Chapter 1. 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 an important motivator when discussing foraging and vigilance behaviours in any species. If an individual forgoes vigilance in favor of greater foraging efficiency, they leave themselves exposed to increased predation risk which can have profound negative impacts on their survival. If the same individual were to prioritize vigilance over foraging, the decreased foraging efficiency can negatively affect their fitness. Individuals must therefore carefully balance the time spent performing both foraging and vigilance behaviours. Group foraging can decrease individual vigilance by virtue of increasing the 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 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 (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 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* (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, 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. 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; 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 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 (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 urban-living than specialist species and can benefit from urban areas (Callaghan et al., 2019; Ducatez et al., 2018). Physiological, morphological, and behavioural adaptations being observed in many urbanized species, and are expected to improve a species ability to exploit urban advantages (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 (De León et al., 2019; Gotanda, 2020; Isaksson, 2018; Lowry et al., 2013; Marzluff, 2001; Meillère et al., 2015; J. C. Withey & Marzluff, 2009; J. Withey & Marzluff, 2005). 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).

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 (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 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 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.

References

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: a dynamic game. *The American Naturalist*, *150*(3), 373–392. https://doi.org/10.1086/286070

Bednekoff, P. A. (2001). Coordination of safe, selfish sentinels based on mutual benefits. *Annales Zoologici Fennici*, *38*(1), 5–14.

Bednekoff, P. A. (2015). Sentinel behavior: a review and prospectus. In *Advances in the Study of Behavior* (Vol. 47, pp. 115–145). Elsevier. https://doi.org/10.1016/bs.asb.2015.02.001

Bednekoff, P. A., & Woolfenden, G. E. (2003). Florida scrub-jays ( *Aphelocoma coerulescens* ) are sentinels more when well-fed (even with no kin nearby). *Ethology*, *109*(11), 895–903. https://doi.org/10.1046/j.0179-1613.2003.00926.x

Bednekoff, P. A., & Woolfenden, G. E. (2006). Florida scrub-jays compensate for the sentinel behavior of flockmates. *Ethology*, *112*(8), 796–800. https://doi.org/10.1111/j.1439-0310.2006.01227.x

Blumstein, D. T. (1999). Selfish sentinels. *Science*, *284*(5420), 1633–1634. https://doi.org/10.1126/science.284.5420.1633

Bolwig, N. (1959). A study of the behaviour of the chacma baboon, *Papio ursinus*. *Behaviour*, *14*(1–4), 136–162. https://doi.org/10.1163/156853959X00054

Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T., & Cornwell, W. K. (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*(6), 845–858. https://doi.org/10.1111/oik.06158

Clutton-Brock, T. H., O’Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S., & Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science*, *284*(5420), 1640–1644. https://doi.org/10.1126/science.284.5420.1640

De León, L. F., Sharpe, D. M. T., Gotanda, K. M., Raeymaekers, J. A. M., Chaves, J. A., Hendry, A. P., & Podos, J. (2019). Urbanization erodes niche segregation in Darwin’s finches. *Evolutionary Applications*, *12*(7), 1329–1343. https://doi.org/10.1111/eva.12721

Dharmakumarsinhji, R. S. (1954). *Birds of Saurashtra, India*. The Author, Bhavnagar.

Ducatez, S., Sayol, F., Sol, D., & Lefebvre, L. (2018). Are urban vertebrates city specialists, artificial habitat exploiters, or environmental generalists? *Integrative and Comparative Biology*, *58*(5), 929–938. https://doi.org/10.1093/icb/icy101

Eastcott, E., Kern, J. M., Morris-Drake, A., & Radford, A. N. (2020). Intrapopulation variation in the behavioral responses of dwarf mongooses to anthropogenic noise. *Behavioral Ecology*, *31*(3), 680–691. https://doi.org/10.1093/beheco/araa011

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*(4), 664–671. https://doi.org/10.1111/j.1474-919X.2006.00567.x

Fleischer, A. L., Bowman, R., & Woolfenden, G. E. (2003). Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildland habitats. *The Condor*, *105*(3), 515–527. https://doi.org/10.1093/condor/105.3.515

Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic? *Applied Geography*, *32*(2), 514–521. https://doi.org/10.1016/j.apgeog.2011.06.013

Gaston, A. J. (1977). Social behaviour within groups of jungle babblers (*Turdoides striatus*). *Animal Behaviour*, *25*(4), 828–848.

Gotanda, K. M. (2020). Human influences on antipredator behaviour in Darwin’s finches. *Journal of Animal Ecology*, *89*(2), 614–622. https://doi.org/10.1111/1365-2656.13127

Hailman, J. P., McGowan, K. J., & Woolfenden, G. E. (2010). Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelocoma c. Coerulescens*). *Ethology*, *97*(1–2), 119–140. https://doi.org/10.1111/j.1439-0310.1994.tb01034.x

Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Hollén, L. I., Bell, M. B. V., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, *18*(8), 576–579. https://doi.org/10.1016/j.cub.2008.02.078

Horrocks, J. A., & Hunte, W. (1986). Sentinel behaviour in vervet monkeys: who sees whom first? *Animal Behaviour*, *34*(5), 1566–1568. https://doi.org/10.1016/S0003-3472(86)80226-3

Huels, F. D., & Stoeger, A. S. (2022). Sentinel behavior in captive meerkats (*Suricata suricatta* ). *Zoo Biology*, *41*(1), 10–19. https://doi.org/10.1002/zoo.21644

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

Kern, J. M., & Radford, A. N. (2013). Call of duty? Variation in use of the watchman’s song by sentinel dwarf mongooses, *Helogale parvula*. *Animal Behaviour*, *85*(5), 967–975. https://doi.org/10.1016/j.anbehav.2013.02.020

Kern, J. M., & Radford, A. N. (2014). Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk. *Animal Behaviour*, *98*, 185–192. https://doi.org/10.1016/j.anbehav.2014.10.012

Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. *Environmental Pollution (Barking, Essex: 1987)*, *218*, 988–995. https://doi.org/10.1016/j.envpol.2016.08.049

Kern, J. M., & Radford, A. N. (2018). Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proceedings of the National Academy of Sciences*, *115*(24), 6255–6260. https://doi.org/10.1073/pnas.1801000115

Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11–20. https://doi.org/10.1016/0003-3472(95)80149-9

Lima, S. L. (1998). Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. In A. P. Møller, M. Milinski, & P. J. B. Slater (Eds.), *Advances in the Study of Behavior* (Vol. 27, pp. 215–290). Academic Press. https://doi.org/10.1016/S0065-3454(08)60366-6

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews of the Cambridge Philosophical Society*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Maccarone, A. D. (1987). Sentinel behaviour in American crows. *Bird Behavior*, *7*(2), 93–95. https://doi.org/10.3727/015613887791918105

Manser, M. (2018). Meerkats – identifying cognitive mechanisms underlying meerkat coordination and communication: Experimental designs in their natural habitat. In N. Bueno-Guerra & F. Amici (Eds.), *Field and Laboratory Methods in Animal Cognition* (1st ed., pp. 286–307). Cambridge University Press. https://doi.org/10.1017/9781108333191.015

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian Ecology and Conservation in an Urbanizing World* (pp. 19–47). Springer US. https://doi.org/10.1007/978-1-4615-1531-9\_2

Marzluff, J. M., McGowan, K. J., Donnelly, R., & Knight, R. L. (2001). Causes and consequences of expanding American crow populations. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian Ecology and Conservation in an Urbanizing World* (pp. 331–363). Springer US. https://doi.org/10.1007/978-1-4615-1531-9\_16

Marzluff, J. M., & Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation*, *130*(2), 301–314. https://doi.org/10.1016/j.biocon.2005.12.026

McGowan, K. J., & Woolfenden, G. E. (1989). A sentinel system in the Florida scrub jay. *Animal Behaviour*, *37*, 1000–1006. https://doi.org/10.1016/0003-3472(89)90144-9

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*(8), e0135685. https://doi.org/10.1371/journal.pone.0135685

Morris-Drake, A., Christensen, C., Kern, J. M., & Radford, A. N. (2019). Experimental field evidence that out-group threats influence within-group behavior. *Behavioral Ecology*, *30*(5), 1425–1435. https://doi.org/10.1093/beheco/arz095

Olson, R. S., Haley, P. B., Dyer, F. C., & Adami, C. (2015). Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *Royal Society Open Science*, *2*(9), 150135. https://doi.org/10.1098/rsos.150135

Ostreiher, R., & Heifetz, A. (2017). The sentinel behaviour of Arabian babbler floaters. *Royal Society Open Science*, *4*(2), 160738. https://doi.org/10.1098/rsos.160738

Ostreiher, R., & Heifetz, A. (2019). The sentineling-foraging trade-off in dominant and subordinate arabian babblers. *Ethology*, *125*(2), 98–105. https://doi.org/10.1111/eth.12833

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

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. *Pakistan Journal of Zoology*, *52*(5), 1701–1708. https://dx.doi.org/10.17582/journal.pjz/20170420070416

Rauber, R., Clutton-Brock, T. H., & Manser, M. B. (2019). Drought decreases cooperative sentinel behavior and affects vocal coordination in meerkats. *Behavioral Ecology*, *30*(6), 1558–1566. https://doi.org/10.1093/beheco/arz112

Rauber, R., & Manser, M. B. (2021). Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats. *Animal Behaviour*, *171*, 129–138. https://doi.org/10.1016/j.anbehav.2020.11.014

Santema, P., & Clutton-Brock, T. (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Animal Behaviour*, *85*(3), 655–661. https://doi.org/10.1016/j.anbehav.2012.12.029

Santema, P., Teitel, Z., Manser, M., Bennett, N., & Clutton-Brock, T. (2013). Effects of cortisol administration on cooperative behavior in meerkat helpers. *Behavioral Ecology*, *24*(5), 1122–1127. https://doi.org/10.1093/beheco/art039

Schulte-Hostedde, A. I., Mazal, Z., Jardine, C. M., & Gagnon, J. (2018). Enhanced access to anthropogenic food waste is related to hyperglycemia in raccoons (*Procyon lotor*). *Conservation Physiology*, *6*. https://api.semanticscholar.org/CorpusID:51609895

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 Ecosystems*, *22*, 1019–1026. https://doi.org/10.1007/s11252-019-00885-3

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57.

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

Walker, L., York, J., & Young, A. (2016). Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behavioral Ecology*, *27*(5), 1461–1470. https://doi.org/10.1093/beheco/arw064

Withey, J. C., & Marzluff, J. M. (2009). Multi-scale use of lands providing anthropogenic resources by American Crows in an urbanizing landscape. *Landscape Ecology*, *24*(2), 281–293. https://doi.org/10.1007/s10980-008-9305-9

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

Wright, J., Berg, E., De Kort, S. R., Khazin, V., & Maklakov, A. A. (2001a). Cooperative sentinel behaviour in the Arabian babbler. *Animal Behaviour*, *62*(5), 973–979. https://doi.org/10.1006/anbe.2001.1838

Wright, J., Berg, E., De Kort, S. R., Khazin, V., & Maklakov, A. A. (2001b). Safe selfish sentinels in a cooperative bird: *Safe selfish sentinels*. *Journal of Animal Ecology*, *70*(6), 1070–1079. https://doi.org/10.1046/j.0021-8790.2001.00565.x

Wright, J., Maklakov, A. A., & Khazin, V. (2001). State-dependent sentinels: An experimental study in the Arabian babbler. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1469), 821–826. https://doi.org/10.1098/rspb.2000.1574