



Research Article

Captive Rearing Sage-Grouse for Augmentation of Surrogate Wild Broods: Evidence for Success

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ABSTRACT Both species of North American sage-grouse (*Centrocercus* spp.) have experienced declines in distribution and abundance. Translocation of adult birds from a stable population to a small or declining population has been a management tool used by wildlife managers to support population persistence in these areas. Captive rearing chicks and releasing them into wild surrogate broods is an untested alternative to augment declining populations of sage-grouse. We developed techniques to successfully rear sage-grouse chicks in captivity, evaluated explanatory variables that could influence hatch and captive-rearing success, and estimated the survival of domestically hatched (DH) chicks to 28 days of age following introduction to a surrogate wild brood. We collected 304 eggs from radiomarked female greater sage-grouse (*C. urophasianus*) during 2004–2007 in 3 study areas in northwestern Colorado. Estimated hatching success of collected eggs was 0.745 (SE = 0.022, 95% CI = 0.700–0.786) and was negatively influenced by the number of days an egg was stored and the percent egg weight loss that occurred during storage and incubation. We monitored 175 DH chicks in captivity for 1–10 days before introduction and adoption into surrogate wild broods. Model-averaged captive-rearing success was 0.792 (SE = 0.045, 95% CI = 0.686–0.865) across years, and was positively influenced by initial chick mass at hatch and daily weight gain in captivity but negatively influenced by the number of days the egg was stored and advancing hatch date. We were able to radiomark and monitor 133 DH chicks adopted into surrogate wild broods until 28 days of age. Eighty-eight percent of DH chicks were successfully adopted within 24 hours. Our overall estimate of DH chick survival to 28 days (0.423; 95% CI = 0.257–0.587) was comparable to published wild-hatched chick survival. Predation and exposure-related deaths accounted for 26.3% and 25.6% of the known fates, respectively. Our captive-rearing protocols and techniques were successful for collecting greater sage-grouse eggs, hatching and rearing chicks in captivity, and releasing chicks into wild surrogate broods. This success further implies that captive rearing and release can be a potential management strategy to demographically and genetically reinforce or augment small populations of sage-grouse. © 2015 The Wildlife Society.

KEY WORDS artificial incubation, bolstering populations, captive-rearing success, *Centrocercus urophasianus*, chick adoption, chick survival, Colorado, egg collection, greater sage-grouse, hatch success.

Historically, sage-grouse (*Centrocercus* spp.) in North America were widespread in their distribution; however, over the last 50 years both species have shown population declines and range reductions (Schroeder et al. 2004) due to the fragmentation, degradation, and destruction of the sagebrush (*Artemisia* spp.) habitats that the species rely on for food and cover (Connelly et al. 2011a, b). The Gunnison sage-grouse (*C. minimus*) has been reduced to 10% of its presettlement habitat and now occurs in only 7 small disjunct

populations in Colorado and Utah (Schroeder et al. 2004). Similarly, the more widespread greater sage-grouse (*C. urophasianus*) has been reduced to 56% of its presettlement habitat with population declines of 17–47% throughout much of its range (Connelly and Braun 1997, Schroeder et al. 2004). In a recent range-wide comprehensive analysis of lek count data of greater sage-grouse males from 1965 to 2007, Garton et al. (2011) estimated 44% of the 24 populations investigated had a declining overall carrying capacity (–1.8% to –11.6% per year), and that at least 54% of these populations are predicted to decline below an effective population size over the next 30 years. Currently both species of sage-grouse have been petitioned for federal protection under the Endangered Species Act (U.S. Fish and Wildlife

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Service 2010, U.S. Department of Interior 2013). The decline in both species demands that managers develop alternative management approaches to stabilizing vulnerable populations.

Many wildlife agencies consider using translocations as a strategy to supplement declining populations (Reese and Connelly 1997). Historical and recent efforts have focused on trapping reproductively active birds from larger and apparently stable populations and translocating them to areas with declining populations (Musil et al. 1993, Reese and Connelly 1997, Baxter et al. 2013). Efforts at translocation have been relatively unsuccessful (5–12% reported by Reese and Connelly 1997, but see Baxter et al. 2013), which is likely attributable to the high site fidelity of adults to traditional breeding, nesting, and wintering areas, inexperience of yearling birds on new breeding grounds (i.e., reduced nest initiation rates), and the long-range movement patterns that the species is capable of making across a landscape (Patterson 1952, Berry and Eng 1985, Musil et al. 1993). Reese and Connelly (1997) made several recommendations to increase the success of a translocation but still viewed translocations as experimental and limited in their ability to substantially increase population numbers. In comparison to earlier translocation efforts, Baxter et al. (2013) observed lower survival of translocated compared to resident females into an isolated population in Utah, but after the initiation of a predator removal program both resident and translocated survival increased, suggesting that translocation success can be improved with concomitant habitat and population management.

A potential alternative to translocating adult sage-grouse would be to supplement broods of successful females with wild sage-grouse chicks that were hatched and raised in captivity. Potential benefits of using domestically hatched chicks include 1) increased productivity of the recipient brood as a result of artificially increased nest success of collected eggs from the wild; 2) increased survival of brood-mates because of dilution of predation risk in a brood with more chicks, increased predator detection, or reduction in exposure time depending on date of introduction into a surrogate brood (i.e., in captivity during pre-flight development); 3) increased familiarity with seasonal habitats, dispersal and migration routes, and corridors provided by brood females, brood-mates, and local juveniles and adults; 4) increased proportion of yearlings that successfully breed (i.e., initiate a nest for females and establish a territory on a lek for males) compared to translocated yearlings; and 5) fewer concerns about which populations could take advantage of this management option (not just non-migratory, isolated, and buffered populations). The feasibility and benefits, as well as risk and cost of this method, have not been widely and rigorously tested among grouse species, although success has been documented in piping plovers (*Charadrius melodus*; Powell et al. 1997, Roche et al. 2008) and Houbara bustards (*Chlamydotis undulate*; van Heezik and Seddon 1998, van Heezik et al. 1999). The main issues determining the feasibility and benefits of translocating captive-reared chicks for sage-grouse hinges upon success-

fully hatching and raising chicks in captivity, and ultimately the successful adoption of unrelated offspring into surrogate wild broods.

Therefore, our objective was to experimentally assess egg collection, chick captive-rearing husbandry, and wild brood chick supplementation protocols within an extant, viable source population of greater sage-grouse before they are used as an alternative to translocations in more vulnerable or declining Gunnison or greater sage-grouse populations. Specifically, we investigated 1) if eggs could be collected from both laying and incubating females and replaced with artificial acrylic sage-grouse eggs with minimal disturbance to the nesting female (i.e., limited number of visits to the nest), 2) the influence of egg characteristics and artificial incubation conditions on the hatching success of collected eggs, 3) the impact of domestically hatched (DH) chick characteristics and husbandry protocols on captive-rearing success of chicks (i.e., placement into surrogate wild broods), 4) if DH chicks could be introduced and adopted into surrogate wild broods and the conditions under which this was most successful, and 5) how DH chick characteristics and surrogate wild brood conditions (e.g., brood size, female age, study area) influenced survival to 28 days post-hatch.

STUDY AREA

We conducted our research in 3 study areas in northwestern Colorado (Fig. 1). Populations of greater sage-grouse (hereafter, sage-grouse) in all areas were stable (A. D. Apa, Colorado Parks and Wildlife, unpublished report). Average straight-line distance between areas was 76.8 km (SE = 15.4) with a maximal distance of 101 km. The Axial Basin study area was centered on 7 active sage-grouse leks and consisted of rolling topography ranging from 1,800 m to 2,350 m in elevation in Moffat County, Colorado, USA (Fig. 1). Axial Basin encompassed the northern and eastern portion of the study area and was bisected by the Yampa River to the north and bounded by it on the east. The northernmost area of the Danforth Hills comprised the south and southwestern portion of this study area and ranged in elevation from 2,000 m to 2,350 m. The Cold Springs Mountain study area included 4 sage-grouse leks that encompassed parts of the eastern edge of the Uinta Mountain Range that extends approximately 30 km into the northwest corner of Colorado and included portions of the Vermillion Basin on the east. Topography consisted of mountainous areas, rolling hills, and mesas ranging in elevation from 1,900 m to 2,900 m. Numerous canyons and drainages bisected the region running generally west to east across the landscape. The area was bounded by the Green River to the south and Vermillion Creek to the east. This area extended approximately 5 km west into Utah and 15 km north into Wyoming. The North Moffat study area was located 20 km north of Maybell, Colorado, USA and was centered on 3 active leks. This site consisted of low elevation sagebrush flats (1,600–1,900 m) on the east side of the Little Snake River, and was located in between the other study areas.

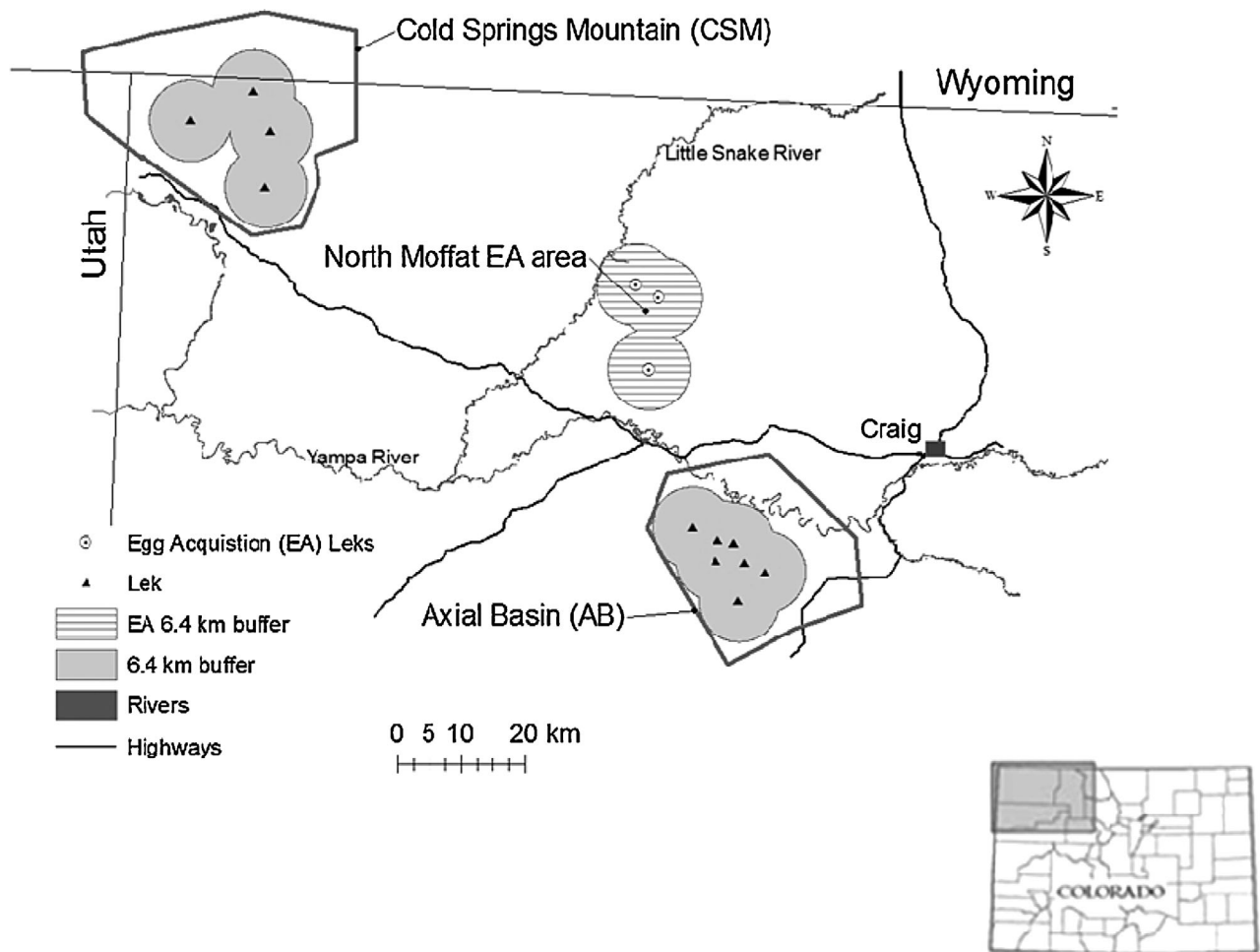


Figure 1. Study area map of Axial Basin and Cold Springs Mountain study areas 2004–2007 (boundary lines in grey), and North Moffat egg acquisition (EA) area in Moffat County, Colorado, Dagget County, Utah, and Sweetwater County, Wyoming, USA. We collected eggs from Axial Basin (2004, 2006, and 2007), Cold Springs Mountain (2006 and 2007), and North Moffat (2005 and 2006) study areas. We released domestically hatched chicks into Axial Basin (2004–2007) and Cold Springs Mountain (2006 and 2007) study areas.

The climate of northwestern Colorado was semiarid and received 20.3–50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The mean annual temperature for Moffat County was 6.3°C (Braun and Hoffman 1979) but was cooler in areas of higher elevation like Cold Springs Mountain (4.4°C; U.S. Department of Interior 1978). Big sagebrush (*A. tridentata* spp.) rangeland communities within the area comprised approximately 60% of the land area, whereas the remainder was comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas were dominated by Wyoming big sagebrush (*A. t. wyomingensis*), whereas higher elevation areas on Cold Springs Mountain and in the Danforth Hills were mainly mountain big sagebrush (*A. t. vaseyana*) with pockets of mountain shrub communities. A combination of private landowners and state and federal (Bureau of Land Management, hereafter BLM) agencies managed the land. Land use was primarily cattle and sheep production, agriculture, mineral exploration and extraction, and ecotourism (hunting, fishing, and outdoor recreation activities). Predator communities were similar

across areas with the coyote (*Canis latrans*), American badger (*Taxidea taxus*), bobcat (*Lynx rufus*), common raven (*Corvus corax*), and several species of small to medium raptors the main threats to survival of young chicks and broods (Schroeder et al. 1999, Schroeder and Baydack 2001).

METHODS

Radiomarking Females for Egg Acquisition and Surrogate Brood Hens

Protocols for the use of sage-grouse eggs and chicks were approved by the University of Idaho Animal Use and Care Committee (Protocol 2005–45). We collected sage-grouse eggs in Axial Basin (2004–2007), Cold Springs Mountain (2006–2007), and North Moffat (2005–2006) study areas. Each year (2004–2007), we radiomarked 30–35 female sage-grouse from at least 1 study area as egg acquisition females. In 2004, we released captive-reared chicks back into their original brood. In 2005–2007, we radiomarked an additional 60 females per year in the Axial Basin (2005–2007) and Cold Springs Mountain (2006–2007) areas as potential surrogate females for placement of captive-reared chicks. We captured

females at night with spotlights and nets (Giesen et al. 1982, Wakkinen et al. 1992) from all-terrain vehicles and on foot near or on known leks during mid-March through late-April. We fitted each female with an 18-g, 540-day necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Inc., Isanti, MN) and a size 16 individually numbered aluminum leg band. We aged females as yearlings (<1-year old) or adults (≥ 2 years old) based on color, shape, and wear of primary feathers (Eng 1955, Cruden 1963). Each year, we tried to make certain that >60% of egg acquisition females were adults to ensure a high probability of nest initiation, clutch size, nest success, and renest rates (i.e., yearling females have been observed to have lower nest initiation and success rates, smaller clutches, and are less likely to renest than adults; Schroeder et al. 1999, Hausleitner 2003, Connelly et al. 2011a, Taylor et al. 2012).

Collection, Storage, and Artificial Incubation Procedures

We monitored egg acquisition females to determine nesting status (laying or incubating) and tried to collect approximately 50% of the eggs (or 3–6 eggs/nest) during laying so that these eggs could be stored at cool temperatures and synchronized with incubation start date of potential nesting surrogate females. To collect eggs during laying, we located females between 0900 and 1200 every day for 3–4 days, and returned to this location later in the same day to search for evidence of nesting. If we found a nest during laying, we removed 50% of the eggs while the female was off the nest, and replaced them with artificial acrylic sage-grouse eggs to encourage continued nesting behavior. We monitored all radiomarked egg acquisition females weekly after egg collection to determine nest fate (i.e., hatched, depredated, or abandoned) and post-nesting status (i.e., if renested) to evaluate possible influence of egg removal.

We transported collected eggs to the hatching facilities where we either stored them or immediately placed them into a cabinet incubator. We placed stored eggs at a 45° angle, small-end down, in a refrigerator set at 10–15°C and turned them twice daily until we placed them into the incubator (Harvey 1993). Depending upon the number of eggs laid, we sometimes visited a nest more than once to remove half the complete clutch (3–5 eggs). We termed these eggs as laying eggs.

We monitored the remaining egg acquisition females (those not designated for collection of eggs during laying) every 3–4 days until localization and confirmation of nest incubation. We then flushed the female from the nest and removed the entire clutch to simulate a depredation. We placed eggs collected from incubating females, termed incubating eggs, in a portable incubator, transported them to the hatching facility, and placed them into an incubator. We monitored females every 3–4 days to determine renesting status.

Placement of eggs collected from laying females into the incubator was staggered and not random but depended upon the number of surrogate females nesting, the number of days an egg had been stored, and the number of eggs currently in

the incubator. In anticipation of placing 3 similar-aged, captive-reared chicks per wild surrogate brood, we placed 4–6 of the oldest stored eggs in the incubator for every 2 surrogate females nesting in the wild. Based on a captive-rearing success rate of 70–80% and a probable nest depredation rate of 40–60% (Hausleitner 2003), at least 3 captive-reared chicks would survive to be placed into a wild surrogate brood. We followed similar strategies with incubating egg acquisition females. We collected a complete clutch only when there were at least 4–6 potential wild surrogate females nesting that all started incubating within 4–5 days of each other. Placement of both laying and incubating eggs into the incubator occurred on the day that we confirmed nest incubation for the wild surrogate females.

For each egg, we recorded female band number, nesting status, and age, as well as number of days stored, study area, and collection date. We individually marked each egg in pencil with a unique identification based on nesting female band number and number of eggs collected in from the clutch, and weighed it to the nearest 0.01 g using an electronic scale before we stored it or placed it into the incubator. We incubated eggs in a large cabinet incubator (Georgia Quail Farm [GQF] model Sportsman 1202, Savannah, GA). The incubator maintained temperature and relative humidity at 37.5°C and 58%, respectively, and rotated eggs automatically every 4 hours for the first 24 days of incubation (Huwert 2004).

We weighed eggs on the day when we placed them in the incubator, and then at 4-day intervals (day 4, 8, 12, 16, 20, and 24) for the first 24 days of incubation to monitor weight loss. On day 24, we removed eggs from the incubator and placed them horizontally into a hatcher (GQF Sportsman Model 1550 Hatcher) with individual hatching trays (Huwert 2004). We stopped turning the eggs, reduced the temperature to 37.2°C, and raised the relative humidity to 80% (Huwert 2004). For both the incubator and hatcher, we recorded temperatures twice a day and checked humidity at least once per week to maintain optimum conditions.

Captive Rearing Domestically Hatched Chicks

Technicians wore camouflaged ghillie suits whenever they interacted with chicks to reduce the probability of chicks imprinting on humans. We weighed (to the nearest 0.01 g) each chick within 3 hours of hatch and attached an individually numbered plastic leg band. Once completely dry, we transferred chicks into small 1.5-m \times 1.5-m predator-proof enclosures within 24 hours. Chicks had access to an artificial female brooder and native vegetation (i.e., sagebrush, grasses, and forbs) in enclosures. We placed chicks into outside enclosures from <1 hour after sunrise until 1 hour before sunset to maximize exposure to natural conditions. At dusk, we moved chicks into an inside enclosure.

We fed chicks hourly a mixture of house crickets (*Acheta domesticus*), meal worms (*Tenebrio* spp.), wax worms (Family Phalidae), and flightless fruit flies (*Drosophila* spp.). We placed food on the ground allowing chicks to feed naturally and ad libitum. We provided chicks access to water and shade

throughout the day. We moved enclosures and artificial female brooders 4–5 m from the previous location every 2–3 days. In addition, <10 chicks of similar ages were kept in enclosures at any time to reduce competition for food, and to minimize stress and possible disease transmission. We weighed chicks to the nearest 0.01 g each evening to estimate weight gain. We moved chicks that lost weight or acted lethargic or malnourished to smaller heated boxes and provided them with additional feeding opportunities until they showed signs of improvement. For most chicks, this was within 24–48 hours, although several chicks did not improve and died during this time.

Brood Augmentation and Monitoring of Domestically Hatched Chicks

We placed approximately 3 chicks ($\bar{x} = 3.0$, $SE = 0.2$, range = 1–8) with each surrogate brood; however, on a couple of occasions we placed more chicks into a brood because of depredation of entire or partial surrogate broods or because there was a limited number of available surrogate broods. We determined timing of chick placement into a wild brood by the number of hatched chicks in captivity, the number of chicks expected to hatch, and the number of potential brooding surrogate females available. Ultimately, we attempted to retain a maximum of 12–15 chicks in captivity at any time if there were at least >5 brooding surrogate females available. We radiomarked captive-reared chicks with a 1.4-g, 40–60-day transmitter (model A4330, Advanced Telemetry Systems) attached externally along the dorsal midline between the wings (Burkpile et al. 2002) <2 hours before placement into a surrogate brood. We transported chicks using small coolers equipped with padding, separators, and a heating source to reduce stress and maintain a constant 35°C temperature. The transport times to Cold Springs Mountain were approximately 3 hours, whereas those in Axial Basin were normally <1 hour. Where we released captive-reared chicks depended upon the availability of radio-marked females with broods of similar ages in an area (i.e., chicks were not necessarily released back into the same area that they originated from).

We released chicks into wild surrogate broods either <1 hour after sunrise or <1 hour before sunset. We first located the radiomarked female brooding her similarly aged (± 3 days) wild-hatched chicks. We flushed the female, collected all the wild-hatched chicks, and placed them in the heated cooler with the captive-reared chicks. We held all chicks for approximately 10 minutes within coolers to allow female time to return to area after being flushed. The holding time also provided a heat source and an opportunity for DH and wild-hatched chicks to mix. We released all chicks simultaneously at the location where the female flushed and monitored female behavior from >50 m. We returned the next morning (0900–1200) and assessed adoption success. We classified an adoption as successful if the chick was <25 m from the female and the chick had moved from the release site. We monitored surrogate wild broods with DH chicks daily through 28 days of age to assess survival and causes of mortality. We circled the brood at a distance of

30–50 m assuming that chicks within this radius were alive. If a DH chick was not with the surrogate brood, we tried to determine its fate immediately by back-tracking to the previous day's location and searching for a radio signal.

Data Analysis

We employed both an information-theoretic approach, and frequentist methods where appropriate, to ascertain the best-supporting models describing the impact of explanatory variables on hatching success of collected eggs, and captive-rearing success of DH chicks (Burnham and Anderson 2002, Stephens et al. 2005). We conducted logistic regression modeling (Hosmer and Lemeshow 1989) to determine the influence of explanatory factors on hatching success and captive-rearing success of individual chicks using the known fate model in Program MARK (White and Burnham 1999). When used with the logit link function, the known fate model in Program MARK is identical to logistic regression in standard statistical software (Hosmer and Lemeshow 1989, Stevens et al. 2011). To determine the best-approximating models of collected egg hatching success probabilities, we developed a set of a priori candidate models using the fixed effects of year and study area where egg was collected with 5 potential explanatory variables of hatching success (Table 1). To estimate the initial egg mass at time of laying, we regressed mass of each collected egg as a function of egg age for each egg type (laying, incubating, or salvage), year, and study area combinations. We estimated the y -intercept (i.e., mass at time of laying) for each egg given its age and mass at the time of collection (Bishop et al. 2008). We used these estimates of egg hatch weight to calculate percent egg weight loss during storage and incubation. Within the hatching success model set, we compared 22 combinations of additive models with explanatory variables, as well as interaction terms with the grouping variables of year and study area.

Similarly, we developed 30 a priori candidate models to predict captive-rearing success using the fixed effect of year collected with the best-supported hatching success variable(s), and the 4 potential explanatory variables of captive-rearing success (Table 1). In all associated analyses, we assessed multicollinearity between variables using the variance inflation factor (VIF) and removed any variables with VIF indices >2.5 (Allison 1995, Kutner et al. 2004). We did not use any other tests to assess multicollinearity among variables. We ranked candidate models with Akaike's Information Criterion corrected for small sample sizes (AIC_c) and used ΔAIC_c , Akaike model weights (w_i), and deviance to evaluate how well each model fit our data (Burnham and Anderson 2002). We used t -tests with an $\alpha = 0.10$ after information criteria methods to estimate differences in the means of influential variables between successful eggs and chicks from those that failed. We chose to use a larger alpha than the usual level of 0.05 to reduce the chances of Type II error. For both model sets, we also calculated generalized likelihood-ratio r -squared values (R_L^2) for each logistic regression model to investigate individual model performance relative to the null constant

Table 1. Explanatory variables used in models to evaluate captive-rearing protocols of greater sage-grouse chicks in captivity from hatch to 10 days of age in northwestern Colorado, USA, 2004–2007. Analyses of captive-rearing success included captive-rearing explanatory variables but also hatching success variables from the best-supported models from the hatching success analyses. Likewise, analyses of chick survival included chick survival and brood adoption explanatory variables but also captive-rearing variables from the best-supported models from the chick survival analyses.

Type	Code	Description	Data type
Hatching	Area	Study area where egg was collected (Axial Basin, Cold Springs Mountain, North Moffat); variable also accounts for the transportation and storage effects on the collected egg to the hatching facility	Categorical
	EggType	Nesting status at time of egg collection: laying, incubating, or salvage (eggs collected from abandoned or depredated nests)	Categorical
	StorDays	Number of days egg was stored in refrigerator	Integer
	EggWt	Estimated egg mass at time of laying to the nearest 0.01 g	Continuous
	PEggLoss	Percent of egg mass lost during the incubation process from time laid (EggWt) through 24 days incubation (combined storage and incubation period)	Percent
	IncuDate	Estimated date (Julian) that incubation began for both female-initiated and artificially initiated incubation	Integer
	FmAge	Age of maternal female at time of nesting (yearling or adult)	Categorical
Captive rearing	HatchDate	Date (Julian) that egg hatched	Integer
	DayCap	Days raised in captivity for hatched chicks; day 0 (hatch) to brood adoption date	Integer
	IniWt	Initial, dry mass (<3 hr post-hatch) to the nearest 0.01 g of chicks at hatch	Integer
	DWtGn	Daily weight gain to the nearest 0.01 g of chicks from hatch to brood adoption (final mass–initial mass/days in captivity)	Continuous
	SurArea	Study area at which domestically hatched chick was placed; either Axial Basin or Cold Springs Mountain; variable also accounts for transportation effects of chicks to study areas	Categorical
Chick survival and brood adoption	FinalWt	Final mass to the nearest 0.01 g of chicks before placement in surrogate wild broods	Continuous
	SurFmAge	Age of the surrogate female (adult, yearling, or unknown)	Categorical
	AdoptDate	Date (Julian) of introduction (adoption) of chick into surrogate wild brood	Integer
	BrdSiz	Number of chicks in the surrogate wild brood (both wild observed and domestically hatched)	Integer
	AgeDiff	Difference in age of domestically hatched chick from surrogate wild brood	Integer

models (Menard 2000). We used the *cvTools* Package in Program R, version 2.10.0 (R Development Core Team 2009) to preform cross validation procedures on the data to estimate prediction success for each model.

We used the known fate option in Program MARK (White and Burnham 1999) to investigate factors of survival from hatch to 28 days post-hatching for DH chicks. Because we monitored DH chicks every day, we confirmed mortality events within 24–36 hours for 92.7% of chicks. Because the known fate model does not account for potential dependence among DH chicks assigned to the same brood (Bishop et al. 2008), we estimated overdispersion ($\hat{c} = 2.14$) by conducting 5,000 bootstrap simulations in Program MARK using a highly parameterized model ($K = 15$). We incorporated chick type (DH or wild-hatched), sex, year hatched, study area, hatch date, brood size, and brood hen age, with the best-supported model of chick survival over time (either a linear or quadratic trend, based on a 4-day or 7-day time interval, or constant). The most likely cause of overdispersion in broods with radiomarked wild-hatched chicks (both with and without DH chicks) was due to the non-independence of mortality events among brood-mates (e.g., mortality of brood hen and complete loss of brood, predator killing more than 1 DH chick in a brood). Therefore, we based our model selection criterion on AIC_c adjusted for overdispersion ($QAIC_c$). We assessed multicollinearity as before. We used $\Delta QAIC_c$, Akaike model weights (w_i), and deviance to rank each model in the model sets (Burnham and Anderson 2002). We carried out the model evaluation by first determining the best-supported age structure model based on a linear trend, a quadratic trend, or based on 4-day or 7-day time intervals. We then retained this age-structured model combined with fixed effects (year and study area) and the best-supported captive-rearing model to evaluate

5 models of survival to 28 days of age that included brood adoption and chick survival explanatory variables (Table 1). We ranked models using $QAIC_c$ and model weights (w_i) to evaluate support for our candidate models given the observed data (Burnham and Anderson 2002).

RESULTS

Egg Collection and Hatching

We collected 304 eggs from 63 radiomarked and 2 unmarked wild sage-grouse from 2004 to 2007. Egg collection dates ranged from 4 April to 20 May and averaged 22 April for all years. We collected eggs on average 14 days later from Cold Springs Mountain (3 May) than the other 2 areas (19 April) and 5 days earlier for laying females compared to incubating females among all areas. We collected the majority of eggs from adult females (65.2%) during their first nesting attempt (92.1%).

We monitored 65 nests after egg removal and were able to document the nesting fate of 58.5% (38/65) of these nests. The remaining monitored nests either had complete clutches removed (27.7%; 18/65), or the final fate of the nest was not determined (13.8%; 11/65). Our inability to determine nesting fate or post-nesting status of remaining females was primarily due to extended periods between successive locations (>10 days). We observed 6 cases when the nest failed <72 hours after egg removal and replacement with artificial eggs (5 abandoned and 1 depredated). Apparent nesting success of females that had partial clutches removed during laying or incubation was 24.1% (7/29) and 22.2% (2/9), respectively. However, we observed that eggs removed during laying were more likely to result in nest abandonment (27.6%; 8/29) than eggs removed during incubation (11.1%; 1/9). In 2006 and 2007, to maximize eggs collected per

female and to reduce depredation and abandonment of nests after collection events, we removed all eggs from both laying and incubating females. We were able to monitor 37 females after the loss of the first nest due to depredation, abandonment, or removal of complete clutches. Female re-nesting rates (51.2%: 19/37) when the nesting status was known after loss of first nest was comparable among nest loss causes (removal of all eggs, abandonment, and depredation; 53%, 16%, 32%, respectively).

We collected 152 laying, 104 incubating, and 35 salvage (collected after nest abandonment or female mortality) eggs from 39, 21, and 7 radio-marked females, respectively. We also collected 13 eggs opportunistically from 2 unmarked nesting females. The mean number of eggs collected from laying, incubating, and salvage females was 3.8 ± 0.3 (SD), 5.1 ± 0.4 , and 3.4 ± 0.6 , respectively. We collected 58.2% of all eggs during laying, and stored 88.9% (135/152) of these for at least 1 day ($\bar{x} = 7.3 \pm 0.2$). We detected high multicollinearity between the explanatory variables egg type (laying, incubating, or salvage) and number of days stored (VIF = 7.9), and retained the continuous variable (number of days stored) instead of the binary variable (egg type). All remaining VIF values among continuous and categorical variables were between 1.0 and 1.9 and were retained in the model set.

The best-supported model from our egg hatching success model set included percent egg weight loss, egg hatch weight, and number of days stored (Table 2). This model predicted that hatching success decreased as percent egg loss increased, decreased as days stored in a refrigerator increased, and was higher for eggs that weighed more at laying. An additional model was supported by the data ($w_i = 0.28$) and also included percent egg weight loss, egg hatch weight, and storage days, as well as incubation date (Table 2). No other models were $< 2 \Delta AIC_c$ units from the best-supported model indicating that the remaining covariates had limited influence on hatching success within this model set (Table 2).

The model-averaged β -values from the best-supported models suggest that hatching success was negatively associated with percent egg weight loss ($\beta = -0.164$, $SE = 0.026$, 95% CI = -0.216 to -0.112 ; Fig. 2a) as well as storage days ($\beta = -0.087$, $SE = 0.026$, 95% CI = -0.141 to -0.033 ; Fig. 2b). For eggs that failed, an additional 1% loss in mass above the desired 11–14% total egg mass loss during incubation (Apa et al. 2010) decreased the odds of hatching by 15.1% (95% CI = 10.6–19.4%). Odds of an egg not hatching also increased by 8.3% (95% CI = 3.3–13.2%) for each additional day stored before placement into the incubator. The β estimates for egg hatch weight ($\beta = -0.081$, $SE = 0.038$, 95% CI = -0.156 to 0.007) and incubation date ($\beta = -0.013$, $SE = 0.013$, 95% CI = -0.038 to 0.012) were both negative; however, the confidence intervals overlapped 0.

Model-averaged artificial hatching success among all areas during our study was 0.745 ($SE = 0.022$, 95% CI = 0.700–0.786), with apparent yearly hatching success ranging from 0.587 to 0.861. Hatching success was greater for eggs collected from incubating females (88.9%) compared to those from laying females (59.2%); however, this difference is also apparent when comparing eggs that were (58.5%) or were not (85.6%) refrigerated. In eggs collected from laying females, the majority of hatching failures occurred after development had started (81.6%), specifically during the last 14 days of incubation based on examination of failed eggs. Only 9.2% of these eggs failed because the chick did not develop (possible infertility). Eggs from incubating females showed similar rates of no development (8.3%), but unlike laying eggs, only 2.8% failed after development had started. Eggs that failed to hatch compared to those that hatched were stored for more days (5.6 days and 3.1 days, respectively; $t_{145} = -4.9$, $P < 0.001$), and lost a higher percentage of estimated initial egg mass during storage and incubation (20.1% and 14.2%, respectively; $t_{85} = -5.1$, $P < 0.001$).

Table 2. Best-supported logistic regression models to predict hatchability (S) of artificially incubated greater sage-grouse eggs collected from a wild, viable population in northwestern Colorado, USA, 2004–2007 using Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) in Program MARK. Only those models with normalized Akaike model weights > 0.01 are shown.

Model description ^a	AIC_c	ΔAIC_c^b	K^c	Deviance	w_i^d	Likelihood ^e	R_L^{2f}	Prediction success ^g
$S(PE_{eggLoss} + StorDays + EggWt)$	525.68	0.00	4	517.60	0.45	1.00	0.162	0.77
$S(PE_{eggLoss} + StorDays + EggWt + IncuDate)$	526.64	0.97	5	516.53	0.28	0.62	0.164	0.74
$S(PE_{eggLoss} + StorDays)$	528.57	2.89	3	522.53	0.11	0.24	0.154	0.80
$S(PE_{eggLoss} + StorDays + IncuDate)$	528.98	3.31	4	520.91	0.09	0.19	0.157	0.77
$S(Year \times Area + PE_{eggLoss} + StorDays + EggWt)$	530.89	5.21	10	510.46	0.03	0.07	0.174	0.69
$S(Year \times Area + PE_{eggLoss} + StorDays + IncuDate + EggWt)$	531.91	6.24	11	509.39	0.02	0.04	0.175	0.65
$S(Year \times Area + PE_{eggLoss} + StorDays)$	532.19	6.52	9	513.84	0.02	0.04	0.168	0.63

^a Area = study area where egg was collected (Axial Basin, Cold Springs Mountain, North Moffat), EggWt = estimated initial egg mass prior to incubation (artificial or natural) or storage, IncuDate = date egg was placed into incubator (Julian date), PE_{eggLoss} = percent egg mass lost during storage and artificial incubation or natural and artificial incubation period ([estimated initial egg mass – egg mass on day 24 of incubation]/24 days [length of incubation]), StorDays = number of days egg was stored in a refrigerator, Year = year egg was collected (2004–2007).

^b ΔAIC_c = the difference between the AIC_c value of the top model and successive models.

^c K = no. of parameters in model.

^d w_i = normalized Akaike model weight.

^e Likelihood = w_i/w_{top} , where w_{top} = normalized Akaike model weight for the top model (Burnham and Anderson 2002).

^f $R_L^2 = 1 - [\ln(L_m)/\ln(L_o)]$, where L_m = maximized likelihood for model of interest, and L_o = maximized likelihood for intercept only model (Menard 2000).

^g We calculated prediction success via cross validation using the cvTools Package (Program R, version 2.10.0; R Development Core Team 2009).

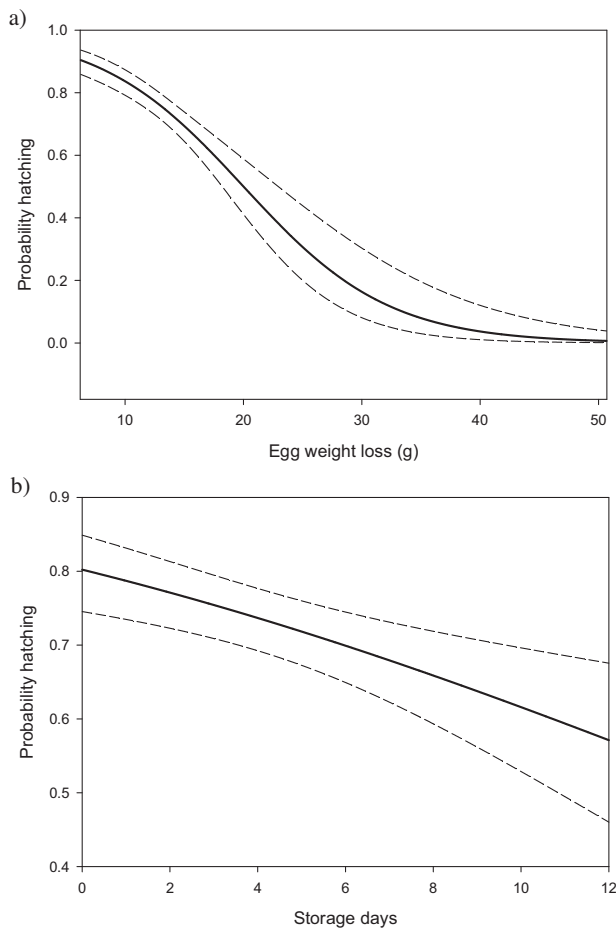


Figure 2. Probability of a collected greater sage-grouse egg hatching relative to a) percent egg mass lost during refrigeration and artificial incubation and b) number of days stored in a refrigerator before placement into an incubator at a captive breeding facility in northwestern Colorado, USA, 2004–2007. Predictions (solid line) and 95% confidence intervals (dashed lines) were based on the best-supported model.

Captive Rearing

We kept 196 DH chicks in captivity for 1–10 days ($\bar{x} = 4.1 \pm 0.2$) before introduction and adoption into surrogate wild broods. We euthanized 21 chicks (10.7%) because of abnormalities observed at hatch. These abnormalities included badly splayed legs, seizures, spasms, and curved necks. We removed euthanized chicks from further analyses before investigating the effects of captive-rearing husbandry practices. An additional 25 chicks (12.8%) showed signs of mild splayed legs and curled toes upon hatching, but conditions improved within 48 hr and we retained them in our study. We documented 32 chick mortalities in captivity during our study, with 50% occurring on days 3 and 4. We did not directly identify specific causes of death. We also had 11 chick mortalities that were due to human error (primarily in the first year and related to husbandry protocols; $n = 9$) and in transport to surrogate brood locations ($n = 2$).

The number of days we retained chicks in captivity varied among years ($\bar{x} = 4.1$ days, $SE = 0.2$) and reflected annual variations in number and initial hatch weights of chicks,

timing and nesting success of surrogate wild females, age and condition (i.e., positive weight gain) of chicks, and environmental conditions (e.g., precipitation, cold temperatures). We did not detect multicollinearity among any of the categorical or continuous explanatory variables used to assess captive-rearing success ($1.1 < VIF < 1.8$).

The 3 best-supported models for predicting captive-rearing success of chicks included initial weight and daily weight gain of DH chicks, and storage days of eggs (Table 3). Additionally, 2 models included hatch date, and 1 model included percent egg weight loss. These 3 models accounted for 0.843 of the weight in the model set (Table 3), and no other models were within 2 AIC_c units of these best-supported models indicating that the remaining covariates and the fixed effect (year) had limited influence on captive-rearing success within this model set.

The model-averaged β estimates for the explanatory variables indicated initial weight ($\beta = 0.475$, $SE = 0.094$, 95% $CI = 0.292$ – 0.659) and daily weight gain ($\beta = 0.611$, $SE = 0.118$, 95% $CI = 0.380$ – 0.842) had a positive influence on captive-rearing success (Fig. 3a and b). The odds of a chick being successfully captive reared increased 61.0% (95% $CI = 33.9$ – 93.3%) for every additional gram at time of hatching, and 84.2% (95% $CI = 46.2$ – 132.0%) for each additional gram gained per day. Conversely, model-averaged β estimates for storage days ($\beta = -0.144$, $SE = 0.037$, 95% $CI = -0.217$ to -0.071) and hatch date ($\beta = -0.037$, $SE = 0.019$, 95% $CI = -0.075$ to -0.001 ; Fig. 3c and d) had a negative influence on captive-rearing success. The odds of a chick being successfully captive reared decreased 13.4% (95% $CI = 7.2$ – 19.5%) for each additional day an egg was stored, and 3.6% (95% $CI = 0.1$ – 7.2%) for each day increase in hatch date. Percent egg weight loss also had a negative influence on captive-rearing success, although the 95% confidence interval overlapped 0, suggesting limited support for this variable ($\beta = -0.045$, $SE = 0.055$, 95% $CI = -0.063$ to 0.153). Estimated prediction success was slightly lower for captive-rearing variables, although models that incorporated at least initial weight, daily weight gain, and hatch date, as well as storage days had an adequate success rate (≥ 0.511 ; Table 3).

Model-averaged captive-rearing success was 0.792 ($SE = 0.045$, 95% $CI = 0.686$ – 0.865), and differed from the apparent captive-rearing success of 0.679 during our study. Across all years, initial weight, daily weight gain, storage days, and hatch date were different between chicks that were placed into surrogate broods and those that died in captivity. Mean initial mass at hatch for all chicks was 30.55 g ($SE = 0.21$), but chicks that died in captivity were 2.01 g lighter than chicks that were placed with surrogate broods (29.03 g and 31.04 g, respectively; $t_{173} = 4.2$, $P < 0.001$). Similarly, chicks that died compared to those that survived during captive rearing gained less weight/day (0.59 g/day and 1.00 g/day, respectively; $t_{107} = 2.1$, $P = 0.037$), were stored longer as eggs before incubation (4.7 days and 2.7 days, respectively; $t_{60} = -2.6$, $P = 0.011$), and hatched later (25 May and 18 May, respectively; $t_{86} = -1.9$, $P = 0.061$).

Table 3. Best-supported logistic regression models to predict captive-rearing success (S) of domestically hatched greater sage-grouse chicks collected from a wild, viable population in northwestern Colorado, USA, 2004–2007 using Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) in Program MARK. Only those models with normalized Akaike model weights >0.01 are shown.

Model description ^a	AIC_c	ΔAIC_c ^b	K ^c	Deviance	w_i ^d	Likelihood ^e	R_L^{2f}	Prediction success ^g
$S_{(IniWt + DWtGn + HatchDate + StorDays)}$	274.81	0.00	5	264.60	0.41	1.00	0.210	0.58
$S_{(IniWt + DWtGn + StorDays)}$	276.02	1.21	4	267.88	0.23	0.55	0.200	0.57
$S_{(IniWt + DWtGn + HatchDate + PEggLoss + StorDay)}$	276.23	1.41	6	263.93	0.20	0.49	0.212	0.54
$S_{(Year + HatchDate + IniWt + DWtGn + StorDays)}$	278.49	3.68	8	261.98	0.07	0.16	0.218	0.51
$S_{(Year + IniWt + DWtGn + StorDays)}$	280.47	5.66	7	266.08	0.02	0.06	0.205	0.58

^a HatchDate = hatch date of collected egg (Julian date), IniWt = dry hatch mass to the nearest 0.01 g of chicks at time of hatch (<6 hr post-hatch), DWtGn = daily weight gain to the nearest 0.01 g of chicks from hatch to brood adoption (final mass–initial mass/age), PEggLoss = percent egg mass lost during storage and artificial incubation or natural and artificial incubation period ([estimated initial egg mass–egg mass on day 24 of incubation]/24 days [length of incubation]), StorDays = number of days egg was stored in a refrigerator, Year = year egg was collected (2004–2007).

^b ΔAIC_c = the difference between the AIC_c value of the top model and successive models.

^c K = no. of parameters in model.

^d w_i = normalized Akaike model weight.

^e Likelihood = w_i/w_{top} , where w_{top} = normalized Akaike model weight for the top model (Burnham and Anderson 2002).

^f $R_L^2 = 1 - [\ln(L_m)/\ln(L_o)]$, where L_m = maximized likelihood for model of interest, and L_o = maximized likelihood for intercept only model (Menard 2000).

^g We calculated prediction success via cross validation using the cvTools Package (Program R, version 2.10.0; R Development Core Team 2009).

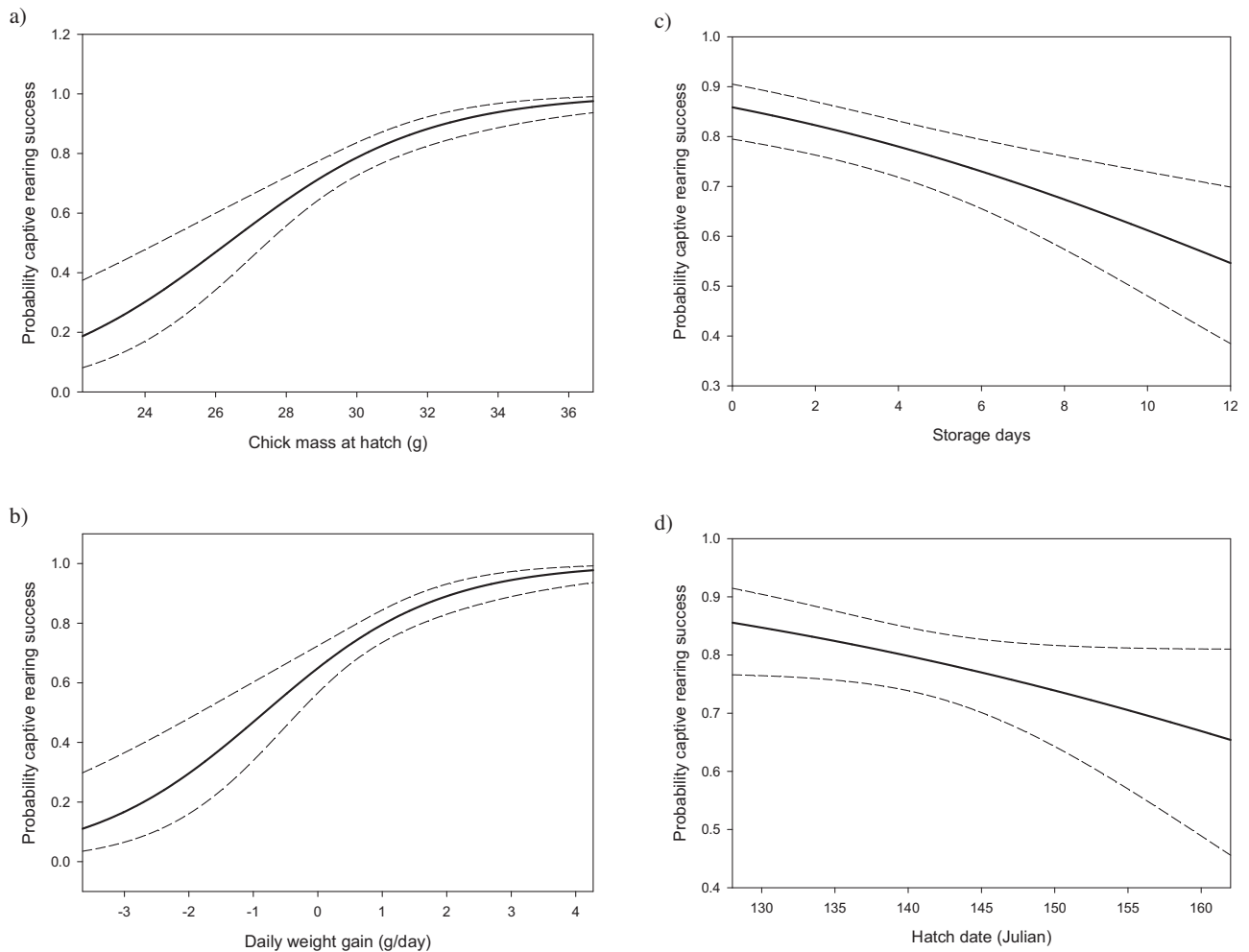


Figure 3. Model predictions with 95% confidence intervals (dashed lines) of the probability of a domestically hatched (DH) greater sage-grouse chick surviving in captivity at captive breeding facilities in northwestern Colorado, USA, 2004–2007 (time in captivity was always <10 days of age; $\bar{x} = 4.1$, $SE = 0.2$). We present probability of captive-rearing success as a function of DH chick mass at hatch (a), as a function of daily weight gain (g/day) of DH chicks in captivity from hatch to introduction into surrogate wild broods (b), as a function of the number of days an egg is refrigerated (c), and as a function of hatch date (d) derived from the best-supported model.

Post-Release DH Chick Survival

We radiomarked and monitored the survival of 133 DH chicks for 2,178 exposure days and introduced the 133 chicks into surrogate wild broods in 53 separate release events during either early morning or late evening periods. Adoption success of DH chicks into wild surrogate broods at 24 hours post release was 88.7% (118/133). Our release of chicks in the morning was less successful (41.7%, 5/12) than evening releases (93.4%, 113/121). Of the 15 adoption failures, 9 (60.0%) had been in captivity for ≥ 5 days ($\bar{x} = 6.3$ days, $SE = 0.3$).

We observed most mortalities of adopted chicks occurring within the first 5–7 days post-release with predation accounting for 26.3% ($n = 35$). We could not determine cause-specific mortality associated with depredation events in most cases (54.3%; 19/35); however, in cases where we could, mammalian and avian predation accounted for 34.3% (12/35) and 11.4% (4/35) of the mortalities, respectively. These cause-specific mortality estimates should be viewed as approximate because mammalian predation is more likely overestimated and avian is likely underestimated because of the potential of scavenging by mammals. Unexplained causes (chick body recovered whole with no signs of predation) accounted for 25.6% ($n = 34$) of the mortalities. Most (30) cases occurred from 2 to 8 days post-adoption and 4 cases ranged from 10 to 18 days post-adoption. Most causes could probably be attributed to exposure (chick not brooding and thermoregulating with surrogate female), starvation (not able to feed or locate food in the wild), or a combination of both. The remaining chicks that were censored before 28 days included chicks that did not brood with the surrogate female 24–48 hours after adoption (12%), had radio transmitter failure (3.0%), or had a missing or unknown fate (4.5%).

We examined 4 models of age structure, and 26 models that incorporated the best-supported age-structured model with fixed effects of surrogate study area and additional explanatory variables (Tables 1 and 4) to predict DH survival to 28 days. The quadratic trend model was the best-supported age structure model (no other model being within 2 $QAIC_c$; Table 4) and revealed that survival initially declined during the first 8–12 days post-adoption but then increased through day 14–28. Among the full model set including covariates (Table 4), the best-supported model incorporated the quadratic trend in chick age, plus weight at adoption and adoption date. Two models were within 2 $QAIC_c$ units of the best-supported model (Table 4), and also included the quadratic trend in chick age, weight at adoption, and adoption date, but 1 model also included the effect of surrogate study area and another included difference in age between the chick and its wild brood-mates. These 3 models accounted for 0.73 of the model weight within the model set. We did not include the explanatory variables weight at adoption, daily weight gain, or days in captivity in any single model because of observed multicollinearity between these variables ($VIF > 5$). We did not detect multicollinearity among any of the other categorical or continuous variables used to assess chick survival to 28 days (tolerance > 7.0 ; $1.2 < VIF < 2.4$).

The model-averaged β estimate for weight at adoption ($\beta = 0.046$, $SE = 0.021$, 95% $CI = 0.004$ – 0.088 ; Fig. 4) had a positive influence on DH chick survival to 28 days. The odds of a chick surviving increased 4.7% (95% $CI = 0.4$ – 9.2%) for every addition gram in chick mass at the time of adoption into wild broods. Conversely, the model-averaged β estimate for adoption date ($\beta = -0.056$, $SE = 0.016$, 95% $CI = -0.088$ to -0.024 ; Fig. 5) had a negative influence on chick survival to 28 days. The odds of a chick surviving to 28 days decreased 5.4% (95% $CI = 2.4$ – 8.4%) for each day increase in adoption date. The model-averaged β estimates for both surrogate study area (at Cold Springs Mountain) and age difference from wild brood-mates indicated they had a negative influence on chick survival, although both 95% confidence intervals overlapped 0 indicating limited support for either variable in the model set (surrogate study area: $\beta = -0.427$, $SE = 0.349$, 95% $CI = -1.11$ to 0.257 ; age difference: $\beta = -0.037$, $SE = 0.072$, 95% $CI = -0.178$ to 0.104). The sum of $QAIC_c$ weights ($\sum w_i$) for variables used in the model set further indicated that only weight at adoption ($\sum w_i = 0.73$) and adoption date ($\sum w_i = 0.97$) were strongly supported ($\sum w_i > 0.5$).

Daily survival decreased from day 1 to 12 before steadily increasing from day 13 to 28 for DH chicks (Fig 6a). Cumulative survival of DH chicks to 28 days of age was 0.423 (95% $CI = 0.257$ – 0.587 ; Fig. 6b). The fixed effects of year and surrogate study area had limited support within the model set, but sample sizes were too small to incorporate any interaction terms between these grouping variables within the survival analyses. However, the proportion of DH chicks surviving to 28 days was substantially lower for chicks transported to Cold Springs Mountain (11.8%; 4/34) compared to the Axial Basin (41.4%; 41/99).

DISCUSSION

Our results demonstrate that by using developed husbandry protocols (Apa et al. 2010) it is feasible to collect eggs from wild hens, successfully incubate and hatch the eggs in captivity, and release hatched chicks into wild surrogate broods. We further suggest that these techniques can be used to bolster or augment vulnerable sage-grouse populations for conservation and management while managers continue other conservation measures to improve and expand grouse habitat. Previous studies have shown that eggs can be collected and successfully hatched, and chicks raised in captivity (Pyrah 1964, Johnson and Boyce 1990, 1991, Huwer 2004), but our study is the first to demonstrate that these captive-rearing methods can be used to successfully introduce young captive reared chicks into wild broods that could potentially bolster and reinforce vulnerable populations in the short-term while maintaining breeding potential within source populations.

We demonstrated that wild eggs can be collected and replaced with artificial eggs during both egg laying and incubation. However, in both cases, the disadvantages associated with egg collection might preclude their use. The alternative method that we suggest is to remove all eggs in a clutch during laying or very early during incubation

Table 4. Model selection results to predict survival (S) of domestically hatched (DH) greater sage-grouse chicks introduced into wild, surrogate greater sage-grouse broods to 28 days of age in northwestern Colorado, USA, 2004–2007. We introduced DH chicks into broods between 1 and 10 days of age ($\bar{x} = 4.1$, $SE = 0.2$). We ranked models based on Akaike's Information Criterion corrected for overdispersion ($c = 2.14$) and small sample size ($QAIC_c$) in Program MARK.

Model description ^a	$QAIC_c$	$\Delta QAIC_c$ ^b	K ^c	Deviance ^d	w_i ^e
$S_{(TT + AdoptDate + FinalWt)}$	461.93	0.00	5	451.91	0.34
$S_{(TT + AdoptDate + FinalWt + SurArea)}$	462.53	0.60	6	450.50	0.25
$S_{(TT + AdoptDate + AgeDiff + FinalWt)}$	463.66	1.73	6	451.64	0.14
$S_{(TT + DWtGn + AdoptDate)}$	464.58	2.65	5	454.57	0.09
$S_{(TT + AdoptDate)}$	465.19	3.26	4	457.18	0.07
$S_{(TT + CapDays + AdoptDate)}$	466.26	4.33	5	456.25	0.04
$S_{(TT + AdoptDate + AgeDiff)}$	466.98	5.05	5	456.96	0.03
$S_{(TT + Area + AdoptDate)}$	467.01	5.08	5	456.99	0.03
Age structure					
$S_{(TT)}$	470.16	8.23	3	464.15	0.01
$S_{(Week)}$	477.11	15.18	4	469.10	0.00
$S_{(.)}$	491.45	29.52	1	489.45	0.00
$S_{(T)}$	491.78	29.85	2	487.78	0.00

^a T = linear trend in age, TT = quadratic trend in age, Week = weekly trend in age, CapDays = number of days raised in captivity (hatch to brood adoption date), DWtGn = daily weight gain to the nearest 0.01 g from hatch to brood adoption (final mass–initial mass/age), FinalWt = final mass to the nearest 0.01 g at time of introduction into wild surrogate brood, AgeDiff = difference in age between DH chick and surrogate wild brood, AdoptDate = date of introduction into surrogate wild brood, SurArea = study area of surrogate wild brood (Axial Basin or Cold Springs Mountain), Year = (2004–2007).

^b $\Delta QAIC_c$ = the difference between the $QAIC_c$ value of the best-supported model and successive models.

^c K = no. of parameters in model.

^d Deviance = $-2 \times \log$ likelihood ($-2\text{Log}[L]$).

^e w_i = normalized Akaike model weight.

(female incubated <4 days) to simulate a depredation event. We believe this is most effective because it requires fewer radiomarked females (approx. 2 times fewer) and less intensive monitoring of these nesting females, reduces additional stress on and disturbance to females and the risk of nest abandonment or depredation, maximizes the number of eggs collected per clutch (Taylor et al. 2012), and retains the reneesting potential of the female (Schroeder 1997, Gregg et al. 2006). Although we did not monitor the ultimate fates of most renests because of increased demands of captive

rearing and monitoring wild broods and DH chicks, we did document lower than average nest survival for nests with partial clutches removed (23.7%), and relatively high rates of reneesting (51.2%) among egg acquisition females. This would suggest that the effect on production potential within source populations might be moderated by increased instances of reneesting if full clutches are removed primarily from females early in the incubation process. Furthermore, at least twice as many females would be needed if only partial clutches are removed (during laying or incubation) as

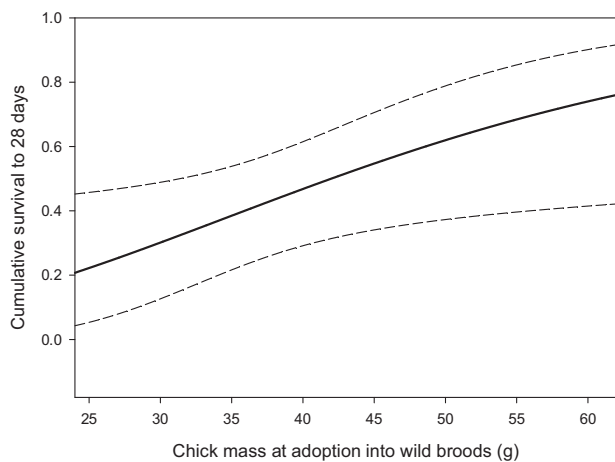


Figure 4. Model-based estimates of cumulative survival to 28 days of age with 95% confidence intervals (dashed lines) of radiomarked domestically hatched greater sage-grouse chicks introduced into surrogate wild-broods at <10 days of age ($\bar{x} = 4.1$, $SE = 0.2$) in northwestern Colorado 2004–2007 in relation to mass of chicks at time of introduction into wild broods. Average mass of chicks at introduction was 36.9 g ($SE = 0.6$ g).

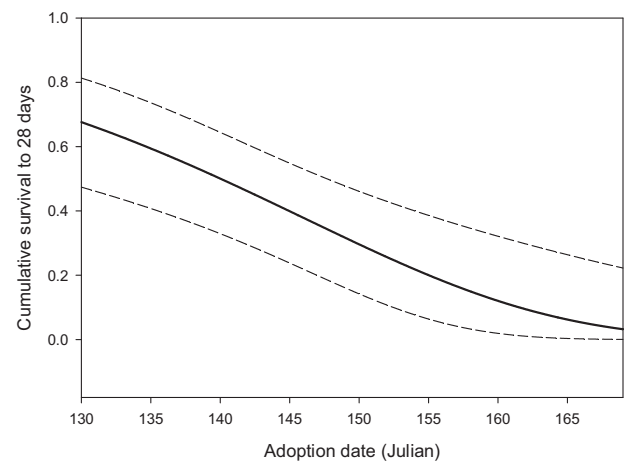


Figure 5. Model-based estimates of cumulative survival to 28 days of age with 95% confidence intervals (dashed lines) of radiomarked domestically hatched greater sage-grouse chicks introduced into surrogate wild-broods at <10 days of age ($\bar{x} = 4.1$, $SE = 0.2$) in northwestern Colorado 2004–2007 in relation to date of introduction of chicks into wild broods. Average adoption date of chicks into surrogate wild broods was 24 May ($\bar{x} = 144.0$, $SE = 0.8$).

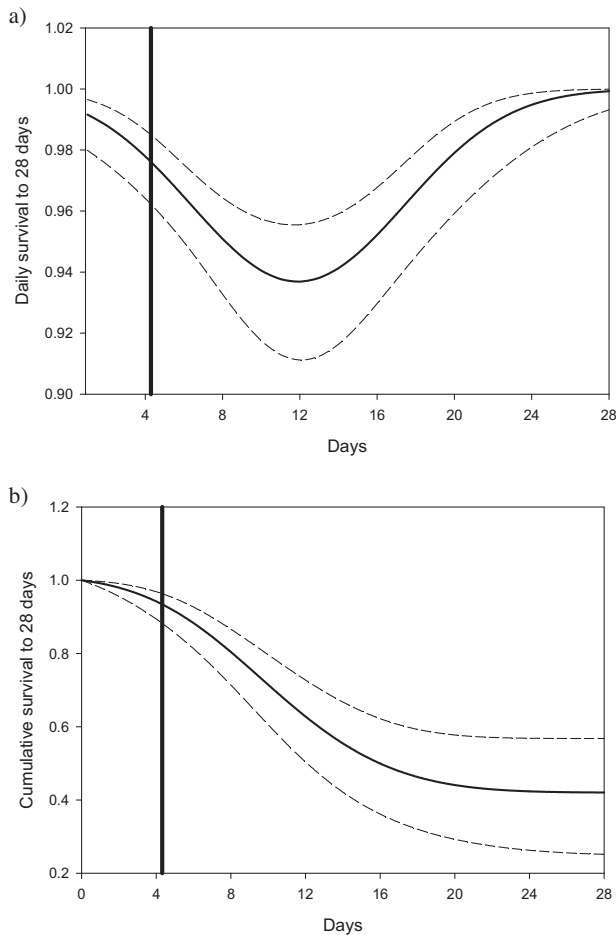


Figure 6. Survival estimates with 95% confidence intervals (dashed lines) of radiomarked domestically hatched greater sage-grouse chicks introduced into surrogate wild-broods at <10 days of age in northwestern Colorado, USA, 2004–2007 in relation to a) daily and b) cumulative survival based on the model average from the 4 best-supported, competitive models. Solid horizontal line represents the average age ($\bar{x}=4.1$, $SE=0.2$) that chicks were introduced into surrogate wild broods.

compared to removal of all eggs from incubating females to reach the same number of eggs that might be needed to meet captive-rearing purposes. Regardless of egg collection protocol used, these methods would still be less of an impact on the source populations than removing breeding age females from these populations such as in a traditional translocation. This might be an issue within potentially vulnerable source populations where manager may not want to remove breeding-age adults for translocation purposes (e.g., some Gunnison sage-grouse populations). Additionally, eggs can be collected from different populations to enhance genetic variability in the target population. However, genetic testing should be conducted prior to any collection to determine the suitability of genetically reinforcing a population and to reduce the potential for outbreeding depression (Edmands 2007).

Our estimated hatching success (0.745) from artificial incubation is similar to or above reported captive-rearing programs involving galliforms (51% and 80%, Johnson and Boyce 1991; 51%, West et al. 2002; 82% and 68%, Huwer

2004). Despite the high degree of variability within and between studies, we demonstrated that it is possible to successfully hatch sage-grouse eggs (>70%) in captivity using artificial incubation protocols. We found strong support for a decrease in the hatching success of stored eggs before placement into artificial incubators (8.4% decline for each additional day stored). Huwer (2004) found little evidence for a storage effect, although storage duration was not known precisely for most eggs. Studies among commercial poultry producers (Mayes and Takeballi 1984, Meijerhof 1992, Hassan et al. 2005) and game farms and wildlife populations (Hamilton et al. 1999, Demirel and Kirikci 2009) reported hatching success was reduced by increased storage time.

In addition to egg storage length, we found that percent weight lost from laying through the first 24 days of incubation including storage was an important predictor of egg hatching success. The recommended weight loss for successful hatch of domestically raised poultry and game bird eggs is 11–15% (Ar 1991, Harvey 1993) and requires proper monitoring of egg weight loss during storage and incubation, and maintaining consistency in the artificial incubator environment. However, the percent loss will often vary depending on the species, environmental adaptations of eggs within different species and populations (e.g., the size and mass of the eggs, thickness of the shell), and incubation environment under captive-rearing conditions (e.g., altitude, ambient humidity and temperature, internal humidity and temperature in the incubator; Ar and Rahn 1980, Hulet et al. 1987, Anderson-Brown and Robbins 2002).

Our observed chick mass at hatching was within the 29–31-g average reported in other studies of wild-hatched sage-grouse (Bean 1941, Petersen 1980, Burkepille et al. 2002, Gregg et al. 2007), which suggests that our DH chicks were probably not adversely affected by the collection and incubator protocols. However, chick mass at hatch and daily weight gain were significantly greater for chicks that survived to be ultimately placed into surrogate wild broods compared to chicks that died during the captive-rearing process. Numerous avian studies report that hatch mass contributes to greater survival and growth in nidifugous young (Erikstad et al. 1998, Pelayo and Clark 2003, Lusk et al. 2005). Possible explanations for this positive relationship include greater available nutrient reserves in hatchlings and eggs (i.e., yolk sack; Ricklefs et al. 1978, Bolton 1991, Anderson and Alisauskas 2002), higher quality body composition and functional maturity (Anderson and Alisauskas 2002), improved thermoregulation (Duncan 1988, Rhymer 1988), increased growth rates (Erikstad et al. 1998, Lusk et al. 2005, Le Fer et al. 2007), and improved motor performance for feeding and evading predation (Anderson and Alisauskas 2001, Goth and Evans 2004).

In addition to initial hatching weight, weight gain per day during captivity was the only other predictor of captive-rearing success. The majority of our DH chicks showed negative or no weight gain from hatch through day 2 with positive weight gains occurring from day 3 or after. Most

chicks spent proportionally more time brooding than feeding in their first 3 days, and became more active with greater weight gain each day after. Foraging time and efficiency increases with age and coincides with periods of rapid weight gain and feather development (between 5 and 20 days in age) among precocial species (Powell et al. 1997). Under wild conditions, sage-grouse chicks will leave the nest with the maternal female shortly after hatching (<24 hr; Schroeder et al. 1999), whereas in captivity chicks are often not exposed to conditions that promote activity but rely rather on only innate behaviors for development of foraging and motor skills. As a result, DH chicks might take longer to develop those skills and thus be susceptible to longer periods of time with low weight gains.

While chicks are in captivity, managers might need to sort them by weight to ensure that proper development is achieved by providing additional feedings and care to lighter chicks. Additional care should be given to the post-hatching environment to ensure that it is clean and natural, that chicks are raised with similar aged individuals in small groups (<8–10 chicks), and that disease testing and post-necropsies are conducted. Furthermore, in a captive-rearing program managers can take advantage of the relationship between egg size, initial hatching weights, and daily weight gains and can allocate the needed assistance and resources to achieve desired growth and survival rates. Under certain circumstances (e.g., chicks with low initial weight or low weight gain), it may be better to keep chicks longer in captivity (>10 days) to make sure adequate foraging skills and weight gain have been achieved before placing chicks into wild surrogate broods. West et al. (2002) recommended that Attwater's prairie-chicken (*Tympanuchus cupido attwateri*) chicks <1 week old not be transported between facilities because of their poor adaptability to environmental change. Chicks raised in captivity and then released might be more susceptible to stress related to unpredictable weather and food conditions, which might be additive to those already experienced in captivity (Dickens et al. 2009).

Causes of death and cases of fatal congenital defects of our chicks decreased over the 4 years, as a result of improved husbandry protocols. Aside from the first year, there was no contaminant or foreign substances identified that resulted in deaths of chicks (i.e., deaths in the first year were due to chicks ingesting artificial turf used as substrate in the inside brooder). Similarly, the number of chicks that needed to be euthanized because of congenital defects decreased with time as incubator protocols were refined (Apa et al. 2010), and were comparable to other captive-rearing studies on precocial avian young (Powell et al. 1997, Naldo et al. 1998, West et al. 2002). The incidents of either splayed legs or curled toes also decreased over time because we made refinements in husbandry protocols to reduce occurrences of prolonged hatching time and high incubation temperatures, and made the surface of the floor in the hatching unit more suitable for chicks (Naldo et al. 1998).

Our results confirm that female sage-grouse will readily adopt DH chicks into wild surrogate broods, verifying the observations of natural brood adoption by previous

researchers (Gregg and Crawford 2009, Dahlgren et al. 2010). Adoption rates of DH chicks did not vary through 10 days of age; however, success rates did vary with evening adoptions (<1 hr before sunset) more successful than morning adoptions (<1 hr after sunrise). Evening adoptions may have been more successful because once chicks are placed with surrogate broods the female had an opportunity to gather and brood all the chicks for the night. This is in contrast to morning adoptions when brood females started moving soon after the augmentation event. This period of time before sunset and overnight probably allowed the DH chicks the opportunity to immediately bond with the surrogate female and brood. This might be particularly important for older chicks that are raised in captivity for >4 days of age and thus less susceptible to imprinting or behavior cues from the surrogate female. We suspect that brood adoption failures were mainly the result of chick condition (e.g., weak, stressed) or age, rather than female unwillingness to brood or aggression of wild-hatched chicks toward DH chicks.

Our overall estimate of DH chick survival to 28 days (0.423; 95% CI = 0.257–0.587) was similar to wild-hatched radiomarked chick survival within the same study areas (wild-hatched chicks in broods with DH chicks: 0.399; 95% CI = 0.293–0.514; wild-hatched chicks in broods without DH chicks: 0.441; 95% CI = 0.299–0.532; Thompson 2012). These estimates are consistent with estimates across North America for wild sage-grouse chicks. In the northern Great Basin, survival to 28 days of age was 0.39 (SE 0.024) and ranged from 0.13 to 0.65 over 4 years (Gregg 2006, Gregg et al. 2007, Gregg and Crawford 2009, Dahlgren et al. 2010). Survival in Alberta, Canada to 30 days of age was 43.3% (Aldridge 2005), and Burkepile et al. (2002) reported apparent survival of 21–32% to 21 days of age in Idaho. These comparisons suggest that our captive-rearing techniques produced sage-grouse chicks that survived as well as wild-hatched chicks under natural conditions. However, our survival curves showed that DH chicks were still prone to high mortality rates after the mean adoption age (\bar{x} = 4.1 days of age, SE = 0.2) into wild broods, and that the critical time for DH chicks was between hatch and 12–14 days of age (Fig. 6). Future research is needed to determine if keeping chicks longer in captivity might by-pass the period at which they are at the most risk (first 21 days).

Previous studies on wild-hatched galliform chicks reported >70% of all mortalities occurred within the first 21 days posthatch, and greater than 80% of these were attributed to predation (Zwickel and Bendell 1967, Riley et al. 1998, Pitman et al. 2006, Gregg et al. 2007, Manzer and Hannon 2007). The next most commonly reported mortality was from exposure, which was often not differentiated from malnutrition or starvation in these field studies. Evidence suggests that mortalities due to exposure or starvation are rare (7–13%) in the wild (Riley et al. 1998, Gregg 2006, Manzer and Hannon 2007). Among our DH chicks, mortalities due to either exposure or starvation (or a combination of both) ranked as high as those from predation (26.3% and 25.6%, respectively) suggesting that at least a

quarter of DH chicks released into surrogate broods before 10 days of age are unable to adapt and survive. Domestically hatched chicks may be more vulnerable during this time because of possible developmental and behavioral limitations, and the additive stress of captive rearing and unpredictable conditions in the wild (e.g., extreme temperature fluctuations, food sources, and distances between food and brood locations).

Finally, we detected decreased survival with increasing adoption date. Reasons for the predicted decrease in survival with advancing adoption date are not readily apparent but could be possibly related to variability in arthropod availability and abundances (Johnson and Boyce 1991, Huwer et al. 2008, Gregg and Crawford 2009) as a result of precipitation and range conditions, thermal stress related to habitat limitations (Bell et al. 2010), or peaks in predator numbers following reproduction cycles occurring at this time (Hannon and Martin 2006). Additional research would be needed to address these questions to determine if DH chicks would be more susceptible to these potential effects than wild-hatched chicks in an area, and if keeping chicks in captivity longer would ameliorate these effects.

MANAGEMENT IMPLICATIONS

The success of the captive-rearing protocols used in this study indicates that captive rearing might be a potential management strategy to demographically or genetically reinforce or augment small populations of sage-grouse. However, before these techniques are used, federal and state agencies will need to consider what source populations are available and the cost of setting up and maintaining a captive-rearing facility for the period needed to achieve their goals.

When considered, we believe it advantageous to collect entire clutches from predominately adult females immediately after the start of incubation because it results in the maximum number of eggs collected per female monitored, as well as the potential for the females to reneest. Managers will need to follow a strict and approved husbandry protocol to ensure success of captive-rearing objectives (Apa et al. 2010). These include the following: daily monitoring of incubators, actively moving enclosures, frequently changing substrates in brooders, using native vegetation and substrates, disinfecting areas that chicks used, and keeping chicks for relatively short times in captivity in small groups (6–10 chicks), which most likely will reduce the risk of deaths due to bacterial infection (West et al. 2002, Apa et al. 2010). Finally, as with other efforts such as translocation of adult birds, the augmenting of surrogate wild broods with captive-reared chicks, is only a “halfway technology” (Frazer 1992) and must be done in conjunction with other habitat and population management efforts to address and ameliorate the ultimate causes of population decline and vulnerability.

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