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

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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 ($\bar{x} = 44.4$ 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

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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 (Schroeder 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) (Autenrieth 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[a]	No. of chicks	No. of broods	No. of surveys per brood	Age of brood (d) when fate was determined[b]	Fate appraisal[c]	Vital rate[d]	Survival analysis[e]
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		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	KF
Beck et al. 2003	UT	1973–2000	WING	UNK					JH	NA
Blomberg et al. 2013	NV	2003–2011	DF		96	6	45		B1	AP, HF
Bryne 2002	OR	1998–2000	UNK		58	UNK	1-Aug		HS	NA
Bui et al. 2010	WY	2007–2008	DF		UNK	2	35		HS	NA
Bunnell et al. 2004	UT	1998–1999	UNK, BRW, DOG		UNK	UNK	UNK		HS	NA
Burkepile et al. 2002	ID	1999–2000	R	65	28	70	70		C1	AP
Burnett 2013	UT	2011–2012	DV		UNK	UNK	UNK		HS	NA
Cardinal and Messmer 2016	ID, UT, WY	2011–2012	DF, NS		20	7	50		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, HF	UNK
Chi 2004	UT	2000–2002	DV		30	13	40		B1	AP
Coggins 1998[f]	OR	1995–1996	UNK		23	UNK	1-Aug		B1, HS	AP
Connelly and Braun 1997	USA	VAR[h]	WING	UNK					JH	NA
Cook 2015	UT	2012–2013	DV		43	16–25	50		B2	NS
Dahlgren et al. 2006	UT	2003–2004	DOG, BRW		UNK	UNK	late-July to 1 Aug		BH, HS	NA
Dahlgren et al. 2010a	UT	2006–2007	DF, DOG, R	25	21	1	35–56			
Dahlgren et al. 2010b	UT	2005–2006	R	150	42	21–42	42		C2	NS
Davis 2002	NV, OR	1998–2000	DV, WI		14	8–38	1-Aug		B1, HS, JH	AP
Davis et al. 2014	CA	2007–2009	DF, DV		25	4	7, 14, 30, 60	HD, FL	B1	AP
Dinkins et al. 2012	WY	2008–2010	DV		83	3	21	HD	HS	NA
Drut 1992	OR	1989–1991	UNK		18	≤12	42, 84		B1, HS	AP
Dunbar et al. 2005	NV, OR	1999–2001	DF		UNK	1	15 Jul–1 Aug		B1, HF	NA
Duvuvuei et al. 2017	UT	2009–2012	DF, DV, R, NS	UNK	47	2	50	HD, NSD	B2	NS
Dzialak 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		CH	NA
Flack 2017	UT	2015–2016	DF, DV		38	14	50	FL, RD	B1	AP
Gibson et al. 2011	CA	1968–1998	WI	UNK					JH	NA
Gibson et al. 2017	NV	2005–2012	DF, NS	862	120	6	42	HD, RD, NSD	C2, HF, HS	LYS
Graham 2013	UT	2010–2012	DV		10	14	50		B1, HS	AP
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		HS, SU	NA
Hagen and Loughin 2008	OR	1993–2005	WI	UNK					JH	NA

(*Continued*)

Table 1. (Continued).

Paper	Area	Years	Method[a]	No. of chicks	No. of broods	No. of surveys per brood	Age of brood (d) when fate was determined[b]	Fate appraisal[c]	Vital rate[d]	Survival analysis[e]
Hagen et al. 2018	CO	1978–1983	WI	UNK					JH	NA
Harju et al. 2013	WY	2008	DV		11	5	35	RD	B1, HS	AP
Hausleitner 2003	CO	2001–2002	DV, DF, NS, WI	UNK	UNK	6–12	42		C1, CH, JH, HS, SU	AP
Herman-Brunson 2007	ND	2005–2006	DF, R	UNK	13	6–9, 52–78, UNK	21, 1 Aug, 35–42 to 1 Jan		B1, C2, HS	AP, KM
Holloran 2005	WY	1998–2004	DF, DV, WI	UNK	86	UNK	1–15 Aug	DFD, HD, RD	C2	KF
Huwer et al. 2008[g]	CO	2002–2003	DV	UNK	UNK	648	27		C2	KF
Jensen 2006	WY	2004–2005	UNK	UNK	UNK	UNK	Aug		B1, SU	AP
Kaczor et al. 2011	ND, SD	2005–2006	DF, DV		43	3–5	35	RD	HS	NA
Kirol et al. 2015	WY	2008–2009	DV, NS		35	6	36	HD, RD, NSD	B2, HS	KM
Knerr 2007	UT	2005–2006	DF, DV	46	9	21–22	50	DFD	C1, B1, HS	AP
LeBeau et al. 2014	WY	2009–2010	DV, NS		31	5	14, 35–37	HD, RD, NSD	B2	AG
LeBeau et al. 2017[f]	WY	2011–2014	DV, NS		123	5	35	HD, RD, NSD	B2	AG
Lyon 2000	WY	1998–1999	DV		27	UNK	21	HD	B1, HS	AP
Mabray 2015	WY	2008–2011	DV		8	UNK	UNK	HD	HS	NA
Moynahan 2004	MT	2001–2003	DF, DV		115	7–8	30	HD, DI, RD, FL	B2	NS
Olsen 2019[f]	OR, NV, CA	2015–2017	DF	UNK	UNK	5	34	HD,RD	C2	GLM
Orning 2014	WY	2011–2012	UNK, NS		8	UNK	35	NSD	C1	AP
Parsons 2019	SD	2016–2017	DF		26	3	49	RD	HF, HS	NA
Perkins 2010	UT	2008–2009	DV, NS	NA	12	14–21	50		B1, C1, HS	AP
Peterson et al. 2016	UT	2012–2016	BRW	UNK	UNK	UNK	UNK		CH, HS	NA
Pratt and Beck 2019	MT, WY	2011–2015	NS		157	1	35	NSD	B2, HS	COX
Rebholz 2007	NV	2004–2005	R	115	21	18	18		B1, C2, HS	AP, KM, COX
Reinhart et al. 2013	UT	2005–2006	DV, DF	UNK	UNK	21	50		SU	NA
Robinson and Messmer 2013	UT	2005–2006	DV		UNK	25	50		B1	AP
Sandford et al. 2017	UT	2012–2015	DF, DV, NS		56	14–21	50	RD, FL, NSV	B1, HS	AP
Schreiber et al. 2016	WY	2011–2013	NS	UNK	37	3–7	70	RD, NSD	C2	LE
Schroeder 1997	WA	1992–1996	UNK	515	99	1	50		C1, B1	AP
Schroff 2016	MT	2014–2015	UNK		UNK	UNK	35		SU	NA
Sika 2006	MT	2003–2005	DF		73	2–3	30	FL	B2	NS
Slater 2003	WY	2001–2002	DV		17	3	14, late-July		B1, HS	AP
Smith 2009	UT	2007–2008	UNK	14	2	14–21	50		C1, HS	AP
Smith 2016	WY	2011–2013	DV, NS		UNK	5	35	HD, RD, NSD	B1, HF, HS	AP
Smith et al. 2019	WY	2013–2015	DV, NS		58	5	35	HD, RD, NSD	HS	NA
Sveum 1996	WA	1992–1993	DV		38	<16	1 Aug		B1, HS	AP
Tack 2009	MT, SK	2007–2008	DF, DV	212	37	10–16	50		B1, C1, HS	AP
Thacker 2010	UT	2008–2009	DV		15	8–12	42		B2	AP
Thompson et al. 2006	WY	1999–2003	DV		82	1–2	14	HD, RD	HS	NA
Walker 2008	WY, MT	2003–2006	DF, DV, NS	1475	222	7–11	35	DFD, DI, HD, FL, NSV	B1, B2,C1, HF	AP, GLM

Westover 2012[f]	UT	1998–2012	DF	UNK	14	50–56	DI, RD	JH	NA
Wik 2001	ID	2000–2001	DV, DF	17	23–35	70	DFD, HD	B1, HS, SU	AP
Wing 2014	UT	2012–2013	DF, NS	28	7	50	RD, NSV	B1, HS	AP

[a] BRV = brood route with vehicle, BRW = brood route by walking transect, DF = daytime flush, DV = daytime visual, R = radio-marked chicks, NS = nighttime spotlight, WI = wing survey.

[b] The final date or age of the chicks when the investigator assessed fate.

[c] DI = distance between consecutive surveys or distance grouse flew after survey, DFD = brood fate assessed by daytime flush if multiple survey types were used, HD = hen distractive behavior (i.e. wing-display, flushing short distances, etc.), NSD = brood fate assessed by nighttime spotlight survey if multiple survey types were used, NSV = nighttime spotlight survey used to validate another survey's fate determination, RD = repeated detection/non-detection and FL = flocking with conspecifics.

[d] B1 = brood success, B2 = brood survival, C1 = chick success, C2 = chick survival, CH = chicks: hen ratio, BH = broods: hen ratio, HF = hen's fitness, JH = juvenile: hen ratio, HS = habitat selection, SU = spatial-use.

[e] AP = apparent values of brood or chick success, AG = Anderson-Gill, ANOVA = analysis of variance, COX = Cox proportional, GLM = generalized linear model, KF = Known-fate, KM = Kaplan-Meier, LE = logistic exposure, LYS = Lukacs' young survival model, NA = brood or chick survival or success not estimated by author or there was enough not information for us to do so, and NS = nest survival.

[f] The author used their own or another author's previously examined data, but also used included previously unexamined data.

[g] The author used human-imprinted chicks to estimate diet selection and chick survival. Authors surveyed chicks 24 times per day thus the extraordinary survey number.

[h] VAR = Author quantified long-term productivity among states in the USA. Years vary.

n = 16), radio-tagged chicks (16.0%; n = 13), wing surveys (9.9%; n = 8), brood vehicle routes (2.5%; n = 2), brood walking routes (2.5%; n = 2) and pointing dog surveys (4.9%; n = 4). Fifty-nine studies (72.8%) made >1 visit per brood (Table 1). Nine papers included results from a daytime survey, but the text included insufficient information to classify whether they explicitly tried to flush the hen and her brood (i.e. whether they conducted a daytime flush survey or daytime visual survey). We assumed that researchers used a daytime visual survey (rather than a flush survey) if the text said that researchers explicitly 'located', 'observed' or 'confirmed' chicks or broods but didn't explicitly state that they flushed birds. Nighttime survey methods were primarily used to determine final brood fate (n = 10) or validate the results of daytime surveys (n = 3). Daytime flush surveys were also used to determine final brood fate (n = 10). Only 2 papers (Hausleitner 2003, Schreiber et al. 2016) used a nighttime survey method throughout the sampling period as their primary brood survey method.

Studies varied widely in numerous ways: goal(s) of the brood sampling; study design; sample size of brood or chicks included in the study; how they determined brood or chick fate; and statistical methodology used to obtain estimates from the survey data (Table 1). Of the 67 studies that monitored broods, 63 reported the number of broods monitored (i.e. sample size), which varied from 2–272 ($\bar{x}$ = 49.7) broods. The sample size for 10 studies that reported the number of monitored radio-marked chicks varied from 25–518 chicks ($\bar{x}$ = 185.7; Table 1). Eight other studies (those that did not include radio-marked chicks) reported chick numbers which varied from 14–1475 chicks ($\bar{x}$ = 251.7; Table 1). Sixty-three studies reported estimates of >1 measure of any metrics related to chicks or broods but varied widely regarding when they recorded brood fate relative to days after hatch ($\bar{x}$ = 44.4, range = 14–84 days) or date of presumed brood independence (range = 15 Jul–15 Aug). The frequency with which the same broods or chicks were re-surveyed varied among the primary survey methods used from 1.19–1.43 surveys per brood per week for daytime flush surveys, 1.62–1.92 surveys per brood per week for daytime visual surveys (without data from the obvious outlier of Huwer et al. 2008), 3.71–3.85 surveys per brood per week for radio-marked chick monitoring, and 2.25–3.50 surveys per brood per week for nighttime surveys. The study that included the most frequent revisits to broods included 168 daytime visual surveys per week over 27 days for a study designed to estimate chick diet and survival rates of human-imprinted, released (rather than wild) chicks (Huwer et al. 2008). None of the 81 studies recorded the proportion of hens or broods that were flushed during their brood surveys. Five of 12 studies that used radio-marked chicks reported mortalities caused by capture or handling, and 4 of the 12 studies reported censoring survival data when a chick's fate was unknown (i.e. went missing). Thirty-five studies used the following indirect or ancillary clues to classify brood status or fate: hen distracting behavior (57.1%; n = 20), hens observed without chicks on >1 consecutive surveys (60.0%; n = 21), the presence of other yearling or adult sage-grouse (17.1%; n = 6), or large hen movements (≥ 1–3 km) relative to prior survey(s) (11.4%; n = 4). Brood survival ranged from 10 to 100% (Table 1). Statistical methods used to estimate 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 we 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 whowish 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 distractive 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 grouse 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 indication 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) 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, Bunnefeld 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 detection of brood-less hens or males compared to hens with broods, and detection rates may be affected by environmental factors. Additionally, we found few studies (n = 2) that used brood walking routes (i.e. line or strip transects). Brood walking routes are difficult to implement on large scales without substantial costs and, therefore, are impractical for monitoring productivity in most gamebirds.

Appropriate sampling design is needed to increase the accuracy of brood productivity parameters. Measures of annual fecundity and their relationship to habitat characteristics are likely underestimated if studies fail to explicitly account for imperfect detection of broods. Moreover, past studies varied widely regarding the brood age when surveys were conducted and this variation limits comparability among studies if detection rates or daily survival vary by brood age (and both typically do; Riley et al. unpubl.). Brood surveys are often designed to estimate survival during a biologically relevant time period (e.g. from hatch until the date when chick fate is independent of hen fate). By having a discrete time period, hypothetically, researchers can standardize the sampling frequency to conduct brood surveys. However, there is no clear consensus regarding what that time period is for broods given the contradictory evidence about when chicks can survive without a hen (Dahlgren et al. 2010b, Thompson 2012) and that age will vary among species and perhaps even among populations within species. We need more information regarding the precision and accuracy of different levels of brood survey effort to achieve defensible survival estimates for most species. Future researchers could standardize the frequency and duration of surveys per brood based on life history (e.g. when thermoregulation or flight is possible, etc.), behavior (e.g. flight versus hiding when reacting to surveyors, etc.), and length of the time when chicks are dependent on the hen. Additionally, researchers could use simulations to evaluate how much sampling effort is needed to estimate survival, resource selection or occupancy (Bailey et al. 2007) during an explicit range of brood ages.

Accurate estimates of demographic parameters, and the habitat features that affect those parameters, are essential for management (MacKenzie et al. 2002, Royle and Link 2006). Brood surveys are commonly used to estimate fecundity and resource selection of gamebirds (Ludwig et al. 2010, Anderson et al. 2015, Sandford et al. 2017, Geaumont and Graham 2020) and past investigators have used numerous brood survey methods, but very few sage-grouse studies that have used brood survey methods have measured or accounted for detection probability. Incorporation of detection probability is more common in resource selection studies including survival models that accommodate detection probabilities and resource covariates (Lebreton et al. 1992) and occupancy models that incorporate detection functions (MacKenzie et al. 2002, Royle and Link 2006, Kéry and Royle 2016).

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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References

Aldridge, C. L. and Boyce, M. S. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. – Ecol. Appl. 17: 508–526.

Aldridge, C. L. and Brigham, R. M. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. – Condor 103: 537–543.

Amundson, C. L. and Arnold, T. W. 2010. Effects of radiotransmitters and plasticine bands on mallard duckling survival. – J. Field Ornithol. 81: 310–316.

Andersen, P. K. and Gill, R. D. 1982. Cox's regression model for counting processes: a large sample study. – Ann. Stat. 10: 1100–1120.

Anderson, L. C. et al. 2015. Greater prairie-chicken brood-site selection and survival in the Nebraska sandhills. – J. Wildl. Manage. 79: 559–569.

Andes, A. K. et al. 2012. Use of a thermal camera to aid in capturing northern bobwhite quail chicks. – Wildl. Soc. Bull. 36: 371–375.

Apa, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. – MSc thesis, Univ. of Idaho.

Asymhr, L. et al. 2012. Successful adult willow grouse are exposed to increased harvest risk. – J. Wildl. Manage. 76: 940–943.

Atamian, M. T. et al. 2010. Landscape-level assessment of brood rearing habitat for sage-grouse in Nevada. – J. Wildl. Manage. 74: 1533–1543.

Autenrieth, R. E. et al. 1982. Sage grouse management practices. Western States Sage-Grouse Committee Tech. Bull. No. 1. – Idaho Dept of Fish and Game, Boise, ID, USA.

Bailey, L. L. et al. 2007. Sampling design tradeoffs in occupancy studies with imperfect detection: examples and software. – Ecol. Appl. 17: 281–290.

Baxter, J. J. et al. 2013. Evaluating survival of greater sage-grouse chicks in Strawberry Valley, Utah, by use of microtransmitters: does handling time negatively influence survival rates? – W. N. Am. Nat. 73: 419–425.

Beck, J. L. et al. 2003. Changes in the distribution and status of sage-grouse in Utah. – W. N. Am. Nat. 63: 203–214.

Blomberg, E. J. et al. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. – J. Avian Biol. 44: 149–158.

Blomberg, E. J. et al. 2019. Detecting capture-related mortality in radio-marked birds following release. – Avian Conserv. Ecol. 13: 1–19.

Braun, C. E. and Schroeder, M. A. 2015. Age and sex identification from wings of sage-grouse. – Wildl. Soc. Bull. 39: 182–187.

Braun, C. E. et al. 2015. Fall population structure of sage-grouse in Colorado and Oregon. Wildlife Technical Report 005-2015. – Oregon Dept of Fish and Wildlife, Salem, OR, USA.

Broms, K. et al. 2010. Using statistical population reconstruction to estimate demographic trends in small game populations. – J. Wildl. Manage. 74: 310–317.

Buckland, S. T. et al. 2015. Distance sampling: methods and applications. – Springer Int.

Bui, T. et al. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. – Condor 112: 65–78.

Bunnefeld, N. et al. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. – J. Anim. Ecol. 78: 485–492.

Bunnell, K. D. et al. 2004. Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. – J. Range Manage. 57: 524–531.

Burkepile, N. A. et al. 2002. Attachment of radiotransmitters to one-day-old sage-grouse chicks. – Wildl. Soc. Bull. 30: 93–96.

Burnett, A. C. 2013. Modeling habitat use of a fringe greater sage-grouse population at multiple spatial scales. – MSc thesis, Utah State Univ.

Bryne, M. W. 2002. Habitat use by female greater sage-grouse in relation to fire at Hart Mountain National Antelope Refuge, Oregon. – MSc thesis, Oregon State Univ.

Cardinal, C. J. and Messmer, T. A. 2016. Ecology of greater sage-grouse populations inhabiting the northwestern Wyoming Basin. – Hum. Wildl. Inter. 10: 188–204.

Casazza, M. L. et al. 2011. Linking habitat selection and brood success in greater sage-grouse. – In: Sandercock, B. K. et al. (eds), Ecology, conservation and management of grouse. Studies in avian biology, No. 39. Univ. of California Press, Berkeley and Los Angeles, CA, USA, pp. 151–167.

Caudill, D. et al. 2014. Effects of climatic variation and reproductive tradeoffs vary by measure of reproductive effort in greater sage-grouse. – Ecosphere 5: 154.

Chi, R. Y. 2004. Greater sage-grouse reproductive ecology and Tebuthiuron manipulation of dense big sagebrush on Parker Mountain. – MSc thesis, Utah State Univ.

Clement, M. J. et al. 2017. Accounting for imperfect detection of groups and individuals when estimating abundance. – Ecol. Evol. 7: 7304–7310.

Coates, P. S. et al. 2017. Greater sage-grouse (*Centrocercus urophasianus*) nesting and brood-rearing microhabitat in Nevada and California-spatial variation in selection and survival patterns. – US Geological Survey Open-File Report 2017-1087.

Coggins, K. A. 1998. Relationship between habitat changes and productivity of sage grouse at Hart Mountain National Antelope Refuge, Oregon. – MSc thesis, Oregon State Univ.

Connelly, J. W. and Braun, C. E. 1997. Long-term changes in sage-grouse *Centrocercus urophasianus* population in western North America. – Wildl. Biol. 3: 229–234.

Connelly, J. W. and Schroeder, M. A. 2007. Historical and current approaches to monitoring greater sage-grouse. – In: Reese, K. P. and Bowyer, R. T. (eds), Monitoring populations of sage-grouse. Exp. Stn Bull. 88. College of Natural Resources, Univ. of Idaho, USA, pp. 3–9.

Connelly, J. W. et al. 2006. Sage grouse ecology. Study II: mortality patterns of juvenile greater sage-grouse. Project W-160-R-33. – Idaho Dept of Fish and Game, Boise, ID, USA.

Cook, A. 2015. Greater sage-grouse seasonal habitat models, response to juniper reduction and effects of capture behavior on vital rates, in northwest Utah. – MSc thesis, Utah State Univ.

Dahlgren, D. K. et al. 2006. Greater sage-grouse response to sagebrush management in Utah. – Wildl. Soc. Bull. 34: 975–985.

Dahlgren, D. K. et al. 2010a. Evaluation of brood detection techniques: recommendations for estimating greater sage-grouse productivity. – W. N. Am. Nat. 70: 233–237.

Dahlgren, D. K. et al. 2010b. Achieving better estimates of greater sage-grouse chick survival in Utah. – J. Wildl. Manage. 74: 1286–1294.

Dahlgren, D. K. et al. 2012. Use of dogs in wildlife research and management. – In Silvy, N. J. (ed.), The wildlife techniques manual: research, Vol. 1. John Hopkins Univ. Press, pp. 140–153.

Davis, D. M. 2002. Breeding season habitat use and response to management activities by greater sage-grouse on Sheldon National Wildlife Refuge, Nevada. – MSc thesis, Oregon State Univ.

Davis, D. M. et al. 2014. Demography, reproductive ecology and variation in survival of greater sage-grouse in northeastern California. – J. Wildl. Manage. 78: 1343–1355.

Dinkins, J. B. et al. 2012. Greater sage-grouse *Centrocercus urophasianus* select nest sites and brood sites away from avian predators. – Auk 129: 600–610.

Dinsmore, S. J. et al. 2002. Advanced techniques for modeling avian nest survival. – Ecology 83: 3476–3488.

Drut, M. S. 1992. Habitat use and selection by sage-grouse broods in southeastern Oregon. – MSc thesis, Oregon State Univ.

Dunbar, M. R. et al. 2005. Normal hematologic and biochemical values for prelaying greater sage-grouse *Centrocercus urophasianus* and their influence on chick survival. – J. Zoo Wildl. Med. 36: 422–429.

Duvuvuei, O. V. et al. 2017. Contribution of translocated greater sage-grouse to population vital rates. – J. Wildl. Manage. 81: 1033–1041.

Dzialak, M. R. et al. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. – PLoS One 6: e26273.

Fischer, R. A. et al. 1996. An investigation on fire effects within xeric sage grouse brood habitat. – J. Range Manage. 49: 194–198.

Flack, M. B. 2017. Ecology of greater sage-grouse inhabiting the southern portion of the Rich–Morgan–Summit sage-grouse management area. – MSc thesis, Utah State Univ.

Flanders-Wanner, B. L. et al. 2004. Validity of prairie grouse harvest-age ratios as production indices. – J. Wildl. Manage. 68: 1088–1094.

Flint, P. L., et al. 1995. Estimating prefledging survival – allowing for brood mixing and dependence among brood mates. – J. Wildl. Manage. 59: 448–455.

Foster, M. A. et al. 2013. Greater sage-grouse in the southeast Montana sage-grouse core area. – Montana Fish, Wildlife and Parks in partnership with U.S. Dept. of the Interior, Bureau of Land Management, Helena, MT, USA.

Geaumont, B. A. and Graham, D. L. 2020. Factors affecting sharp-tailed grouse brood habitat selection and survival. – Wildl. Biol. 2020: wlb.00633

Gibson, G. et al. 2017. Weather, habitat composition and female behavior interact to modify offspring survival in greater sage-grouse. – Ecol. Appl. 27: 168–181.

Gibson, R. M. et al. 2011. Hunting lowers population size in greater sage-grouse. – In: Sandercock, B. K. et al. (eds), Ecology, conservation and management of grouse. Studies in Avian Biology, No. 39. Univ. of California Press, Berkeley and Los Angeles, CA, USA, pp. 307–315.

Graham, S. E. 2013. Greater sage-grouse habitat selection and use patterns in response to vegetation management practices in Northwestern Utah. – MSc thesis, Utah State Univ.

Gregg, M. A. and Crawford, J. A. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. – J. Wildl. Manage. 73: 904–913.

Gregg, M. A. et al. 2007. Use of implanted radio-signal transmitters to estimate survival of greater sage-grouse chicks. – J. Wildl. Manage. 71: 646–651.

Gruber, N. W. 2012. Population dynamics and movements of translocated and resident sage-grouse on Anthro Mountain, Utah. – MSc thesis, Utah State Univ.

Guttery, M. R. et al. 2013. Effects of landscape-scale environmental variation on greater sage-grouse chick survival. – PLoS One 8: e65582.

Gutzwiller, K. J. 1990. Minimizing dog-induced bias in game bird research. – Wildl. Soc. Bull. 18: 351–356.

Hagen, C. A. 1999. Sage grouse habitat use and seasonal movements in a naturally fragmented landscape, northwestern Colorado. – MSc thesis, Univ. of Manitoba.

Hagen, C. A. 2003. A demographic analysis of lesser prairie-chicken populations in southwestern Kansas – survival, population viability and habitat use. – PhD thesis, Kansas State Univ.

Hagen, C. A. and Loughin, T. M. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample sizes. – J. Wildl. Manage. 72: 1369–1375.

Hagen, C. A. et al. 2007 A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. – Wildl. Biol. 13: 42–50.

Hagen, C. A. et al. 2018. Estimating sex-ratio, survival and harvest susceptibility in greater sage-grouse: making the most of hunter harvests. – Wildl. Biol. 2018: wlb.00362.

Hansen, M. C. et al. 2015. Comparison of 3 surveys for estimating forest grouse population trends: forest grouse indices. – Wildl. Soc. Bull. 30: 93–96.

Harju, S. M. et al. 2013. Occurrence and success of greater sage-grouse broods in relation to insect-vegetation community gradients. – Hum. Wildl. Inter. 7: 214–229.

Hausleitner, D. 2003. Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. – MSc thesis, Univ. of Idaho.

Herman-Brunson, K. E. 2007. Nesting and brood-rearing habitat selection of greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. – MSc thesis, South Dakota State Univ.

Holloran, M. J. 2005. Greater sage-grouse *Centrocercus urophasianus* population response to natural gas field development in western Wyoming. – PhD thesis, Univ. of Wyoming.

Huwer, S. L. et al. 2008. Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. – J. Wildl. Manage. 72: 1622–1627.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). – MSc thesis, Univ. of Wyoming.

Kaczor, N. W. et al. 2011. Resource selection during brood-rearing by greater sage-grouse. – In: Sandercock, B. K. et al. (eds), Ecology, conservation and management of grouse. Studies in avian biology no. 39. – Univ. of California Press, Berkeley and Los Angeles, CA, USA, pp. 169–177.

Keppie, D. M. 1977. Inter-brood movements of juvenile spruce grouse. – Wilson Bull. 89: 67–72.

Kéry, M. and Royle, J. A. 2016. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS, Vol. 1. – Elsevier, pp. 551–628.

Kirol, C. P. et al. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. – Ecol. Appl. 25: 968–990.

Knerr, J. S. 2007. Greater sage-grouse ecology in western Box Elder County, Utah. – MSc thesis, Utah State Univ.

Kubisiak, J. F. 1978. Brood characteristics and summer habitats of ruffed grouse in central Wisconsin. Tech. Bull. 108. – Wisconsin Dept of Natural Resources, Madison, WI, USA.

Larson, M. A. et al. 2001. Survival of ruffed grouse chicks in northern Michigan. – J. Wildl. Manage. 65: 880–886.

LeBeau, C. W. et al. 2014. Short-term impacts of wind energy development on greater sage-grouse fitness. – J. Wildl. Manage. 78: 522–530.

LeBeau, C. W. et al. 2017. Greater sage-grouse habitat selection and survival, and wind energy infrastructure. – J. Wildl. Manage. 81: 690–711.

Lebreton, J. D. et al. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Leopold, A. 1933. Game management. – Univ. of Wisconsin Press.

Lott, D. E. and Mastrup, S. N. A. 1999. Facultative communal brood rearing in California quail. – Condor 101: 678–681.

Ludwig, G. X. et al. 2010. Individual and environmental determinants of early brood survival in black grouse *Tetrao tetrix*. – Wildl. Biol. 16: 367–378.

Lukacs, P. M. et al. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. – Condor 106: 927–932.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse (*Centrocercus urophasianus*) near Pinedale, Wyoming. – MSc thesis, Univ. of Wyoming.

Mabray, S. T. 2015. Microhabitat selection by greater sage-grouse hens in southern Wyoming. – MSc thesis, Utah State Univ.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.

McGowen, P. J. K. et al. 2012. Galliformes science and species extinctions: what we known and what we need to know. – Anim. Biodivers. Conserv. 35: 321–331.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse *Centrocercus urophasianus* in north-central Montana 2001–2004. – PhD thesis, Univ. of Montana.

Nichols, J. D. et al. 2000. A double-observer approach for estimating detection probability and abundance from point counts. – Auk 117: 393–408.

Olsen, A. C. 2019. Greater sage-grouse demography, habitat selection and habitat connectivity in relation to western juniper and its management. – PhD thesis, Oregon State Univ.

Orange, J. P. et al. 2016. Evaluating the efficacy of brood flush counts: a case study in two quail species. – W. N. Am. Nat. 76: 485–492.

Orning, E. K. 2014. Effect of predator removal on greater sage-grouse *Centrocercus urophasianus* ecology in the bighorn basin conservation area of Wyoming. – MSc thesis, Utah State Univ.

Parsons, L. A. 2019. Greater sage-grouse survival, breeding ecology, resource selection and West Nile virus prevalence on the eastern fringe of their range. – PhD thesis, South Dakota State Univ.

Perkins, C. J. 2010. Ecology of isolated greater sage-grouse populations inhabiting the Wildcat Knolls and Horn Mountain, southcentral Utah. – MSc thesis, Utah State Univ.

Peterson, S. L. et al. 2016. Response of greater sage-grouse to surface coal mining and habitat conservation in association with the mine. – Hum. Wildl. Inter. 10: 205–216.

Pratt, A. C. and Beck, J. L. 2019. Greater sage-grouse response to Bentonite mining. – J. Wildl. Manage. 83: 866–878.

Rebholz, J. L. 2007. Influence of habitat characteristics on greater sage-grouse reproductive success in the Montana Mountains, Nevada. – MSc thesis, Oregon State Univ.

Reinhart, J. S. et al. 2013. Inter-seasonal movements in tri-state greater sage-grouse: implications for state-centric conservation plans. – Hum. Wildl. Inter. 7: 182–181.

Riley, I. P. 2019. Sampling methods for lek and brood counts of greater sage-grouse: accounting for imperfect detection. – MSc thesis, Univ. of Idaho.

Robinson, J. D. and Messmer, T. A. 2013. Vital rates and seasonal movements of two isolated greater sage-grouse populations in Utah's west desert. – Hum. Wildl. Inter. 7: 182–194.

Royle, J. A. and Link, W. A. 2006. Generalized site occupancy models allowing for false positive and false negative errors. – Ecology 87: 835–841.

Sandercock, B. K. 1994. The effect of manipulated brood size on parental defence in a precocial bird, the willow ptarmigan. – J. Avian Biol. 25: 281–286.

Sandercock, B. K. et al. 2008. Demographic sensitivity of population change in the northern bobwhite: a life-stage simulation analysis. – J. Wildl. Manage. 72: 970–982.

Sandford, C. P. et al. 2017. Greater sage-grouse resource selection drive reproductive fitness under a conifer removal strategy. – Range Ecol. Manage. 70: 59–67.

Sands, J. P. and Pope, M. D. 2010. A survey of galliform monitoring programs and methods in the United States and Canada. – Wildl. Biol. 16: 342–356.

Schaub, M. and Royle, J. A. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. – Methods Ecol. Evol. 5: 1316–1326.

Schreiber, L. A. et al. 2016. Greater sage-grouse apparent nest productivity and chick survival in Carbon County, Wyoming. – Wildl. Biol. 22: 37–44.

Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. – Condor 99: 933–941.

Schroeder, M. A. et al. 2004. Distribution of sage-grouse in North America – Condor 106: 363–376.

Schroff, S. 2016. Nest site selection and brood home ranges of greater sage-grouse (*Centrocercus urophasianus*) in the Centennial Valley, Montana – MSc thesis. Montana State Univ.

Sedinger, J. S. 2007. Improving understanding and assessment of greater sage-grouse populations. – In: Reese, K. P. and Bowyer, R. T. (eds), Monitoring populations of sage-grouse. College of Natural Resources Exp. Stn Bull. 88. Univ. of Idaho, Moscow, USA, pp. 43–55.

Sika, J. 2006. Breeding ecology, survival rates and causes of mortality of hunted and nonhunted greater sage-grouse in central Montana. – MSc thesis, Montana State Univ.

Slater, S. J. 2003. Sage-grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. – MSc thesis, Univ. of Wyoming.

Smith, L. S. 2009. Greater sage-grouse and energy development in northeastern Utah: implications for management. – MSc thesis, Utah State Univ.

Smith, K. T. 2016. Identifying habitat quality and population response of greater sage-grouse to treated Wyoming big sagebrush habitats. – PhD thesis, Univ. of Wyoming.

Smith, K. T. et al. 2019. Reconstructing greater sage-grouse diets: diet selection, body condition and food availability at brood-rearing sites. – Condor 121: 1–12.

Steen, J. B. and Haugvold, O. A. 2009. Cause of death in willow ptarmigan *Lagopus l. lagopus* chicks and the effect of intensive, local predator control on chick production. – Wildl. Biol. 15: 53–59.

Storch, I. 2007. Conservation status of grouse worldwide: an update. – Wildl. Biol. 13: 5–12.

Summers, R. W. et al. 2004. An experimental study of the effects of predation on the breeding productivity of capercaillie and black grouse. – J. Appl. Ecol. 41: 513–525.

Sveum, C. M. 1996. Habitat selection by sage grouse hens during the breeding season in south-central Washington. – MSc thesis, Oregon State Univ.

Tack, J. D. 2009. Sage-grouse and the human footprint: implications for conservation of small and declining populations. – MSc thesis, Univ. of Montana.

Taylor, R. L. et al. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. – J. Wildl. Manage. 76: 336–347.

Thacker, E. T. 2010. Greater sage-grouse seasonal ecology and responses to habitat manipulations in northern, Utah – MSc thesis, Utah State Univ.

Thompson, K. M. et al. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. – W. N. Am. Nat. 66: 332–342.

Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. – PhD thesis, Univ. of Idaho.

Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. – PhD thesis, Univ. of Montana.

Western Association of Fish and Wildlife Agencies 2015. Greater sage-grouse population trends: an analysis of lek count databases 1965–2015. – Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.

Westover, M. D. 2012. Habitat selection of greater sage-grouse *Centrocercus urophasianus* and northern river otters *Lontra canadensis* in Utah. – MSc thesis, Brigham Young Univ.

Wik, P. A. 2001. Ecology of greater sage-grouse in southcentral Owyhee County, Idaho. – MSc thesis, Univ. of Idaho.

Wing, B. R. 2014. The role of vegetation structure, composition and nutrition in greater sage-grouse ecology in northwestern Utah. – MSc thesis, Utah State Univ.

Wing, L. et al. 1944. Brood habits and growth of 'blue grouse'. – Auk 61: 426–440.

Williams, B. K. et al. 2002. Analysis and management of animal populations. – Academic Press.

Willis, M. J. et al. 1993. Sage grouse in Oregon. Wildlife research report 15. – Oregon Dept of Fish and Wildlife, Salem, OR, USA.

Wisdom, M. J. and Mills, L. S. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. – J. Wildl. Manage. 61: 302–312.

Zwickel, F. C. 1982. Demographic composition of hunter-harvested blue grouse in east central Vancouver Island, British Columbia. – J. Wildl. Manage. 46: 1057–1061.