RESEARCH ARTICLE

Meta-analysis shows that overabundant deer (Cervidae) populations consistently decrease average population abundance and species richness of forest birds

Robert Crystal-Ornelas,[1,a,*,] **Jeffrey A. Brown,**[1,2] **Rafael E. Valentin,**[1,3] **Caroline Beardsley,**[1] **and Julie L. Lockwood**[1,]

[1] Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, New Jersey, USA
[2] Global Institute of Sustainability, Arizona State University, Tempe, Arizona, USA
[3] Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA
[a]Current address: Lawrence Berkeley National Lab, Berkeley, California, USA
*Corresponding author: rcrystalornelas@lbl.gov

ABSTRACT

Local-scale studies have shown that an overabundance of Cervidae species (deer, elk, moose) impacts forest bird communities. Through meta-analysis, we provide a generalized estimate of the overall direction and magnitude of the indirect effects overabundant cervids have on avian species. We conducted 2 distinct meta-analyses that synthesized data on 130 bird species collected from 17 publications. These analyses compared bird species' population abundance and/or species richness at sites with overabundant cervids to sites with lower cervid abundance or without cervids. We evaluated whether the impacts of overabundant cervids are generally in the same direction (positive, negative) across avian species and locations and if effects vary in magnitude according to avian nesting location and foraging habitat. We found that where cervids were overabundant, there was a significant decrease in mean bird population abundance and species richness. Species that nest in trees, shrubs, and on the ground showed the largest decreases in abundance, as did species whose primary habitat is forest and open woodland and species that are primarily insectivores or omnivores. We did not find significant decreases in abundance for avian species that nest in cavities, whose primary habitat is grassland or scrub, nor for species that mainly eat seeds. Our results indicate that overabundant cervids, likely through their direct effects on vegetation and indirect effects on insects and forest birds, negatively impact individual bird populations and decrease overall avian species richness.

Keywords: avian, cervid, forest ecology, indirect effects, trophic cascades

---

LAY SUMMARY

- Local-scale studies suggest that when cervid species (deer, elk, moose) are overabundant, forest bird populations and communities are negatively impacted.
- We synthesized data from 17 publications to provide a global summary of the average impacts that overabundant cervids have on bird species abundance and richness.
- Forest bird abundance and richness decline where cervid species are overabundant, likely because they alter vegetation that birds use as components of habitat and the resources that vegetation provides birds.
- The highest magnitude abundance declines are seen in populations of tree, shrub, and ground-nesting avian species, species whose primary habitat is forest and open woodland, and species that are insectivores or omnivores.
- Our results suggest that, to maintain forest bird biodiversity, wildlife and land managers should consider actions to keep cervid species from becoming overabundant or reduce populations where they are already overabundant.

Un meta-análisis muestra que las poblaciones sobreabundantes de ciervos (Cervidae) disminuyen consistentemente la abundancia poblacional y la riqueza de especies promedio de las aves del bosque

RESUMEN

Los estudios a escala local han demostrado que una sobreabundancia de especies de Cervidae (ciervo, uapití, alce) impacta en las comunidades de aves del bosque. A través de un meta-análisis, proporcionamos una estimación generalizada de la dirección global y la magnitud de los efectos indirectos que los cérvidos sobreabundantes tienen en las especies de aves. Realizamos 2 meta-análisis distintos que sintetizaron datos sobre 130 especies de aves recopilados de 17 publicaciones.

Estos análisis compararon la abundancia poblacional y/o la riqueza de especies de aves en sitios que presentan cérvidos sobreabundantes con sitios con menor abundancia de cérvidos o sin cérvidos. Evaluamos si los impactos de los cérvidos sobreabundantes van generalmente en la misma dirección (positiva, negativa) para todas las especies de aves y las ubicaciones, y si los efectos varían en magnitud según la ubicación de anidación y el hábitat de alimentación de las aves. Encontramos que donde los cérvidos eran sobreabundantes, había una disminución significativa de la abundancia poblacional y la riqueza de especies promedio de las aves. Las especies que anidan en árboles, arbustos y en el suelo mostraron las mayores disminuciones en abundancia, al igual que las especies cuyo hábitat principal es el bosque y las arboledas abiertas, y las especies que son principalmente insectívoros u omnívoros. No encontramos disminuciones significativas en la abundancia de las especies de aves que anidan en cavidades, cuyo hábitat principal es el pastizal o el matorral, ni para las especies que se alimentan principalmente de semillas. Nuestros resultados indican que los cérvidos sobreabundantes, probablemente a través de sus efectos directos sobre la vegetación y los efectos indirectos sobre los insectos y las aves del bosque, impactan negativamente poblaciones individuales de aves y disminuyen la riqueza global de las especies de aves.

Palabras clave: aves, cérvidos, ecología forestal, efectos indirectos, cascadas tróficas

INTRODUCTION

Bird populations are declining globally due to a combination of direct and indirect effects (Gaston et al. 2003, Butchart et al. 2010, Rosenberg et al. 2019). Direct effects, such as diminishing forest cover due to land use changes (Northrup et al. 2019) or increasing nest predation rates (Ims et al. 2019), immediately affect birds. In contrast, processes such as trophic cascades indirectly affect bird communities through more complex processes, including intermediate species. One such example of an indirect effect can be seen in forest communities, where increases in cervid populations (deer, elk, moose) may cause declines in breeding birds by cervids consuming large amounts of forest vegetation and altering understory structure (deCalesta 1994, Anderson 2007, Baiser et al. 2008, Graham et al. 2014). If such indirect trophic effects are common, then an increase in hunting pressure on cervids or other actions that protect forest understory from over-browsing (e.g., installing fencing, reintroducing top predators; Nilsen et al. 2007, Dávalos et al. 2015, Nagashima et al. 2019) would be broadly necessary for bird conservation. However, previous work shows that certain avian species may increase or decrease in abundance in the presence of cervids (Holt et al. 2011, Okuda et al. 2012; but see Chollet and Martin 2013 for evidence of general avian decline). Because cervid management is costly (Macdonald et al. 2017), difficult to implement in some locations (e.g., urban forests; Nilsen et al. 2007), and/or is controversial (Storm et al. 2007, Kugeler et al. 2016, Ramsey et al. 2017), the generality of negative cervid effects on birds should be investigated. Although there is research on how cervids impact avian populations and communities (deCalesta 1994)—and even efforts to synthesize the existing evidence base (Chollet and Martin 2013)—this question has never been systematically addressed through meta-analysis. Such a quantitative synthesis of the existing evidence base, which draws statistical inferences from directly comparable studies, will provide wildlife and land managers with

additional guidance on whether such impacts are common, under what circumstances they may manifest strongly, and which bird species are most affected.

Cervid populations in many locations have increased in abundance over historical levels due to removal of their natural predators (Woodroffe 2000, Ballard et al. 2001), reductions in hunting pressure (Warren 2011), and dietary supplementation from agriculture and suburban landscaping (Côté et al. 2004, Milner et al. 2014). When in high abundance, cervids can excessively browse favored vegetation and stall forest regeneration, remove key understory plants, and allow nonnative species to establish more easily (Anderson 2007, McWilliams et al. 2018). Although the vegetation that cervids consume varies by species and location, these impacts consistently alter forest composition and function (McLaren et al. 2004, Beguin et al. 2016). Changes to vegetation may especially impact avian species by altering the availability or quality of resources, including shelter, food, or nesting substrates (Allombert et al. 2005, Hegland et al. 2005, Dolman and Wäber 2008).

Syntheses that integrate data of cervid impacts on avian species play a key role in reconciling differences in the evidence base. One large-scale synthesis found continent-wide decreases in forest bird abundance with overabundant deer (Chollet and Martin 2013), although the analysis did not consider community impacts, nor was it based on a search of the published literature. Without a quantitative meta-analysis, managers in locations that have not been the subject of local-scale studies are left without generalized recommendations for cervid management aimed at the conservation of forest birds (Fuller et al. 1995, Loss et al. 2015). Here, we aim to provide such recommendations by conducting 2 meta-analyses that use published data to synthesize the effects of overabundant cervids on avian population abundance and richness and to investigate which bird species are most vulnerable to over-browsing habitat change.

TABLE 1. To conduct our meta-analyses on cervid impacts on avian abundance and species richness, we developed a set of a priori inclusion criteria to identify suitable published articles. The first column lists each of the inclusion criteria. To be included in our meta-analyses, a published article needed to include certain focal species (Population), have similar experimental designs (Treatment/Control), and measurements (Outcome). In the second column, we describe the reason for each inclusion criterion. For an article to be included in either of our meta-analyses, the study had to meet all 4 inclusion criteria.

	Criteria	Rationale
1	Species in the family Cervidae and one or more avian species (Population)	The goals of our meta-analyses were to assess the impact of overabundant cervids on individual avian species abundance and species richness. Thus, we included only articles that had both focal cervid species and avian species.
2	Sites with cervids present (Treatment)	We required that studies included a treatment group with cervids present.
3	Sites with cervids absent or at low densities (Control)	We required that each study had a control group where cervids were absent or at substantially lower densities than the treatment group.
4	Metric of abundance or richness (Outcome)	Articles had to quantify individual avian species abundance or avian species richness.

METHODS

Search Strategy

We developed a search strategy that minimized bias when identifying the cohort of studies for our review (Koricheva et al. 2013, 2014). We conducted the systematic search in September 2020 using the literature search software *Publish or Perish* (version 7.26; https://harzing.com/pophelp/index.htm). We searched Google Scholar and Web of Science for articles related to cervid browsing impacts on birds and accepted articles from any language and any publication year. We used the following search term strings to identify candidate articles:

("deer*" OR "ungulate*") AND "bird* OR songbird*" AND ("impact*" OR "effect*")
("~deer" OR "~ungulate") AND "~bird OR songbird" AND ("~impact" OR "~effect")

Initially, we included the search term "avia*" but the results yielded no new articles, except for articles from unrelated fields (e.g., aviation). We retained all Web of Science search results for screening. Google Scholar returned thousands of potential articles from which we sorted by relevance and selected the top 700 articles in each search (Wang Wei et al. 2016). We did not initially restrict our search to articles only on the link between cervids and forest breeding birds, but all returned publications contained information on birds in primarily forested habitats.

Study Inclusion Criteria and Screening

Our search yielded 2,988 candidate articles. After removing duplicates, we screened the remaining articles (n = 2,023) against a set of inclusion criteria (Table 1). Articles had to meet all 4 criteria (Population, Treatment, Control, and Outcome; modified from Huang et al. 2006) to be included in our analyses. We required that each article investigates the impacts of species in the family Cervidae (deer, elk, moose) on a focal avian species or group of avian species (Population). Articles had to include treatment groups with cervid populations that the original authors considered "overabundant" (Treatment) and control groups that had no cervid or low cervid population densities (Control). In all included studies, authors considered unmanipulated cervid populations to be overabundant and, in many cases, the overabundance was a result of supplemental feeding or loss of natural predators (deCalesta 1994, Tymkiw et al. 2013, Chollet et al. 2015), or the introduction of deer to environments that lacked predators such as islands (Chollet et al. 2015). Low cervid densities (Controls) resulted from culls or exclosure treatments (Gill and Fuller 2007). Researchers confirmed low cervid density plots using camera traps or field transects (Graham et al. 2014, Carpio et al. 2015). We included articles in our meta-analyses if they quantified cervid population impacts on avian species' population abundance or overall avian species richness (Outcome).

We screened all potential articles against inclusion criteria in 3 steps. We first screened titles of all 2,023 articles and removed 1,166 articles that were not relevant (e.g., did not include either cervids or birds in the study or were not ecological papers). Next, we read the abstracts of the remaining 857 articles and removed all that did not contain information on how cervids impact avian abundance and/or richness. Finally, we read the remaining 298 articles in their entirety to determine if they, in addition to examining the relationship between cervids and avian species, contained the quantitative data (e.g., mean, sample size, measure of variation) for treatment and control groups necessary for computing overall effect sizes for our meta-analyses. When we excluded articles from the meta-analyses, we noted the reason for exclusion in our database. We used a Preferred Reporting Items for Systematic Reviews and Meta-Analysis diagram (Moher et al. 2009) to depict article exclusion during the screening process
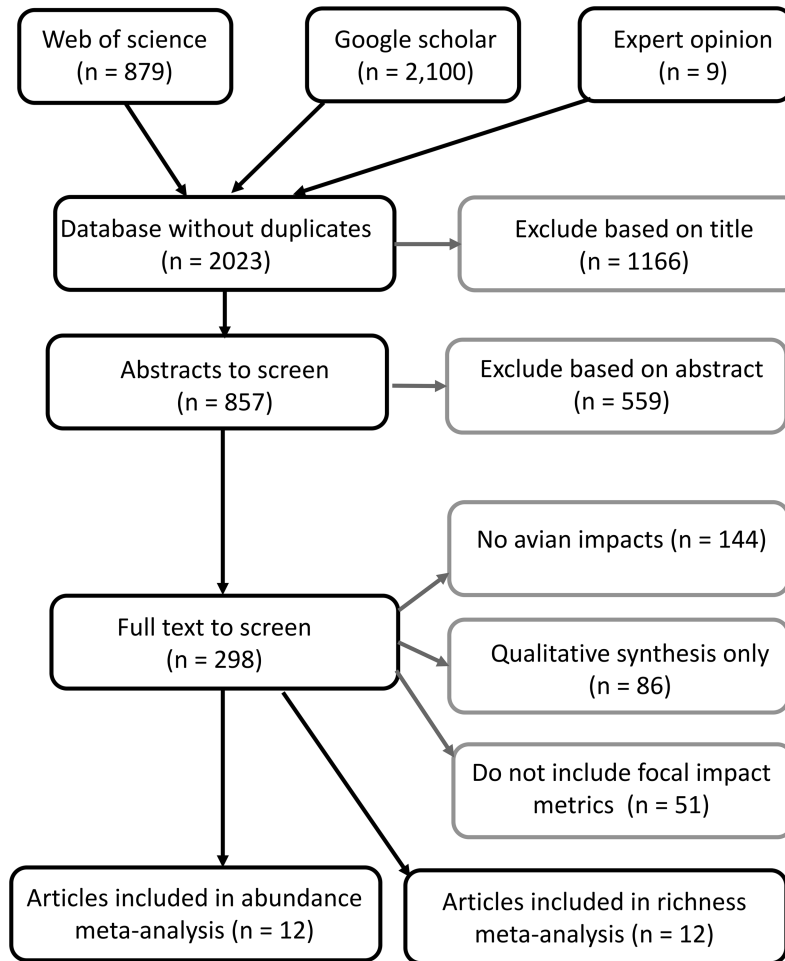
FIGURE 1. To conduct our meta-analyses that investigate deer impacts on avian abundance and richness, we first searched Web of Science and Google Scholar to locate studies in the published literature. Gray boxes indicate articles that were not consistent with our inclusion criteria, and black boxes indicate articles that were included in the next step of the screening process, and ultimately in the meta-analyses.

(Figure 1). After vetting each article against inclusion criteria, we found 17 articles that included data related to individual avian species abundance and/or species richness. Because a single article can contain both avian abundance and richness data, 7 articles were included in both the population abundance analysis and richness analysis, and ultimately each meta-analysis consisted of 12 articles (Table 2). The minimum threshold number of studies for a meta-analysis is between 5 and 10 publications (Koricheva et al. 2013).

Data Extraction
We extracted data for 22 categories from each article (Table 3; Crystal-Ornelas et al. 2021). Given a single article could provide abundance data for more than one species, when we extracted abundance data, we arranged our dataset by article (i.e. the full publication) and recorded the response of each avian species to the presence or absence of cervids (i.e. measurements within the publication). Each avian species in one article was assigned as a new row in our database and we recorded abundance statistics for each species.

We extracted data on publication characteristics (e.g., author, journal, publication year) as well as experimental design (e.g., focal avian species, focal cervid species, country where the study took place, study length [in days]). We determined whether the study occurred on an island or mainland and relied on information provided within each article to identify whether cervid populations were native or nonnative. Additionally, since research suggests cervid populations may disproportionately impact forest birds that nest on the ground or in shrubs, we included natural history information of each avian species to investigate links between deer impacts and avian nesting traits, primary habitat, and diet (Baiser et al. 2008, del Hoyo et al. 2013, Rodewald 2015). We collected information

TABLE 2. We list each of the 17 articles included in our meta-analyses that synthesizes research on deer impacts on forest bird populations and communities. We provide information on the focal cervid species in each published article, the length of each experiment, and whether the article was included in our abundance meta-analysis, richness meta-analysis, or both. If the article was used in our abundance meta-analysis, we provide the number of avian species studied in the original published article.

Article	Focal cervid species	Experiment length	Abundance data	Species with abundance data	Richness data
Anderson (2007)	Rocky Mountain elk (*Cervus elaphus nelsoni*)	3 days	✓	16	✓
Berger et al. (2001)	Moose (*Alces alces*)	1 month 15 days	✓	12	
deCalesta (1994)	White-tailed deer (*Odocoileus virginianus*)			N/A	✓
Carpio et al. (2015)	Red deer (*Cervus elaphus*)	7 months	✓	1	
Chollet et al. (2015)	Mule deer (*Odocoileus hemionus*)	20 years		N/A	✓
Graham et al. (2014)	Sika deer (*Cervus nippon*) and Red deer (*Cervus elaphus*)	5 years	✓	34	✓
McShea and Rappole (1992)	White-tailed deer (*Odocoileus virginianus*)	10 days		N/A	✓
McShea and Rappole (2000)	White-tailed deer (*Odocoileus virginianus*)	9 years	✓	3	
Tymkiw et al. (2013)	White-tailed deer (*Odocoileus virginianus*)	5 years	✓	27	✓
Okuda et al. (2012)	Sika deer (*Cervus nippon*)	N/A	✓	32	✓
Martin et al. (2011)	Black-tailed deer (*Odocoileus hemionus*) and Fallow deer (*Dama dama*)	3 months	✓	30	✓
Martin et al. (2010)	Black-tailed deer (*Odocoileus hemionus*)	3 months		N/A	✓
Chollet et al. (2016)	Black-tailed deer (*Odocoileus hemionus*)	13 years	✓	17	✓
DeGraaf et al. (1991)	White-tailed deer (*Odocoileus virginianus*)	2 years	✓	6	✓
Seki et al. (2014)	Sika deer (*Cervus nippon*)	1 month		N/A	✓
Martin et al. (2008)	Black-tailed deer (*Odocoileus hemionus*)	3 months	✓	13	
Cardinal et al. (2012)	White-tailed deer (*Odocoileus virginianus*)	1 year 6 months	✓	1	

on nesting location (brood parasite, building, cavity, cliff, ground, shrub, tree), primary habitat (forest, grassland, marsh, open woodland, riparian, scrub, town), and diet (meat, insects, nectar, omnivore, seeds) from the Cornell Lab of Ornithology's All About Birds database (https://www.allaboutbirds.org/news/). While the study primarily focused on forest birds (forest and open woodland habitat), 26 species associated with other habitat types (e.g., Brownheaded Cowbird [*Molothrus ater*] and rook [*Corvus frugilegus*]) were observed across the studies and were therefore included in this analysis.

We extracted data on mean individual species' population abundance or overall species richness from treatment sites (cervids present and overabundant) and control sites (cervids absent or at low abundance). In addition to mean abundance or richness, we extracted standard deviation and sample size for treatment and control groups. We took several steps to locate missing data if authors did not report the mean, standard deviation, or sample size in their article. First, we used *WebPlotDigitizer* (4.1; Rohatgi 2018) to extract mean and standard deviation from article figures when possible. We also examined supplementary information for any missing data. Finally, we emailed the corresponding author on the article and requested the missing data (*n* = 7 requests, *n* = 2 responses). We converted all measures of variation to standard deviation. One article (Martin et al. 2008) did not include any measure of variation for the 13 pairs of abundance measurements (i.e. only presented mean abundance at the site with overabundant cervids and the mean abundance at the site without cervids) we extracted for this analysis.

We used the R package *mice* (V3.12.0; van Buuren and Groothuis-Oudshoorn 2011) to impute a small number of missing standard deviations based on mean, sample size, and standard deviation values contained in the rest of the dataset.

Analysis: Choosing an Effect Size

We used the meta-analytic effect size Hedges' *g* to compare across all sites with low cervid population abundance to sites where cervids were overabundant (Hedges and Olkin 1985, Willms et al. 2017). The Hedges' *g* statistic represents an overall effect size for pairs of averages and accounts for sample size and standard deviation for each measurement. This effect size is frequently used in ecological meta-analyses because it incorporates a correction for small sample size and is appropriate when synthesizing 5 or more measurements, as were the case for both of our meta-analyses (Koricheva et al. 2013, Schwarzer et al. 2015). Also, Hedges' *g* is more appropriate than proportion-based effect sizes (e.g., response ratio, odds ratio) when articles have treatment or control sites with a 0-mean effect estimate since a 0 in the denominator of a proportion-based effect size would lead to an undefined summary effect (Hedges et al. 1999). In our meta-analyses, the value of Hedges' *g* represents the average effect of cervid overabundance on forest bird population abundance or overall species richness. A positive value for *g* suggests that overabundant cervid populations increase the abundance or richness of associated breeding birds, and a negative value for *g* suggests that cervid populations decrease bird abundance or richness. Generally, an

TABLE 3. To create the database for our meta-analysis, we extracted data from each article that quantified impacts that cervids have on individual avian species abundance or species richness. Most categories allowed for open responses according to information provided within the article. However, some categories had predefined subcategories, and in these instances, we provide the subcategories within the description.

Category	Description
Unique ID	This is a unique identification code that links measurements in our database to articles
Publication year	Year article was published
Cervid common name	Cervid species common name
Cervid Latin name	Cervid species Latin name
Avian common name	Avian species common name
Avian Latin name	Avian species Latin name
Avian family	Avian taxonomic family
Nesting location	Where does avian species nest (brood parasite, building, cavity, cliff, ground, shrub, tree; based on del Hoyo et al. 2013, Rodewald 2015)?
Primary habitat	What habitat is avian species most often associated with (forest, grassland, marsh, open woodlands, riparian, scrub, towns; based on Cornell Lab of Ornithology 2020)?
Diet	What is avian species primary diet (meat, insects, nectar, omnivore, seeds; based on Cornell Lab of Ornithology 2020)?
Native or introduced	Is cervid population native to study location or introduced?
Island or mainland	Did study occur on island or mainland?
Latitude	Study site latitude
Longitude	Study site longitude
Country	Country where study took place
Experiment length	Length of study as reported by article authors (in days)
Mean (control)	Mean individual avian species abundance or mean species richness at site without cervids
Mean (treatment)	Mean individual avian species abundance or mean species richness at sites with cervids
Standard deviation (control)	Standard deviation for avian abundance or richness mean at sites without cervids
Standard deviation (treatment)	Standard deviation for avian abundance or richness mean at sites with cervids
Sample size (control)	Number of sites measured for avian abundance or richness without cervids
Sample size (treatment)	Number of sites measured for avian abundance or richness with cervids

absolute value of Hedges' g less than 0.2 is considered a weak effect size, whereas a g value exceeding 0.8 is considered a strong effect (Cohen 1988, Koricheva et al. 2013).

Meta-analytic Models

We performed both meta-analyses using the R software package (3.6.3; R Core Team 2019) *metafor* (2.1.0; Viechtbauer 2017). For both meta-analyses, we first calculated an overall effect size using a random-effects model and restricted maximum likelihood estimation because the data for our meta-analyses came from heterogeneous studies (Koricheva et al. 2013). In these random-effects models, we assigned each article's unique identifier as a random effect to control for nonindependence when we extracted multiple measurements from a single article (Schwarzer et al. 2015), though we note that we did not control for multiple studies conducted in the same natural system (e.g., the Haida Gwaii archipelago; Martin et al. 2010, Chollet et al. 2015). In both models, we gave greater weight to measurements with lower associated variance size using the inverse-variance method (i.e. if the sample size were equal in 2 different studies, the study with lower variance would be given greater weight when computing the overall effect size; Koricheva et al. 2013). We calculated 95% confidence intervals (95% CIs) for summary effect sizes. When CIs exclude zero, this suggests that mean avian abundance or species richness significantly differs between control and overabundance plots.

To examine whether cervids disproportionately impact population abundance for species with certain nesting locations, we implemented a mixed-effects meta-regression (Raudenbush et al. 2009, Koricheva et al. 2013). We conducted similar mixed-effects meta-regressions for primary avian habitat and diet. We performed all 3 meta-regressions using only abundance data because the richness dataset aggregates information from species with a variety of nesting and habitat locations. In our mixed-effects model, we used nesting location, habitat, or diet as the fixed predictor variable and assigned the unique article identifier as a random effect. We followed recommendations in other meta-analyses and excluded any nesting substrates, habitats, or diets in our database with fewer than 7 published effect sizes (Ferreira et al. 2016 suggests $n > 3$, Blouin et al. 2019 suggests $n > 10$; we took the average as the recommendation).

Test for Publication Bias

Publication bias occurs if statistically nonsignificant results are published less often than significant results (Gurevitch et al. 2018). We used publication bias histograms to

visually assess whether our dataset was biased toward high-magnitude positive or negative effect sizes (Basche and DeLonge 2017, Thapa et al. 2018). If effect sizes are approximately normally distributed, this suggests that the meta-analytic dataset lacks publication bias.

RESULTS

Our meta-analyses compiled data from 17 different articles that included the effects of 8 cervid species (Table 2) on 130 avian species to quantify the magnitude of the effects of overabundant cervid browsing on populations and communities of breeding forest birds. The effect sizes that we included in our abundance meta-analysis represented avian species from 35 families. Of the 130 species, 36 were classified as decreasing by the International Union for Conservation of Nature (IUCN) with the remaining species listed as stable ($n = 53$), increasing ($n = 39$), or unknown ($n = 2$) (IUCN 2020).

On average, each article contributed abundance data for 16 species (SD = 12.22), with a maximum number of 34 abundance measures and a minimum of 1. The average study duration across both meta-analyses was 3.58 years (SD = 5.79), with the longest study duration being 20 years and the shortest 3 days. Most research took place in the United States ($n = 7$), followed by Canada ($n = 5$) and Japan ($n = 2$). A total of 9 articles contained data from island-based studies. Impacts represent 8 members of Cervidae, with 5 articles in our database investigating nonnative cervid populations, 11 focused on native populations, and 1 study that included both native and nonnative cervid species.

Population Abundance
Our random-effects model found a significant association between overabundant cervids and "moderate" declines in avian abundance according to the Hedges' g statistic ($g = -0.424$, 95% CI: -0.753 to -0.094, $P \leq 0.05$; Figure 2; Cohen 1988). The high level of heterogeneity in our dataset ($Q[df = 190] = 851.92$, $P < 0.0001$) indicated that moderating variables (e.g., nesting location, habitat, or diet) may be driving differences in how bird species respond to cervid overabundance. Our publication bias histogram for the population abundance meta-analysis did not show strong publication bias (Figure 3A).

Our mixed-effects meta-regression examining the differential impact of nesting location showed that ground-nesting species were associated with the largest drops in abundance with the presence of overabundant cervids ($g = -0.515$, 95% CI: -0.819 to -0.212, $P < 0.001$; Figure 4A). Shrub and tree nesting species were also associated with significant moderate declines in abundance ($g = -0.420$, 95% CI: -0.718 to -0.122, $P < 0.01$ and $g = -0.415$, 95% CI: -0.711 to -0.119, $P < 0.01$, respectively). Cavity nesting

species were not associated with a decline in abundance (P = not significant [n.s.]).

Our mixed-effects meta-regression for primary habitat found that forest birds showed the steepest declines in abundance with overabundant cervid populations ($g = -0.435$, 95% CI: -0.750 to -0.119, $P < 0.01$; Figure 4B). Species whose primary habitat is open woodland were also associated with significant moderate declines in abundance ($g = -0.416$, 95% CI: -0.734 to -0.098, $P < 0.05$). Although some species in the study were associated primarily with grasslands and scrub habitat, these species were not associated with significant declines in abundance.

Our final mixed-effects meta-regression found that insectivorous and omnivorous birds were associated with significant moderate declines in abundance ($g = -0.375$, 95% CI: -0.666 to -0.083, $P < 0.05$ and $g = -0.429$, 95% CI: -0.791 to -0.066, $P < 0.05$, respectively; Figure 4C). Species that primarily forage on seeds were not associated with declines in abundance (P = n.s.).

Species Richness
Our random-effects model analyzing species richness found that overabundant cervid populations significantly decreased mean species richness of forest breeding birds with a "moderate" decline ($g = -0.650$, 95% CI: -1.231 to -0.068, $P < 0.05$; Figure 5). Based on the publication bias histogram for our richness meta-analysis (Figure 3B), there is no evidence of publication bias, though we note that this meta-analysis included a small number of effect sizes ($n = 14$).

DISCUSSION

As bird populations broadly decline around the globe (Gaston et al. 2003, Butchart et al. 2010, Rosenberg et al. 2019), it is important to synthesize existing local-scale studies to identify the average impacts that overabundant cervid species have on forest birds. Through quantitative synthesis, we found that, on average, sites with overabundant cervids were associated with moderately lower abundance and species richness as compared to sites that had either no cervids or had relatively small cervid populations. Our meta-analyses strongly suggest that controlling cervid populations may help native forest avian biodiversity. While many of the studies in our meta-analyses identified the negative impact of cervids on birds at smaller spatial scales, our synthesis provides wildlife and land managers with a broad and quantitative foundation for consideration of cervid management programs to support bird conservation initiatives.

Birds that primarily place their nests in shrubs, trees, and on the ground are less abundant at sites with overabundant cervids. Given the influence that deer, elk, and moose have
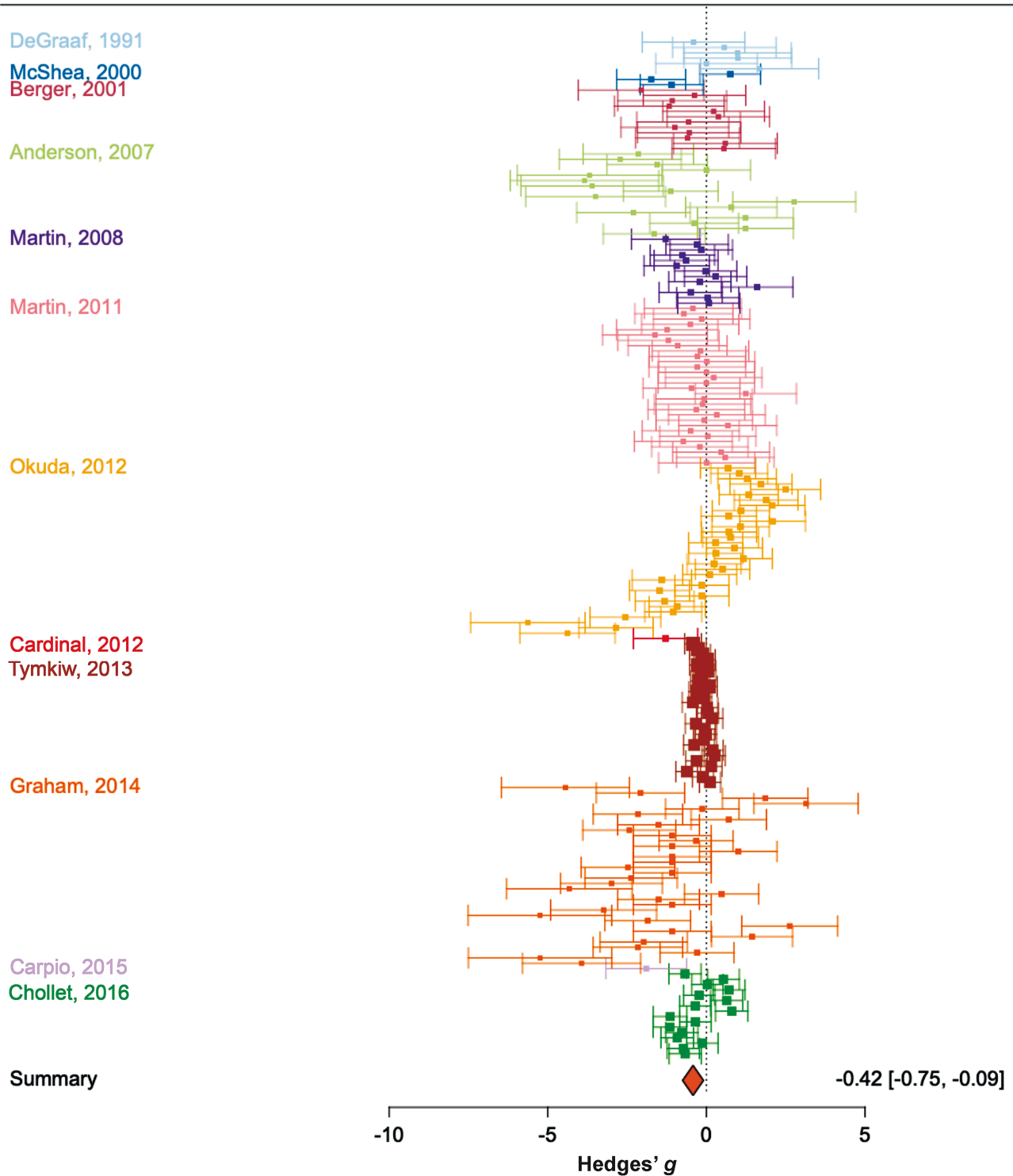
FIGURE 2. Forest plot for a random-effects model of cervid impacts on individual avian species abundance. We included 192 abundance effect sizes from 12 articles. Each effect size is color-coded according to the original article that contained avian abundance data. The mixed-effects model identified a significant average negative effect of cervids on individual species abundance, indicated by the orange diamond at the bottom of the forest plot.

on forest understory composition (McLaren et al. 2004, Anderson 2007, Kelly 2019), over-browsing of shrub vegetation likely results in a reduction in locations suitable for placing nests or an increased vulnerability of nests placed in altered shrub vegetation structure to reptilian and mammalian predators (Cox et al. 2012, Vetter et al. 2013, Fulton 2018).
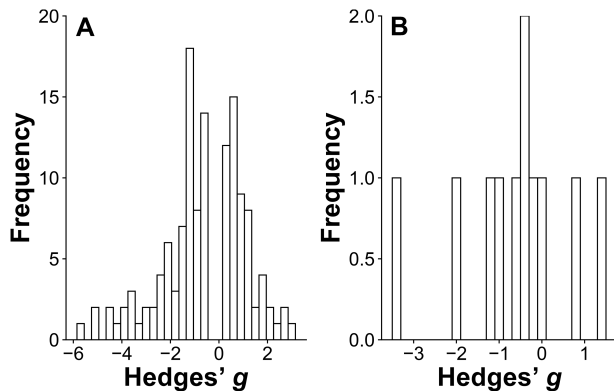
FIGURE 3. Our publication bias histograms show the frequency distribution of effect sizes for our 2 meta-analyses. (A) The publication bias histogram for our individual avian abundance meta-analysis is both symmetrical and centered on an effect size of 0. This suggests that our abundance meta-analysis database was an unbiased sample of the published evidence base. (B) The publication bias histogram for our avian richness meta-analysis is approximately symmetrical given the small sample size ($n = 14$) for this meta-analysis.

We did not expect to find a negative effect of overabundant cervids on birds that nest in trees. One might intuitively predict that birds nesting in trees would be unaffected by cervids browsing on forest understory. However, tree nesting species may decrease over the long term if over-browsing results in a shift in canopy tree composition or a change in the frequency or location of treefall gaps (Suominen et al. 1999, McWilliams et al. 2018, Collins et al. 2020). Either effect can reduce the number of tree species that are preferred by birds for nest placement, alter canopy architecture to disfavor nest survival, or alter the incidence of micro-successional forest habitats that some birds evolved to exploit (Edworthy and Martin 2013, Johnson et al. 2017). More likely, shrub and tree nesting birds that are primarily insectivorous may be declining due to the loss of insects that live exclusively in the understory, live in the canopy, or originate in the understory and move to the canopy through their lifecycle (Chollet et al. 2015). For example, in just a year, overabundant deer resulted in reduction of litter, mostly through reduction of litter quality, and this reduction in understory litter directly reduced insect populations (Shik and Kaspari 2010, Compson et al. 2013, Chollet et al. 2020).

Published local-scale studies suggested that exposure of nests to predators and trampling of nests by cervids would reduce ground-nesting bird abundance (Holloran and Anderson 2003, Baiser et al. 2008) and that substantial impacts would be seen in forest-dwelling birds (Jirinec et al. 2017). Our meta-analysis establishes the generality of these local-scale studies and suggests that on average, overabundant cervids will be associated with significant drops in avian abundance. However, the exact mechanism by which overabundant cervids affect ground-nesting birds cannot be teased apart in our meta-analysis, necessitating the need for local studies to explicitly explore these impacts.

We acknowledge that our meta-analytic approach, as beneficial as it can be for summarizing research, can obscure important species-by-species results. For example, elk overabundance in the United States was associated with a decrease in ground-nesting Fox Sparrow (*Passerella iliaca*) abundance and an increase in ground-nesting Savannah Sparrow (*Passerculus sandwichensis*) abundance (Anderson 2007). These changes are likely reflective of how cervids alter forest structure and associated food resources as Fox Sparrows prefer forested habitat and will be negatively impacted by a lack of forest regeneration, while Savannah Sparrows prefer open habitat which deer browse may facilitate.

The differential response of specific bird nesting behavior to habitat changes and how cervids shape understory vegetation drive the findings of our second meta-regression. We found that the sharpest declines in avian abundance were associated with birds whose primary habitat is forest and open woodland. In addition to altering patterns in canopy gaps and regeneration (Suominen et al. 1999, McWilliams et al. 2018, Collins et al. 2020), cervid overabundance can also promote establishment of nonnative plants that alter forest structure (Baiser et al. 2008). These changes may homogenize forests limiting the diversity of resources that forest specialists may need, and these changes in forest composition have been associated with decreased avian abundance over time (Rooney 2009, Brown et al. 2019). Additionally, forest habitat specialists may not utilize nonnative resources as readily as species associated with multiple habitats and may be less tolerant of disturbances caused by deer leading to a reduction in population (Devictor et al. 2008, Aslan and Rejmanek 2010). Thus, overabundant deer populations may negatively impact forest specialist birds by acting as a form of disturbance and altering habitat quality. However, it is less clear how species associated with other habitat types, such as scrub and grassland, but still found in forests or forest edges are impacted. Although we found no negative correlation between birds associated with non-forest habitat and cervid abundance, we emphasize that there were no studies in this work specifically in non-forest systems. The lack of studies highlights potential areas for further investigation but may also be limited due to the cervids' primary association with forests.

Our third meta-regression indicated that avian species that are insectivores or omnivores were associated with declines in abundance when cervids were overabundant. This corresponds with recent research that suggests mass declines in insect abundance may be associated with declines in avian abundance (Bowler et al. 2019). While
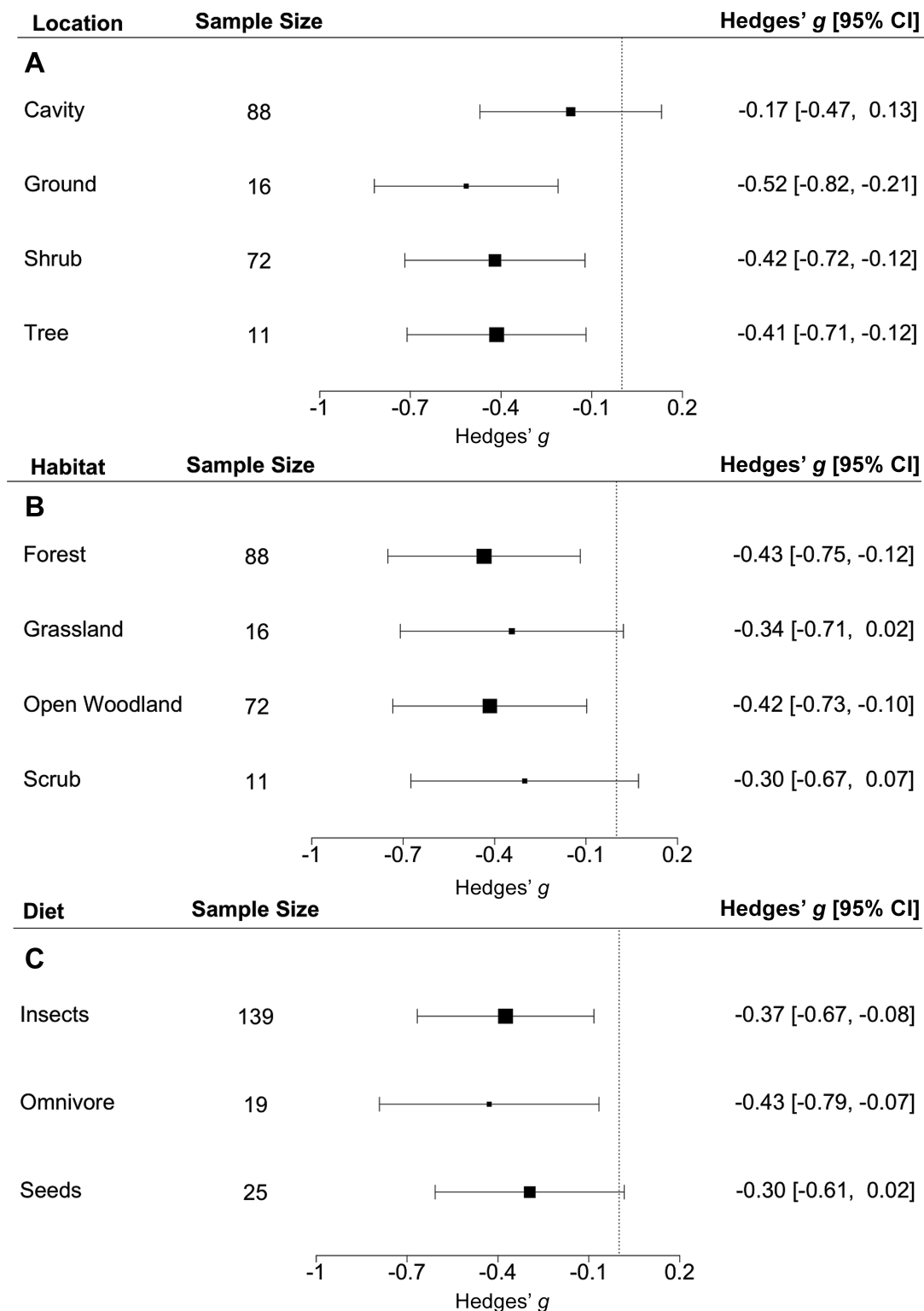
Location	Sample Size		Hedges' *g* [95% CI]
A			
Cavity	88		-0.17 [-0.47, 0.13]
Ground	16		-0.52 [-0.82, -0.21]
Shrub	72		-0.42 [-0.72, -0.12]
Tree	11		-0.41 [-0.71, -0.12]

Habitat	Sample Size		Hedges' *g* [95% CI]
B			
Forest	88		-0.43 [-0.75, -0.12]
Grassland	16		-0.34 [-0.71, 0.02]
Open Woodland	72		-0.42 [-0.73, -0.10]
Scrub	11		-0.30 [-0.67, 0.07]

Diet	Sample Size		Hedges' *g* [95% CI]
C			
Insects	139		-0.37 [-0.67, -0.08]
Omnivore	19		-0.43 [-0.79, -0.07]
Seeds	25		-0.30 [-0.61, 0.02]

FIGURE 4. The forest plot for our mixed-effects meta-regression shows that changes to individual avian species abundance depend on avian species: (A) nesting location, (B) primary habitat, and (C) diet. The right side of each forest plot provides summaries of effect sizes for each nesting location or habitat and the associated confidence interval. Positive values for Hedges' *g* indicate that the presence of cervids corresponded to an increase in avian abundance while negative values suggest that cervids decreased avian abundance. Cervids significantly decreased abundance for species that nest on the ground, in shrubs, and in trees and species whose primary habitat is forest and open woodland. Abundance also significantly decreased for the species that were either insectivores or omnivores.
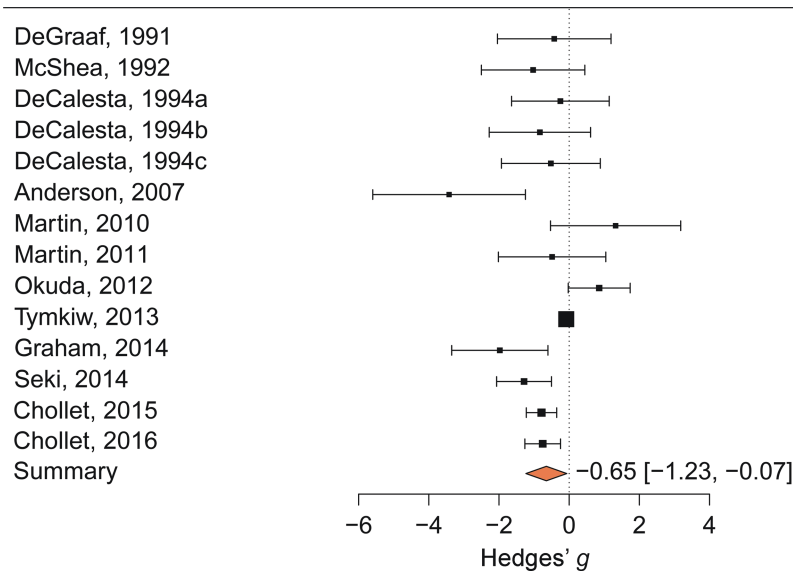
FIGURE 5. Results of our random-effects meta-analysis of cervid impacts on avian species richness. We extracted the data from 12 unique articles that included 14 richness measurements. Article identifiers are listed along the left column of the forest plot. The model suggested that the presence of cervids significantly decreased mean avian species richness as indicated by the orange diamond at the bottom of the forest plot ($P = 0.035$).

pinpointing the mechanism of this decline remains to be explored (Tallamy and Shriver 2021), shifts in insect communities across forest strata may have an impact on forest birds (Carson and Root 2000, Eschtruth and Battles 2008, Chollet et al. 2015, Møller 2019). Research shows that excessive understory herbivory is linked to a reduction in insect richness, which in turn may limit food for insectivores (deCalesta 1994, Allombert et al. 2005, Bowler et al. 2019, Møller 2019). In addition to the decline of insectivorous species, we were surprised to see a decline in omnivores. A previous study suggests omnivores will not experience the same impacts from shifting food sources (Bowler et al. 2019), but increased cervid abundances may also correlate with other more complex food web interactions. Specifically, overabundant cervids can alter rodent and lizard populations and omnivorous birds may prey directly on, or compete directly with, these taxa for food (Fleming 1979, Bolzoni et al. 2012, Mohanty et al. 2016). Thus, changes in rodent and lizard populations may indirectly impact birds, although we acknowledge our findings for omnivores were based on a relatively small sample size. We did not locate enough published research on nectivores or carnivores to synthesize research on these species, and we note that we had no frugivores in our meta-analyses. The lack of frugivores is likely because most frugivores are tropical species with ranges that do not overlap with cervids (although there are exceptions, e.g., Cedar Waxwings [*Bombycilla cedrorum*]), and other fruit-eating species tend to be omnivorous (e.g., Hooded Crows [*Corvus cornix*]).

The results of our meta-analyses establish the generality of previous local-scale research that recommends management

of overabundant cervid populations to protect forest birds. However, the existing evidence for different cervid management strategies presents mixed results for avian populations. The evidence published thus far suggests that management solutions can themselves trigger complex trophic dynamics, where the links between cervid management actions and bird population recovery are less than clear (Kelly 2019). For example, a long-term study in the eastern United States showed that, after the installation of deer-proof fencing, forest vegetation returned to a density and composition characteristic of moderately browsed locations within 10–20 years after the removal of white-tailed deer (Kelly 2019). However, the authors could not determine how their relatively small-scale cervid exclusion efforts may cascade through to the bird populations and communities they investigated (Kelly 2019). On the other hand, evidence from research on the Haida Gwaii archipelago in Canada suggested that cervid culling over a 13-year period resulted in the rapid return of native plant species and an eventual (~10 years later) increase in avian species (Chollet et al. 2016). Additionally, recent research shows that a threatened songbird's population (San Clemente Bell's Sparrow [*Artemisiospiza belli clementeae*]) has rebounded after cervid removal and associated native vegetation recovery (Meiman et al. 2020). These varying results may be due to a lack of long-term research and highlight the need for additional long-term cervid exclusion and monitoring efforts.

Finally, our systematic search for evidence to inform the relationship between cervid overabundance and forest bird status revealed some research gaps that limited our ability to provide a more comprehensive meta-analysis. Although our meta-analyses had a global scope, all the articles with quantitative

information suitable for inclusion were conducted in the northern hemisphere. This geographical bias almost certainly does not reflect the role that cervid species play in forest dynamics and bird conservation within southern hemisphere locations such as New Zealand or the Patagonia region of Argentina (Simberloff and Rejmánek 2011). Similarly, although we identified nearly 300 published articles with potentially relevant data for our meta-analyses, we could only include 17 articles in our meta-analyses. This was because the studies either (1) were not designed so that bird population abundance or richness could be compared between sites that differed substantially in cervid abundance or (2) did not provide relevant basic information on effect sizes, sample sizes, or data variation. The former issue highlights the need for careful observation or experimental design that ensures (through point counts or camera traps) that cervids are at low density or absent in control sites and overabundant in treatment sites. Studies that clearly delineate control and treatment sites and make their data readily reusable (Martin et al. 2011, Cardinal et al. 2012) ensure that the study directly assessed the trophic links between cervid browse and bird populations. The latter issue is a common problem across the ecological and wildlife sciences, with our efforts adding to the growing call for data to be Findable, Accessible, Interoperable, and Reusable (FAIR; Wilkinson et al. 2016). Submitting data to long-term repositories (e.g., figshare, Dryad) is a way that researchers can make their data more FAIR and also increase the efficiency of syntheses and meta-analyses like ours. We note that in an effort to strictly adhere to our inclusion criteria for this meta-analysis we excluded studies that would have almost certainly been incorporated into a narrative review on this same subject. However, robust meta-analyses can only incorporate existing evidence that fits inclusion criteria (Gurevitch et al. 2018). Given these limitations to our conclusions, we strongly suggest that our synthesis be updated in the future to reflect future accumulation of more and varied research on cervid overabundance and avian populations declines.

ACKNOWLEDGMENTS

LITERATURE CITED

Allombert, S., A. J. Gaston, and J.-L. Martin (2005). A natural experiment on the impact of overabundant deer on songbird populations. Biological Conservation 126:1–13.

Anderson, E. M. (2007). Changes in bird communities and willow habitats associated with fed elk. The Wilson Journal of Ornithology 119:400–409.

Aslan, C. E., and M. Rejmanek (2010). Avian use of introduced plants: Ornithologist records illuminate interspecific associations and research needs. Ecological Applications 20:1005–1020.

Baiser, B., J. L. Lockwood, D. La Puma, and M. F. J. Aronson (2008). A perfect storm: Two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions 10:785–795.

Ballard, W., D. Lutz, and L. H. Carpenter (2001). Deer–predator relationships: A review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.

Basche, A., and M. DeLonge (2017). The impact of continuous living cover on soil hydrologic properties: A meta-analysis. Soil Science Society of America Journal 81:1179–1190.

Beguin, J., J. Tremblay, N. Thiffault, D. Pothier, and S. D. Côté (2016). Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps. Ecosphere 7:e01488.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson (2001). A mammalian predator–prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11:947–960.

Blouin, M., J. Barrere, N. Meyer, S. Lartigue, S. Barot, and J. Mathieu (2019). Vermicompost significantly affects plant growth. A meta-analysis. Agronomy for Sustainable Development 39:34.

Bolzoni, L., R. Rosà, F. Cagnacci, and A. Rizzoli (2012). Effect of deer density on tick infestation of rodents and the hazard of tick-borne encephalitis. II: Population and infection models. International Journal for Parasitology 42:373–381.

Bowler, D. E., H. Heldbjerg, A. D. Fox, M. de Jong, and K. Böhning-Gaese (2019). Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology 33:1120–1130.

Brown, J. A., J. L. Lockwood, J. D. Avery, J. Curtis Burkhalter, K. Aagaard, and K. H. Fenn (2019). Evaluating the long-term effectiveness of terrestrial protected areas: A 40-year look at forest bird diversity. Biodiversity and Conservation 28:811–826.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, et al. (2010). Global biodiversity: Indicators of recent declines. Science 328:1164–1168.

van Buuren, S., and K. Groothuis-Oudshoorn (2011). *mice*: Multivariate Imputation by Chained Equations in R. Journal of Statistical Software 45:1–68.

Cardinal, E., J.-L. Martin, J.-P. Tremblay, and S. D. Côté (2012). An experimental study of how variation in deer density affects vegetation and songbird assemblages of recently harvested boreal forests. Canadian Journal of Zoology 90:704–713.

Carpio, A. J., J. Oteros, J. Vicente, F. S. Tortosa, and J. Guerrero-Casado (2015). Factors affecting Red-legged Partridge (*Alectoris rufa*) abundance on big-game hunting estates: Implications for management and conservation. Ardeola 62:283–297.

Carson, W. P., and R. B. Root (2000). Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. Ecological Monographs 70:73–99.

Chollet, S., C. Bergman, A. J. Gaston, and J.-L. Martin (2015). Long-term consequences of invasive deer on songbird communities: Going from bad to worse? Biological Invasions 17:777–790.

Chollet, S., M. Maillard, J. Schörghuber, S. J. Grayston, and J.-L. Martin (2020). Deer slow down litter decomposition by reducing litter quality in a temperate forest. Ecology 102:e03235.

Chollet, S., and J.-L. Martin (2013). Declining woodland birds in North America: Should we blame Bambi? Diversity and Distributions 19:481–483.

Chollet, S., S. Padié, S. Stockton, S. Allombert, A. J. Gaston, and J.-L. Martin (2016). Positive plant and bird diversity response to experimental deer population reduction after decades of uncontrolled browsing. Diversity and Distributions 22:274–287.

Cohen, J. (1988). Statistical Power Analyses for the Social Sciences. Lawrence Erlbaum Associates, Hillsdale, NJ, USA.

Collins, R. J., C. A. Copenheaver, J. N. Barney, and P. J. Radtke (2020). Using invasional meltdown theory to understand patterns of invasive richness and abundance in forests of the northeastern USA. Natural Areas Journal 40:336–344.

Compson, Z. G., K. J. Adams, J. A. Edwards, J. M. Maestas, T. G. Whitham, and J. C. Marks (2013). Leaf litter quality affects aquatic insect emergence: Contrasting patterns from two foundation trees. Oecologia 173:507–519.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller (2004). Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 3:113–147.

Cox, W. A., F. R. Thompson, and J. Faaborg (2012). Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landscape Ecology 27:659–669.

Crystal-Ornelas, R., J. A. Brown, R. E. Valentin, C. Beardsley, and J. L. Lockwood (2021). Data from: Meta-analysis shows that overabundant deer (Cervidae) populations consistently decrease average population abundance and species richness of forest birds. Ornithological Applications 123:4. doi:10.6084/m9.figshare.12001368

Dávalos, A., V. Nuzzo, and B. Blossey (2015). Single and interactive effects of deer and earthworms on non-native plants. Forest Ecology and Management 351:28–35.

deCalesta, D. S. (1994). Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. The Journal of Wildlife Management 58:711–718.

DeGraaf, R. M., W. M. Healy, and R. T. Brooks (1991). Effects of thinning and deer browsing on breeding birds in New England oak woodlands. Forest Ecology and Management 41:179–191.

Devictor, V., R. Julliard, and F. Jiguet (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514.

Dolman, P. M., and K. Wäber (2008). Ecosystem and competition impacts of introduced deer. Wildlife Research 35:202–214.

Edworthy, A. B., and K. Martin (2013). Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. The Journal of Wildlife Management 77:770–776.

Eschtruth, A. K., and J. J. Battles (2008). Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecological Applications 18:360–376.

Ferreira, V., J. Koricheva, J. Pozo, and M. A. S. Graca (2016). A meta-analysis on the effects of changes in the composition of native forests on litter decomposition in streams. Forest Ecology and Management 364:27–38.

Fleming, T. H. (1979). Do tropical frugivores compete for food? American Zoologist 19:1157–1172.

Fuller, R. J., R. D. Gregory, D. W. Gibbons, J. H. Marchant, J. D. Wilson, S. R. Baillie, and N. Carter (1995). Population declines and range contraction among lowland farmland birds in Britain. Conservation Biology 9:1425–1441.

Fulton, G. R. (2018). Avian nest predation in Australian temperate forest and woodland: A review. Pacific Conservation Biology 24:122–133.

Gaston, K. J., T. M. Blackburn, and K. K. Goldewijk (2003). Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London, Series B: Biological Sciences 270:1293–1300.

Gill, R. M. A., and R. J. Fuller (2007). The effects of deer browsing on woodland structure and songbirds in lowland Britain: Deer browsing, woodland structure and songbirds. Ibis 149:119–127.

Graham, C. T., M. W. Wilson, T. Gittings, T. C. Kelly, S. Irwin, O. F. M. Sweeney, and J. O'Halloran (2014). Factors affecting the bird diversity of planted and semi-natural oak forests in Ireland. Bird Study 61:309–320.

Gurevitch, J., J. Koricheva, S. Nakagawa, and G. Stewart (2018). Meta-analysis and the science of research synthesis. Nature 555:175–182.

Hedges, L. V., J. Gurevitch, and P. S. Curtis (1999). The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Hedges, L. V., and I. Olkin (1985). Statistical Method for Meta-analysis. Academic Press, Orlando, FL, USA.

Hegland, S. J., K. Rydgren, and T. Seldal (2005). The response of *Vaccinium myrtillus* to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy. Canadian Journal of Botany 83:1638–1644.

Holloran, M. J., and S. H. Anderson (2003). Direct identification of Northern Sage-grouse (*Centrocercus urophasianus*) nest predators using remote sensing cameras. Canadian Field-Naturalist 117:308–310.

Holt, C. A., R. J. Fuller, and P. M. Dolman (2011). Breeding and post-breeding responses of woodland birds to modification of habitat structure by deer. Biological Conservation 144:2151–2162.

del Hoyo, J., S. H. M. Butchart, N. Collar, A. Stattersfield, and L. Bennun (2013). Handbook of the Birds of the World: New Species and Global Index. Lynx Ediciones, Barcelona, Spain.

Huang, X., J. Lin, and D. Demner-Fushman (2006). Evaluation of PICO as a knowledge representation for clinical questions. AMIA Annual Symposium Proceedings 2006:359–363.

Ims, R. A., J.-A. Henden, M. A. Strømeng, A. V. Thingnes, M. J. Garmo, and J. U. Jepsen (2019). Arctic greening and bird nest predation risk across tundra ecotones. Nature Climate Change 9:607–610.

IUCN (2020). The IUCN Red List of Threatened Species. http://www.iucnredlist.org/

Jirinec, V., D. A. Cristol, and M. Leu (2017). Songbird community varies with deer use in a fragmented landscape. Landscape and Urban Planning 161:1–9.

Johnson, K., G. Sadoti, and J. Smith (2017). Weather-induced declines in piñon tree condition and response of a declining bird species. Journal of Arid Environments 146:1–9.

Kelly, J. F. (2019). Regional changes to forest understories since the mid-twentieth century: Effects of overabundant deer and other factors in northern New Jersey. Forest Ecology and Management 444:151–162.

Koricheva, J., J. Gurevitch, and L. Gómez-Aparicio (2014). Uses and misuses of meta-analysis in plant ecology. The Journal of Ecology 102:828–844.

Koricheva, J., J. Gurevitch, and K. Mengersen (2013). Handbook of Meta-Analysis in Ecology and Evolution. Princeton University Press, Princeton, NJ, USA.

Kugeler, K. J., R. A. Jordan, T. L. Schulze, K. S. Griffith, and P. S. Mead (2016). Will culling white-tailed deer prevent Lyme disease? Zoonoses and Public Health 63:337–345.

Loss, S. R., S. S. Loss, T. Will, and P. P. Marra (2015). Linking place-based citizen science with large-scale conservation research: A case study of bird-building collisions and the role of professional scientists. Biological Conservation 184:439–445.

Macdonald, N., G. Nugent, K. A. Edge, and J. P. Parkes (2017). Eradication of red deer from Secretary Island, New Zealand: Changing tactics to achieve success. In Island Invasives: Scaling Up to Meet the Challenge (C. R. Veitch, M. N. Clout, A. R. Martin, J. C. Russell, and C. J. West, Editors) Occasional Paper SSC no. 62. IUCN, Gland, Switzerland. pp. 256–260.

Martin, J. L., S. Allombert, and A. J. Gaston (2008). The effects of deer and squirrels on forest birds: Community structure, population density, and reproduction. In Lessons from the Islands: Introduced Species and What They Tell Us About How Ecosystems Work (A. J. Gaston and T. E. Golumbia, Editors). Canadian Wildlife Service, Ottawa, Ontario, Canada. pp. 93–99.

Martin, J.-L., S. A. Stockton, S. Allombert, and A. J. Gaston (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. Biological Invasions 12:353–371.

Martin, T. G., P. Arcese, and N. Scheerder (2011). Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. Biological Conservation 144:459–469.

McLaren, B. E., B. A. Roberts, N. Djan-Chékar, and K. P. Lewis (2004). Effects of overabundant moose on the Newfoundland landscape. Alces 40:45–49.

McShea, W. J., and J. H. Rappole (1992). White-tailed deer as keystone species within forest habitats of Virginia. Virginia Journal of Science 43:177–186.

McShea, W. J., and J. H. Rappole (2000). Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14:1161–1170.

McWilliams, W. H., J. A. Westfall, P. H. Brose, D. C. Dey, A. W. D'Amato, Y. L. Dickinson, M. A. Fajvan, L. S. Kenefic, C. C. Kern, K. M. Laustsen, S. L. Lehman, et al. (2018). Subcontinental-Scale Patterns of Large-Ungulate Herbivory and Synoptic Review of Restoration Management Implications for Midwestern and Northeastern Forests. U.S. Department of Agriculture, Forest Service, Northern Research Station NRS-GTR-182, Madison, WI, USA.

Meiman, S. T., E. E. DeLeon, and A. S. Bridges (2020). Reproductive success of the threatened San Clemente Bell's Sparrow (*Artemisiospiza belli clementeae*) in recovering habitats is similar to success in historical habitat. The Condor: Ornithological Applications 122:2.

Milner, J. M., F. M. Van Beest, K. T. Schmidt, R. K. Brook, and T. Storaas (2014). To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. The Journal of Wildlife Management 78:1322–1334.

Mohanty, N. P., S. Harikrishnan, K. Sivakumar, and K. Vasudevan (2016). Impact of invasive spotted deer (*Axis axis*) on tropical island lizard communities in the Andaman archipelago. Biological Invasions 18:9–15.

Moher, D., A. Liberati, J. Tetzlaff, D. G. Altman, and PRISMA Group (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. PLoS Medicine 6:e1000097.

Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. Ecology and Evolution 9:6581–6587.

Nagashima, K., T. Shimomura, and K. Tanaka (2019). Early-stage vegetation recovery in forests damaged by oak wilt disease and deer browsing: Effects of deer-proof fencing and clear-cutting. Landscape and Ecological Engineering 15:155–166.

Nilsen, E. B., E. J. Milner-Gulland, L. Schofield, A. Mysterud, N. C. Stenseth, and T. Coulson (2007). Wolf reintroduction to Scotland: Public attitudes and consequences for red deer management. Proceedings of the Royal Society B: Biological Sciences 274:995–1003.

Northrup, J. M., J. W. Rivers, Z. Yang, and M. G. Betts (2019). Synergistic effects of climate and land-use change influence broad-scale avian population declines. Global Change Biology 25:1561–1575.

Okuda, K., Y. Seki, and K. Masaaki (2012). Effects of vegetation modification due to high deer density on breeding bird communities in Oku-Nikko, Japan. Journal of the Japanese Forest Society 94:236–242.

R Core Team (2019). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramsey, D. S. L., D. M. Forsyth, C. J. Veltman, S. J. Richardson, R. B. Allen, W. J. Allen, R. J. Barker, P. J. Bellingham, C. L. Jacobson, S. J. Nicol, A. W. Robertson, and C. R. Todd (2017). A management experiment reveals the difficulty of altering seedling growth and palatable plant biomass by culling invasive deer. Wildlife Research 44:623.

Raudenbush, S., H. Cooper, L. Hedges, and J. Valentine (2009). The handbook of research synthesis and meta-analysis. In The Handbook of Research Synthesis and Meta-Analysis (H. Cooper, L. V. Hedges, and J. C. Valentine, Editors). Russell Sage Foundation, New York, NY, USA. pp. 295–315.

Rodewald, P. (2015). The Birds of North America. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsna.org

Rohatgi, A. (2018). WebPlotDigitizer. Version 4.1. Pacifica, CA, USA. https://automeris.io/WebPlotDigitizer

Rooney, T. P. (2009). High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202:103–111.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra (2019). Decline of the North American avifauna. Science 366:120–124.

Schwarzer, G., J. R. Carpenter, and G. Rücker (2015). Meta-Analysis with R. Springer International Publishing, Switzerland.

Seki, S.-I., D. Fujiki, and S. Sato (2014). Assessing changes in bird communities along gradients of undergrowth deterioration in deer-browsed hardwood forests of western Japan. Forest Ecology and Management 320:6–12.

Shik, J. Z., and M. Kaspari (2010). More food, less habitat: How necromass and leaf litter decomposition combine to regulate a litter ant community. Ecological Entomology 35:158–165.

Simberloff, D., and M. Rejmánek (2011). Encyclopedia of Biological Invasions. University of California Press, Berkeley, CA, USA.

Storm, D. J., C. K. Nielsen, E. M. Schauber, and A. Woolf (2007). Deer–human conflict and hunter access in an exurban landscape. Human–Wildlife Conflicts 1:53–59.

Suominen, O., K. Danell, and R. Bergstrom (1999). Moose, trees, and ground-living invertebrates: Indirect interactions in Swedish pine forests. Oikos 84:215.

Tallamy, D. W., and W. G. Shriver (2021). Are declines in insects and insectivorous birds related? Ornithological Applications 123:1. doi:10.1093/ornithapp/duaa059

Thapa, R., S. B. Mirsky, and K. L. Tully (2018). Cover crops reduce nitrate leaching in agroecosystems: A global meta-analysis. Journal of Environmental Quality 47:1400.

Tymkiw, E. L., J. L. Bowman, and W. G. Shriver (2013). The effect of white-tailed deer density on breeding songbirds in Delaware: Effect of deer density on songbirds. Wildlife Society Bulletin 37:714–724.

Vetter, D., G. Rücker, and I. Storch (2013). A meta-analysis of tropical forest edge effects on bird nest predation risk: Edge effects in avian nest predation. Biological Conservation 159:382–395.

Viechtbauer, W. (2017). Metafor: Meta-analysis package for R. https://cran.r-project.org/web/packages/metafor/metafor.pdf

Wang Wei, J., B. P. Lee, and L. Bing Wen (2016). Citizen science and the urban ecology of birds and butterflies: A systematic review. PLoS One 11:e0156425.

Warren, R. J. (2011). Deer overabundance in the USA: Recent advances in population control. Animal Production Science 51:259–266.

Wilkinson, M. D., M. Dumontier, I. J. J. Aalbersberg, G. Appleton, M. Axton, A. Baak, N. Blomberg, J.-W. Boiten, L. B. da Silva Santos, P. E. Bourne, J. Bouwman, et al. (2016). The FAIR Guiding Principles for scientific data management and stewardship. Scientific Data 3:160018.

Willms, J., A. Bartuszevige, D. W. Schwilk, and P. L. Kennedy (2017). The effects of thinning and burning on understory vegetation in North America: A meta-analysis. Forest Ecology and Management 392:184–194.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. Animal Conservation 3:165–173.