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 a sentinel. This individual is tasked with watching over other group-members, alerting them of potential dangers or threats. Similarly, animal sentinels take on the role of a sentinel by exhibiting constant vigilance over other group-members from a prominent, usually exposed, position, and making alarm calls when sources of danger are detected [1,2]. Observations of sentinel behaviour have very likely been made by naturalists and researchers for centuries and the earliest descriptions of sentinel behaviour in animals appear in mid-XXth century research articles, mostly associated with the behaviour of birds and mammals. As they are 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 [3–8]. Studies have also been conducted on sentinel behaviour in certain mongoose and primate species [9–14]. In avian species, sentinel systems have been described and exhaustively researched in species of the *Aphelocoma* [15–19], *Argya* [20–25], and *Turdoides* genera [26,27]. 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.

Sentinel behaviour is an effective strategy to help balance a fundamental trade-off between foraging and vigilance [28]. These two behaviours are considered mutually exclusive and are equally important. Time spent performing each behaviour must be carefully managed [29,30]. Were one to forgo vigilance, they would expose themselves to an increased risk of mortality due to predation. 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 a cooperative or selfish behaviour. 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 [31]. 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 through group-size effects [32]. However, this behaviour could be driven by selfish, state-dependent decisions. Originally hypothesized by Bednekoff, an important contributor to research on sentinel behaviour, this state-dependent model for sentinel decision-making revolves around an individual’s energetic reserves and requirements [33,34]. 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 to perform sentinel behaviour [3,25,28,35]. These two hypotheses are not mutually exclusive, and sentinel behaviour invariably provides benefits to other individuals in the group and could benefit the sentinel itself. 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 [36,37], suggesting dominant males could be using sentinel behaviour to also gather information about other groups and defend against intrusion. 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. If a sentinel is present, then other group-members could reduce their individual vigilance and increase their foraging efficiency as vigilance is ensured by the sentinel [38]. A sentinel cannot be vigilant in perpetuity, and eventually will relinquish the position in favour of foraging for food. It is therefore crucial that sentinels coordinate their efforts to minimize the “gaps” in coverage and ensure the safety of the group [1,33,34]. This 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[1,19,34]. This definition is not universally used, resulting in possible misidentification of sentinel behaviour in non-sentinel species.

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 [39,40]. 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 [41], it is inevitable that animal species will 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 when compared to more generalist species if the conditions to which they are adapted to are no longer present. Since urbanization can cause habitat loss or fragmentation, and increases the frequency and severity of anthropogenic disturbances [42,43], 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 [44]. However, not all species suffer equally. Generalist species are better suited to forage in most conditions than specialist species and could even benefit from living and foraging in urban areas [39,40]. Such species could adapt at many levels, with physiological, morphological, and behavioural adaptations being observed in many species [42,43,45,46]. 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 urbanized species. As a result, urbanized species - henceforth referred to as synurbic species - could increase in abundance in urban areas [47]. 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, with the latter species’ abundance consistently increasing over the years, correlating with the increase in the size and number of urban areas and cities [48–51]. Adaptations to urban living have also been observed in these species, such as preferring anthropogenic foods and greatly increased tolerance to human proximity[48,50,51]. 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 [9,52]. In such scenarios, species have adapted their use of sentinel behaviour, increasing their individual vigilance despite the presence of a sentinel. 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 in a quicker manner than in wilder, less disturbed areas, resulting in greater body mass and energetic reserves [53,54]. If Bednekoff’s model of state-dependent decision-making holds true, individuals should then be able to perform sentinel behaviour earlier, more often and/or for longer [33,34]. 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. The associated increase in abundance of these species could be contributing to the loss of biodiversity in and around urban areas, exacerbating an already devastating problem. 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 their success in urban areas.

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 [48,49]. 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 [55]. 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 could increase the duration of time spent being vigilant, reducing the overall time spent foraging. The time spent foraging is expected to remain unchanged if sentinel effectiveness is not affected by the foraging environment, with an increase in the duration of time spent foraging when compared to foraging in the absence of a sentinel. By observing the behaviour of foraging American crows, I could make inferences about how the use of sentinel behaviour is impacted by the foraging environment, and by extension urbanization. Synurbic nest predators like the American crow could negatively affect the survival of other species like the Common Nighthawk [48,56], contributing to the decrease in biodiversity observed around urban centers. Therefore, studies such as mine could help determine the role of adapted behaviours on the success of urbanized species like the American crow.

Research Objectives

In chapter 1, I performed a scoping review on the currently available literature on intrinsic and extrinsic factors affecting sentinel decision-making in terrestrial and avian species. I discuss these factors in relation to urbanization with the objective to determine if and how urbanization could alter this behaviour, either directly or indirectly. The purpose of this chapter is to help predict and explain the results of the Chapter 2’s observational study. I hypothesize that sentinel behaviour is affected by both intrinsic and extrinsic factors, and that while some factors are unchangeable, many of the factors identified can be affected by urbanization.

In chapter 2, I investigate the results of an observational study I undertook in summer 2022. Its objective was to determine how American crows alter their use of sentinel coverage 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 perceive their environment and utilize the added vigilance provided by the sentinel. I hypothesize that foragers will 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.

Chapter 1 of this thesis will 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 the effects urbanization could have on forager use of the added protection of a sentinel. In turn, these results could help explain why certain social species, including the American crow, are so successful in urban areas and how sentinel behaviour could contribute to this success.

References

1. Bednekoff PA. 2015 Sentinel behavior: a review and prospectus. In *Advances in the Study of Behavior*, pp. 115–145. Elsevier. (doi:10.1016/bs.asb.2015.02.001)

2. Blumstein DT. 1999 Selfish sentinels. *Science* **284**, 1633–1634. (doi:10.1126/science.284.5420.1633)

3. Huels FD, Stoeger AS. 2022 Sentinel behavior in captive meerkats ( *Suricata suricatta* ). *Zoo Biol.* **41**, 10–19. (doi:10.1002/zoo.21644)

4. Rauber R, Manser MB. 2021 Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats. *Anim. Behav.* **171**, 129–138. (doi:10.1016/j.anbehav.2020.11.014)

5. Rauber R, Clutton-Brock TH, Manser MB. 2019 Drought decreases cooperative sentinel behavior and affects vocal coordination in meerkats. *Behav. Ecol.* **30**, 1558–1566. (doi:10.1093/beheco/arz112)

6. Santema P, Clutton-Brock T. 2013 Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Anim. Behav.* **85**, 655–661. (doi:10.1016/j.anbehav.2012.12.029)

7. Santema P, Teitel Z, Manser M, Bennett N, Clutton-Brock T. 2013 Effects of cortisol administration on cooperative behavior in meerkat helpers. *Behav. Ecol.* **24**, 1122–1127. (doi:10.1093/beheco/art039)

8. Manser M. 2018 Meerkats – identifying cognitive mechanisms underlying meerkat coordination and communication: experimental designs in their natural habitat. In *Field and Laboratory Methods in Animal Cognition* (eds N Bueno-Guerra, F Amici), pp. 286–307. Cambridge University Press. (doi:10.1017/9781108333191.015)

9. Eastcott E, Kern JM, Morris-Drake A, Radford AN. 2020 Intrapopulation variation in the behavioral responses of dwarf mongooses to anthropogenic noise. *Behav. Ecol.* **31**, 680–691. (doi:10.1093/beheco/araa011)

10. Kern JM, Radford AN. 2018 Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proc. Natl. Acad. Sci.* **115**, 6255–6260. (doi:10.1073/pnas.1801000115)

11. Kern JM, Radford AN. 2014 Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk. *Anim. Behav.* **98**, 185–192. (doi:10.1016/j.anbehav.2014.10.012)

12. Kern JM, Radford AN. 2013 Call of duty? Variation in use of the watchman’s song by sentinel dwarf mongooses, *Helogale parvula*. *Anim. Behav.* **85**, 967–975. (doi:10.1016/j.anbehav.2013.02.020)

13. Horrocks JA, Hunte W. 1986 Sentinel behaviour in vervet monkeys: who sees whom first? *Anim. Behav.* **34**, 1566–1568. (doi:10.1016/S0003-3472(86)80226-3)

14. Bolwig N. 1959 A study of the behaviour of the chacma baboon, *Papio ursinus*. *Behaviour* **14**, 136–162. (doi:10.1163/156853959X00054)

15. Bednekoff PA, Woolfenden GE. 2003 Florida scrub-jays ( *Aphelocoma coerulescens* ) are sentinels more when well-fed (even with no kin nearby): sentinel behavior by Florida scrub-jays fed peanuts. *Ethology* **109**, 895–903. (doi:10.1046/j.0179-1613.2003.00926.x)

16. Hailman JP, McGowan KJ, Woolfenden GE. 2010 Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelocoma c. coerulescens*). *Ethology* **97**, 119–140. (doi:10.1111/j.1439-0310.1994.tb01034.x)

17. Bednekoff PA, Woolfenden GE. 2006 Florida scrub-jays compensate for the sentinel behavior of flockmates. *Ethology* **112**, 796–800. (doi:10.1111/j.1439-0310.2006.01227.x)

18. Fleischer AL, Bowman R, Woolfenden GE. 2003 Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildland habitats. *The Condor* **105**, 515–527. (doi:10.1093/condor/105.3.515)

19. McGowan KJ, Woolfenden GE. 1989 A sentinel system in the Florida scrub jay. *Anim. Behav.* **37**, 1000–1006. (doi:10.1016/0003-3472(89)90144-9)

20. Edelaar P, Wright J. 2006 Potential prey make excellent ornithologists: adaptive, flexible responses towards avian predation threat by Arabian babblers *Turdoides squamiceps* living at a migratory hotspot: predation threat flexibility in babblers. *Ibis* **148**, 664–671. (doi:10.1111/j.1474-919X.2006.00567.x)

21. Ostreiher R, Heifetz A. 2017 The sentinel behaviour of Arabian babbler floaters. *R. Soc. Open Sci.* **4**, 160738. (doi:10.1098/rsos.160738)

22. Ostreiher R, Heifetz A. 2019 The sentineling-foraging trade-off in dominant and subordinate arabian babblers. *Ethology* **125**, 98–105. (doi:10.1111/eth.12833)

23. Ostreiher R, Mundry R, Heifetz A. 2021 On the self-regulation of sentinel activity among Arabian babbler groupmates. *Anim. Behav.* **173**, 81–92. (doi:10.1016/j.anbehav.2021.01.002)

24. Wright J, Berg E, De Kort SR, Khazin V, Maklakov AA. 2001 Cooperative sentinel behaviour in the Arabian babbler. *Anim. Behav.* **62**, 973–979. (doi:10.1006/anbe.2001.1838)

25. Wright J, Maklakov AA, Khazin V. 2001 State-dependent sentinels: an experimental study in the Arabian babbler. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 821–826. (doi:10.1098/rspb.2000.1574)

26. Gaston AJ. 1977 Social behaviour within groups of jungle babblers (*Turdoides striatus*). *Anim. Behav.* **25**, 828–848.

27. Rafay M, Ahmad G, Ruby T, Abdullah M, Rasheed F, Abid M. 2020 Breeding and feeding behaviour of jungle babbler(*Turdiodes striata dumont*, 1923) in agro-ecological zones of district layyah, pakistan. *Pak. J. Zool.* **52**, 1701–1708. (doi:https://dx.doi.org/10.17582/journal.pjz/20170420070416)

28. Wright J, Berg E, De Kort SR, Khazin V, Maklakov AA. 2001 Safe selfish sentinels in a cooperative bird: *Safe selfish sentinels*. *J. Anim. Ecol.* **70**, 1070–1079. (doi:10.1046/j.0021-8790.2001.00565.x)

29. Lima SL, Dill LM. 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640. (doi:10.1139/z90-092)

30. Lima SL. 1998 Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. In *Advances in the Study of Behavior* (eds AP Møller, M Milinski, PJB Slater), pp. 215–290. Academic Press. (doi:10.1016/S0065-3454(08)60366-6)

31. Ridley AR, Nelson-Flower MJ, Thompson AM. 2013 Is sentinel behaviour safe? An experimental investigation. *Anim. Behav.* **85**, 137–142. (doi:10.1016/j.anbehav.2012.10.017)

32. Lima SL. 1995 Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20. (doi:10.1016/0003-3472(95)80149-9)

33. Bednekoff PA. 2001 Coordination of safe, selfish sentinels based on mutual benefits. *Ann. Zool. Fenn.* **38**, 5–14.

34. Bednekoff PA. 1997 Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.* **150**, 373–392. (doi:10.1086/286070)

35. Clutton-Brock TH, O’Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser M. 1999 Selfish sentinels in cooperative mammals. *Science* **284**, 1640–1644. (doi:10.1126/science.284.5420.1640)

36. Morris-Drake A, Christensen C, Kern JM, Radford AN. 2019 Experimental field evidence that out-group threats influence within-group behavior. *Behav. Ecol.* **30**, 1425–1435. (doi:10.1093/beheco/arz095)

37. Walker L, York J, Young A. 2016 Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behav. Ecol.* **27**, 1461–1470. (doi:10.1093/beheco/arw064)

38. Hollén LI, Bell MBV, Radford AN. 2008 Cooperative sentinel calling? Foragers gain increased biomass intake. *Curr. Biol.* **18**, 576–579. (doi:10.1016/j.cub.2008.02.078)

39. Ducatez S, Sayol F, Sol D, Lefebvre L. 2018 Are urban vertebrates city specialists, artificial habitat exploiters, or environmental generalists? *Integr. Comp. Biol.* **58**, 929–938. (doi:10.1093/icb/icy101)

40. Callaghan CT, Major RE, Wilshire JH, Martin JM, Kingsford RT, Cornwell WK. 2019 Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos* **128**, 845–858. (doi:10.1111/oik.06158)

41. UN Department of Economic and Social Affairs. 2018 68% of the world population projected to live in urban areas by 2050, says UN. *U. N.* See https://www.un.org/development/desa/en/news/population/2018-revision-of-world-urbanization-prospects.html.

42. Isaksson C. 2018 Impact of urbanization on birds. In *Bird Species: How They Arise, Modify and Vanish* (ed DT Tietze), pp. 235–257. Cham: Springer International Publishing. (doi:10.1007/978-3-319-91689-7\_13)

43. Marzluff JM. 2001 Worldwide urbanization and its effects on birds. In *Avian Ecology and Conservation in an Urbanizing World* (eds JM Marzluff, R Bowman, R Donnelly), pp. 19–47. Boston, MA: Springer US. (doi:10.1007/978-1-4615-1531-9\_2)

44. Aronson MFJ *et al.* 2014 A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B Biol. Sci.* **281**, 20133330. (doi:10.1098/rspb.2013.3330)

45. Meillère A, Brischoux F, Parenteau C, Angelier F. 2015 Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. *PLOS ONE* **10**, e0135685. (doi:10.1371/journal.pone.0135685)

46. Lowry H, Lill A, Wong BBM. 2013 Behavioural responses of wildlife to urban environments. *Biol. Rev. Camb. Philos. Soc.* **88**, 537–549. (doi:10.1111/brv.12012)

47. Francis RA, Chadwick MA. 2012 What makes a species synurbic? *Appl. Geogr.* **32**, 514–521. (doi:10.1016/j.apgeog.2011.06.013)

48. Marzluff JM, McGowan KJ, Donnelly R, Knight RL. 2001 Causes and consequences of expanding American Crow populations. In *Avian Ecology and Conservation in an Urbanizing World* (eds JM Marzluff, R Bowman, R Donnelly), pp. 331–363. Boston, MA: Springer US. (doi:10.1007/978-1-4615-1531-9\_16)

49. Marzluff JM, Neatherlin E. 2006 Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biol. Conserv.* **130**, 301–314. (doi:10.1016/j.biocon.2005.12.026)

50. Withey JC, Marzluff JM. 2009 Multi-scale use of lands providing anthropogenic resources by American Crows in an urbanizing landscape. *Landsc. Ecol.* **24**, 281–293. (doi:10.1007/s10980-008-9305-9)

51. Withey J, Marzluff J. 2005 Dispersal by juvenile American crows influences population dynamics across a gradient of urbanization. *The Auk* **122**, 205–221. (doi:10.1093/auk/122.1.205)

52. Kern JM, Radford AN. 2016 Anthropogenic noise disrupts use of vocal information about predation risk. *Environ. Pollut. Barking Essex 1987* **218**, 988–995. (doi:10.1016/j.envpol.2016.08.049)

53. Stofberg M, Cunningham S, Sumasgutner P, Amar A. 2019 Juggling a “junk-food” diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosyst.* **22**, 1019–1026. (doi:https://doi.org/10.1007/s11252-019-00885-3)

54. Schulte-Hostedde AI, Mazal Z, Jardine CM, Gagnon J. 2018 Enhanced access to anthropogenic food waste is related to hyperglycemia in raccoons (*Procyon lotor*). *Conserv. Physiol.* **6**.

55. Maccarone AD. 1987 Sentinel behaviour in American crows. *Bird Behav.* **7**, 93–95. (doi:10.3727/015613887791918105)

56. Latta SC, Latta KN. 2015 Do urban american crows (*Corvus brachyrhynchos*) contribute to population declines of the common nighthawk (*Chordeiles minor*)? *Wilson J. Ornithol.* **127**, 528–533. (doi:10.1676/14-181.1)