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REVIEW

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Methodology matters when estimating deer abundance: a global systematic review and recommendations for improvements

David M. Forsyth[1] | Sebastien Comte[1] | Naomi E. Davis[2] | Andrew J. Bengsen[1] | Steeve D. Côté[3] | David G. Hewitt[4] | Nicolas Morellet[5] | Atle Mysterud[6]

[1]Vertebrate Pest Research Unit, New South Wales Department of Primary Industries, 1447 Forest Road, Orange, NSW 2800, Australia

[2]School of BioSciences, The University of Melbourne, Parkville, Victoria 3010, Australia

[3]Département de biologie & Centre d'études Nordiques, Université Laval, Québec G1V 0A6, Canada

[4]Caesar Kleberg Wildlife Research Institute, Texas A&M University–Kingsville, Kingsville, Texas 78363, USA

[5]Université de Toulouse, INRAE, CEFS, Castanet-Tolosan, France

[6]Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

Correspondence

David M. Forsyth, Vertebrate Pest Research Unit, New South Wales Department of Primary Industries, 1447 Forest Road, Orange, NSW 2800, Australia.
Email: dave.forsyth@dpi.nsw.gov.au

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Abstract

Deer (Cervidae) are key components of many ecosystems and estimating deer abundance or density is important to understanding these roles. Many field methods have been used to estimate deer abundance and density, but the factors determining where, when, and why a method was used, and its usefulness, have not been investigated. We systematically reviewed journal articles published during 2004–2018 to evaluate spatio-temporal trends in study objectives, methodologies, and deer abundance and density estimates, and determine how they varied with biophysical and anthropogenic attributes. We also reviewed the precision and bias of deer abundance estimation methods. We found 3,870 deer abundance and density estimates. Most estimates (58%) were for white-tailed deer (*Odocoileus virginianus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*). The 6 key methods used to estimate abundance and density were pedestrian sign (track or fecal) counts, pedestrian direct counts, vehicular direct counts, aerial direct counts, motion-sensitive cameras, and harvest data. There were regional differences in the use of these methods, but a general pattern was a temporal shift from using harvest data, pedestrian direct counts, and aerial direct counts to using pedestrian sign counts and motion-sensitive cameras. Only 32% of estimates were accompanied by a measure of precision. The most precise estimates were from vehicular spotlight counts and from capture–recapture analysis of images from motion-sensitive cameras. For aerial direct counts, capture–recapture methods provided the most precise estimates. Bias was robustly assessed in only 16 studies. Most abundance estimates were negatively biased, but capture–recapture methods were the least biased. The usefulness of deer abundance and density estimates would be substantially improved by 1) reporting key methodological details, 2) robustly assessing bias, 3) reporting the precision of estimates, 4) using methods that increase and estimate detection probability, and 5) staying up to date on new methods. The automation of image analysis using machine learning should increase the accuracy and precision of abundance estimates from direct aerial counts (visible and thermal infrared, including from unmanned aerial vehicles [drones]) and motion-sensitive cameras, and substantially reduce the time and cost burdens of manual image analysis.

KEYWORDS

abundance, aerial survey, bias, deer, density, image classification, machine learning, motion-sensitive cameras, precision, red deer, roe deer, white-tailed deer

Deer (family Cervidae) are key ecological, economic, and socio-cultural components of many ecosystems (Gordon et al. 2004, Linnell et al. 2020). Some deer species and populations are declining and have a high risk of extinction (International Union for Conservation of Nature and Natural Resources [IUCN] 2019), but others are considered overabundant (Côté et al. 2004, Valente et al. 2020). Deer have been widely introduced to new locations (Long 2003), and they now occur on all continents except Antarctica (Mattioli 2011). Harvesting of deer populations is an important activity in many places (Hewitt 2011, Putman et al. 2011). Deer management can therefore have many objectives, ranging from increasing threatened populations to reducing overabundant populations.

Reliable estimates of population abundance (N) or density (N/area) are important to understanding the roles of deer in ecosystems, to determining whether populations are declining, stable, or increasing, and to evaluating management effectiveness (Williams et al. 2002). The true abundance of wild deer populations can seldom be known. Rather, estimates of N ($\hat{N}$) are subject to sampling error, the totality of which is typically expressed as a standard error (SE) or confidence interval (CI; Thompson et al. 1998, Williams et al. 2002), or their Bayesian equivalents (SD or credible interval [CrI]). The relative precision of estimates can be compared using the coefficient of variation (CV), which is the ratio of the sample variability to the estimated value (Thompson et al. 1998). The smaller the CV, the more precise and useful the estimate is. It is also desirable to know the difference between N and $\hat{N}$ (i.e., bias or accuracy; McCullough 1982, Pollock and Kendall 1987). The smaller the bias, the more useful the estimate. Knowing the true abundance of deer such that the bias of an estimator can be robustly assessed typically requires either stocking enclosures (White et al. 1989) or collaring a sample of animals (Hewison et al. 2007). Mean square error (MSE), the sum of the variance and the squared bias, is another measure of the usefulness of an estimator (Cochran 1977, Hone 2008). The estimator with the lowest MSE is most desirable.

The earliest field methods for estimating deer abundance or density involved people counting groups of deer (McCutchen 1938) or their signs (e.g., fecal pellets; Bennett et al. 1940) from the ground. Fixed-wing aircraft were first used to directly count deer in the 1940s (Buechner et al. 1951). Efforts have since focused on increasing the detection probability (p) of deer in field surveys by using technologies such as helicopters (Thompson and Baker 1981, Bartmann et al. 1986), thermal infrared imagers (Croon et al. 1968, Havens and Sharp 1998), and motion-sensitive cameras (Macaulay et al. 2020). The most recent review of deer abundance estimation methods is that of Morellet et al. (2011), but this was restricted to Europe, was not systematic (Moher et al. 2015), and did not consider motion-sensitive cameras. Given the widespread need to understand and manage deer populations, we conducted a global systematic review of methods used to estimate deer abundance during 2004–2018 to address 3 questions: what were the spatio-temporal trends in deer abundance estimation methods, which technique(s) have provided estimates with the best precision (i.e., smallest CV) and least bias, and how can the usefulness of deer abundance estimates for research and management be improved?

METHODS

Systematic literature reviews

Our literature searches followed the PRISMA-P statement (Moher et al. 2015) and we assessed only publications written in English. We systematically searched the Web of Science™ for articles published during 2004–2018 reporting estimates of deer abundance or density (which, for brevity, we sometimes collectively refer to as abundance). We used the following topic search terms and Boolean operators: (TS = ("deer") AND TS = ("abundance" OR "density")) NOT TS = ("deer mice" OR "deer mouse"). We restricted document type to articles and to the Web of Science categories agriculture multidisciplinary, biodiversity conservation, biology, ecology, environmental sciences, environmental studies, forestry, plant sciences, and zoology. We conducted this search on 23 December 2018. Our analyses of spatio-temporal patterns in deer abundance and density estimation, and the precision of deer abundance and density estimates, used data from free-ranging deer populations (i.e., we excluded fenced populations). We also excluded indices of abundance, except if they were calibrated against absolute abundance (Morellet et al. 2007), because the reliability and comparability of these is often uncertain (Anderson 2001). We included estimates of abundance or density that were reported in articles as unpublished data or cited from gray literature. We also included estimates of abundance or density that were reported from published articles not identified by the Web of Science search. For each deer abundance and density estimate, we extracted the following information: species (IUCN 2019), year of field data collection, country, region (Europe, North America, South America, Asia, Australasia, or Africa), study area location (latitude, longitude), and study area size (ha). If study area location or size were not provided, then we estimated these from the study area description. To enable assessment of the precision of estimates, we extracted the SE, CI, SD, or CrI for each estimate. We also identified the primary reason for estimating deer abundance and density from each publication, and for those with a clearly articulated management objective, we determined whether the objective was to increase, maintain, or decrease deer abundance. We qualitatively assigned each method to 1 of 3 relative cost categories (low, medium, or high) for summary purposes.

For studies to be included in our analysis of the accuracy or bias of deer abundance estimation methods, 2 criteria needed to be met (Pollock and Kendall 1987, McCullough and Hirth 1988): the deer population had to be physically closed to immigration, emigration, and temporary movements; and the number of deer in the population had to be known with complete, or near-complete, certainty. In practice, this meant that the population was either introduced to the enclosure immediately prior to the assessment being undertaken, or the population was subject to capture and marking or some other intensive monitoring immediately prior to the assessment. The Web of Science™ search described above identified only 1 journal article that met these criteria. To increase our sample size, we conducted a second search of the Web of Science™ for articles published from January 1990 (when the Web of Science™ collection begins) to 2020 using the following topic search terms and Boolean operators: (TS = ("deer") AND (TS = ("abundance" OR "density") OR TS = ("accuracy" OR "bias" OR "estimation"))) NOT TS = ("deer mice" OR "deer mouse"). We again restricted document type to articles written in English and to the Web of Science categories agriculture multidisciplinary, biodiversity conservation, biology, ecology, environmental sciences, environmental studies, forestry, plant sciences, and zoology. We conducted this search on 8 October 2020 and it revealed an additional 3 journal articles that met our criteria. To further increase the potential number of studies of the bias of deer abundance estimation methods, we next searched the reference lists in these publications and our own reference collections, primarily to identify studies not covered by the Web of Science™ searches. This search revealed an additional 11 journal articles and 1 book chapter that met our criteria. These 16 studies of accuracy or bias were insufficient for quantitative analysis. Therefore, we qualitatively report the magnitude (i.e., small, moderate, or large) and direction (i.e., underestimate or overestimate) of biases in deer abundance estimation methods.

Explanatory variables and statistical analyses

Study area size and deer density (i.e., deer abundance/study area size) could explain variation in methodology and precision of estimates. We considered 6 other biophysical and anthropogenic variables that could also be influential explanatory variables: elevation (m above sea level), tree cover (% canopy), net primary productivity (NPP; $\times 10^9$ g carbon [C]), night light (values from 0 [low light] to 63 [intense light]), human density (people/km^2), and Global Human Influence Index (GHII; values from 0 [lowest influence] to 64 [highest influence]; Supporting Information S1). The 3 anthropogenic variables (night light, human density, and GHII) were, however, all strongly positively correlated (Table S1.2). We therefore used only 1 anthropogenic variable, GHII, in subsequent analyses because, in our assessment, this variable represents the complexity of human influences on the landscape better than night light or human density alone. In particular, GHII includes information on human population density, urban areas, roads, navigable rivers, and agricultural land uses. For each deer abundance estimate, we extracted the value of each variable as the mean of all raster cells whose center was within a circular buffer of the study area location. We calculated the radius of the buffer for each estimate as the radius of a circle with a surface area matching the study area size.

We analyzed regional and temporal trends in methodology using multinomial logistic regression (Venables and Ripley 2002). We included the biophysical and anthropogenic variables, and their interactions, in these models, and we used a stepwise model selection approach (Murtaugh 2009) to identify the model with the smallest Akaike's Information Criterion value corrected for small sample size (AIC_c; Burnham and Anderson 2002). We compared the precision of methods by calculating the CV for estimates that were accompanied by a measure of precision: $CV = SD/\hat{N}$, where SD is the standard deviation (or is derived from the reported CI or CrI) and $\hat{N}$ is the estimated abundance or density (Thompson et al. 1998). We first evaluated the factors affecting whether precision was reported (i.e., whether a CV could be calculated) using a probit generalized linear model (GLM). We then evaluated the effects of methodology on the CV using a gamma GLM with a log link function (McCullagh and Nelder 1989). All analyses were performed in the R statistical environment (R Core Team 2020).

RESULTS

Breadth of deer abundance estimates

Our systematic review of deer abundance and density estimates published during 2004–2018 returned 2,632 peer-reviewed journal articles. Of these, we removed 599 because they did not target deer species ($n = 598$) or had been retracted (n = 1). We subsequently excluded 1,122 articles that did not provide a quantitative estimate of deer abundance and 200 articles that reported indices of abundance. We removed an additional 124 articles that referenced secondary sources that were published before 2004 (n = 50), were already included (n = 51), or were reviews lacking key methodological details (n = 23). We discarded 47 publications that used simulated rather than field data and 27 publications that were conducted in fenced areas. From the remaining 513 articles, we identified 5,470 deer abundance and density estimates published in 133 journals during 2004–2018. We retained 3,870 estimates derived from field data collected between 1980 and 2017. We excluded 1,600 estimates because field data were collected before 1980 (n = 346 estimates, insufficient to make robust inference for that period), estimates could not be attributed to a year and therefore could not be linked to explanatory variables (n = 613), or estimates lacked key methodological details (n = 641; including many from secondary sources [gray literature or expert knowledge]).

Our sample included abundance estimates for 27 of the 56 deer species recognized by the IUCN, but 58% of all estimates were for white-tailed deer (*Odocoileus virginianus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*), and 90% were for 10 species (Supporting Information S2). Most estimates came from North America (43%) and Europe (38%), followed by Asia (15%). South America and Australasia accounted for only 3% and 1% of the estimates, respectively (Figure 1). We pooled estimates from Asia and Australasia for most subsequent analyses. There were no estimates from Africa, where just 1 deer species (red deer) occurs in 2 small areas (IUCN 2019).

Why estimate deer abundance or density?

Half of the 3,870 estimates (n = 1,945) were used to improve knowledge of the ecology of the deer species, and 30.3% were used for improving field and statistical methods for estimating deer abundance (Supporting Information S3).

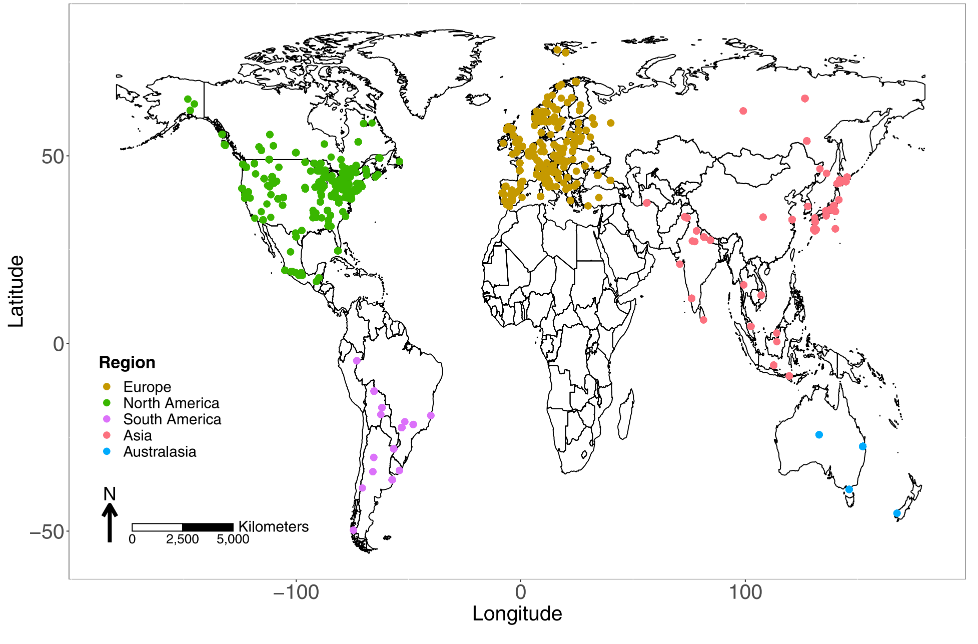

FIGURE 1 Locations of study areas in which deer abundance or density was estimated in articles published during 2004–2018.

The remaining estimates were used for understanding the impacts of deer on natural assets and human activities. Impacts on natural assets included provision of prey for predators (7.5%), impacts on native vegetation (3.2%), and competition with other wildlife for food (0.8%). Impacts on human activities included damage to forestry (5.2%), vehicle collisions (1.1%), wildlife diseases (0.9%), and damage to agricultural production (crops, 0.5%; livestock, 0.3%).

Only 8.4% of estimates were linked to clearly stated management objectives (Supporting Information S3). Reducing deer abundance or density was the most common management objective in Europe and North America, indicating the success of managing native deer on those continents during the 1900s (Côté et al. 2004, Linnell et al. 2020, Valente et al. 2020), and in Australasia, where all deer are non-native (Davis et al. 2016, King and Forsyth 2021). In contrast, maintaining deer abundance was the most common management objective in Asia and South America, reflecting the high proportion of deer species of conservation concern in those regions (IUCN 2019). Increasing deer abundance was an uncommon management objective outside of North America (Supporting Information S3).

Which method, where, and when?

Six first-order data collection methods for estimating deer abundance emerged from the data (Figure 2A): pedestrian sign (track or fecal pellet) counts, pedestrian direct counts, vehicular direct counts, aerial direct counts, motion-sensitive cameras, and harvest data. The probability of each of the 6 methods being used varied in space and time (Figure 2B–E; Supporting Information S4), suggesting that cultural traditions and sometimes cost were important determinants of use (Rabe et al. 2002, Morellet et al. 2011). In Europe, the dominant methods were pedestrian direct counts, pedestrian sign counts, and vehicular direct counts, with aerial direct counts and motion-sensitive cameras seldom used (Figure 2B). In North America, harvest data, pedestrian direct counts, and aerial direct counts dominated until the 2000s, after which the use of motion-sensitive cameras increased rapidly (Figure 2C). In South America, pedestrian sign counts dominated in the 1980s and 1990s, but thereafter were superseded by aerial direct counts, vehicular direct counts, and pedestrian direct counts (Figure 2D). In Asia–Australasia, harvest data dominated until about 2000, after which pedestrian direct counts and pedestrian sign counts dominated (Figure 2E). In all 4 regions, the use of vehicular direct counts and motion-sensitive cameras have increased since 2000.

Pedestrian sign counts

Pedestrian sign counts were used across all situations except for study areas >1,000,000 ha (Figure 3; Supporting Information S4). Three types of sign counts were used: snow tracks, fecal pellets, and browsing signs. The use of snow-track counts has steadily declined since the 1980s and was seldom used in the 2010s (Supporting Information S4). This method was used in large, snow-covered, low-elevation forested areas in eastern Europe and North America with high deer densities (>20 deer/km^2), particularly where human influence (including accessibility) was high (GHII > 40). Fecal pellet counts have been used to estimate deer abundance since the 1930s (Bennett et al. 1940), and this method dominated during 1980–2018 (Supporting Information S4). In contrast to snow-track counts, pellet counts can be used in any environment, but pellet decomposition rates can vary with environmental conditions such as humidity and tree cover (Campbell et al. 2004). Most deer abundance estimates from pellets were count-based, either using quadrats (80.1%; Fattorini et al. 2011, Mandujano 2014) or distance sampling on cleared or uncleared transects (13.1%; Marques et al. 2001, Anderson et al. 2013, Simard et al. 2013). Browsing impact was used in 1 Canadian study to estimate white-tailed deer density, following calibration with known densities (Koh et al. 2010).

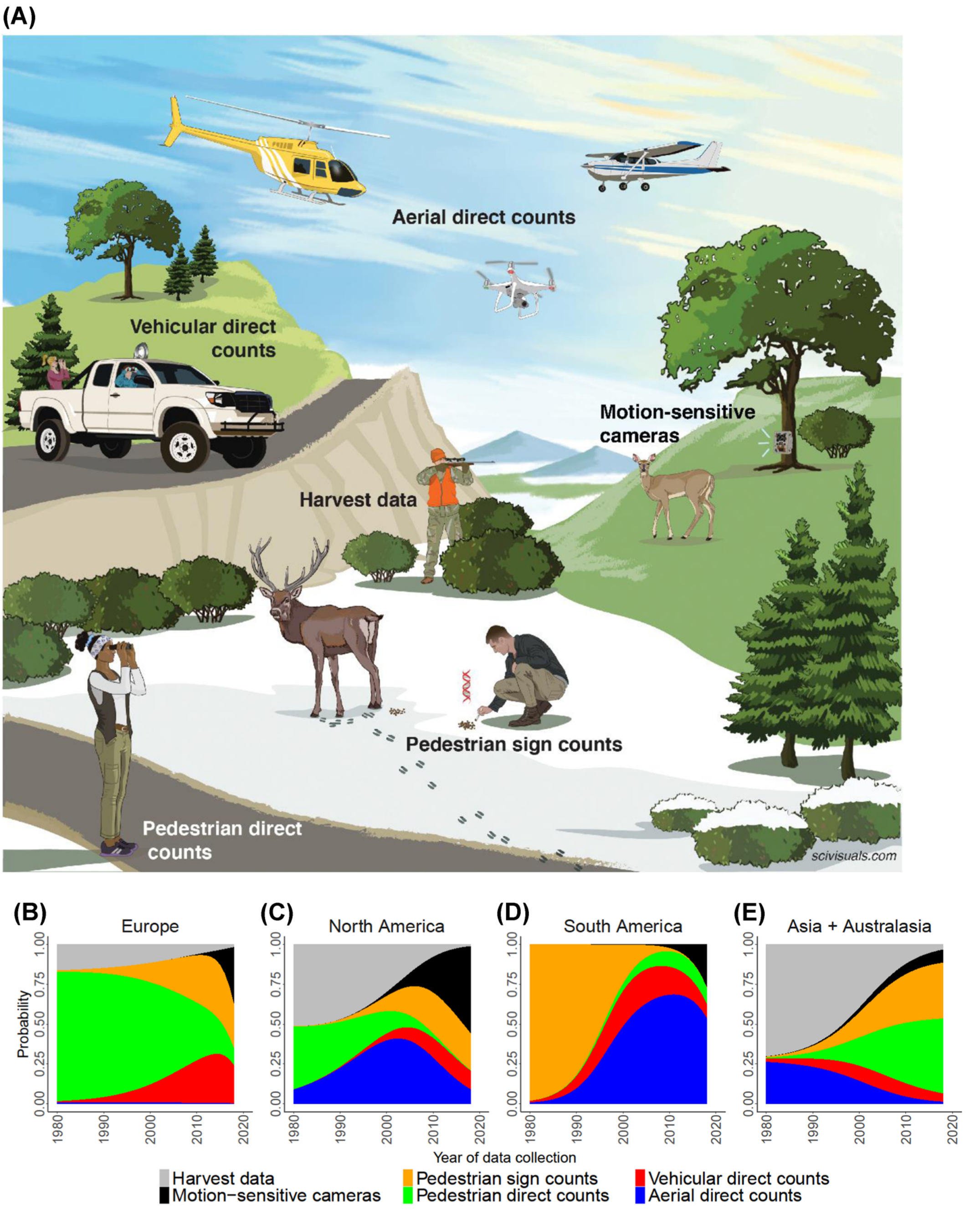

FIGURE 2 The 6 first-order field methods for estimating deer abundance or density in articles published during 2004–2018 (A), and spatio-temporal variation in the probability of each method being used (B–E).

Most methods that use animal signs to estimate population abundance rely strongly on assumptions about relationships between sign density and ancillary data such as daily defecation and decomposition rates (Marques et al. 2001, Campbell et al. 2004). Ancillary data are often used in models as point estimates without consideration of sampling error. Sign count methods also often assume constant sign accumulation rates and detection probabilities. Consequently, sign counts incorporate many sources of uncertainty and are more commonly used to

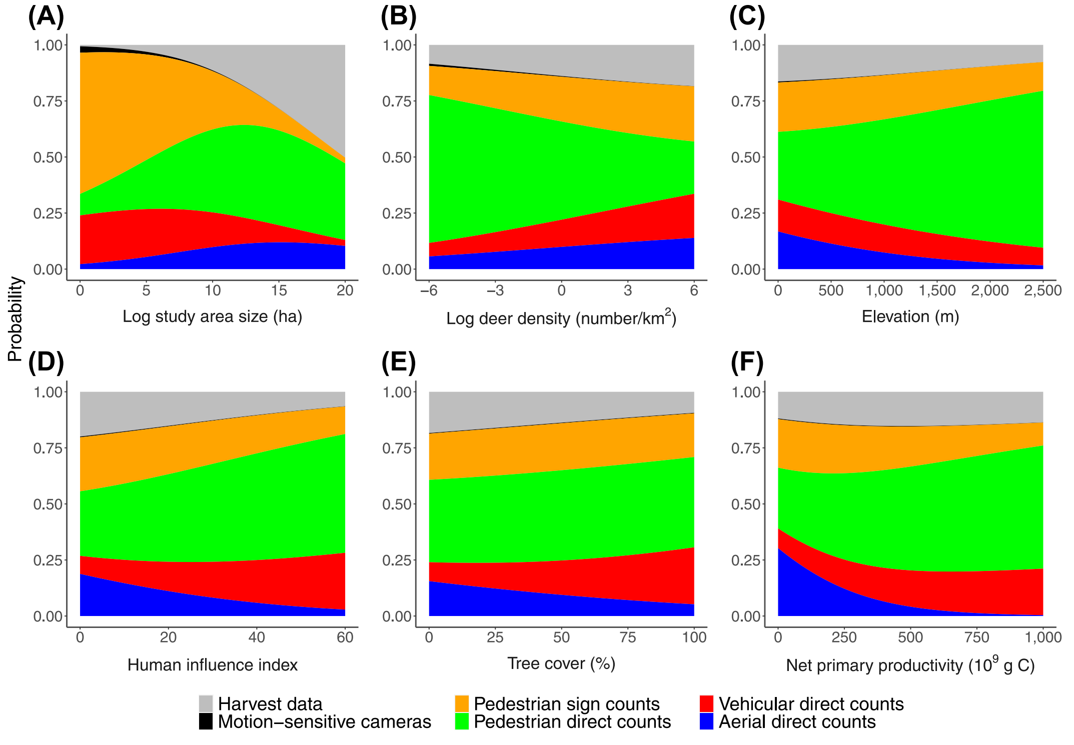

FIGURE 3 Effects of explanatory variables on the probability of the 6 first-order methods being used to estimate deer abundance or density in articles published during 2004–2018.

calculate indices of relative abundance rather than estimates of absolute abundance (Anderson 2001, Simard et al. 2013). One innovation that can overcome these limitations is the use of DNA extracted from fecal pellets with capture–recapture (CR) models to estimate deer abundance. First used in 2006 (Brinkman et al. 2011), this method has been rapidly adopted (Supporting Information S4) and is now being used in combination with other methods such as motion-sensitive cameras that can identify individual deer (see Motion-sensitive cameras section).

Pedestrian direct counts

Pedestrian direct counts were mostly used in large study areas (>20,000 ha) and at high elevations (>1,000 m; Figure 3; Supporting Information S4). There was no significant temporal change in the proportional use of the 3 pedestrian direct count methods (drive count, vantage point count, and walked count; Supporting Information S4).

Drive counts involve a line of beaters driving deer out of a well-defined area toward a cordon of stationary observers (Maillard et al. 2010). This method was mostly used at low elevation and with low tree cover. It was not used in areas of high human influence, probably because of an increased risk of vehicle collisions when deer were flushed. The use of drive counts has decreased in some areas, following recognition that they are negatively biased (i.e., underestimate true population density; Hewison et al. 2007, Maillard et al. 2010).

Vantage point counts used stationary observers, usually at elevated locations, to count the number of deer in defined survey blocks over a fixed interval. Vantage point counts were used at high elevation (>1,500 m) and in areas of low net primary productivity (<250 × 10^9 g C), low deer density (<1 deer/km^2), and high human influence (GHII > 40).

The walked count method, in which observers counted deer while walking, was used in smaller areas and higher tree cover relative to the previous 2 pedestrian count methods. Detections from walked counts were used with mark–recapture analyses when a large proportion of the population was visually marked (Garel et al. 2014) or fitted with tracking devices (McClure et al. 2005). Of the 670 estimates made using walked counts, 23.3% used distance sampling methods to account for imperfect detection of deer (Focardi et al. 2002, Thomas et al. 2010) by estimating the number of animals not observed because of decreasing detection probability with increasing distance from the observer.

Thermal imagers have been used to improve the precision and accuracy of walked counts with distance sampling (5.1%) in Europe (Gill et al. 1997, Focardi et al. 2013, La Morgia et al. 2015), and on vantage point counts (0.8%) in the United States (Hinton et al. 2017).

Vehicular direct counts

Three visual count techniques were used from vehicles: diurnal, and nocturnal with either a spotlight or thermal imager. The use of vehicular direct counts declined with increasing study area size but increased with deer density (Figure 3; Supporting Information S4). Vehicular direct counts were used in preference to aerial direct counts (see below) in areas of high human influence, likely because of the presence of good road and track networks, and in dense forest, where deer are more likely to be seen from a slow-moving vehicle than from an aerial platform.

Nocturnal counts from a vehicle, using a spotlight or thermal imager, are typically preferred to daytime visual counts because they maximize detection probability, especially in forests (Garel et al. 2010). Nocturnal spotlight counts steadily replaced daytime counts during 1980–2018 (Supporting Information S4). A thermal imager was first used to estimate deer abundance from a vehicle in Europe in 1999 (Gill et al. 1997), followed by North America in 2002 (Conner et al. 2016). Since then, nocturnal counts with a thermal imager have become the dominant vehicle-based method in those 2 regions. By 2018, diurnal visual counts had been almost completely replaced by nocturnal spotlight and thermal imaging counts in all regions.

Nocturnal surveys were used in large areas, at high elevations, and with dense tree cover but low net primary productivity (Supporting Information S4). Nocturnal surveys were used more in areas of high human influence and high deer densities. Thermal imagers were mostly used in areas at low elevation with low net primary productivity, denser tree cover, and greater human influence, the latter likely because they were less intrusive for people than a visible light from a spotlight.

Of the 477 estimates from vehicular ground counts, 47.2% used distance sampling, 2.5% used mark–recapture (spotlight only), and 0.8% used double-observer methods (diurnal only), in which the number of animals present but not detected is estimated using concurrent counts from 2 observers. The use of distance sampling was more frequent when observing with thermal imagery (84.4%) than with diurnal counts (42.5%) or spotlights (28.8%).

Aerial direct counts

The lower use of aerial direct counts in areas of high net primary productivity, elevation, tree cover, and human influence (Figure 3; Supporting Information S4) likely relates to the increased safety risks of flying aircraft in these environments. Also, the detectability of deer from aircraft declines with increasing tree cover (Cogan and Diefenbach 1998, McMahon et al. 2021).

A key advantage of aerial direct counts over pedestrian and vehicular counts is that large areas can be surveyed quickly using robust sampling designs (e.g., randomly or systematically located transects; Caughley 1974, Pettorelli et al. 2007). Most estimates used manual visual observation from a helicopter (49.7%) or fixed-wing aircraft (28.0%). Thermal imagery was used in 6% of estimates, almost always from fixed-wing aircraft (88.9%); however, 16.4% of aerial estimates did not report the platform used. Aerial methods were mostly used in North America (76.6%).

Helicopters rapidly replaced fixed-wing aircraft in the 1990s, the latter being used in areas of low elevation, high tree cover, and high net primary productivity (Supporting Information S4). Fixed-wing aircraft were used in relatively small areas with low human influence and low deer density. The only use of unmanned aerial vehicles (UAVs; i.e., drones) was to supplement walked counts of Père David's deer (*Elaphurus davidianus*) in China when grass was too high for deer to be observed when walking (Yuan et al. 2017); therefore, we considered this study to be a pedestrian direct count. The limited use of UAVs to estimate deer abundance until 2018 is likely due to their restricted flight range relative to the spatial scales of interest and the difficulties detecting and identifying deer (Chrétien et al. 2016, Fust and Loos 2020, Corcoran et al. 2021).

Several methods have been used to estimate and account for detection probability in analyses of aerial direct counts. If a sample of deer is radio-collared, then sightability correction models can be fitted to the observed and not-observed data and used to estimate abundance (Pollock and Kendall 1987). This approach, however, was used in only 3 studies in North America (McCorquodale et al. 2013) and 1 in Europe (Solberg et al. 2007). Double-observer methods (Pollock and Kendall 1987) were used to correct for imperfect detection in 23.1% of strip count surveys. Distance sampling (DS; Thomas et al. 2010), which also adjusts for incomplete counts in strip count surveys, was used in 11.9% of aerial direct counts. Capture–recapture methods were also used (8.4%) to account for imperfect detection of deer on the transect line (McCorquodale et al. 2013). Some estimates used a combination of these methods: double-observer DS (2.0%), double-observer mark–recapture (0.5%), and mark–recapture DS (0.3%; Burt et al. 2014).

Thermal imagers were first used from an aerial platform in North America in 1967 (Croon et al. 1968) but thereafter were little used until the late 1990s (Havens and Sharp 1998, Duguay and Farfaras 2011). The use of thermal imagers has subsequently increased in North America. This technology was used once outside North America, in Europe in 2008 (Franke et al. 2012). Thermal imagers were primarily used in small areas at low elevation (Supporting Information S4). Aerial direct counts conducted with a thermal imager used strip count (63.2%), DS (28.9%), and double-observer (7.9%) methods to analyze the data extracted from the video (DeNicola and Williams 2008, Kissell and Nimmo 2011). Thermal imagers cannot always distinguish species of deer, or other larger herbivores, and conditions for their optimal use may be infrequent (Croon et al. 1968, Havens and Sharp 1998, Daniels 2006, Franke et al. 2012, Chrétien et al. 2016). The simultaneous use of thermal and RGB (visible) imagery can substantially improve deer detection rates in aerial direct counts (Franke et al. 2012, Chrétien et al. 2016).

Automated detection of deer in images (RGB and thermal infrared) collected from aerial platforms (including UAVs) can reduce the biases and costs associated with manual detection of deer (either directly from aircraft by observers or in images collected from aircraft; Kellenberger et al. 2018, Eikelboom et al. 2019, Corcoran et al. 2021). This recent development is discussed further below (Improving the usefulness of deer abundance and density estimates).

Motion-sensitive cameras

Motion-sensitive cameras have revolutionized the study of wildlife (Nichols and Karanth 2011, Burton et al. 2015, Glover-Kapfer et al. 2019), and were first used to estimate deer abundance in 1992 (North America: Jacobson et al. 1997). This method has increasingly been used to estimate deer abundance and density in all regions except Australasia (Figure 2), reflecting a more general uptake of motion-sensitive cameras to study wildlife (Burton et al. 2015, Glover-Kapfer et al. 2019). This temporal trend likely reflects the major advances in camera technology and affordability, and also in statistical methods for estimating deer abundance from camera data (e.g., spatial capture-recapture models; Royle et al. 2013, Parsons et al. 2017, Macaulay et al. 2020).

Motion-sensitive cameras have been used mostly over small to medium areas (<10,000 ha) at low elevation and with low deer density (<1 deer/km^2; Figure 3; Supporting Information S4). The risks of vandalism and theft (Glover-Kapfer et al. 2019, Meek et al. 2019), and privacy concerns, limit the use of cameras in areas of high human influence (Figure 3D). Analyses of data from camera images used CR models (Amstrup et al. 2005; 65.6%), unspecified methods (17.4%), N-mixture models (Royle 2004; 13.7%), or random encounter models (Rowcliffe et al. 2008; 3.2%).

The process of manually searching images for objects of interest and encoding that information (tagging) has been a significant limitation of using motion-sensitive cameras to estimate deer abundance (Swanson et al. 2015). The recent application of machine learning to the detection of objects such as deer in camera images is removing this limitation and substantially reducing the costs of image processing (Tabak et al. 2019). This emerging technology is discussed further below (Improving the usefulness of deer abundance and density estimates).

Harvest data

Harvest data were used to estimate abundance and density in 3 ways: hunting bags (19.7%), in integrated models including additional information (38.4%; Stergar and Jerina 2017), or by population reconstruction (sex–age–class survival and hunting mortality; Tanentzap et al. 2009). The use of harvest data to estimate deer abundance has declined in all regions, especially since 2000, such that it is now uncommon (Figure 2). Hunting bags were mostly used at low elevation and in areas of low net primary productivity and high deer density (Supporting Information S4). Integrated models were used for large study areas (≥50,000 ha), at high elevation, and with dense tree cover (Supporting Information S4). Population reconstruction models were used for small areas with low deer density, low human influence, low tree cover, and high net primary productivity (Supporting Information S4). Harvest data relies on honest reporting by a representative sample of hunters and is potentially subject to significant reporting bias, hunter selectivity and differential vulnerability of deer age–sex classes, and to errors in deer aging (Roseberry and Woolf 1991).

Reporting of precision

Surprisingly, only 1 in 3 estimates of deer abundance or density were accompanied by a measure of precision. The probability of reporting precision was much higher for estimates in South America (0.71; 95% CI = 0.61–0.81) and Australasia (0.69; 0.52–0.85) than in Asia (0.30; 0.22–0.39), North America (0.29; 0.21–0.37), and Europe (0.21; 0.14–0.28; Supporting Information S5). Given the importance of including precision of estimates in population dynamic (Calder et al. 2003) and management (Milner-Gulland and Shea 2017) models, the low percentage of estimates accompanied by a measure of precision is concerning.

The reporting of precision increased during 1980–2017 for 5 of the 6 first-order methods (Figure 4; Supporting Information S5). Pedestrian sign count methods were more likely to report precision than the other 5 first-order methods but showed negligible temporal increase (Figure 4). At the end of our review period, >80% of estimates from vehicular direct counts, motion-sensitive cameras, and harvest data reported precision (Figure 4); however, reporting of precision was significantly lower for pedestrian sign counts, pedestrian direct counts, and aerial direct counts.

Precision of estimates

Of the 1,247 estimates of deer abundance or density for which CVs could be calculated, only 329 (26.4%) were ≤0.25, a commonly used minimum threshold considered useful for management and research (Skalski et al. 2005). Overall, the median CV was 0.42, and the lower and upper deciles were 0.15 and 1.62, respectively.

There were sufficient estimates (i.e., ≥30) to make inferences about the relative precision of 14 second-order methods from 5 first-order methods, representing 87.8% of all the estimates for which a CV could be calculated. Because only 1.5% of estimates based on harvest data reported precision, despite there being well-developed methods for doing so (Skalski et al. 2005), we did not include this first-order method in the analysis. Neither the median nor the 2.5th percentile of any of these 14 methods was <0.25 (Figure 5). The smallest mean CVs were obtained using ground vehicle spotlight (0.41 and 0.36 with and without DS, respectively) and CR from motion-sensitive camera images (0.39),

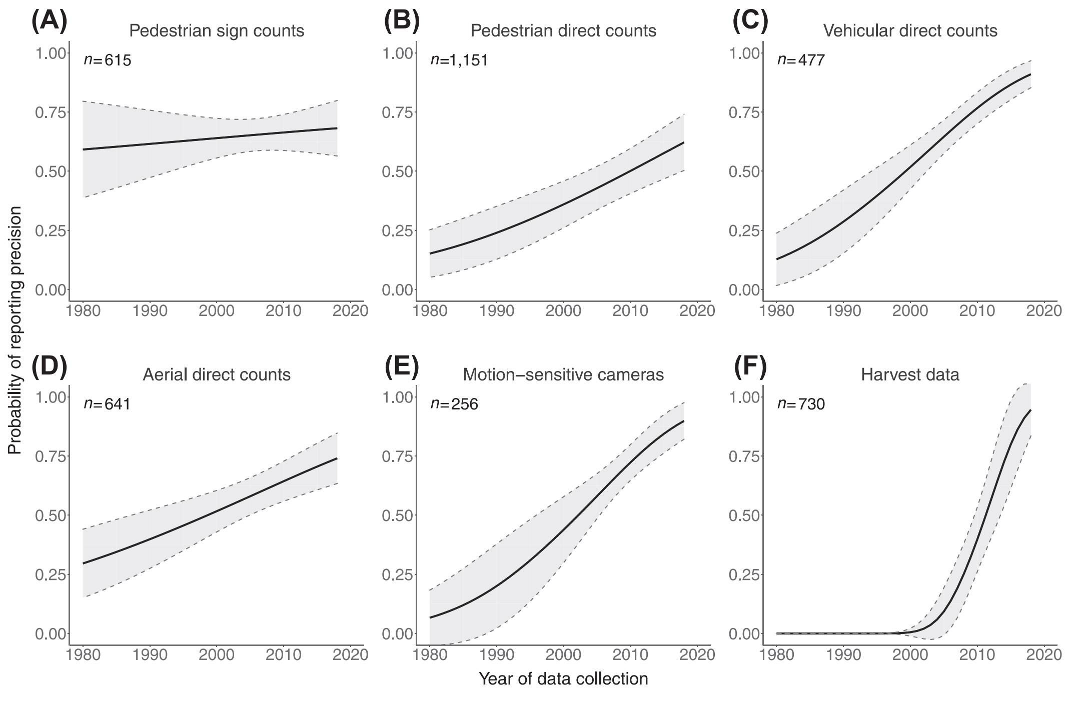

FIGURE 4 Temporal trends in the probability (mean and 95% CIs) of reporting precision for deer abundance and density estimates in articles published during 2004–2018.

followed by aerial direct counts using CR (0.48). The least precise estimates were for diurnal vehicular direct counts (1.09) and visual pedestrian direct counts (1.03), likely reflecting that deer typically seek cover in thicker vegetation during the day (Beier and McCullough 1990, Ager et al. 2003), increasing variability in the detection probability. Fecal pellet counts without DS were much less precise (0.99) than those with DS (0.63).

The precision of estimates steadily decreased (i.e., became poorer) after 1980 (Supporting Information S6). This trend likely reflects more complete incorporation of processes generating precision into the estimation process (Williams et al. 2002, Skalski et al. 2005), rather than truly less precise estimates. The precision of estimates increased significantly (i.e., improved) with high deer densities and if the survey was not for management purposes but decreased significantly with increasing study area size and elevation (Supporting Information S6).

Only 89 (27.3%) of the estimates with a management objective provided a measure of precision. Those estimates were, on average, less precise than research-focused estimates (management estimates: 0.76 [0.52–1.11], research estimates: 0.51 [0.38–0.68]). The required precision of an estimate varies with each study's objectives, but the large relative precision of nearly all deer abundance estimates (for the subset that reported precision) is concerning.

The use of field methods that enabled the probability of detecting deer (p) to be estimated generally gave more precise estimates of abundance. Examples include DS for fecal pellet counts (Marques et al. 2001) and CR analysis of motion-sensitive camera images (Macaulay et al. 2020).

Bias of deer abundance estimation methods

Our systematic review of studies reporting the accuracy or bias of deer abundance estimation methods identified 15 peer-reviewed journal articles and 1 book chapter that met our inclusion criteria (Supporting Information S7). We used a longer timeframe for this review than for the deer abundance and density estimates described above

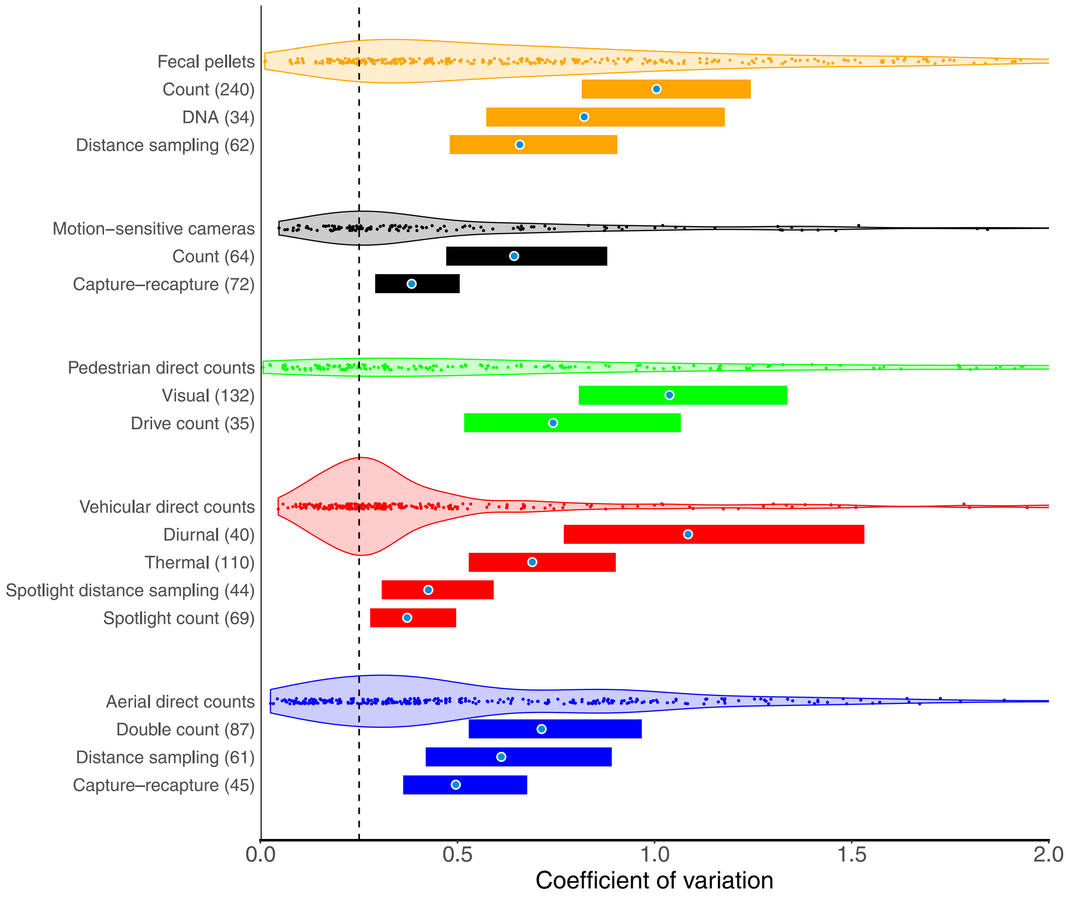

FIGURE 5 Relative precision of deer abundance and density estimates in articles published during 2004–2018 for 5 first-order and 14 second-order methods (the latter with ≥30 estimates). We had an insufficient number of harvest data estimates to include this first-order method. Violin plots summarize all estimates for each of the 5 first-order methods. Bar plots are outputs from a generalized linear model, with circles indicating mean values and blocks indicating the 95% range of the estimates. Sample sizes are in parentheses. The dashed vertical line indicates the threshold value of 0.25, a commonly used threshold for assessing whether estimates will be useful for research and management. Violin plots are right-truncated at 2.0.

because of the rarity of studies reporting accuracy or bias. The 16 publications reporting accuracy or bias spanned from the 1970s (LeResche and Rausch 1974) to 2020 (Beaver et al. 2020). We evaluated bias for only 3 of the 6 first-order methods: pedestrian direct counts, vehicular direct counts, and aerial direct counts (Table 1). Most assessments revealed negative bias, but the magnitude varied greatly. Capture–recapture methods, either pedestrian direct count or aerial direct count, were the least negatively biased (<10% underestimation of *N*). Pedestrian direct counts (drive, vantage point, and walked methods) and vehicle spotlight counts had the largest negative biases (>25% underestimation). Of the aerial direct count methods, strip counts and DS had minor or moderate negative biases (8–25% underestimation). An abundance estimate can be biased but its CIs include the true abundance (White et al. 1989), emphasizing the importance of reporting CIs or CrIs. Despite the widespread use of pedestrian sign counts, motion-sensitive cameras, and harvest data methods to estimate deer abundances, their biases have not been robustly assessed.

TABLE 1 Key features of methods used to estimate deer abundance and density globally in articles published during 2004–2018. The 6 first-order methods are shown, with their sub-methods listed only if key features differ substantially.

				Most suitable for study areas with these attributes:			
Method	Relative precision	Bias[a]	Relative cost	Size (ha)	Tree cover (%)	Deer density	Comments
Pedestrian sign counts							Most of the sub-methods are low-cost; bias not evaluated
Fecal pellet count	Poor		Low	All	All	All	Require deposition and decay rates to be estimated
Fecal pellet distance sampling	Moderate		Low	All	All	All	As above
Fecal pellet DNA	Moderate		High	Small	All	All	DNA may not amplify; laboratory processing costs can be substantial
Snow tracks			Low	Large	Medium, high	Medium, high	Need snow cover; require calibration with true deer density
Browsing signs			Low	All	Medium, high	All	Require calibration with true deer density
Pedestrian direct counts							Can be affected by evasive movement or avoidance behavior of deer in response to people (some analysis methods account for this); can have strong observer effects
Drive		Moderate negative (Hewison et al. 2007); major negative (Maillard et al. 2010)	Moderate	Medium, large	Low	All	People need to be excluded from the survey area
Vantage point			Low	Small, medium	Low	Low	Requires elevated areas; relatively unobtrusive to people; using a thermal imager could increase detections

TABLE 1 (Continued)

Method	Relative precision	Bias[a]	Relative cost	Most suitable for study areas with these attributes: Size (ha)	Tree cover (%)	Deer density	Comments
Capture–recapture		Minor negative and positive (Vincent et al. 1996); major positive (McCullough and Hirth 1988)	High	Small	All	Medium, high	Potential animal welfare issues (including mortality) with capture
Walked	Poor	Minor negative (Vincent et al. 1996); major negative (Hewison et al. 2007)	Moderate	Small	Low	Medium, high	Relatively unobtrusive to people; using a thermal imager could increase detections
Vehicular direct counts							Can be used in densely populated and densely treed areas; can be affected by evasive movement or avoidance behavior of deer in response to vehicles (some analysis methods account for this); requires a road or track network that representatively samples study area; can be strong observer effects
Diurnal	Poor		Low	All	All	All	Lower detection probability compared with nocturnal (thermal imager, spotlight) methods
Thermal imaging	Moderate		Medium	Small, medium	All	High	Imagers are expensive but increase detection probability; less intrusive for people than spotlight
Spotlight	Best	Major negative (McCullough 1982)	Low	Small, medium	Low, moderate	All	Intrusive for people in built-up areas
Spotlight distance sampling	Best		Low	Small, medium	Low, moderate	All	See above

(Continues)

TABLE 1 (Continued)

Method	Relative precision	Bias[a]	Relative cost	Most suitable for study areas with these attributes: Size (ha)	Tree cover (%)	Deer density	Comments
Aerial direct counts							Surveys can be completed quickly in suitable conditions; can use robust sampling designs; detection probability is lower for fixed-wing aircraft than for helicopters; thermal imaging cannot always distinguish species, or deer from other large mammals; infrequent conditions for optimal use of thermal imaging; state-of-the-art thermal imagers are expensive; manual image analysis is labor-intensive and subject to often unquantified errors, but machine learning algorithms will standardize and automate detection of deer in images; can be strong observer effects; UAVs[b] currently have a limited range (often line-of-sight)
Strip count		Quadrat count moderately negatively biased (LeResche and Rausch 1974, Bartmann et al. 1986); total count majorly negatively biased (Beasom et al. 1986, Zabransky et al. 2016); strip count by a UAV equipped with thermal sensor had minor (evening surveys) or moderate (morning and all surveys) negative bias (Beaver et al. 2020)	Moderate	Medium, large	Low, medium	Medium, high	Assumption of perfect detection usually strongly violated; accuracy increases with increasing observer experience

TABLE 1 (Continued)

				Most suitable for study areas with these attributes:			
Method	**Relative precision**	**Bias**[a]	**Relative cost**	**Size (ha)**	**Tree cover (%)**	**Deer density**	**Comments**
Double count			Moderate	Medium, large	Low, medium	Medium, high	Partially accounts for imperfect detection
Distance sampling	Variable	Minor negative or none (White et al. 1989)	Moderate	Medium, large	Low, medium	Medium, high	Need ≥70 detections; partially accounts for imperfect detection
Capture–recapture	Best	Minor negative (Rice and Harder 1977) or minor positive (Bartmann et al. 1987)	High	Small, medium	Low, medium	Medium, high	Best precision and least bias; animals must be marked, which is costly and can have animal welfare issues
Sightability models		Negative (magnitude not reported; Cogan and Diefenbach 1998)	High	All	Low, medium	Medium, high	Deer must be captured for model development (see above); visibility and undercounting of group size contributes to negative bias
Motion-sensitive cameras							High cost of cameras, and they can be stolen or vandalized; privacy concerns in high human-use areas; manual image analysis is labor-intensive and subject to often unquantified errors, but machine learning algorithms will standardize and automate detection of deer in images; data analysis methods are developing rapidly; accuracy unknown
Count	Moderate		High	Small, medium	All	Low, medium	Analysis methods less developed

(Continues)

TABLE 1 (Continued)

Method	Relative precision	Bias[a]	Relative cost	Most suitable for study areas with these attributes: Size (ha)	Tree cover (%)	Deer density	Comments
Capture–recapture	Best		High	Small, medium	All	Low, medium	Analysis methods well developed
Harvest data			Low	All	All	All	Relies on honest reporting by representative sample of hunters; subject to reporting bias, hunter selectivity, differential vulnerability, and aging errors; precision and bias unknown

[a]Bias classes are approximately as follows: minor, <10%; moderate, 10–25%; major, >25%.

[b]UAV, unmanned aerial vehicle (drone).

DISCUSSION

Improving the usefulness of deer abundance and density estimates

Reliable estimates of population abundance or density will continue to be essential for deer research and management globally. The field and analytical methods to be used depend on many factors, including objective of the study, the budget, and logistics. Human safety should also be considered (Mayle et al. 1999). A key criterion for selecting a method should be that it provides a relatively unbiased estimate with precision that meets the study's objectives, such as estimating the probability that 2 abundance estimates differ by ≥10%. Mean square error could be useful for evaluating abundance estimators (Cochran 1977, Hone 2008). The precision, biases, and costs of the main methods used to estimate deer abundance are influenced by their suitability for study areas of differing size, tree cover, and deer density (Table 1). More generally, this review has identified 5 opportunities for significantly improving the usefulness of deer abundance and density estimates.

1. Improved methodological reporting
   A large proportion of studies did not report basic information such as the year that data were collected, survey protocols, or the makes and models of key equipment such as motion-sensitive cameras or thermal imagers. This information is important for repeatability and for interpretation (Burton et al. 2015, McMahon et al. 2021). At a minimum, methods should be reported in sufficient detail such that they could be repeated. Space is limited in journal articles, but additional methodological details can now be placed online (e.g., supporting information).
2. Assess the bias of key methods
   The biases of most deer abundance estimation methods have not been evaluated in the field, including the increasingly popular motion-sensitive camera and fecal DNA methods (Table 1). The small number of robust assessments of bias reflects the difficulty of knowing the true abundance of a deer population. Given the potential impacts of biased abundance estimates for deer research and management, we recommend that priority be given to assessing the biases of current and emerging methods.
3. Report the precision of estimates
   Statistical comparison and evaluation of estimates require estimates of precision such as CIs, SEs, or CVs. The target precision for a deer abundance estimate depends on the study objective and can be explored in a simulation study. In the absence of a simulation study, field methods that provide the most precise estimates should be used. For pedestrian and vehicular surveys, visual daytime methods have the poorest precision; thus, using spotlights or thermal imagers (from a vehicle) or motion-sensitive cameras should be preferred. Most studies did not report precision. Journal reviewers and editors should expect that precision be reported for all deer abundance estimates, and readers should be skeptical of estimates not accompanied by a measure of precision.
4. Use methods that increase and estimate detection probability
   The probability of detecting deer varies with many factors but declines with increasing tree cover for several direct visual count methods such as vehicle spotlight counts (Focardi et al. 2001) and aerial direct counts (Cogan and Diefenbach 1998, Franke et al. 2012). Not accounting for imperfect detection leads to negatively biased density estimates (i.e., underestimates). We strongly encourage the use of well-established methods to maximize, estimate, and account for p. Motion-sensitive cameras, fecal pellet DNA, and thermal imagers can all improve p in densely treed areas, where conventional visual counts usually miss large proportions of the population (Focardi et al. 2001, Brinkman et al. 2011, Bessone et al. 2020, Corcoran et al. 2021). Detection probability can be estimated and accounted for using multiple observers, DS, or mark–recapture methods (Thomas et al. 2010, Burt et al. 2014). Applying machine learning to images collected from aerial platforms enables p to be modeled as a function of variables (e.g., tree cover) in the image (see below).

5. Stay up to date on new methods
During this review, we identified several emerging field methods that hold considerable promise for deer abundance estimation. First, the declining cost of genetic analysis means that techniques using information collected from feces, hair, and tissue to identify individuals is becoming more feasible for estimating deer abundance at management scales (Brinkman et al. 2011, Brazeal et al. 2017). Second, recent advances in statistical methods allow deer abundance and density to be estimated using motion-sensitive camera images using either spatial CR (Parsons et al. 2017, Macaulay et al. 2020, Bengsen et al. 2022) or point-based DS (Bessone et al. 2020) methods. Third, methods that identify individuals using multiple techniques, such as fecal DNA and motion-sensitive cameras, and perform analyses using spatial CR methods (Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2013) are promising for providing relatively precise deer abundance estimates (Furnas et al. 2020), at least for small- to medium-sized study areas. Fourth, recent rapid advances in sensor technology and the automated processing of images mean that RGB, thermal infrared, and satellite imagery from aerial platforms (sometimes in combination; Franke et al. 2012, Chrétien et al. 2016) are providing increasingly more accurate, precise and cheaper estimates of deer abundance (Hollings et al. 2018, Kellenberger et al. 2018, Eikelboom et al. 2019, Beaver et al. 2020, Corcoran et al. 2021). Fifth, the application of machine learning to automate and standardize objects in images collected from aerial platforms and motion-sensitive cameras is transforming wildlife monitoring (Kellenberger et al 2018, Eikelboom et al. 2019, Greenberg et al. 2019, Tabak et al. 2019, Corcoran et al. 2021). Convolutional neural networks (Goodfellow et al. 2016) can detect animals, such as deer, by comparing features in training and testing images using the spectral value of an individual pixel and proximity to other pixels (Kellenberger et al. 2018, Corcoran et al. 2021). Useful application of machine learning methods requires the rates of precision (reduced from 1.0 by false positives, including double-counts of true objects) and recall (reduced by false negatives) to be quantified (Kellenberger et al. 2018, Eikelboom et al. 2019, Tabak et al. 2019). The automated processing of images greatly reduces the labor needed to search and tag images, although time is needed to train the detection algorithm (Kellenberger et al. 2018, Eikelboom et al. 2019, Greenberg et al. 2019). Machine learning standardizes the deer detection process, which can be explicitly modeled as a function of covariates within the image (Franke et al. 2012, Kellenberger et al. 2018, McMahon et al. 2021).

RESEARCH IMPLICATIONS

Our global systematic review has revealed the substantial effort expended estimating deer abundance and density, particularly in Europe and North America. There is, however, opportunity to substantially improve the usefulness of estimates by 1) reporting key methodological details, 2) assessing the bias of current and emerging methods, 3) reporting the precision of estimates, 4) using methods that increase and estimate detection probability, and 5) staying up to date on new methods. The automation of image analysis using deep neural network methods should increase the accuracy and precision of abundance estimates from direct aerial counts (RGB and thermal infrared, including from UAVs) and cameras, and substantially reduce the time and cost burdens of image analysis. Adopting these 5 recommendations and following the key principles of wildlife survey design outlined elsewhere (Thompson et al. 1998, Anderson 2001, Borchers et al. 2002, Williams et al. 2002, Skalski et al. 2005, Pierce et al. 2020), will provide stronger inferences about the dynamics of deer populations and their responses to management.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.18846647.v1.

ORCID

David M. Forsyth http://orcid.org/0000-0001-5356-9573
Sebastien Comte https://orcid.org/0000-0001-7984-8159
Andrew J. Bengsen http://orcid.org/0000-0003-2205-4416
Steeve D. Côté https://orcid.org/0000-0002-4875-1917
David G. Hewitt https://orcid.org/0000-0001-7907-3023
Nicolas Morellet https://orcid.org/0000-0002-4274-7044
Atle Mysterud http://orcid.org/0000-0001-8993-7382

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