour of animals.

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