Title: Invertebrates in the Diet of Greater Sage-grouse: A Systematic Map

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ABSTRACT

Greater sage-grouse (*Centrocercus urphasianus*) are considered an umbrella species for the sagebrush-steppe ecosystem. Conservation efforts have been made to protect this species as they have neared Endangered Species status. Protecting the many aspects of their habitat has been crucial to protecting the species, and understanding and protecting their food sources is a critical tool in supporting sage-grouse populations. Insects are known to be a part of their diet, specifically for the juvenile sage-grouse, but which insects and what portion of their diet these insects comprise is not well understood. In this paper, we have conducted systematic mapping of the known research on this topic. Analyses done from 1933 through 1994 were compiled to identify knowledge clusters and gaps on the known invertebrates in the diet diet of these birds, while studies from 1994 through 2023 were analyzed on what insect and arthropod species are found in their habitat. Many knowledge gaps were found to exist with little to no knowledge clusters, and further research into this topic is needed to assist land managers in choosing practices to best benefit sage-grouse populations through encouraging beneficial insect diversity and abundance.

KEYWORDS: *Centrocercus urophasianus*, arthropods, insects, terrestrial food web, ecological reclamation, ecosystem restoration

The Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) has been considered an umbrella species for the sagebrush-steppe ecosystem (e.g., Rowland et al. 2006). Sage-grouse populations span 11 US states and two Canadian provinces, within which historical habitat has decreased by 50-60% (Schroeder et al. 2004, Wann et al. 2025). The sage-grouse was listed as 'warranted but precluded' from listing under the US Fish and Wildlife Service's Endangered Species Act in 2010 (USFWS 2010). Since this listing decision, an unprecedented number of conservation efforts have taken place in the western US and Canada, which has led to a non-warranted Endangered Species Act listing decision in 2015 (USFWS 2016). A habitat assessment framework (HAF) has been developed for sage-grouse based on a hierarchical system which includes species range, population areas and dispersal, homerange of small or isolated groups, and seasonal habitats (Stiver et al. 2015). This framework ranks seasonal habitat for sage-grouse such as lekking (Spring), early and late brood-rearing (early Summer and late Summer), and Winter habitats. The HAF further goes on to describe habitat suitability with consideration to vegetation composition and structure as well as environmental and anthropogenic threats (Stiver et al. 2015). While it is well-known that sage-grouse rely on sagebrush (*Artemesia* spp.) for cover throughout their lifecycle and as a primary food source in winter months, less is known about other components of the sage-grouse diet, though several studies have been done highlighting the importance of forbs in the sage-grouse diet (e.g., Kirol et al. 2012, Curran et al. 2015, Dumroese et al. 2015, Dumroese et al.2016, Pennington et al. 2016). It is also known that invertebrates are critical to sage-grouse at various stages of their lifecycle (e.g., Klebenow & Gray 1968, Drut et al. 1994), though no work has been done to synthesize the types of invertebrates sage-grouse eat and the importance of insects to sage-grouse at various stages of their lifecycle or across seasonality.

Invertebrates are often the first animals to respond to ecosystem changes and are a useful proxy for measuring ecosystem functionality (Longcore 2003). Invertebrates provide a large number of ecosystem services which are critical to the sagebrush-steppe, such as pollination, biodiversity, nutrient cycling, and as a primary source of protein to higher trophic levels (e.g., Archer & Pyke 1991, Belovsky & Slade 2000, Curran et al. 2022ab, Curran et al. 2024, Tallamy 2009). Regarding their importance to higher trophic levels, it has been documented that sage-grouse chick mortality rates increase if a lack of invertebrates are available for consumption during the first ten days post-hatch (Johnson & Boyce, 1990). Insects play a role in the sage-grouse diet at various life stages, with insect matter making up as much as 75% of the juvenile birds' diet soon after hatching and decreasing to approximately ten percent by Fall (Klebenow & Gray 1968). As well as varying with life-stage, insects found to be a part of the sage-grouse diet vary with habitat location and seasons (Patterson 1952). Previous studies are limited, do not cover the entire sage-grouse range, and have various objectives. Cataloging the current state of knowledge about insects in sage-grouse diet is important as land management practices (e.g., grazing, reclamation, restoration) are likely to directly impact insect diversity and abundance. For example, it was found that post-fire restoration seeding techniques influence insect populations differently and that increasing forb composition on natural gas well pads is likely to improve insect habitat within sagebrush ecosystems (Rohde et al. 2019, Curran et al. 2022ab, Curran et al. 2024). As efforts have increased to maintain and improve sage-grouse habitat through reclamation and restoration (Stahl & Curran 2017), improving the knowledge of insects in their diet will be helpful.

Currently, a comprehensive catalogue of invertebrates within the sage-grouse diet does not exist. A systematic map approach would be useful to enhance knowledge on this topic to assist in guiding conservation efforts (e.g., land management practices such as reclamation and restoration) focused around sage-grouse and their ecosystem. Systematic maps have been helpful for other natural resource management issues (James et al. 2016, Elmore et al. 2021, Elmore et al. 2023). Unlike systematic reviews which aim to answer a specific question, systematic mapping focuses on collecting evidence around a topic in order to describe and organize known information while identifying knowledge gaps and knowledge clusters (James et al. 2016). Identifying knowledge gaps can help guide new research questions, whereas identifying knowledge clusters can help guide existing research or help inform policy and management decisions (James et al. 2016). Another benefit to a systematic map approach is that a repeatable process can be developed which can be revisited periodically to advance knowledge clusters and determine how knowledge gaps are being filled (James et al. 2016).

Our objective was to develop a systematic map regarding the invertebrate component of the sage-grouse diet. In doing so, we sought to determine geographic areas where studies associated with invertebrates in the sage-grouse diet have occurred, seasonality of studies, the age of birds being studied, and methods used to study insects in the sage-grouse diet. We describe our methodology so future researchers can repeat this type of work as more information is gathered.

METHODS

We followed guidelines for systematic mapping set out by James et al. (2016) to answer the primary question: What insects are a known part of the Greater sage-grouse diet? From this primary question, secondary questions arose: How does the insect portion of the sage-grouse diet differ throughout the sage-grouse lifecycle? How do seasonality and geography affect the insect portion of the sage-grouse diet?

Literature search

We performed all searches in English and only literature available in English was included. While no geographical limit was imposed, the search terms are specific to North America which was reflected in search results.

We conducted all searches in July of 2023. The databases searched included Google Scholar, ScienceDirect, ProQuest, ProQuest Dissertation and Theses Global, Wildlife & Ecology Studies Worldwide, and Web of Science. We conducted two searches within each database using the following search strings:

(sage grouse OR centrocercus urphasianus) AND (insect$ OR arthropod$ OR invertebrate$)

(sage grouse OR centrocercus urphasianus) AND (diet$)

When applicable, a wildcard (*) was added to search terms. With each search, we saved the first 100 results. In searches where fewer than 100 results were returned, all were saved, and we excluded any repeated papers found in previous searches. A total of 547 papers were found in the initial search, from which we found 22 additional papers within their associated citations which may have been relevant to our questions.

Literature screening and inclusion

We reviewed the found literature and excluded those that did not address our primary or secondary questions as well as those without original, meaningful data. We ensured team agreement of at least 80% on the literature to be included by having authors FMMB and MFC independently review their titles and abstracts (see Elmore et al. 2021 for a similar example).

Data extraction and synthesis

The data found selected studies was separated into two categories: (1) insects found in sage-grouse stomach or crop analyses, or (2) insects abundant in areas of known sage-grouse habitat where diet composition was not confirmed. For the latter, we further classified studies into categories based on both the stage of the sage-grouse life cycle at which time the study occurred and whether the study was conducted in undisturbed, disturbed or managed habitat. For the habitat type, we classified studies as:

(1) undisturbed sagebrush, (2) grazed areas, (3) mowed areas, (4) areas disturbed by wildfire, or (5) areas within energy development fields. From these studies, we extracted and organized data into tables by location, time, sage-grouse age, and invertebrates found by frequency and total volume where available.   As the latter studies do not confirm insects are actually in the sage-grouse diet, a summary table is provided in Supplemental File A (Bott et al. 2026), but information in this paper is focused in the former studies.

RESULTS

A total of 569 papers were returned in our initial search with 22 more papers which were not found in initial searching being added after reviewing the literature found in our initial searches (Figure 1; Supplemental File A – Bott et al. 2026). A total of 503 papers were eliminated after screening titles and abstracts because they did not specifically address our questions or have insect-specific data. Papers that had potential to provide answers to our question were then read in entirety to determine if they should be included in final mapping efforts. At this stage and additional 19 papers were eliminated from our mapping effort, leaving 37 relevant papers with 12 studies examining and confirming insects in the sage-grouse diet (category 1 above; Supplemental File A – Bott et al. 2026) and 25 studies documenting insects located near sage-grouse nesting or brood-rearing sites (category 2 above; Supplemental File A - Bott et al. 2026). Figure 1 depicts the work flow of our selection process.

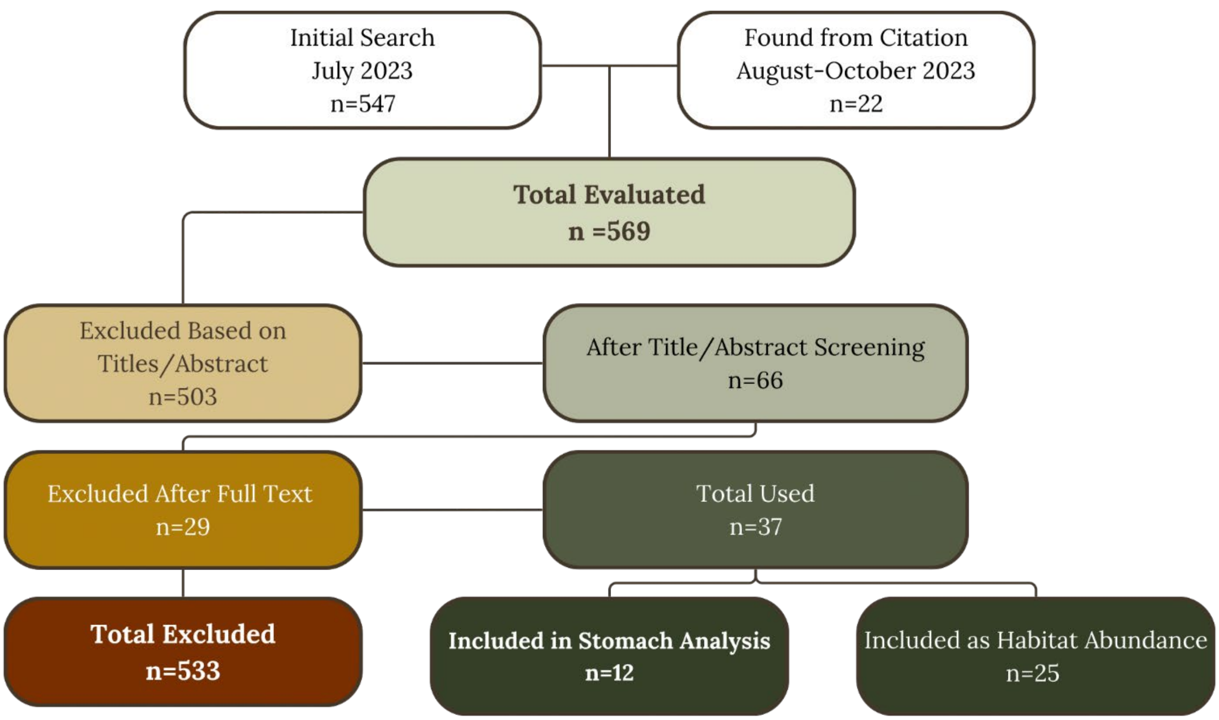

Figure 1. Schematic of mapping stages, including search and screening stages, leading to final articles and studies included in this systematic map of invertebrates in the sage-grouse diet.

Studies which analyzed sage-grouse stomach or crop contents ranged from 1933-1994, whereas studies which focused on insects adjacent to sage-grouse nesting or brood-rearing habitat ranged from 1994-2023. Locations of studies were recorded with the best available information in the paper, which varied from specific coordinates to generalized counties or regions where studies were conducted (Figure 2).

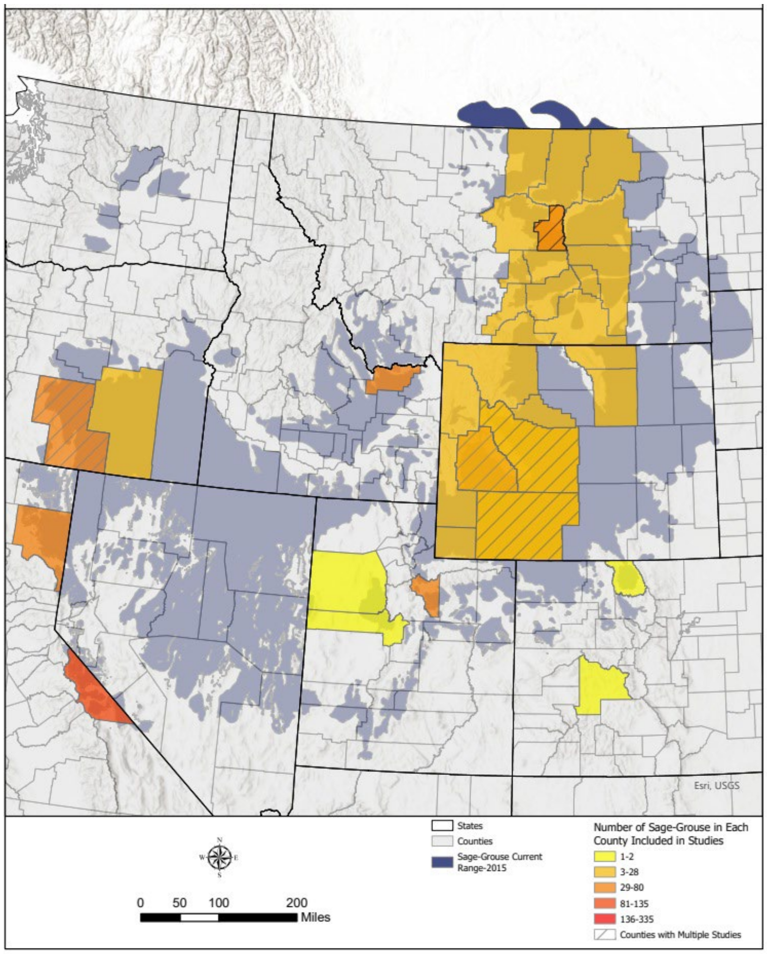

Figure 2. A map depicting where sage-grouse studies have taken place along with the range of birds in each area laid over the range of sage-grouse (in grey).

As studies which conducted stomach or crop analysis did not follow consistent methodologies, included different numbers of birds, and were conducted with different sampling methods, we kept all data stored in Supplemental File A (Bott et al. 2026) and decided to use a Tree Map from the Microsoft Excel Package to depict which insects show up most commonly in the sage-grouse diet (Figure 3).

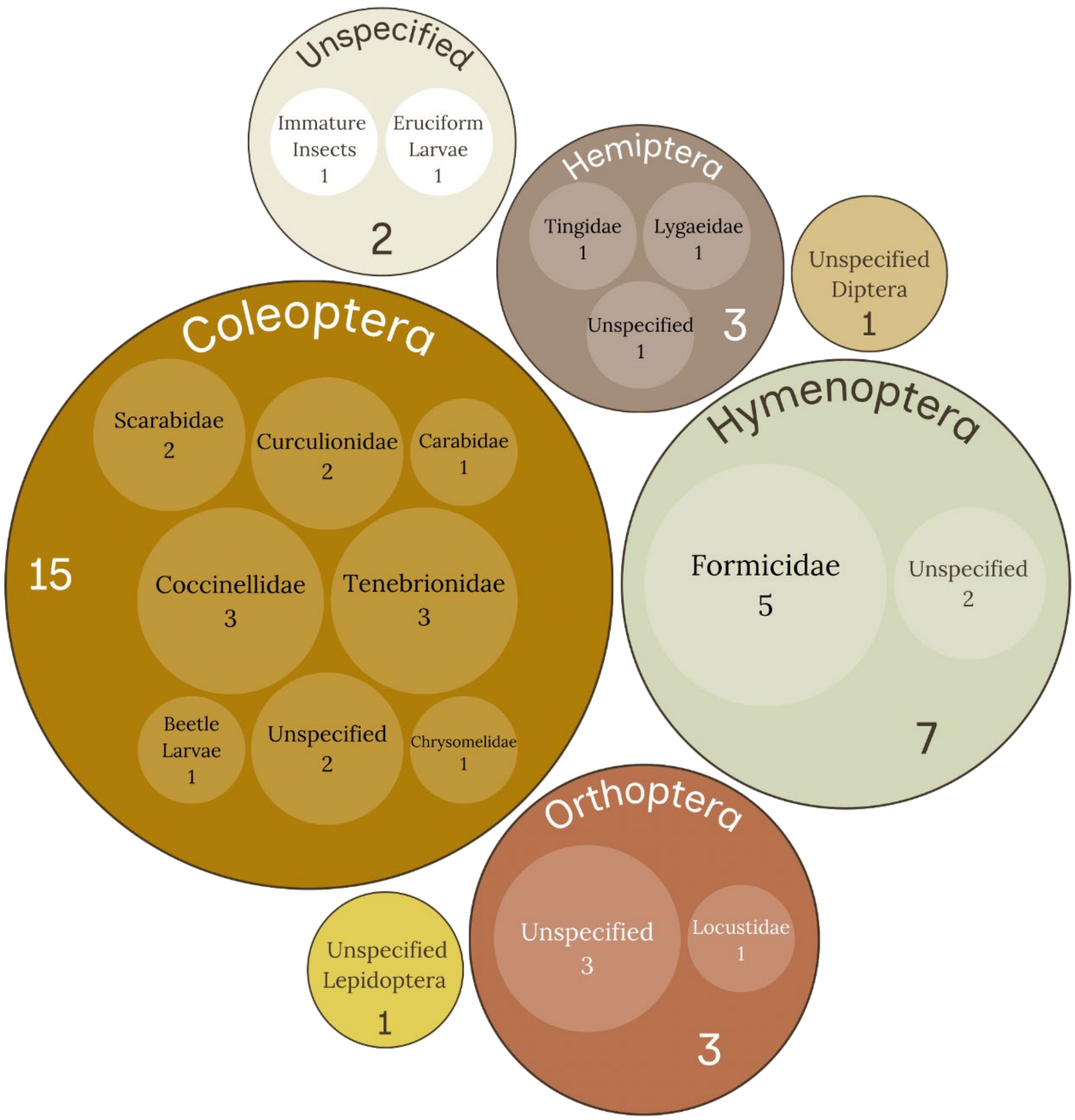

Figure 3. A tree map depicting which insects show up in studies from the systematic map. As studies were not consistent across time and space, we decided to show this at the coarsest level available across studies.

Ants (Formicidae) were found to be crucial species in five of 12 studies to sage-grouse diet. Grasshoppers (Orthoptera), lady bugs (Coccinellidae), and darkling beetles (Tenebriondae) were found to be crucial in 3 of 12 studies. Klebenow and Gray (1968) suggest juvenile sage-grouse switch from ants to leaf beetles (Chyrsomelidae) as their primary source of insect protein after ~5 weeks post-hatch. These most common insects are high in calcium, slow moving, and typically found in large groups (e.g., Ahearn 1971, Carlislse et al. 2012).

DISCUSSION

In comprising this systematic map, a handful of limitations were evident. Current regulations make obtaining licenses to kill sage-grouse, especially juvenile sage-grouse, difficult and highly limited, likely contributing to declines in analyses related to sage-grouse crop or stomach contents. Data of this type were not found from our systematic mapping effort past 1994. While other methods of analyzing sage-grouse diet have been used, they provide less definitive data. The taxonomy of sage-grouse has also changed, in 2000, Greater sage-grouse *(Centrocercus urophasianus*) and Gunnison sage-grouse (*Centrocercus minimus*) were designated as separate species, making older data difficult to categorize as one or the other (Young et al. 2000). Similarly, continuously evolving changes to insect taxa, and the degree of insect taxonomy provided in different studies (e.g., insects described to the genus vs. family level) introduced inconsistencies in data.

Promising methods to track insects have been proposed in recent decades. For example, Hagler and others (2001) reviewed existing techniques and have developed methods to track insects from floral sources and potentially through fecal studies utilizing enzyme-linked immunosorbent assay (ELISA) techniques (Hagler et al. 2019). Sullins and others (2018) were able to utilize deoxyribonucleic acid (DNA) barcoding to gain a better understanding of the diet of the Lesser prairie-chicken (*Tympanuchus pallidicinctus*). Curran and others (2020) were able to utilize 3-dimensional videography to track insect movement across floral resources which would be easily translatable to capture sage-grouse or other animals utilizing insects as a food source. As technology continues to advance, it is becoming increasingly likely that the need for lethal management techniques to monitor the diet of sage-grouse and other animals which rely heavily on insects will be unnecessary in the future.

MANAGEMENT IMPLICATIONS

Previous research shows insects respond differently to various land management treatments associated with reclamation and restoration in the western United States (e.g., Curran et al 2022 ab; 2024, Rohde et al. 2019). Understanding exactly which insects are in the sage-grouse diet may inform future practices to help introduce or maintain sage-grouse benefitting insect populations. As sage-grouse are considered and umbrella species of the sagebrush-steppe ecosystem of western North America, understanding plant-insect interactions which may benefit grouse would help inform future land management practices. In addition to helping sage-grouse populations thrive, enhancing insect abundance and diversity has shown to improve juvenile growth and survival of songbirds across the globe according to a recent meta-analysis (Grames et al. 2023).

Our research shows that there are major knowledge gaps in this area. There are no true knowledge clusters, as only 12 studies across over the last century have been conducted to understand insects in the sage-grouse diet. As the vast majority of terrestrial birds rear their young on insects, and because insects are clearly important to the sage-grouse diet, more research is needed in this field.

Information gleaned from this systematic map can be utilized by other researchers to determine if insects found in studies within sage-grouse habitat areas are those actually utilized by grouse. For example, habitat restoration after natural gas disturbance in Sublette County, Wyoming, USA found significantly higher levels of insects from the Formicidae and Chrysomelidae families when Rocky Mountain bee plant (*Cleome serrulata*) was used in seed mixes alongside with later successional native plant species (Curran et al. 2019, Curran et al. 2022ab, Curran et al. 2024.). Whilst a 146x increase of leaf beetles were found within one year of seeding (Curran et al. 2022a), the impacts of reclaiming sites with native plants, in Wyoming (USA), can contribute to positive impacts on insect populations for at least 12 years (Curran et al. 2024).

As more knowledge is gained about how insect communities interact with specific vegetation, habitat restoration plans may be tailored specifically to attract sage-grouse preferred insects and forbs. Terrestrial food webs are critical components of ecosystems (Tallamy 2009, Tallamy and Shropshire 2009). This systematic map clearly shows more research needs to be conducted to improve the overall knowledge of the sage-grouse diet and to improve our overall understanding of sagebrush-steppe ecosystem recovery in the arid and semi-arid environments associated with the Rocky Mountain western portions of North America.

While it should not be expected that species of plants which attract insects, or all insects within the sage-grouse diet will be present or able to persist across the wide range of sage-grouse habitat, recent advancements in ecological research are rapidly developing. Enhancing the availability of native plant material available for reclamation and restoration projects will be paramount for future projects (e.g., Curran et al. 2015, NASMDBDELSCNSC 2020, Winkler et al. 2024). Developing suitable provisional methods to guide where best to utilize certain floral species which attract insects local to specific area and advancements in understanding reclamation and restoration in arid and semi-arid ecosystems found in western Northa America are rapidly advancing (e.g., Crow et al. 2018, Bertuol-Garcia et al. 2023, Shackelford et al. 2022). Further research to understand terrestrial food web connectivity between vegetation and insects and higher trophic levels is likely to provide numerous benefits to reclamation and restoration practitioners, as well as to the wildlife dependent on management practices, including the Greater sage-grouse, an umbrella species of the sagebrush-steppe ecosystems which are critical to western North America. As recent research has shown it is not uncommon for understories (e.g., forbs and grasses) to be degraded within large stands of sagebrush in the western US (Copeland et al. 2024), it may be especially important to understand these plant-insect interactions not only to improve terrestrial food webs, but also to assist with enhancement of understory vegetation communities where they have been degraded.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICS STATEMENT

The work summarized in this manuscript did not analyze new data collected from studies of wildlife or humans.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. A list of the primary sources of data is available in the supplementary material of this article.

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