**Introduction**

Sentinel behavior is a form of coordinated vigilance observed in social species, where an individual adopts a prominent exposed position to perform constant vigilance and make alarm calls in response to threats while others forage or engage in other activities. The most recognizable sentinel species is the meerkat with sentinels adopting a bipedal stance to increase their field of view. The presence of a sentinel can result in increased foraging efficiency and biomass intake while reducing predation risk in foragers. Sentinel behaviour is therefore incredibly beneficial to foragers but appears to be at the detriment of the sentinel. While performing sentinel behaviour, an individual incurs the loss of foraging opportunities raising interest in the underlying mechanisms behind what appeared to be a form of altruism in nature. More recently, a state-dependent model for sentinel decision-making has garnered support from empirical studies on this behaviour, where individuals decide to perform sentinel behaviour based on their energetic levels and the benefits it offers the sentinel. Studies on satiation and body mass support this explanation, but the decision to perform sentinel behaviour is not only affected by these internal factors. Sex and risk can also affect an individual’s decision to perform the behaviour. Studying how internal and external influences can affect sentinel behaviour can shed light on how individual choose to participate in social behaviours and can provide insights into the evolution of cooperative behaviours.

Behavioural plasticity is crucial for individuals faced with changing environment, where failure to adapt could result in inefficiencies that can negatively impact survival. Studies on urban adaptation have shown that individual behaviours can change to best take advantage of city living, though comparatively fewer studies have been performed on social behaviours. Changes in social behaviours, like sentinel behaviour, can be adaptive in cities, affecting the success of urban social species. A wholistic understanding of the factors involved in social behaviour decision-making could then help us predict how these behaviours can change in urban environments.

The objective of this scoping review is to identify and analyse the factors that affect sentinel behaviour. By reviewing studies that investigate both intrinsic and extrinsic factors, we aim to identify common patterns and trends in sentinel behavior across different species and environments. To best understand sentinel decisions in individuals, we will search for empirical studies on the behaviour of non-aquatic vertebrates, excluding studies that did not test the effects of a factor on sentinel behaviour. We will analyse the main trends observed and synthesize these findings to understand the influence of internal and external factors. We will then discuss how urbanization can affect sentinel behaviour by altering the factors involved in sentinel decisions.

Gaining a wholistic perspective of the factors involved in the decision to perform sentinel behaviour can benefit the understanding of decisions involved in other similar social behaviours. Other antipredator behaviours such as the coordination of vigilance in foragers could be affected by the same factors involved in sentinel behaviour. The presence of predators can increase the need for vigilance, resulting in an increase in the behaviour. Conservation ecologists can use this change in behaviour to better understand an individual’s perception of its environment. This can help guide urban planning in reducing sources of stress in at-risk species. The effects of social factors on social behaviours, such as dominance hierarchies and the number of individuals in a group can also affect social vigilance behaviours in the same manner as sentinel behaviour. By understanding the effects of social factors on sentinel behaviour, we could better interpret changes in social behaviours and possibly infer changes in social structures and dynamics in populations. This could reduce the time and effort required in sampling whole populations and making quick assessments of the direction of changes at the population level. Likewise, energy-related factors can change the availability of energy resources required to perform costly social behaviours. Increased presence and quality of food sources could increase the energetic reserves of an individual, increasing its ability to perform sentinel behaviour. Understanding how human activity can impact social behaviours can help minimize our effects on urban wildlife. Sentinel behaviour could also be used to help monitor sentinel species at risk, informing conservation ecologists on the relative health and stress in at-risk populations, and can help guide policies aimed at reducing the success of particularly successful sentinel species like corvids.

The need for a comprehensive review of factors influencing sentinel behavior is highlighted by the complexity of urban environments and their effects on wildlife behavior. Urbanization can lead to adaptations in social behaviors, including sentinel behavior, yet there remains a gap in understanding how urbanization affects sentinel behavior. By conducting a thorough review of the literature on sentinel behaviour, this study aims to provide a comprehensive overview of the factors influencing this social behavior

**Discussion**

**Intrinsic Factors:**

Our review identified several intrinsic and extrinsic factors that can influence sentinel behavior in avian and mammal species. The common intrinsic factors tested were sex, maturity, body mass and satiation. The effects of sex were consistent throughout species, with males engaging in sentinel behaviour more than females The difference in sentinel behaviour could be attributed to differences in energetic investment between sexes, with males having more energy available for activities outside of reproduction. Male reproduction is less energetically costly than in females (sperm vs. egg production) which would result in additional energy able to be allocated towards other behaviours including sentinel behaviour. This is especially true during the breeding season when females could be investing considerable amounts of time and energy into caring for young. In red-winged blackbirds (*Agelaius phoeniceus*), males assume the role of nest guarding through sentinel behaviour, with nest success associated with closer and higher perches. Likewise in Zebra finch, sentinels, which were most often males, alerted their partners when threats approached the nest, resulting in incubating individuals flushing their nests earlier than when sentinels were absent. The benefits from sentinel behaviour could therefore extend past increased foraging efficiency and increased biomass intake, but also to increased nest success and mate survival.

Sentinel behaviour could also play a role in male intrasexual competition over mates and territories. When encountering a foreign male’s solo song, dominant male white-browed sparrow weavers (*Plocepasser mahali*) increased their sentinel effort despite already sentineling more than other group members. The increased sentinel behaviour of dominant male individuals could be to detect and gather information about the intruding individual. The use of sentinel behaviour for non-antipredator vigilance is also observed in mammal species. When encountering signs of rival groups, dwarf mongoose (*Helogale* parvula) more regularly engaged in sentinel behaviour to gather more information about the threat. Since dominant males are most often usurped by out-group individual rather than subordinates, early detection and monitoring of rivals is essential for dominant males to maintain their position in the group. This interaction between sex and dominance, an extrinsic factor, is often reported in studies, with dominant males sentineling more than other group members. Consistent with the hypothesis of differing energetic investment between sexes, subordinate males sentineled more than subordinate females in both mammal and avian species.

Another intrinsic factor identified in our review was maturity. Older and more experienced individuals sentineled more than younger individuals. Younger individuals could be inefficient sentinels as they lack the experience to identify potential threats. The misidentification of a threat could result in mortality or to unnecessary energetic expenditure. If a threat is undetected by the sentinel, foragers could be at greater risk of predation due to their reliance on the sentinel’s vigilance, resulting in injury or death. Though less detrimental to an individual’s immediate survival, inappropriate alarm calls are detrimental to foraging efficiency and diminish the benefits provided by sentinel behaviour. Correct identification of threats is therefore crucial for effective sentinel behaviour. Older individuals could have had greater exposure to potential threats present in the environment and can better recognize and vocalize the presence of a threat. Younger individuals could also take advantage of the sentinel behaviour of more experienced individuals to learn to identify threats. Social learning helps mitigate the costs of learning about threats by reducing the risk of injury or mortality of learning through direct exposure to danger.

Older and more experienced individuals could also have greater energetic resources to allocate to sentinel behaviour. Mature adults could have more efficient foraging strategies and no longer need to allocate as much energy to growth and development, reducing the costs of performing sentinel behaviour. In comparison, maturing young could have a different allocation of energy and could be less capable of spending energy being sentinel and instead favouring foraging to compensate for the lower foraging efficiency and their growth.

Energetic resources therefore play a considerable role in an individual’s decision to perform sentinel behaviour. The selfish state-dependent model proposes that an individual will perform sentinel behaviour if the alternative is foraging without a sentinel present, a considerably more dangerous option. However, sentinel behaviour is only favourable if the individual has sufficient energetic reserves to perform this behaviour. The results of studies on the effects of satiation and body mass on sentinel behaviour are consistent with this hypothesis, with heavier and more satiated individuals sentineling more than lighter, unsatiated individuals. Sentinel behaviour is unfavourable for individuals lacking sufficient energetic levels to perform it as the long periods of vigil are lost foraging opportunities for the individual. Instead, it would be most beneficial to forage quickly and maintain sufficient individual vigilance to limit the risk of predation. Individuals capable of more efficient foraging, achieving the minimal energetic threshold to perform sentinel behaviour quicker than other individuals, therefore sentinel earlier and more than other group members. This was supported by the results of studies on dwarf mongoose and, Arabian babblers (*Turdoides squamiceps*), and Florida scrub-jays (Aphelocoma coerulescens) which found that fed individuals often immediately commenced sentinel behaviour. Satiated individuals also decreased their foraging behaviour and sentineled more and longer than unsatiated individuals. In response to the increased sentinel behaviour of a group member, other members compensated and decreased their own sentinel behaviour. These findings suggest that upon achieving sufficient energetic reserves, sentinel behaviour could be the most beneficial activity for the individual.

Originally believed to be a selfless behaviour, sentinel behaviour as explained by the state-dependent model for sentinel decision-making could be a result of selfish decisions made by the individual to satisfy their personal needs. The energetic state of the individual appears to be trade off for increased the increased individual safety provided by sentinel behaviour. When under risk of predation, sentinels could identify threats and reach a safe refuge earlier than foragers. Intrinsic factors identified by our review can affect the energetic investment and reserves of individuals, altering their behaviour. Though the benefits of sentinel behaviour are mainly antipredator vigilance, dominant males could have ulterior motives for performing the behaviour, further altering their propensity to perform sentinel behaviour.

**Extrinsic Factors:**

Our review has also identified several extrinsic factors that can affect sentinel behaviour. Dominance, group size, and risk play significant roles in shaping sentinel behavior in mammal and avian species. These factors influence sentinel decision-making often in conjunction with intrinsic factors. Social hierarchies within groups can significantly affect sentinel behaviour, with dominant individuals sentineling more than subordinates. Dominant individuals could have greater access to resources, either through more effective foraging strategies or receiving gifts from other members of the group, reducing the lost foraging opportunity cost of performing the behaviour. The differences in sentinel behaviour between dominant and subordinate individuals could also reflect the differences in benefits received by the sentinel. Dominant, usually male, individuals could also be using the behaviour for non-antipredator benefits, but instead to guard against outgroup rivals and territory intrusions as previously discussed. Subordinates do contribute to a group’s sentinel behaviour but could be compensating for the dominant individual’s sentinel behaviour by reducing theirs. When fed however, subordinate Arabian babblers increased the duration of their sentinel bouts significantly more than dominants in comparison to when unfed, indicating they ended their bouts with a lower energetic state than dominants. This could point to yet another difference in energetic investment among group members, causing a difference in their individual contribution to the group’s sentinel behaviour.

The effects of group size on sentinel behaviour are not surprising. The greater the number of group members, the greater the likelihood of an individual having sufficient energetic reserves to sentinel. Larger groups will therefore see decreased individual sentinel behaviour but more sentinel behaviour at the group level, with fewer and shorter gaps between bouts of sentinel behaviour. In smaller groups, individuals must perform longer bouts of sentinel behaviour, increasing costs of sentinel behaviour for participating group members. Though, larger groups can result in increased competition for limited resources, possibly increasing the reliance on the added vigilance of the sentinel during scramble competition. Larger groups can more effectively distribute the costs of sentinel behaviour among members, while also providing other predation risk-reducing effects through other group-size effects such as the Many Eyes hypothesis.

Increased risk had similar effects on the sentinel behaviour of avian and mammal species, where increased sentinel behaviour was observed in situations of heightened risk. This risk can be from the presence of predators but also the presence of outgroup rivals and territory intruders, which caused an increase in sentinel behaviour. The collection of information on potential threats is essential to the survival of individuals. Earlier detection of predators can reduce the risk of mortality and injury because of an interaction with a predator, increasing survival of group members and mates. The presence of at-risk individuals, such as young individuals, also resulted in an increase in sentinel behaviour, likely to compensate for an increase in predation risk. In meerkats (*Suricata suricatta*), the presence of pups significantly increased the sentinel behaviour of subordinates during foraging trips. The presence of young in the group could increase predation risk if young individuals are more vulnerable or have inefficient vigilance due to a lack of experiences with threats. Their inclusion in foraging groups could therefore increase the group’s risk of predation, resulting in increased sentinel behaviour in adult members. Reduced risk environments, such as in captivity, have shown that captive meerkats behaved similarly to their wild counterparts suggesting that sentinel behaviour is plastic, but does not disappear in the absence of predation risk. Instead, individuals could be upregulating their sentinel behaviour in response to increased perceived threat but maintain a ‘baseline’ level of sentinel behaviour in times of low risk, further supporting the hypothesis that the behaviour is dependent on the selfish motivation of individuals.

Extrinsic factors can also modify the effectiveness of the sentinel, diminishing the benefits provided to the non-sentinel individuals. Factors such as access to adequate sentinel locations, anthropogenic noise and factors that increase environmental uncertainty such as visual obstructions (e.g. tall grasses), shorter lines of sight and novel stimuli can also alter an individual’s need for vigilance and by extension sentinel behaviour. In dwarf mongoose, the presence of anthropogenic noises significantly affected the ability to hear acoustic signals from the sentinel, reducing their effectiveness. Foragers were observed to increase their personal vigilance in response to compensate. The wealth of environmental factors that can increase the anxiety and need for vigilance require further study to assess their impacts on sentinel behaviour.

The likelihood of an individual to perform sentinel behaviour can therefore be affected by extrinsic as well as intrinsic factors, revealing a remarkably plastic behaviour. By altering changing their behaviour, individuals can best manage their own needs for foraging and vigilance based on their energetic reserves and the perceived threats in their environments. This ability to alter their behaviour can be adaptive in highly variable environments. While the benefits are primarily to the sentinel, either increased safety or increased ability to gather information, the presence of a sentinel is advantageous to other group members. Foragers could gain increased biomass intake and foraging efficiency while lowering their risk of predation, thereby increasing the success of sentinel species.

**Coordination of Sentinel Behavior:**

Coordination of sentinels has been identified as the defining feature of true sentinel systems. The adoption of an exposed prominent position from which to perform constant vigilance, and the communication of threats through alarm calls are not behaviours exclusive to sentinel behaviour. These characteristics can not be solely relied upon to describe a sentinel species. Instead, the coordination of sentinel bouts to ensure no overlap and reduce gaps should then appear more frequently in contemporary literature on sentinel behaviour. Despite this, there is a low number of articles that explicitly mention coordination in their definition of sentinel behaviour, though an upward trend is detected in articles published after 2017. However, this is not accompanied by a decrease in the number of articles without this criterion. By not including and testing for the coordination of sentinels, we are exposing ourselves to increased risk of misidentification of sentinel species. The correct identification of sentinel systems is required to further our understanding of the underlying mechanisms behind these complex social behaviours.

**Exploration of Urbanization Effects:**

Urbanization is an important driver of behavioural change. Animals will alter their behaviours to increase success in their environments, and the effects of urbanization on individual behaviours has frequently been studied in a variety of species. Less researched are the effects of urbanization on social behaviour such as sentinel behaviour. The effects of factors such as sex and maturity are unalterable by the environment, both intrinsic and extrinsic factors are predicted to be affected by urbanization. Urban environments often have an increased abundance and predictability of anthropogenic foods. Human food could have considerably more calories, resulting in increased energetic intake and possible satiation. Individuals who have fed on human foods could then shift their preference towards human foods and are more likely to perform sentinel behaviour by having greater energetic reserves. Factors that can affect the energetic levels of individuals could therefore also alter their sentinel behaviour. Additional studies on the effects of anthropogenic food sources on sentinel behaviour could help elucidate one way urbanization can affect the behaviour but could provide additional support to the selfish state-dependent model.

Urbanization also has the effect of increasing the density of individuals in urban areas, increasing the number of groups as well as potentially the number of individuals in the groups. This can have a two-fold effect on sentinel behaviour. Greater group sizes are expected to decrease individual sentinel behaviour as there are a greater number of individuals capable of performing sentinel behaviour. On the other hand, the increase in frequency of interactions with out group rivals is expected to increase the sentinel behaviour of certain group members, typically dominant males. How urbanization can alter the social dynamics of a species is an interesting avenue for future research, and the downstream effects on sentinel behaviour could differ greatly between group-members. Individual-level variations in behaviour could reflect differences in personal motivations and could support the hypothesis that sentinel behaviour could play a role in non-antipredator behaviours.

Urbanization could affect an individual’s perception of the threats in their environment. Disruptive factors such as anthropogenic noise can decrease the effectiveness of sentinels. By disrupting forager-sentinel communication, this can result in foragers relying less on the sentinel’s vigilance, affecting their foraging efficiency. The shortening or obstruction of lines of sight could affect the sentinel’s ability to identify threats in time, possibly increasing the risk of predation to themselves and other group members. If the benefits to the sentinel decrease, then the option to forage without a sentinel could be favored. A surprising finding in future studies could be a decrease in sentinel behaviour and increased reliance on other types of coordinated vigilance in urban environments. Though this would not be expected, the possibility of such a shift in social behaviour in urban environments reinforces the need for further research. Habitat alteration could also beneficially affect sentinel behaviour by increasing the presence of perches and elevated locations from which to sentinel from. Lampposts are frequently used by avian species and are elevated positions that offer wide fields of view. Artificial lighting could also increase the ability of the sentinel to identify threats during dusk and dawn. Microenvironments within urban centers could also cause variations in sentinel behaviour, as urban environments can be highly heterogenous. Factors that contribute to sentinel decision-making could differ wildly between an undeveloped area and a grocery store parking lot. Predation risk due to the presence of urban raptors could also differ within urban environments, with urban green areas being hunting areas for species such as the red-tailed hawk. Studying the differences in sentinel behaviour between different types of urban environment could reveal more subtle factors at play in sentinel decision-making.

**Implications and Future Directions:**

The findings of this review should demonstrate that sentinel behaviour is a plastic behaviour that serves primarily the sentinel, revolving generally around an individual’s need to forage (i.e. to maintain sufficient energetic reserves) and for safety. Several intrinsic and extrinsic factors can alter an individual’s propensity to perform sentinel behaviour through changes in energetic investment and requirements. An individual’s perception of its environment can then further affect an individual’s requirement for information on potential threats, thereby increasing their requirement for sentinel behaviour. Individuals can therefore modify their sentinel behaviour to best meet their personal and energetic requirements. Other group members can then alter their own behaviour to maximise the advantages provided by the sentinel, demonstrating a complex interaction between sentinel and forager. As we continue to research social behaviours, we must continue to take into consideration both intrinsic and extrinsic motivators, as we have shown that they can often interact and significantly alter behaviours. Studying the interaction between intrinsic and extrinsic factors can provide insights into the complex social dynamics and decision-making processes that behind sentinel behavior in animal groups. Further studies are required to continue analyzing this relationship and to better understand how behaviours like sentinel behaviour have evolved and become adaptive.

The effects of urban environments on sentinel behaviour require additional investigations, as human-altered environments continue to expand and affect sentinel species. How sentinel species will respond to urban living conditions must be researched. Factors such as resource availability and anthropogenic disturbances can have significant effects on social behaviours and reveal more about how individuals decide to perform sentinel behaviour. The relative lack of studies on the effects of urbanization on social behaviours, when compared to the abundance of studies on individual behaviours, represents a considerable gap in our understanding of the effects of urbanization on wildlife.

As urbanization continues globally, it is associated with a loss of biodiversity and an increase in the abundance of urbanized species. Some of these species could have adaptive behaviours such as sentinel behaviour, which in turn can contribute to the success of these species in urban environments. By further researching the effects of urbanization on social behaviours, we could infer how social species will react to urban living and help guide urban planning to better protect social species at risk.

Future research should also endeavour to create standardized protocols for testing the effects of factors such as body mass and satiation in a variety of species. These standardized protocols would permit better comparisons between species. Additionally, future research should seek additional sentinel species to determine if there are any species-specific differences in sentinel systems. Many studies focus on a limited number of species, often birds or mammals, neglecting other taxa such as reptiles, and amphibians. The study of a wider variety of sentinel species could help identify general patterns across taxa and understand the evolutionary drivers of sentinel behavior.

Our scoping review has identified several intrinsic and extrinsic factors that can significantly alter sentinel behaviour in avian and mammal species. These effects can often interact with one another, further complicating the role of internal and external influences on this social behaviour. Though the effects of urbanization on sentinel behaviour have yet to be fully understood, its potential effects on an individual’s energetic reserves and the perception of threat in its environment cannot be ignored and demand further study. Future research should focus on this source of variation in social behaviours such as sentinel behaviour. This knowledge can inform conservation efforts and urban planning to mitigate the impacts of human activities on wildlife. Ultimately, this research contributes to a deeper understanding of the intricate relationship between animals and their environments, highlighting the need for conservation strategies that consider both the individual and the ecosystem.