Chapter 2. Sentinel behaviour in mammalian and avian species

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Introduction

Sentinel behaviour 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 (Bednekoff, 2015). A highly recognizable sentinel species is the meerkat with sentinels adopting a bipedal stance. The presence of a sentinel can result in increased foraging efficiency and biomass intake while reducing predation risk in foragers (Clutton-Brock et al., 1999; Hollén et al., 2008; Kern & Radford, 2014). 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 questions about the underlying mechanisms behind sentinel decision-making. 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 receives from performing the behaviour (Bednekoff, 1997, 2001). Studies on satiation and body mass support this explanation (Arbon et al., 2020; Bednekoff & Woolfenden, 2003). Other intrinsic (internal, e.g. age, sex) and extrinsic (external or social, e.g. dominance, risk) factors can also affect an individual’s decision to perform the behaviour (Bednekoff, 2015).

Studying how intrinsic and extrinsic factors can affect sentinel behaviour can shed light on how individuals choose to participate in social behaviours and can provide insights into the evolution of cooperative behaviours. 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. Likewise, resource-related factors can change the availability of energy needed to perform costly social behaviours. Increased presence and quality of food sources can increase the energetic reserves of an individual, increasing its ability to perform sentinel behaviour (Arbon et al., 2020; Bednekoff & Woolfenden, 2003; Manser, 2018). Studies on urban adaptation have shown that individual behaviours change to best take advantage of city living (Gotanda, 2020; Isaksson, 2018; Lowry et al., 2013), though comparatively fewer studies have been performed on social behaviours (Łopucki et al., 2021). Behavioural plasticity is crucial for individuals faced with a changing environment, where failure to adapt could result in inefficiencies that can negatively impact survival. Changes in social behaviours, like sentinel behaviour, can be adaptive in cities and could greatly improve the success of a species in urban areas.

Our objective was to explore the mechanisms underlying sentinel decision-making by identifying and analyzing the factors that affect sentinel behaviour in a scoping review. By reviewing studies that investigate both intrinsic and extrinsic factors, we aimed to identify common patterns and trends in sentinel behaviour across different species and environments. To best understand sentinel decision-making, we searched for empirical studies on the behaviour of non-aquatic vertebrates, excluding studies that did not test the effects of a factor on sentinel behaviour (e.g. articles identifying a new sentinel species). We analyzed the main trends observed and synthesized these findings to understand the influence of intrinsic and extrinsic factors. We then discussed how urbanization can affect sentinel behaviour by altering the factors involved in sentinel decisions. Urbanization can lead to adaptations in social behaviours, including sentinel behaviour, yet there remains a gap in understanding how urbanization affects sentinel behaviour. The need for a comprehensive review of factors influencing sentinel behaviour is highlighted by the complexity of urban environments and their effects on wildlife behaviour.

The synthesis of information on the factors involved in sentinel decision-making can further our understanding of social behaviours in general. Other social antipredator behaviours, such as the coordination of vigilance in foragers, can be affected by the same factors involved in sentinel behaviour. By conducting a thorough review of the literature on sentinel behaviour, this study aimed to provide a comprehensive overview of the factors influencing this social behaviour.

Methods

This scoping review followed the ROSES standards of reporting for scoping and systematic reviews to the best of our ability (Haddaway et al., 2018). The protocol was not pre-published, though our objective was to ensure transparency and maximize the reproducibility of the search performed.

Selection criteria

The inclusion and exclusion criteria for the screening were identified and noted before initiating database searches (Table 1). We searched various databases for studies on the effects of a factor on a quantitative measurement of sentinel behaviour (e.g., frequency, duration, number of bouts, etc.). We only included articles that tested sentinel behaviour in terrestrial or avian vertebrates. Aquatic species can have different methods of identifying threats and communicating their presence. We excluded articles published before 1970 because the definition of sentinel behaviour before this date was nebulous and not consistent with the currently used definition of sentinel behaviour. For inclusion, we defined sentinel behaviour as an individual that adopted a prominent, exposed position and whose purpose was to maintain constant vigilance over other group members, whether coordinated or not (Bednekoff, 2015; Blumstein, 1999). Theoretical or review articles were excluded, though review article citations were screened. We also excluded mixed-species flocks to better observe effects on sentinel behaviour within a species, without the effects of eavesdropping and fake alarm cries performed by other species (Ridley et al., 2014).

Search strategy

On Jan. 24th, 2022, a preliminary search was performed on Web of Science and Google Scholar to find relevant articles and generate a list of exemplar articles using “sentinel behaviour in animals” as a search string. This list of 20 articles was subsequently used to test the comprehensiveness of the final search strategy and screening. Common keywords in the exemplar articles were compiled and used to develop the search string. The final search string we used to search for articles was "Sentinel AND Behavio\*" (Table 2). We filtered the articles by removing articles in fields unrelated to behaviour (e.g., sleep, remote sensing). On Nov. 1st, 2022, we searched through Web of Science Complete, which included Web of Science Core, Current Contents Connect, Zoological Records, SciELO Citation Index, KCI-Korean Journal Database, BIOSIS Citation Index, Data Citation Index. Using the factors identified during the full-text screening of articles, ELICIT was used to search for any articles not present in the databases searched on Nov. 20th,2023 using variations of the search string “How does [factor] affect sentinel behaviour?” (Kung, 2023).

Data collection and analysis

Titles and abstracts were screened three times using the "Metagear" package in R (v.4.2.3, (Lajeunesse, 2015)) by following the inclusion and exclusion criteria (Table 1). Full texts of articles were then screened for inclusion or exclusion based on our criteria. How changes in sentinel behaviour were measured (e.g. total duration, length of bout) and which factors tested by the articles were recorded, as well as the species of interest. We later grouped the factors as either intrinsic or extrinsic (see Table 3). We also kept a record of articles that defined sentinel behaviour, and if that definition included coordination as a defining feature as proposed by Bednekoff (Bednekoff, 2015).

Table 1: Inclusion and exclusion criteria for the scoping review

|  |  |
| --- | --- |
| **Inclusion Criteria** | **Description** |
| Study design | Study must be experimental; testing the effect of one or more factors on some element of sentinel behaviour. |
| Model species | Animal species must be terrestrial or avian, and vertebrate. |
| Date of publication | Article must have been published after 1970. |
| Major concepts | Must be related to behaviour, behavioural ecology, or adjacent and related fields. |
|  |  |
| **Exclusion Criteria** | **Description** |
| Study design | Study must not be descriptive (e.g. X species has a sentinel system), or mathematical/theoretical. |
| Model species | Animal species must not be aquatic and must not be invertebrate. |
| Date of publication | Article must not have been published before 1970. |
| Major concepts | Exclude studies from non-behaviour-related fields (e.g. remote sensing, sentinels of ecosystem health/biodiversity, sleep). |

Table 2: Search string used on November 1st, 2022.

|  |  |
| --- | --- |
| **Element** | **String** |
| Topic | sentinel AND Behavio\* |
| Language | “ENGLISH” |
| Subject | “BEHAVIORAL SCIENCES” |
| NOT Subject | "HEALTH CARE SCIENCES SERVICES" OR "PEDIATRICS" OR "PHARMACOLOGY PHARMACY" OR "MARINE FRESHWATER BIOLOGY" OR "GENERAL INTERNAL MEDICINE" OR "METEOROLOGY ATMOSPHERIC SCIENCES" OR "SUBSTANCE ABUSE" OR "CRIMINOLOGY PENOLOGY" OR "RADIOLOGY NUCLEAR MEDICINE MEDICAL IMAGING" OR "SURGERY" OR "MEDICAL LABORATORY TECHNOLOGY" OR "PUBLIC ENVIRONMENTAL OCCUPATIONAL HEALTH" OR "WOMEN APOS S STUDIES" OR "GEOCHEMISTRY GEOPHYSICS" OR "RESEARCH EXPERIMENTAL MEDICINE" OR "IMAGING SCIENCE PHOTOGRAPHIC TECHNOLOGY" OR "EDUCATION EDUCATIONAL RESEARCH" OR "BUSINESS ECONOMICS" OR "BIOTECHNOLOGY APPLIED MICROBIOLOGY" |

Table 3: List of intrinsic and extrinsic factors identified in retained articles.

|  |  |  |
| --- | --- | --- |
| **Factor Type** | **Factors Identified** | **Number of studies** |
| **Intrinsic** |  |  |
|  | Maturity | 7 |
|  | Body mass | 4 |
|  | Cortisol | 1 |
|  | Dulled epaulets | 1 |
|  | Satiation | 8 |
|  | Sex | 17 |
| **Extrinsic** |  |  |
|  | Anthropogenic disturbances | 4 |
|  | Breeding period | 2 |
|  | Dominance | 12 |
|  | Drought | 1 |
|  | Group activity | 1 |
|  | Group size | 10 |
|  | Habitat | 1 |
|  | Pair status | 1 |
|  | Presence of rivals | 2 |
|  | Presence of young | 4 |
|  | Risk | 7 |
|  | Time of day | 3 |

Results

Our search string yielded 364 articles on Web of Science. Title and abstract screening rejected 274 articles, three articles were unretrievable, and 48 articles were rejected during full-text screening (Figure 1). We retained 42 studies that met the inclusion criteria. Our search of Web of Science Complete and subsequent screening successfully retained 85% of the exemplar articles (17/20 articles, higher than the minimum pre-established threshold of 80%).

We retained 29 articles that conducted studies on sentinel behaviour on avian species, with most studies being performed on *Argya squamiceps* (N=6), *Turdoides spp.* (N=5), *Aphelocoma spp.* (N=5), and red-winged blackbirds (*Agelaius phoeniceus*, N=3) (Table 3). The other 13 studies were conducted on mammal species, namely on meerkats (*Suricata suricatta,* N=7), dwarf mongooses (*Helogale parvula,* N=5), and vervet monkeys (*Chlorocebus aethiops sabaeus*, N=1).

Overall, the effects of extrinsic factors on sentinel behaviour were tested in 13 studies, and 9 studies tested the effects of intrinsic factors on sentinel behaviour (Table 4). The effects of both intrinsic and extrinsic factors were tested in 20 studies, the majority of which were studies testing the interactive effects of sex and dominance on sentinel behaviour. The effects of sex (N=17), dominance (N=12), and group size (N=10) were the most studied factors (Table 3). The effects of satiation (N=8), risk (N=7), and maturity (N=7) were also frequently studied.

A diagram of a flowchart

Description automatically generated

Figure 1: ROSES Flow diagram showing literature sources and inclusion/exclusion process.

Table 4: Number of articles retained by the search strategy separated by factors tested and mention of coordination as a defining feature of sentinel behaviour.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | **Coordination** | |  | **Factors Tested** | | |  |  |
| **Species** |  | **NO** | **YES** |  | **Extrinsic** | **Intrinsic** | **Both** |  | **Nb. of studies** |
| **Avian** |  | **19** | **10** |  | **8** | **7** | **14** |  | **29** |
| ***Agelaius*** |  |  |  |  |  |  |  |  |  |
| *phoeniceus* |  | 2 | 1 |  |  | 2 | 1 |  | 3 |
| ***Aphelocoma*** |  |  |  |  |  |  |  |  |  |
| *californica* |  | 1 |  |  |  | 1 |  |  | 1 |
| *coerulescens* |  | 1 | 3 |  |  | 2 | 2 |  | 4 |
| ***Argya*** |  |  |  |  |  |  |  |  |  |
| *squamiceps* |  | 3 | 3 |  |  |  | 6 |  | 6 |
| ***Furnarius*** |  |  |  |  |  |  |  |  |  |
| *rufus* |  | 1 |  |  | 1 |  |  |  | 1 |
| ***Grus*** |  |  |  |  |  |  |  |  |  |
| *nigricollis* |  |  | 1 |  | 1 |  |  |  | 1 |
| ***Haliaeetus*** |  |  |  |  |  |  |  |  |  |
| *leucephalus* |  | 1 |  |  |  |  | 1 |  | 1 |
| ***Malurus*** |  |  |  |  |  |  |  |  |  |
| *cyaneus* |  | 1 |  |  | 1 |  |  |  | 1 |
| ***Melierax*** |  |  |  |  |  |  |  |  |  |
| *canorus* |  | 1 |  |  |  | 1 |  |  | 1 |
| ***Perdix*** |  |  |  |  |  |  |  |  |  |
| *perdix* |  | 1 |  |  |  |  | 1 |  | 1 |
| ***Plocepasser*** |  |  |  |  |  |  |  |  |  |
| *mahali* |  | 1 |  |  |  |  | 1 |  | 1 |
| ***Pomatostomus*** |  |  |  |  |  |  |  |  |  |
| *ruficeps* |  | 1 |  |  | 1 |  |  |  | 1 |
| ***Saltator*** |  |  |  |  |  |  |  |  |  |
| *atricollis* |  |  | 1 |  | 1 |  |  |  | 1 |
| ***Taeniopygia*** |  |  |  |  |  |  |  |  |  |
| *guttata* |  | 1 |  |  |  | 1 |  |  | 1 |
| ***Turdoides*** |  |  |  |  |  |  |  |  |  |
| *affinis* |  | 1 |  |  |  |  | 1 |  | 1 |
| *bicolor* |  | 1 | 1 |  | 2 |  |  |  | 2 |
| *striata* |  | 2 |  |  | 1 |  | 1 |  | 2 |
|  |  |  |  |  |  |  |  |  |  |
| **Mammalian** |  | **10** | **3** |  | **5** | **2** | **6** |  | **13** |
| ***Cercopithecus*** |  |  |  |  |  |  |  |  |  |
| *aethiops sabaeus* |  | 1 |  |  |  | 1 |  |  | 1 |
| ***Helogale*** |  |  |  |  |  |  |  |  |  |
| *parvula* |  | 4 | 1 |  | 3 |  | 2 |  | 5 |
| ***Suricata*** |  |  |  |  |  |  |  |  |  |
| *suricatta* |  | 5 | 2 |  | 2 | 1 | 4 |  | 7 |
|  |  |  |  |  |  |  |  |  |  |
| **Grand Total** |  | **29** | **13** |  | **13** | **9** | **20** |  | **42** |

To follow up on Bednekoff’s review on sentinel behaviour (Bednekoff, 2015), we recorded the number of studies that explicitly mentioned ‘coordination’ as a characteristic element of sentinel behaviour. Only 33% of the articles retained in this review (14 out of 42 articles) fitted this criterion.

Discussion

Intrinsic Factors

Our review identified several intrinsic and extrinsic factors that could influence sentinel behaviour 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 (Burt, 1996; Burton & Yasukawa, 2001; Gaston, 1977; Horrocks & Hunte, 1986; Mainwaring & Griffith, 2013; Walker et al., 2016; Yasukawa et al., 1992). The difference in sentinel behaviour can be attributed to differences in energetic investment between sexes, with males having more energy available for activities outside of reproduction (Walker et al., 2016). Male reproduction is less energetically costly than for females (sperm vs. egg production) resulting in additional energy that can be allocated towards other behaviours including sentineling (Hayward & Gillooly, 2011). 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 (Yasukawa et al., 1992). Likewise in Zebra finches (*Taeniopygia guttata*), sentinels, which are most often males, alert their partners when threats approached the nest, resulting in incubating individuals flushing their nests earlier than when sentinels are absent (Mainwaring & Griffith, 2013). The benefits from sentinel behaviour could therefore extend past increased foraging efficiency and biomass intake, but also to 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*) increase their sentinel effort despite already sentineling more than other group members (Walker et al., 2016). Similarly, dominant male dwarf mongoose (*Helogale* parvula) more regularly engage in sentinel behaviour when encountering signs of rival groups (Morris-Drake et al., 2019). The increased sentinel behaviour of dominant male individuals could permit earlier intruder detection as well as serving as an antipredator function (Morris-Drake et al., 2019; Walker et al., 2016). Since dominant males are most often usurped by out-group individuals rather than subordinates, early detection and monitoring of rivals is essential for dominant males to maintain their position in the group (Walker et al., 2016).

Another intrinsic factor identified in our review was maturity. Older and more experienced individuals sentineled more than younger individuals (Gaston, 1977; Hailman et al., 2010; Horrocks & Hunte, 1986; Rauber & Manser, 2021; Zacharias & Mathew, 1998). Younger individuals could be inefficient sentinels as they lack the experience to identify potential threats (Zacharias & Mathew, 1998). The benefits of earlier threat detection from sentineling might therefore be decreased in juveniles as they might not be able to correctly identify threats. Instead, juveniles could be taking advantage of the sentinel behaviour of more experienced individuals to learn to identify threats. Older and more experienced individuals could also have greater energetic resources to allocate to sentinel behaviour as a result of having a greater body mass (Wright, Berg, et al., 2001b). In certain species, older individuals could also be more efficient foragers, further mitigating the costs of sentinel behaviour (Lescroël et al., 2019).

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 (Bednekoff, 1997, 2001, 2015). 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 (Bednekoff & Woolfenden, 2003; Clutton-Brock et al., 1999; Huels & Stoeger, 2022; Wright, Berg, et al., 2001a, 2001b; Wright, Maklakov, et al., 2001). 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, Arabian babblers (*Turdoides squamiceps*), and Florida scrub-jays (*Aphelocoma coerulescens*) which found that fed individuals initiated bouts of sentinel behaviour more frequently (Arbon et al., 2020; Bednekoff & Woolfenden, 2003, 2006; Clutton-Brock et al., 1999; Ostreiher et al., 2021; Wright, Maklakov, et al., 2001). 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 (Bednekoff & Woolfenden, 2006). These findings suggest that upon achieving sufficient energetic reserves, sentinel behaviour is the most beneficial activity for the individual.

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 behaviour in mammalian 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 (Gaston, 1977; Ostreiher et al., 2021; Walker et al., 2016; Wright, Berg, et al., 2001a; Zacharias & Mathew, 1998, 1998). Dominant individuals could have greater access to resources, either through more effective foraging strategies or receiving gifts from other members of the group (Ostreiher & Heifetz, 2019). The differences in sentinel behaviour between dominant and subordinate individuals could also reflect the differences in benefits received by the sentinel. Dominant individuals, usually male, could receive additional benefits from sentinel behaviour, such as guarding against outgroup rivals and territory intrusions (Morris-Drake et al., 2019; Walker et al., 2016). Subordinates do contribute to a group’s sentinel behaviour but could be compensating for the dominant individual’s increase in sentinel behaviour by reducing theirs (Hailman et al., 2010). 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 (Ostreiher & Heifetz, 2019). 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, and are consistent with the effects of group size on vigilance (Beauchamp, 2008). The greater the number of group members, the greater the likelihood of at least one individual being capable of sentineling. Larger groups see decreased individual sentinel behaviour, potentially due to increased competition for resources and lower energetic reserves, but more sentinel behaviour at the group level with fewer and shorter gaps between bouts (Hailman et al., 2010; Houslay et al., 2021; Yasukawa & Cockburn, 2009). In smaller groups, individuals must perform longer bouts of sentinel behaviour, increasing the costs of sentinel behaviour for participating group members (Clutton-Brock et al., 1999). 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 (Lima, 1995).

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 (Arbon et al., 2020; Kern & Radford, 2014; Kong et al., 2021; Sorato et al., 2012). This risk can be from the presence of predators but also the presence of outgroup rivals and territory intruders, which cause an increase in sentinel behaviour (Morris-Drake et al., 2019; Walker et al., 2016). The collection of information on potential threats is essential to the survival of individuals. The earlier detection of predators from sentinel behaviour reduces the risk of mortality and injury of a predator encounter, improving survival of the sentinel as well as the other group members. The presence of at-risk individuals, such as young individuals, also increased sentinel behaviour, likely to compensate for an increase in predation risk or as a form of parental care (D’Agostino et al., 1980; Santema & Clutton-Brock, 2013). In meerkats (*Suricata suricatta*), the presence of pups significantly increased the sentinel behaviour of subordinates during foraging trips (Santema & Clutton-Brock, 2013). 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 experience with threats. Their inclusion in foraging groups could therefore increase the group’s risk of predation, resulting in increased sentinel behaviour in adult members to counteract that increased risk. Reduced-risk environments, such as in captivity, have shown that captive meerkats behaved similarly to their wild counterparts suggesting that sentinel behaviour does not disappear in the absence of predation risk (Huels & Stoeger, 2022). 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 (Wright, Berg, et al., 2001b), anthropogenic noise in urban environments (Kern & Radford, 2016) and factors that increase environmental uncertainty such as visual obstructions (e.g. tall grasses) (Kern & Radford, 2014) can also alter an individual’s need for vigilance and by extension sentinel behaviour. In dwarf mongooses, the presence of anthropogenic noises significantly affected the ability to hear acoustic signals from the sentinel, reducing their effectiveness (Eastcott et al., 2020; Kern & Radford, 2016). Foragers were observed to increase their personal vigilance in response (Kern & Radford, 2016). The wealth of environmental factors that can increase risk 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 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 change their behaviour can be adaptive in highly variable environments, such as urban environments. Urbanization is an important driver of behavioural change, and animals will alter their behaviours to increase success in their environments. Urban environments often have an increased abundance and predictability of anthropogenic foods, which are generally more caloric but less nutritious. Feeding on these food sources could increase the availability of energy and lead to an increase in the propensity of an individual to perform sentinel behaviour. Urbanization could also affect an individual’s perception of the threats in their environment. Disruptive factors such as anthropogenic noise can decrease the effectiveness of sentinels (Eastcott et al., 2020; Kern & Radford, 2016). 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. 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 (*Buteo jamaicensis*) (Morrison et al., 2016). Studying the differences in sentinel behaviour between different types of urban environment could reveal more subtle factors at play in sentinel decision-making.

Coordination

Coordination of sentinels has been identified as the defining feature of true sentinel systems (Bednekoff, 2001, 2015; Bednekoff & Woolfenden, 2003, 2006; Goodale et al., 2017). Despite this, few articles explicitly use coordination in their definition of sentinel behaviour. By not including and testing for the coordination of sentinels, we are exposing ourselves to an 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.

Implications and Future Directions

The findings of this review 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. An individual’s foraging environment can then affect an individual’s propensity and ability to perform sentinel behaviour. For example, individuals who have fed on highly caloric anthropogenic foods could have more energy to perform sentinel behaviour. Conversely urban factors such as anthropogenic noise and the shortening or obstruction of lines of sight can also affect the effectiveness of sentinels. Future research is required to uncover subtle environmental effects on sentinel behaviour, and should consider both intrinsic and extrinsic factors, as we have shown that they can often interact and significantly alter behaviours.

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