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Methods

This scoping review followed the ROSES standards of reporting for scoping and systematic reviews to the best of our ability [1]. 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 recorded before initiating database searches. We included primary literature that sought to determine 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. We excluded articles published before 1970, because the definition of sentinel behaviour prior to this date was nebulous and not consistent with the currently used definition of sentinel behaviour, where an individual adopts a raised, prominent position to perform constant vigilance over other group-members and makes alarm calls when sources of danger are detected [2,3]. 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. For inclusion, we defined sentinel behaviour as an individual that adopts a prominent, exposed position and whose purpose is to maintain constant vigilance over other group members, whether coordinated or not. Theoretical or review articles were excluded, though review article citations were screened.

Search strategy

On Jan. 24th, 2022, a preliminary search was performed in 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 1). 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, and exported the list of search results. 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?” [4].

Data collection & analysis

Title and abstract were screened in triplicate using the "Metagear" package in R [5] by following the inclusion and exclusion criteria (Table 2). 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 (e.g. sex, age, body mass) or extrinsic (e.g. anthropogenic noise, presence of predators or outgroup rivals). 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 [2].

Table 1: Search string used on Nov. 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 2: Inclusion and exclusion criteria for 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 | Model species must be terrestrial or avian, and vertebrate. |
| Date of publication | Article must be 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 observational (e.g. X species has a sentinel system), or mathematical/theoretical. |
| Model species | Model species must not be aquatic and must not be invertebrate. |
| Date of publication | Article must not be published before 1970. |
| Major concepts | Exclude studies from non-behaviour related fields (e.g. remote sensing, sentinels of ecosystem health/biodiversity, sleep). |

Results

Our search string collected 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, Supplemental Materials). We retained 42 studies that met the inclusion criteria (Table 2). 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%). The three exemplar articles missed by the search on Web of Science were found by searching and screening the results from ELICIT.org.

We retained 29 articles that conducted studies on sentinel behaviour on avian species, with most studies being performed on *Argya squamiceps* (6), *Turdoides spp.* (5), and *Aphelocoma spp.* (5) (Table 2). The remaining studies were conducted on various other species such as red-winged blackbirds, finches, and cranes. The other 13 studies were conducted on mammal species, with the majority being performed on meerkats (*Suricata suricatta,* 7), and dwarf mongooses (*Helogale parvula,* 5).

Factors tested were grouped as testing either intrinsic (e.g. sex, maturity, satiation, body size) or extrinsic (e.g. group size, dominance, risk). 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. The effects of both intrinsic and extrinsic factors were tested in 20 studies, the majority of which were studies testing the effects of sex and dominance on the sentinel behaviour. The effects of sex (17 articles), dominance (12 articles), and group size (10 articles) were the most studied factors (Table 2). The effects of satiation (8 articles), predation risk (7 articles), and maturity (7 articles) were also frequently studied.

To follow up on Bednekoff’s 2015 review on sentinel behaviour, we recorded the number of studies that explicitly mention ‘coordination’ as a characteristic element of sentinel behaviour. Out of 42, 14 articles fit this criterion. An upward trend is observed after 2017, though this trend is not reflected by a decrease in the number of articles published that do not include coordination as a defining feature of sentinel behaviour (Figure S1).

A diagram of a flowchart

Description automatically generated

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

Table 3: Number of articles retained by the search strategy

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | **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 |
|  |  |  |  |  |  |  |  |  |  |
| **MAMMAL** |  | **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** |

Trends observed

Several trends were observed among the studies looking at factors that could affect sentinel behaviour. The main trends observed were in the effects of sex, dominance, maturity, group size, satiation, body mass and risk. Sex, maturity, satiation, and body mass can be categorized as intrinsic factors, while dominance, group size, and risk are categorized as extrinsic or external factors. These trends were observed among both avian and mammal species, though appeared most frequently in avian species. This is explained by the disparity in the research on sentinel behaviour performed on avian (N=29) and mammal (N=13) species.

Among intrinsic factors, the effects of sex were the most reported. Generally, males of both avian and mammal species have greater sentinel contribution than females. A significant interaction between dominance and sex was often observed. Satiation and body mass had similar effects, with better fed individuals sentineling earlier, more often, and/or for longer than individuals who were either lighter or not satiated. Lastly, more mature, and older individuals generally sentineled more than younger, especially juvenile, individuals.

Among extrinsic factors, the effects of dominance on sentinel behaviour were the most reported. Social hierarchy within the group played a significant role in an individual’s sentinel decision-making, with more dominant individuals having a greater sentinel contribution than subordinates. Dominant males tended to sentinel the most in a group, with males sentineling more than females of the same dominance rank. Consistent with group size effects [6], larger groups resulted in overall greater sentinel coverage than in smaller groups, yet individual contribution to the group’s sentinel effort decreased. Risk, either through environmental uncertainty, anthropogenic disturbances, or the presence of young, predators, or conspecifics from another group caused an increase in sentinel efforts. Dominant males tended to greatly increase their sentinel contribution when risk increased, especially in the presence of rival or outgroup threats.

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Supplemental Material

List of Supplemental Figures

[Figure S1: Number of articles with coordination as a defining feature of sentinel behaviour across time 10](#_Toc155329787)

Coordination as defining feature of sentinel behaviour

Number of articles

Figure S1: Number of articles with coordination as a defining feature of sentinel behaviour across time