Methods for estimating vital rates of greater sage-grouse broods: a review

Ian P. Riley and Courtney J. Conway

Biologists use a variety of methods to estimate productivity and resource selection of birds. The effectiveness and suitability of each method depends on the study’s objectives, but is also influenced by many important traits, including detection probability, disturbance of focal birds and sampling frequency. We reviewed 504 greater sage-grouse Centrocercus urophasianus papers published from 1990 to 2019 to document the most common brood survey methods used by investigators and summarized if and how they used brood survey data to estimate brood survival and detection probability. Of the 504 papers, 16.1% (n = 81) had useful information relevant to the review. The most common methods included daytime visual surveys (46.9%; n = 38), daytime flush surveys (33.3%; n = 27), nocturnal spotlight surveys (19.8%; n = 16), radio-tagged chicks (16.0%; n = 13), wing surveys (9.9%; n = 8), brood routes (4.9%; n = 4) and pointing dogs (4.9%; n = 4). Fifty-nine of the 81 papers used >1 method, only 2 of the 81 papers measured or reported detection probability, and none reported the level of disturbance caused by the method. Studies varied widely regarding the age of the brood when brood fate was confirmed (X = 44.4 days post-hatch, range 14–84 days). The frequency of brood sampling visits also varied greatly among studies (range = 1.19–3.85 surveys/brood/week) and this variation complicates comparison in fecundity and survival estimates across studies. Furthermore, 35 papers used >1 maternal behavior as purported indicators of brood fate, but none of them documented how accurate their indicators were. Future studies could reduce variance in estimates of sage-grouse fecundity and brood survival by employing empirical methods to estimate detection probability, standardizing brood sampling methods and conducting trials to document the effects of hen or brood capture, handling and flushing on brood survival estimates. Moreover, the accuracy of commonly used indicators of brood fate, including maternal behaviors, flocking behavior and distance moved after flush needs verification.

Keywords: breeding productivity, brood survey methods, brood survival, Centrocercus urophasianus, chicks, detection probability

Life history determines the vital rates of plant and animal populations and, hence, measuring vital rates is essential for both basic and applied sciences. For example, vital rates form the basis of population viability models, inform decisions regarding annual harvest limits, and are often triggers for conservation actions. Similarly, resource selection studies are common in wildlife ecology and they are frequently used to inform land management decisions. Hence, estimating and comparing vital rates and resource selection of wildlife populations is a common goal of managers and researchers. Vital rates and resource selection are best if measured by using field methods that maximize accuracy and precision, minimize disturbance to the focal animals, and make estimates comparable across time, space, species and studies.

The need for accurate and precise methods to estimate vital rates and patterns in resource selection are particularly important in wildlife populations that are harvested and those that are rare or declining (i.e. species of conservation concern). Many birds in the order Galliformes are both gamebirds and species of conservation concern due to their declining populations, habitat loss and range contractions (Storch 2007, McGowen et al. 2012). Moreover, population growth rates for Galliformes are particularly sensitive to annual fecundity (i.e. chick survival, brood survival and other measures of productivity) (Hagen 2003, Summers et al. 2004, Sandercock et al. 2008, Taylor et al. 2012). Hence, identifying the environmental factors that affect productivity of gamebirds is necessary for effectively managing their populations. However, the methods commonly used to measure productivity and the inferences from commonly used
analytic methods (Williams et al. 2002) have assumptions that are difficult to meet for many gamebird species. Specifically, detection errors are common for many avian sampling methods but are often not measured by investigators (Nichols et al. 2000, MacKenzie et al. 2002, Williams et al. 2002, Buckland et al. 2015). Moreover, incidental disturbance (i.e. flushing, radio-marking, etc.) caused by field methods is seldom quantified.

The greater sage-grouse Centrocercus urophasianus (hereafter sage-grouse) is both a gamebird and a species of conservation concern in North America due to long-term declines in abundance (Western Association of Fish and Wildlife Agencies 2015) and distribution contraction (Schoeder et al. 2004). Chick survival has a large influence on population growth rates in sage-grouse (Wisdom and Mills 1997, Taylor et al. 2012) and, hence, estimating chick survival, brood survival, and the factors that affect them (e.g. resource selection) will help guide conservation and management decisions (Dahlgren et al. 2006, Atamian et al. 2010, Guttery et al. 2013, Coates et al. 2017). The methods used to estimate chick and brood survival in sage-grouse and the habitat factors that affect those parameters are the same as those used for other gamebirds (Summers et al. 2004, Steen and Haugvold 2009, Sands and Pope 2010, Dahlgren et al. 2012, Orange et al. 2016, Blomberg et al. 2019). These methods (daytime visual and flush surveys, radio-tagging, nighttime spotlight surveys, pointing dog surveys and wing surveys; Dahlgren et al. 2010a, Riley 2019) can potentially influence accuracy, precision and comparability among studies. Our objectives were to summarize the extent to which past sage-grouse studies accounted for detection probability and documented levels of disturbance caused by their field methods. To help guide future research and monitoring efforts on gamebirds, we conducted a thorough review of the methods used in past sage-grouse papers whose objectives were to estimate vital rates and habitat relationships related to sage-grouse chicks and broods.

**Methods**

We reviewed journal articles, theses, dissertations and book chapters (hereafter, papers) that reported one or more demographic parameters associated with sage-grouse chicks or broods habitat selection, occupancy, or movement of broods. In our review, we recorded whether papers measured hen productivity metrics, chick or brood success, or chick or brood survival. We defined productivity as the rate at which breeding-aged hens produce chicks or broods that subsequently are recruited to the population (Leopold 1933, p. 452), chick success as the number of fledged chicks per hen during a specific period of time, brood success as the number of broods that had ≥1 chick fledged per hen during a specific period of time, and chick or brood survival as the probability of chicks or broods alive during a specific period of time, respectively. We used Google Scholar (<https://scholar.google.com/>) to conduct literature searches for papers that used sampling techniques to obtain the demographic data above, including: 1) survey individual radio-tagged hens with their broods or radio-tagged chicks, 2) annual count of sage-grouse wings or tail feathers of different age and sex classes (i.e. wing surveys) and 3) counts of chicks or broods with hens on transects (i.e. brood routes) (Atzenieth et al. 1982, Connelly et al. 2003, Sedinger 2007, Hagen and Loughin 2008). We conducted three separate literature searches for the three types of data enumerated above and used sage-grouse, *Centrocercus* and *Centrocercus urophasianus* as keywords in all three searches. For radio-tagged hens or broods (no. 1 above), we also included the following secondary keywords: chick, brood and survival. For wing surveys (no. 2 above), we also included the following secondary keywords: hunt, harvest, female, juvenile, ratio, wing, production and productivity. For brood routes (no. 3 above), we also included the following secondary keywords: brood, survey and route. We restricted our review to papers that were published or completed from 1990 to 2019. We did not consider earlier studies because we wanted to focus on contemporary field and analytical practices. To ensure we did not overlook any papers, we searched references in previous sage-grouse reviews (Hagen et al. 2007, Taylor et al. 2012). For each paper, we recorded the following information: study duration, field method used (daytime visual surveys, daytime flush surveys, nocturnal spotlight surveys, radio-tagged chicks, wing surveys, brood routes, dog surveys, etc.), number of broods sampled, number of surveys or visits per brood, survey intervals (i.e. days between subsequent visits to a brood), whether broods were intentionally flushed or detected visually (without flushing) during surveys, time of surveys (day or night), the proportion of hens or broods that were flushed during surveys, whether the study reported any effects of their survey methods on hen or brood survival, if detection probability was reported, how brood fate was determined and the response variables estimated (chick or brood survival, brood success, brood presence, brood habitat use, etc.). We assumed that researchers used a daytime flush survey if researchers explicitly reported that chicks or broods were flushed. We thoroughly examined each author’s publication history for evidence that data were reused among multiple papers and we only selected papers that reused data if that paper also included additional or previously unexamined data.

**Results**

Our search produced 1403 results, of which we reviewed 549 papers that met our search criteria. Of those, 81 papers were useful for the review because they included brood survey methods used to estimate ≥1 vital rate associated with broods or chicks (Table 1): 47 journal articles, 31 graduate theses or dissertations and 3 book chapters. Among the 81 papers, the authors used field survey methods to: document brood habitat selection or space-use (54.3%; n = 44), estimate chick or brood success (43.2%; n = 35), estimate chick or brood survival (29.6%; n = 24), estimate an index of hen productivity (i.e. chick, brood or juvenile to hen ratios; 14.8%; n = 12) and address life history questions related to hen productivity (7.4%; n = 6). Most studies (64%, n = 52) used one survey method and 36% (n = 29) used 2 or 3 different survey methods. The most common methods were daytime visual surveys (46.9%; n = 38), daytime flush surveys (33.3%; n = 27), nocturnal spotlight surveys (19.8%;
Table 1. Summary of 81 greater sage-grouse *Centrocercus urophasianus* papers published 1990–2019 that used brood survey methods to estimate productivity or habitat use. Papers that accounted for or estimated chick or brood detection probabilities are in bold. UNK = insufficient information.

| Paper                        | Area | Years         | Method | No. of chicks | No. of broods | No. of surveys per brood | Age of brood (d) when fate was determined | Fate appraisal | Vital rate | Survival analysis |
|------------------------------|------|---------------|--------|---------------|---------------|--------------------------|------------------------------------------|---------------|------------|------------------|
| Aldridge and Brigham 2001    | AB   | 1998–1999     | DF     | 88            | 22            | 1                        | 50                                       | B1, C1        | AP         |                   |
| Aldridge and Boyce 2007      | AB   | 2001–2004     | R      | 41            | 35            | 23                       | 56                                       | C2, HS        | COX        |                   |
| Apa 1998                     | ID   | 1988–1991     | DV     | 9             | UNK           | UNK                      | UNK                                      | HS, SU        | NA         |                   |
| Atamian et al. 2010          | NV   | 2003–2006     | DF     | 29            | 7             | 12, 45                   | HD, RD                                   | B1, HS        | AP         |                   |
| Baxter et al. 2013           | UT   | 2005–2006     | R      | 40            | 19            | 14                       | 49                                       | C2, KS        |            |                   |
| Beck et al. 2003             | UT   | 1973–2000     | WING   | UNK           |               |                          | UNK                                      |               |            |                   |
| Blomberg et al. 2013         | NV   | 2003–2011     | DF     | 96            | 6             | 45                       | C2                                       |               |            |                   |
| Byrne 2002                   | OR   | 1998–2000     | UNK    | 58            | UNK           | 1-Aug                    | H1                                       | HS, NA        |            |                   |
| Bui et al. 2010              | WY   | 2007–2008     | DF     | UNK           | 2             | 35                       | HS                                       | NA, NA        |            |                   |
| Bunnell et al. 2004          | UT   | 1998–1999     | UNK, BRW, DOG | UNK           |               |                          | UNK                                      |               |            |                   |
| Burkleile et al. 2002        | ID   | 1999–2000     | R      | 65            | 28            | 70                       | 70                                       | C1, AP        |            |                   |
| Burnett 2013                 | UT   | 2011–2012     | DV     | UNK           | UNK           | UNK                      | UNK                                      | HS, NA        |            |                   |
| Cardinal and Messmer 2016     | ID, UT, WY | 2011–2012 | DF, NS | 20            | 7             | 50                       | B1, B1, HS, SU, AP                     |               |            |                   |
| Casazza et al. 2011          | CA   | 2003–2005     | DV     | 38            | 16–50         | 50                       | RD                                       | B1, HS        | UNK        |                   |
| Caudill et al. 2014          | UT   | 1998–2010     | DV, R  | UNK           | 142           | 21–25                    | 42–50                                    | B1, B1, HS    | UNK        |                   |
| Chi 2004                     | OR   | 2000–2002     | DV     | 30            | 13            | 40                       | C2                                       | B1, HS        | AP         |                   |
| Coggins 1998                 | USA  | 1995–1996     | UNK    | 23            | 21            | 1-Aug                    | B1, HS                                    | NA, NA        |            |                   |
| Connelly and Braun 1997      | USA  | 1995–1996     | VARw  | WING          | UNK           |                          | UNK                                      |               |            |                   |
| Cook 2015                    | UT   | 2012–2013     | DV     | 43            | 16–25         | 50                       | C1                                       | NA, NA        |            |                   |
| Dahlgren et al. 2006         | UT   | 2003–2004     | DOG, BRW | UNK           |               |                          | UNK                                      | B1, HS, AP    |            |                   |
| Dahlgren et al. 2010a        | UT   | 2005–2006     | DF, DOG, R | 25            | 21            | 1                        | 35–56                                    | B1, HS        | UNK        |                   |
| Davis 2002                   | NV, OR | 1998–2000 | DV, WI | 14            | 8–38          | 1-Aug                    | B1, HS                                    | UNK, AP       |            |                   |
| Davis et al. 2014            | CA   | 2007–2009     | DV, DF | 25            | 4             | 7, 14, 30, 60            | HD, FL                                    | B1, AP        |            |                   |
| Dinkins et al. 2012          | WY   | 2008–2010     | DV     | 83            | 3             | 21                       | HD                                       | NS, NA        |            |                   |
| Drut 1992                    | OR   | 1989–1991     | UNK    | 18            | ≤12           | 42, 84                    | B1, HS                                    | NA, NA        |            |                   |
| Dunbar et al. 2005           | NV, OR | 1999–2001 | DF     | UNK           | 1             | 15 Jul–1 Aug             | B1, HS                                    | NA, NA        |            |                   |
| Duvuuei et al. 2017          | UT   | 2009–2012     | DF, DV, R, NS | UNK           | 47            | 2                        | 50                                       | B1, HS        | UNK        |                   |
| Dziak et al. 2011            | WY   | 2008–2010     | DV     | 22            | 5             | 35                       | HD, DI, RD                               | B2, HS        | COX        |                   |
| Fischer et al. 1996          | ID   | 1990–1992     | BRV    | UNK           | 16            | 15 Aug                   | UNK                                      |               |            |                   |
| Flack 2017                   | UT   | 2015–2016     | DV     | 38            | 14            | 50                       | FL, RD                                   | B1, AP        |            |                   |
| Gibson et al. 2011           | CA   | 1968–1998     | WI     | UNK           |               |                          | UNK                                      |               |            |                   |
| Gibson et al. 2017           | NV   | 2005–2012     | DF, NS | 862           | 120           | 6                        | 42                                       | HD, RD, NS    | C2, HS, LYS |                   |
| Graham 2013                  | NV, OR | 2010–2012 | DV     | 10            | 14            | 50                       | C2, KM                                    |               |            |                   |
| Gregg et al. 2007            | NV, OR | 2001–2002 | R     | 288           | 52            | 28                       | 28                                       | C2, KM        |            |                   |
| Gregg and Crawford 2009      | NV, OR | 2000–2003 | DOG, R | 506           | 83            | 28                       | 28                                       | B2, C2        | KM         |                   |
| Gruber 2012                  | UT   | 2009          | R      | 99            | 24            | 21                       | 20                                       | C2, MS        |            |                   |
| Guttery et al. 2013          | ID, UT | 1999–2009 | R     | 518           | 142           | 26–42                    | 42                                       | C2, MS        |            |                   |
| Hagen 1999                   | CO   | 1997–1998     | DF     | 19            | UNK           | UNK                      | UNK                                      | HS, SU        | NA         |                   |
| Hagen and Loughlin 2008       | OR   | 1993–2005     | WI     | UNK           |               |                          | UNK                                      | NA, NA        |            |                   |

(Continued)
| Paper                  | Area | Years       | Method†  | No. of chicks | No. of broods | No. of surveys per brood | Age of brood (d) when fate was determined†  | Fate appraisal† | Vital rate‡ | Survival analysis§ |
|-----------------------|------|-------------|----------|---------------|---------------|----------------------------|---------------------------------|---------------|-------------|-------------------|
| Hagen et al. 2018     | CO   | 1978–1983   | WI       | UNK           | 11            | 5                          | 35                              | RD            | B1, HS      | NA                |
| Hariju et al. 2013    | WY   | 2008        | DV       | UNK           | 86            | UNK                       | 1–15 Aug                         | DFD, HD, RD   | C2          | KN                |
| Hausleitner 2003      | CO   | 2001–2002   | DV, DF, NS, WI | UNK           | 13            | 6–9, 32–78, UNK           | 21, 1 Aug, 35–42 to 1 Jan        | RD            | B1, HS      | AP                |
| Heuer et al. 2008a    | CO   | 2002–2003   | DV       | UNK           | 86            | UNK                       | 27                              | C2            | C2          | KN                |
| Jensen 2006           | CO   | 2004–2005   | UNK      | UNK           | 11            | 3–5                       | 35                              | RD            | HS          | NA                |
| Kaczor et al. 2011    | ND, SD| 2005–2006   | DF, DV   | UNK           | 86            | UNK                       | Aug                             | B1, SU        | AP          | KN                |
| Kiril et al. 2015     | WY   | 2008–2009   | DF, NS   | UNK           | 11            | 6                         | 36                              | HD, RD, NSF   | B2, HS      | KM                |
| Kneel 2007            | UT   | 2005–2006   | DF, DV   | 46            | 9             | 21–22                      | 50                              | DFD           | B1, HS      | AP                |
| LeBeau et al. 2014    | WY   | 2009–2010   | DF, NS   | UNK           | 13            | 5                         | 14, 35–37                       | HD, RD, NSF   | B2          | KM                |
| Hofer et al. 2017†    | WY   | 2011–2012   | DV       | UNK           | 8             | 5                         | 35                              | HD            | B1, HS      | AP                |
| Lyon 2000             | WY   | 1998–1999   | DV       | UNK           | 115           | 7–8                       | 30                              | HD, DI, RD, FL | B2          | NS                |
| Mabray 2006           | OR, NV, CA | 2015–2017  | DF       | UNK           | 5             | 34                        | 35                              | NSD           | C1          | AP                |
| Moynahan 2004         | MT   | 2001–2003   | DF, DV   | UNK           | 115           | 7–8                       | 30                              | HD, RD        | C2          | GLM               |
| Olsen 2019f           | OR, NV, CA | 2015–2017  | DF       | UNK           | 8             | 34                        | 35                              | NSD           | C1          | AP                |
| Orning 2014           | WY   | 2011–2012   | UNK, NS  | UNK           | 8             | UNK                       | 35                              | NSD           | C1          | AP                |
| Parsons 2019          | SD   | 2016–2017   | DF       | UNK           | 26            | 5                         | 49                              | RD            | B1, C1, HS  | AP                |
| Perkins 2010          | UT   | 2008–2009   | DF, NS   | UNK           | 11            | 14–21                      | 50                              | CH            | HS          | NA                |
| Peterson et al. 2016  | UT   | 2012–2016   | BRW, UNK | UNK           | 157           | 1                         | 15                              | NSD           | B2, HS      | AP                |
| Pratt and Beck 2019   | MT, WY| 2011–2015  | NS       | UNK           | 115           | 18                        | 18                              | HD, DI, RD, FL | B2          | NS                |
| Reinhart et al. 2013  | UT   | 2005–2006   | DF, DV   | UNK           | 12            | 21–50                      | 50                              | SU            | NA          | AP                |
| Robinson and Messmer 2013 | UT | 2005–2006 | DF, DV   | UNK           | 12            | 21–50                      | 50                              | B1            | AP          | KN                |
| Sveum 1996            | WA   | 1992–1996   | UNK      | 515           | 99            | 1                         | 35                              | UNK           | B1, C1, HS  | AP                |
| Tack 2009             | MT, SK| 2007–2008  | DF, DV   | 212           | 37            | 10–16                      | 50                              | HD, RD        | B1, HS      | AP                |
| Thacker 2010          | UT   | 2008–2009   | DF       | UNK           | 15            | 8–12                       | 42                              | B2            | AP          | KN                |
| Walker 2008           | WY, MT| 2003–2006  | DF, DV, NS | 1475          | 222           | 7–11                       | 35                              | DFD, DF, HD, FL, NSV | B1, B2, C1, HF, AP | GLM |

Table 1. (Continued).
A brood is composed of a male (drum) and female (hen) of the same species. A brood may contain one to several chicks. The fate of a brood (i.e., the proportion of chicks that survive to adulthood) is a critical parameter for understanding the success of a species (Zink et al. 2001). The fate of a brood can be determined by various methods, such as radio-tracking, monitoring, and visual observations. The fate of a brood can be influenced by various factors, including environmental conditions, predation, and human activities. Understanding the fate of a brood is essential for conservation and management of bird populations.
survival from survey data varied among papers (Table 1), but 23 papers used statistical methods that required a clear binary decision on brood fate (i.e. dead or alive), 31 papers calculated apparent success, and only 1 of the 81 papers (Dahlgren et al. 2010a) provided estimates of detection probability associated with their survey method(s) (Table 1). Furthermore, 1 paper (Gibson et al. 2017) accounted for chick detection via an extension of a Cormack–Jolly–Seber model (young survival model; Lukacs et al. 2004), but the authors did not report their estimates of chick detection probability.

Discussion

Conservation and monitoring programs are most effective and efficient when they include careful consideration of factors that influence the precision and accuracy of key metrics commonly used to make management and policy decisions, such as vital rates and patterns of resource selection. We reviewed the literature on greater sage-grouse and found substantial variation among studies in methods used; none of the sage-grouse brood survey methods and sampling designs, except wing surveys (reviewed by Connelly and Schroeder 2007) are used in consistent ways (also see Taylor et al. 2012). Some of that variation in survey methods undoubtedly reflects variation in goals of the investigators but the lack of consistency stymies comparisons across studies and populations. Based on our review of 81 papers, 71 studies have primarily used daytime visual surveys and daytime flush count surveys to estimate any metrics related to chick or brood productivity metrics of sage-grouse and nearly all did so without estimating or accounting for variation in detection probability. Indeed, we found only two studies (Dahlgren et al. 2010a, Gibson et al. 2017) that estimated or accounted for detection probability when using data from daytime surveys to estimate brood survival or chick survival, respectively. Perhaps most importantly, we found wide disparity among studies in the cues or triggers used to infer brood fate, and substantial variation among studies in the frequency and duration of surveys per brood. This variation makes comparisons among studies difficult and limits an investigator’s ability to put their study results into proper context. Variation in detection probability among brood survey methods is likely most pronounced at younger brood ages and age-specific variation in detection probability may be more prominent for some methods than others (Riley et al. unpubl.). Moreover, no prior studies explicitly reported the frequency with which hens or chicks were flushed during surveys and so we currently lack estimates regarding the relative disturbance caused by the different brood survey methods. If the frequency with which hens and chicks are flushed is reported in future studies, investigators can make more informed decisions regarding which brood survey methods to use and how many repeated visits to include in their sampling protocol. And studies are needed to document the effects of repeatedly flushing hens and chicks on body condition and survival. Based on our review of the average frequency and duration of past studies, future investigators who wish to estimate brood or chick survival in a manner that maximizes their ability to compare their results to others should survey broods once per week during the first 44 days after hatch for daytime flush surveys, twice per week for daytime visual surveys, and thrice per week for radio-tagged chicks. For investigators who want to estimate chick or brood survival during early stages just after hatching (e.g. post-hatch to 14 DAH), it is important to at least acknowledge that their estimated chick survival or brood fate may be affected by disturbance caused by the methods mentioned above. Researchers who wish to estimate early brood survival may want to consider using a brood survey method that is less disruptive such as nighttime roost-site fecal surveys (Riley and Conway unpubl.). For investigators who want to calculate unmarked chick or brood success with high detection probability, the best approach is likely nighttime spotlight surveys, nocturnal roost-site fecal surveys or dog surveys (Dahlgren et al. 2010a, Riley 2019), or the use of >1 method or >1 observer. Future researchers could increase the accuracy of gamebird vital rates and patterns of resource selection by explicitly estimating and accounting for detection probability with appropriate analytic and sampling approaches.

Past studies have often inferred sage-grouse brood fate based on untested assumptions regarding hen or chick behavior observed during surveys. For example, hens with broods will sometimes act ‘broody’ or use protective or defensive behaviors when approached by humans. However, the validity of these behaviors as reliable cues of brood status (alive or dead) needs verification especially when studies do not account for imperfect detection, rely on a single survey to determine fate, or when no chicks are seen. Hen behaviors such as staying close to the flush site (i.e. flushing short distances), feigning injury (e.g. broken-wing or wing-drag display), or rushing towards the observer have also been used as indicators of brood fate in sage-grouse (Atamian et al. 2010, Lebeau et al. 2017). Willow ptarmigan Lagopus lagopus use some of these defensive behaviors when they have broods (Sandercock 1994), but the validity of this behavior for inferring brood fate has not been quantified with any grousse species to our knowledge. Moreover, some studies have inferred brood fate based on when a hen moves >1 km between subsequent telemetry locations or in response to a flush count survey (Moynahan 2004, Dzialak et al. 2011) or when a hen flocks with other hens (Sandford et al. 2017). However, a large movement in response to flushing is not necessarily an indicator of a recent brood mortality; sage-grouse hens with broods in Nevada that moved further had a lower probability of survival (Gibson et al. 2017), but hens with intact broods (even those with very young broods) in Idaho sometimes moved 1–3 km in a day (Riley and Conway unpubl.). Daily movements of willow ptarmigan broods in Norway were highly variable (typically 14–514 m per day when they were 14–21 days old), but some broods traveled >2 km in one day with no apparent effect on survival (Steen and Haugvold 2009). Hence, the use of hen behaviors to infer brood fate should be used judiciously until future research provides evidence that one or more of these behaviors are indeed reliable indicators of brood fate.

Very few prior studies on gamebirds have estimated detection probability associated with brood survey methods (Andes et al. 2012, Orange et al. 2016, Riley 2019). Chick detection probability during surveys is <100% for
most gamebirds (Wing et al. 1944, Kubisiak 1978, Schroeder 1997, Dahlgren et al. 2010a, Ludwig et al. 2010). For example, chick detection probability was 0.72 (Dahlgren et al. 2010a) for 35–47-day-old sage-grouse chicks in Utah. Brood detection probability is higher than detection probability of individual chicks but is still typically <100%; brood detection probability during daytime flush counts was 0.86–0.95 for 36–47-day old sage-grouse broods in Idaho but was lower for younger-aged broods (Riley et al. unpubl.). Brood detection probability during daytime visual surveys varied with brood age for sage-grouse in Idaho, ranging from 0.618 just after hatch (95% CI = 0.440–0.770) to 0.881 at 47 days after hatch (95% CI = 0.671–0.964) (Riley et al. unpubl.). Nighttime spotlight surveys had high detection probability in Idaho (0.95–1.00) and Utah (1.00) for older sage-grouse broods (35–47 days after hatch) (Dahlgren et al. 2010a, Riley 2019), but detection rates were much lower for younger broods (1–30 day after hatch) (Foster et al. 2013, Riley 2019). We are unaware of any study that has evaluated intrinsic or extrinsic factors that influence detection probability of sage-grouse broods, regardless of the survey method. Future studies are needed on the following topics: 1) how sampling methods influence detection for other species, 2) to sampling methods with minimal disturbance such as nighttime roost-site fecal surveys (Riley 2019) and thermal cameras (Andes et al. 2012) for chick or brood counts and 3) the influence of topography, vegetation, temperature, weather, observers and other factors on detection probability of brood survey methods.

Some brood survey methods for gamebirds may influence survival probabilities due to disturbance caused while flushing the hen or chicks. Intentionally or unintentionally flushing the hen or chicks could decrease survival via increased probability of chick abandonment, increased susceptibility to predation or increased energy expenditure (Riley 2019). Observers intentionally try to flush both the hen and chicks during daytime flush counts, whereas observers try not to do so during daytime visual and nocturnal spotlights counts. However, past studies vary widely regarding the frequency of surveys on individual broods. For example, observers that conducted daytime flush counts flushed hens and chicks from 1 to 14 times. Also, incidental flushes occur even with methods that are not designed to intentionally flush either chicks or the hen (Riley 2019) and not all hens and chicks flush even with methods where observers explicitly try to flush them. Future investigators can help inform others when developing future study design and protocols by quantifying the disturbance caused while conducting brood or chick surveys.

Use of radio-marked chicks or pointing dogs are viewed by some researchers as the most reliable methods to estimate chick or brood survival, but few studies have reported detection probability associated with these methods and whether detection rates vary with brood age or brood size. Pointing dogs are used extensively in Europe and are used less commonly in North America to locate chicks or broods (Connelly et al. 2003, Dahlgren et al. 2012). Pointing dogs located 21 of 22 (96%) 5- to-8-week-old sage-grouse chicks (Dahlgren et al. 2010a), but the accuracy of this method has not been tested on younger sage-grouse broods and detection probability likely varies among dogs (Connelly et al. 2003, Dahlgren et al. 2012, Orange et al. 2017), habitat conditions, trainers, weather, etc. Furthermore, pointing dogs have occasionally eaten chicks and surveyors have incidentally stepped on and killed chicks (typically <14 days after hatch) during surveys (M. Schroeder unpubl., Conway unpubl.). Standardized protocols that include efforts to reduce chick mortality are needed to better assess and reduce biases associated with pointing-dog surveys (Gutzwiller 1990, Dahlgren et al. 2012). Detection probability of radio-marked chicks (Larson et al. 2001, Burkepile et al. 2002, Gregg et al. 2007, Dahlgren et al. 2010b, Steen and Haugvold 2012) is often assumed to be 100%, but lost signals are a form of imperfect detection, and right-censoring of missing signals can produce biased survival estimates (Blomberg et al. 2019). Moreover, adverse reactions to handling or attaching transmitters to chicks may confound survival estimates (Amundson and Arnold 2010, Steen and Haugvold 2009, Taylor et al. 2012, Baxter et al. 2013, Blomberg et al. 2019). Lastly, radio-marked chicks may not accurately estimate brood survival unless researchers are certain that all chicks within a brood are radio-tagged.

Wildlife agencies often rely on field methods like wing surveys and brood routes to obtain population-level information about trends in productivity and other vital rates (Hagen and Loughin 2008, Broms et al. 2010, Sands and Pope 2010, Hansen et al. 2015, Braun et al. 2015). We found very few papers that had used sage-grouse wing surveys to estimate productivity. Moreover, we are unaware of any study that has explicitly quantified classification error of wings which likely varies among observers based on experience, and its accuracy is likely affected by unusual molt patterns (Braun and Schroeder 2015) and wing condition. Several studies have documented the validity of grouse production indices based on wing surveys (Flanders-Wanner et al. 2004, Hansen et al. 2015) or based on a combination of wing surveys and band-recoveries (Hagen et al. 2018). Despite this, production indices are potentially biased if differential hunter kills occur among grouse sex and age classes (Zwickel 1982, Flanders-Wanner et al. 2004, Buneufeld et al. 2009, Asymhr et al. 2012). For example, hunters may select sage-grouse hens or juveniles when they congregate near springs (i.e. density-dependent harvest selection), brood-less hens and males flush more readily than hens with broods (Riley unpubl.), adult males are viewed as trophies (D. Musil unpubl.), and these and other motivations produce sex-biased harvest (Guttery et al. 2015). Documenting sex, age or size biases associated with harvest can help ensure that those biases are accounted for when using wing surveys to estimate population parameters. We found few papers that used brood vehicle routes (n = 2) to quantify sage-grouse vital rates, despite the apparent use of this method by wildlife agencies to inform management and harvest decisions (Willis et al. 1993, Connelly and Schroeder 2007, Sands and Pope 2010). Brood vehicle routes have been used to document temporal trends in brood production (e.g. number of juveniles per hen) for numerous North American gamebirds because agencies can monitor large areas and multiple species in short time spans (Sands and Pope 2010). However, data from brood vehicle routes may not accurately estimate productivity due to: low or unknown detection rates (Hansen et al. 2015), use of convenience sampling to select the survey routes (Sands and Pope 2010), differential
studies that have monitored radio-marked chicks (2.0–51%) (Flint et al. 1995). With sage-grouse, the frequency of brood is rarely reported and, hence, may bias survival estimation (Gren et al. 2010b, Steen and Haugvold 2012, Orange et al. 2015, Sandford et al. 2017, Geaumont and Grainger 2020) and past investigators have used numerous brood survey methods to estimate fecundity and management (MacKenzie et al. 2002, Royle and Link 2006). Brood amalgamation, where >1 chick is adopted by another hen, is an alloparental care strategy common in Galliformes (Keppie 1977, Lott and Mastrup 1999, Dahlgren et al. 2010b, Steen and Haugvold 2012, Orange et al. 2016), but its frequency likely varies among populations and is rarely reported and, hence, may bias survival estimation (Flint et al. 1995). With sage-grouse, the frequency of brood amalgamation varies among populations based on a few studies that have monitored radio-marked chicks (2.0–51%) and broods (8.3–43%) (Connelly et al. 2006, Gregg et al. 2007, Dahlgren et al. 2010b, Gruber 2012). Studies that do not use radio-marked chicks to account for brood amalgamation have an unknown amount of bias introduced into their estimates of chick or brood survival. Hence, more studies are needed to estimate brood amalgamation rates and how they vary among populations, years, brood ages and species.

A common theme among many analytic approaches commonly used to estimate brood survival is that they require a clear binary outcome (e.g. alive or dead) for each individual brood or chick (Andersen and Gill 1982, Dinsmore et al. 2002, Williams et al. 2002, p. 343). It is unclear whether surveys without marked chicks or without complete observations can achieve this outcome; although some authors report that repeated surveys or the use of nighttime surveys is enough to validate brood fate (LeBeau et al. 2017). Given that most brood survey methods have imperfect detection, future studies can reduce variance in survival estimates by using Cormack–Jolly–Seber models (Lebreton et al. 1992, Lukacs et al. 2004, Schaub and Royle 2014), occupancy models (MacKenzie et al. 2002, Kéry and Royle 2016), or by conducting >1 visit, using >1 method or including >1 independent observer (Williams et al. 2002, Buckland et al. 2015, Clement et al. 2017).

Conclusions and recommendations

Sage-grouse and other gamebird populations have declined (Storch 2007, McGowen et al. 2012) and future research on brood survival, hen productivity and resource selection will help inform management decisions including their response to environmental and anthropogenic conditions. The following strategies would help to improve accuracy of parameter estimates and reduce disturbance and their incorporation into gamebird brood monitoring protocols will improve inferences and comparisons across studies.

1. Document the factors that influence detection probability and extent of disturbance to broods and hens for all brood sampling methods used on gamebirds.
2. Minimize inaccuracy and imprecision in estimating brood fate and brood survival by accounting for detection probability with appropriate analytic and sampling approaches.
3. Standardize the frequency and duration of surveys per brood based on life history, behavior and length of the time when chicks are dependent on the hen.
4. Report the frequency of disturbance (e.g. flushing) to hens and chicks for each brood sampling method used.
5. Minimize flushing chicks early in life (typically < 14 days after hatch) when chicks are unlikely to survive without their hen. If estimates of early chick survival or success are needed, acknowledge that the survey method likely influences these estimates of productivity or consider using less invasive brood survey methods such as nighttime roost-site fecal surveys (Riley et al. unpubl.).
6. Conduct studies to validate the utility of using various hen behaviors as reliable indicators of brood fate (i.e. to more reliably assign fate when no chicks are detected).
7. Explicitly state the hen behaviors used to infer brood fate.
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