



Commentary

Individual Heterogeneity and Effects of Harvest on Greater Sage-Grouse Populations

DANNY CAUDILL,^{1,2} *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*

MICHAEL R. GUTTERY,³ *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*

THERON M. TERHUNE, II, *Tall Timbers Research Station and Land Conservancy, Tallahassee, FL 32312, USA*

JAMES A. MARTIN, *Warnell School of Forestry and Natural Resources, Savannah River Ecology Lab, University of Georgia, Athens, GA 30605, USA*

GRETCHEN CAUDILL, *Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, FL 32601, USA*

DAVID K. DAHLGREN, *Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*

TERRY A. MESSMER, *Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA*

ABSTRACT The influence of harvest on wild populations has been the focus of substantial debate, and has widespread implications for the management of wild populations. Traditional views of harvest are based on density-dependent responses of populations to harvest. However, alternate mechanisms can and do induce compensation (e.g., individual heterogeneity). Selective harvest of successful females and their offspring is thought to occur in some grouse populations (e.g., blue grouse [*Dendragapus* spp.], greater sage-grouse [*Centrocercus urophasianus*]), and delaying harvest within a season has been proposed as a viable strategy to overcome this type of selective harvest. However, a recent examination regarding the effects of harvest on greater sage-grouse strongly criticized the recommendation of delayed harvest. Herein, we address the criticism of the delayed harvest strategy and provide an examination of projecting the effects of harvest in the face of individual heterogeneity using deterministic projection models. We demonstrate that under proportional harvesting strategies, given a fixed harvest rate, early additive harvest does not have a larger effect on the population than additive harvest later in the season. Moreover, we show that when higher quality individuals (i.e., individuals with higher survival and reproductive rates) are more susceptible to harvest, individual heterogeneity in harvest effects will induce compensatory dynamics when density-dependent effects are only additive. Conversely, even when density-dependent effects are additive, if lower quality individuals are more susceptible to harvest, heterogeneity will induce partial compensation. Reducing the selectivity of harvest on higher quality individuals (i.e., shifting harvest onto lower quality groups) could reduce the risk of artificial selection and induce partial compensation. Therefore, we recommend managers consider the spatiotemporal patterns of populations and time harvest to maximize the heterogeneity tradeoff between higher and lower quality individuals. © 2017 The Wildlife Society.

KEY WORDS additive, *Centrocercus urophasianus*, compensatory, depensatory, individual heterogeneity, selective harvest, survival.

Effective wildlife conservation is predicated on knowledge of the factors affecting populations. Harvest is one such factor that has received considerable attention and debate (Boyce et al. 1999, Conroy et al. 2005, Lebreton 2005, Servanty et al. 2010, Wolfe et al. 2015). Early investigations bore several similar carrying capacity-based hypotheses, which postulated harvest, under a certain level, does not decrease subsequent

population size (Errington 1945, Allen 1947, Wing 1951, Lack 1954, Errington 1956). Although some evidence contrary to these early hypotheses emerged (Roseberry 1979; Romesburg 1981; Bergerud 1985, 1988a; Connelly et al. 2012), contemporary harvest paradigms are based, at least in part, upon these concepts (e.g., Kokko and Lindström 1998, Boyce et al. 1999). These traditional harvest management regimes and research efforts have focused on demographic parameters and how they respond to harvest (Anderson and Burnham 1976, Roseberry 1979, Bergerud 1985, Hudson 1985, Pollock et al. 1989), where compensatory mortality has been characterized as reducing seasonal density within a population, and consequently decreasing natural mortality (i.e., density-dependent survival; Boyce et al. 1999). The relationship between survival (S_a) and harvest mortality (K)

Received: 21 November 2016; Accepted: 17 January 2017

¹E-mail: danny.caudill@alaska.gov

²Present Address: Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

³Present Address: Alaska Department of Fish and Game, 1800 Glenn Highway, Palmer, AK 99645, USA.

can be illustrated by the general harvest mortality equation: $S_a = S_o(1 - bK)$, where S_o is survival in the absence of harvest and b is a slope coefficient linking harvest to survival (Anderson and Burnham 1976, Burnham and Anderson 1984). Harvest effect hypotheses differ in the value of the slope coefficient (b ; Sandercock et al. 2011), and are a continuum of population responses along which complete compensation and additivity are points (Péron 2013, Koons et al. 2014). In particular, the degree to which harvest is additive ($b = 1$) or completely compensatory ($b = 0$) has received considerable attention (Anderson and Burnham 1976, Roseberry 1979, Pollock et al. 1989, Nichols et al. 1995, Cooley et al. 2009), but little consensus has been reached (Smith and Reynolds 1992, Connelly et al. 2003, Reese et al. 2005, Sedinger and Rotella 2005, Sedinger and Herzog 2012). Lack of consensus could suggest that alternate functional forms of harvest effects exist.

The effect of harvest on wild populations can also be influenced by variation in survival and reproduction between individuals (i.e., individual heterogeneity; Lebreton 2005, Lindberg et al. 2013, Guillemain et al. 2014). Density dependence in survival would likely have to occur at extreme levels to achieve complete compensation for harvest mortality, whereas the effect of individual heterogeneity on harvest could more plausibly induce some level of compensation for harvest mortality, when lower quality individuals (i.e., individuals with lower survival and reproductive rates) are more susceptible than other quality classes to harvest (Lebreton 2005). This mechanism for compensation of harvest mortality is of particular interest because individual heterogeneity in reproductive output and cost of reproduction appears common in many species (Aubry et al. 2009, 2011; Hamel et al. 2009; Cam et al. 2013; Caudill et al. 2014a), and therefore could constitute a prevalent functional form for population response to harvest. Indeed, individual heterogeneity in survival and reproduction can elucidate compensatory relationships between harvest and population dynamics (Lindberg et al. 2013). Alternatively, individual heterogeneity could pose challenges to traditional harvest paradigms, particularly in instances when harvest is artificially selective against higher quality individuals (Caudill et al. 2014a). However, when harvest is selective of higher quality individuals (i.e., individuals with higher survival and reproductive rates) the potential for long-term effects should also be considered in addition to the short-term numerical effects on populations (Festa-Bianchet 2003).

Selective harvest has increasingly become recognized as a potentially significant ecological and economic challenge for management of wild populations (Ashley et al. 2003, Festa-Bianchet 2003, Jørgenson et al. 2007, Allendorf and Hard 2009, Darimont et al. 2009), particularly because selective harvest of organisms can induce rapid phenotypic changes (Coltman et al. 2003, Jørgenson et al. 2007, Darimont et al. 2009). Selective harvest can have unforeseen negative consequences for species fitness in a host of taxa: mammals (Coltman et al. 2003, 2005; Garel et al. 2007; Kvalnes et al. 2016), flora (Law and Salick 2005), and fish (Conover and

Munch 2002, Kuparinen and Merilä 2007, Swain et al. 2007). Selective harvest can tend to increase the frequency of less desirable phenotypes thereby undermining the goal of long-term sustainability of harvest (Allendorf and Hard 2009). Moreover, harvest-induced artificial selection can be at odds with natural selection, resulting in distorted adaptive landscapes (Coltman 2008, Kvalnes et al. 2016). However, theoretical projections suggest that even nonselective harvest can affect evolutionary trajectories (Engen et al. 2014).

Herein we address recent (Blomberg 2015) criticism of altered harvest paradigms and provide projections of the effect of harvest on greater sage-grouse (*Centrocercus urophasianus*) in the face of individual heterogeneity. We provide a theoretical demonstration of projecting the effects of harvest when individual heterogeneity exists, applications of such individual heterogeneity in harvest susceptibility to hypothetical sage-grouse examples, and a new analysis on the effect of individual heterogeneity on sage-grouse survival.

CONCEPTUALIZING AND ESTIMATING HARVEST EFFECTS

Compensatory Mortality (Density-Dependence Induced)

Blomberg's (2015) equation 1 calculates the maximum potential harvest mortality, which is simply the amount of natural mortality left in a season. However, offsetting density dependence in survival to completely compensate for harvest removal likely requires density dependence at levels that border on unrealistically high, even at low harvest rates (Lebreton 2005). Moreover, this traditional characterization of (completely) compensatory harvest mortality (Lack 1954, Errington 1956) could be problematic for several grouse species (Bergerud 1985, 1988a,b; Reese and Connelly 2011; Connelly et al. 2012), particularly because several species (blue grouse [*Dendragapus* spp.]; spruce grouse [*Falciptennis canadensis*]; sage-grouse) inhabit a sea of resources during winter (e.g., conifer needles, sagebrush leaves; Bergerud 1988a), and typically maintain or gain weight during winter (Pendergast and Boag 1973, Redfield 1973, Beck and Braun 1978). Consequently, it is difficult to conceive a plausible scenario in which the time post-harvest to subsequent breeding, mainly winter, is resource limited (i.e., winter bottlenecks; Lack 1954). Furthermore, juvenile sage-grouse exhibit high overwinter survival (Caudill et al. 2014b), and thus do not fit the traditional harvest paradigms (i.e., doomed surplus; Errington 1956).

Another potential issue with the complete compensation hypothesis is that longer lived species have an inherently lower likelihood of compensatory survival because less leeway exists in survival (Hamel et al. 2006, Sedinger et al. 2007); in other words the survival rate is proximate to its upper bound (1). Moreover, in some cases there could also be little natural variability in key demographic parameters if they have been canalized (Gaillard et al. 2000; Gaillard and Yoccoz 2003; Souchay et al. 2013, 2015; Péron et al. 2016). Hence, assessing the variability in demographic rates is vital to understanding the effects of harvest on populations. For example, Blomberg's (2015) maximum potential harvest

mortality rate is numerically close to the target harvest rate and variability in the parameters could cause an inability to discern between competing hypotheses (compensatory or additive mortality). Nevertheless, Blomberg (2015: figure 2) failed to present estimates of variability in these systems, despite well-established methods to estimate variability when combining period-specific survival rates (e.g., delta method; Seber 1982:7–9). Moreover, when survival is very high and harvest very low, numerical instabilities may exist in maximum likelihood estimates (boundary conditions exist), thus further obscuring underlying processes. However, density dependence and compensation for numerical removals likely occur at some level within a season (Boyce et al. 1999), and accordingly alternate mechanisms for compensation could occur and warrant consideration (e.g., individual heterogeneity, immigration). Moreover, these alternate mechanisms could be influenced by timing of harvest (Caudill et al. 2014a,b, 2016b).

Additive Mortality (Lack of Density Dependence)

Blomberg's (2015) equation 2 calculates the realized impact of additive harvest mortality on survival. However, the equation presented does not replicate results therein (i.e., figure 3), nor is the logical derivation clear. The equation would seem to seek the difference between survival with and without harvest (i.e., $I_{s(i)} = S_{o(i)} - S_{a(i)}$; where $I_{s(i)}$ is the impact of harvest on survival during the i th time period) in which case K (kill or harvest rate) in Blomberg's (2015) equation 2 should be $1 - K$. This substitution in the equation does replicate the results therein. Blomberg (2015) states that the equation yields the proportion of harvested individuals that were likely to survive until the subsequent breeding season, and consequently an alternate formulation to achieve this goal would be:

$$I_{s(i)} = K(i) \times \prod_{i=1}^j S_{o(i)}$$

where multiplying the harvest rate (K) by survival from the current to the last period would yield the aforementioned proportion Blomberg's (2015) equation 2 purportedly calculated. This derivation is equivalent numerically to our first solution (i.e., $I_{s(i)} = S_{o(i)} - S_{a(i)}$), and both replicate the results in Blomberg (2015). Regardless, all of these equations are quite deceptive because they calculate a period-specific rate. Hence the results of the equations do not have common bases (i.e., they consist of varying amounts of time) and therefore are not directly comparable. To compare these rates, one must force them to a common scale, which can easily be done by dividing the entire equations by $\prod_{i=1}^j S_{o(i)}$, in

other words standardizing the values by the amount of exposure left in the time series. Once the values are on a common scale, it becomes apparent that the total effect of harvest is in fact equivalent to K (i.e., the harvest rate). Further, consider a hypothetical population with the survival rates reported by Blomberg (2015) for juvenile sage-grouse

(monthly survival = 0.76 for Aug–Sep, 0.88 for Oct–Nov, 0.99 for Dec–Jan, and 0.93 for Feb–Mar), a starting population size in August of $N=1,000$, and an additive ($b=1$) harvest rate of 10%. For a scenario where additive harvest occurs in September, we calculated $S_o=0.499$ (i.e., the product of survival rates from Sep–Mar) and thus under the general harvest mortality equation $S_a=0.499 = S_o (1 - bK)$. Now we calculate that $S_o - S_a = 0.05 = K(i) \times \prod_{i=1}^j S_{o(i)}$, which is the reduction in survival from harvest occurring in this period ($S_{r(i)}$). However, because the population is undergoing natural mortality through time, we must calculate how many individuals are still alive at any given point in time:

$$N_{A(t)} = N \times \prod_{i=1}^t S_{o(i-1)}$$

where $N_{A(t)}$ is the number of individuals alive at the beginning of the t th period, which is simply the product of the original population size and the probability of surviving from the first to the beginning of the current period (t). Note that because the equation calculates population size at the beginning of a period, then $N_{A(1)} = N$ (i.e., $S_{o(0)} = 1$ because no time has elapsed). Thus for harvest in September, we project $N_{A(1 \text{ Sep})} = 760$ and then calculate the effective removal due to harvest as:

$$N_{r(t)} = N_{A(t)} \times S_{r(t)}$$

where $N_{r(t)}$ is the number of individuals removed by harvest that would have otherwise been expected to live. Evaluating this hypothetical harvest in September example, $N_{r(1 \text{ Sep})} = 37.92$. In other words, a 10% additive harvest occurring on juvenile sage-grouse in September would be expected to remove approximately 38 individuals that would have otherwise survived. Now let us only change the hypothetical to shift harvest to November. We calculate that $S_o = 0.746$, $S_a = 0.671$, and $N_{A(1 \text{ Nov})} = 508$, which yields $S_{r(1 \text{ Nov})} = 0.075$ and $N_{r(1 \text{ Nov})} = 37.92$. Again the projected removal of 10% additive harvest occurring in November would be roughly 38 individuals. This fact is not surprising because K is a mortality rate that is inverted to survival via $1 - K$ in the general harvest mortality equation, and when K is relative to the current population (proportional harvesting strategy; Blomberg's [2015] approach) then the rate is also a mortality probability. Total survival is merely the product of several probabilities whose position in the survival vector are irrelevant (i.e., $0.9 \times 0.8 \times 0.7 = x = 0.8 \times 0.7 \times 0.9$), hence once $K(i)$ is relative to $N_{A(t)}$, as in proportional harvesting strategies, the end effect of K does not change through time.

Individual Heterogeneity Effects on Harvest

Blomberg (2015) presented equation 3 for the expected reduction in per capita reproductive success for class x . However, the equation uses the same logic as the previous additive effects on survival equation (i.e., equation 2), which we have shown to be erroneous. We demonstrated that once

Blomberg's (2015) second equation was applied to the current population size during a given period ($N_{A(t)}$), the numerical effect of a constant harvest rate is identical through time. Consequently the third equation therein is logically and numerically flawed, because the first 2 terms in the equation, once corrected, become a constant that is then multiplied by a second constant. Conversely several established methods to calculate the effect of harvest (i.e., b) in the presence of heterogeneity exist (Lebreton 2005, Lindberg et al. 2013), which is germane to the present topic of varying harvest through time. Lebreton (2005) provided a framework to project the effect of heterogeneity on harvest, which we adapt to illustrate the appropriate manner to project the effect of heterogeneity on survival. Individual heterogeneity is at least in part tied to the ideas of frailty (Vaupel et al. 1979, Vaupel and Yashin 1985), reproductive value (Fisher 1930), and individual quality (Cam and Monnat 2000, Sedinger et al. 2008, Hamel et al. 2009, Wilson and Nussey 2010, Aubry et al. 2011). Thus, consider a hypothetical grouse population that consists of 2 subpopulations (i.e., quality classes): a frail group with natural annual survival equal to 0.3 and a robust group with natural annual survival equal to 0.7, thus the population's average natural annual survival is $S_o = 0.5$ (i.e., both groups are equally represented in the population). Harvest rates of 20% and 5% are applied to the frail and robust groups, respectively. If we assume harvest is additive ($b = 1$) and ignore the heterogeneity in harvest and survival (use the population averages), then we can calculate using the general harvest mortality equation:

$$S_a = 0.5(1 - 1 \times 0.125)$$

which yields $S_a = 0.438$; however, this value does not reflect survival once heterogeneity is accounted for. To calculate the population's survival rate in the face of heterogeneity, we formulate:

$$S_{a\ b} = \sum_{x=1}^n w_{(x)} \times S_{o(x)} (1 - bK_{(x)})$$

where $w_{(x)}$ is the proportion of the population in the x th quality class. Applying this heterogeneity effect equation to our hypothetical population and assuming equal representation of the groups in the population (i.e., $w_{(x)} = 0.5$ for both frail and robust), we get $S_{a\ b} = 0.453$. Thus, although the density-dependent slope coefficient is additive ($b = 1$) in our example, heterogeneity has induced partial compensation because $S_{a\ b} > S_a$. To quantify the effect of this compensatory heterogeneity we calculate:

$$b_b = \frac{S_o - S_{a\ b}}{S_o K_{\bar{x}}}$$

where b_b is the slope coefficient linking survival to harvest under individual heterogeneity and is calculated by simply entering our known values into the general harvest mortality equation (where $K_{\bar{x}}$ is the population's mean harvest rate) and solving for b . When we apply this equation to our

hypothetical example, we see that $b_b = 0.76$, and consequently heterogeneity-induced partial compensation for harvest removals, despite the fact that density-dependent effects were additive. If we modify our hypothetical harvest to a structure similar to what has been proposed for sage-grouse where robust individuals are more vulnerable to harvest, we see a different pattern arise. Again let both categories be equally represented in the population ($w_{(x)} = 0.5$ for both frail and robust), and for arguments sake let the heterogeneity among classes be less severe, where natural survival is 0.5 and 0.7 for frail and robust classes, respectively. However, now let harvest (density dependence still fixed to additive) be higher for the robust category, but still low overall at 4%, whereas harvest for the frail category is 1%. Now $S_{a\ b} = 0.584$ and $b_b = 1.1$, heterogeneity in harvest has now induced a depensatory (or super-additive) effect, even though the density-dependent slope coefficient is only additive ($b = 1$). Finally, consider a scenario where all the parameters are as in the previous example, but density-dependent responses are present and exhibit heterogeneity. Let the robust class exhibit weak compensation ($b = 0.9$), whereas the frail class exhibits strong density dependence ($b = 0.1$). Now $S_{a\ b} = 0.587$ and $b_b = 0.857$; despite strong density-dependent compensation in one of the quality classes, the result is relatively weak partial compensation overall. Even relatively small changes in harvest susceptibility can influence the effect size and direction of harvest on survival (Fig. 1), and the effect size of harvest varies with the strength of heterogeneity and the proportion of the population in each quality class (Fig. 2).

In many instances harvest rate objectives are expressed as the average removal rate for the entire population. Our previous equations use a specific harvest rate for each quality class, which causes the populations mean harvest rate to vary as proportions in each quality class change (Fig. 1). The effect of harvest can also be projected using the population's mean harvest rate and the probability of each quality classes' presence in the harvest. We can project the contribution of each quality class to the overall harvest rate as:

$$K_{p(x)} = K_{\bar{x}} \times p_{K(x)}$$

where $K_{p(x)}$ is the harvest rate (out of the entire population) for the x th quality class and $p_{K(x)}$ is the probability that a harvested individual belongs to the x th quality class. The effective harvest rate for any given quality class can then be represented as:

$$K_{(x)} = \frac{K_{\bar{x}} \times p_{K(x)}}{w_{(x)}}$$

Consider a scenario in which harvest of frail individuals is 2:1 odds versus robust individuals (Fig. 3), and conversely a scenario in which the odds are reversed, 1:2, and robust individuals are more susceptible to harvest (Fig. 3). In general, as previously fixing density dependence to $b = 1$ for clarity, when frail individuals are more susceptible harvest is partially compensatory and when robust individuals are more susceptible harvest is depensatory (Fig. 3). However, when

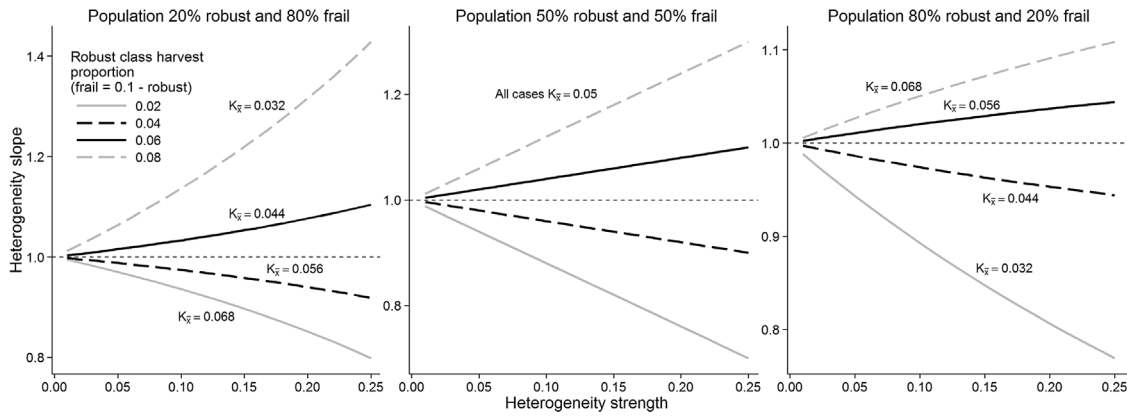


Figure 1. Projected survival effect of harvest heterogeneity on harvest effect size across hypothetical proportions of robust and frail quality classes. Density-dependent harvest effects are fixed at $b = 1$. Heterogeneity strength is the deviation from natural survival (S_o) of 0.5 for each quality class where robust is above and frail is below (i.e., heterogeneity strength = 0.1 indicates $S_{o\text{ Frail}} = 0.4$ and $S_{o\text{ Robust}} = 0.6$). Heterogeneity slope coefficient is the slope parameter linking survival to harvest and in the face of heterogeneity is formulated as $b_b = \frac{S_a - S_o b}{S_o K_{\bar{x}}}$, where S_a is survival adjusted for harvest and heterogeneity and $K_{\bar{x}}$ is the population's mean harvest rate.

the quality classes' availability is greater than its proportion in the harvest, an opposite effect will occur. For example, when frail individuals are more susceptible to harvest, in most instances the projected effect will be partial compensation, but when the proportion of frail individuals in the population exceeds the proportion of frail in the harvest, depensatory harvest effects will be projected (Fig. 3). These general patterns hold true even as the effect of density dependence (b) is altered equally for each quality class, whereby as harvest heterogeneity increases susceptibility towards robust individuals, b_b will be larger than b and the converse is true when frail individuals are more susceptible. However, when $b = 0$ then harvest removals are perfectly compensated for and harvest heterogeneity induces no effect ($b_b = b$).

In addition to the effect of individual heterogeneity on survival, individual heterogeneity in future reproductive output can also influence the end effect of harvest on populations. Reproduction can be incorporated into estimating the effect of individual heterogeneity on harvest via reproductive values (Lindberg et al. 2013). Lindberg et al. (2013) formulated the harvest proportion irrespective of reproductive value as:

$$h = \frac{\sum_{i=1}^n \omega_i b_i}{\sum_{i=1}^n \omega_i}$$

and the harvest proportion weighted by reproductive value as:

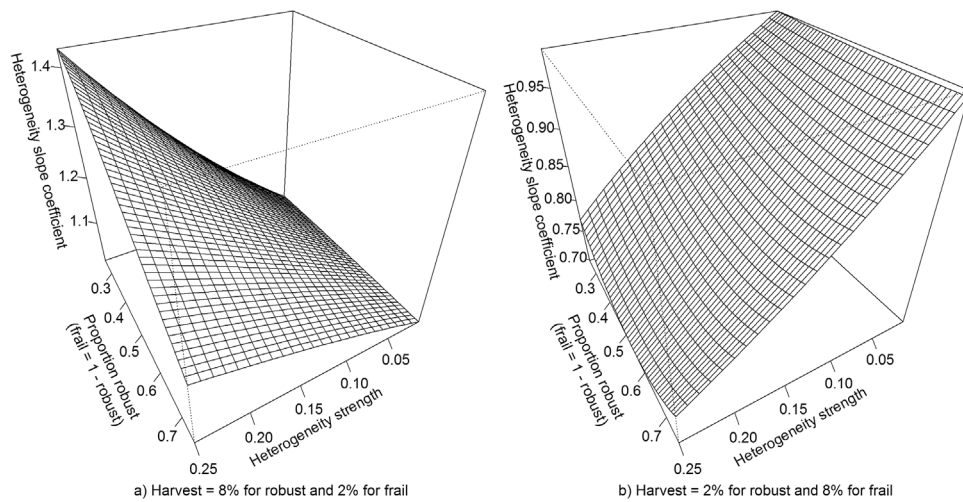


Figure 2. Projected survival effect of 2 converse scenarios where heterogeneity in harvest risk varies by quality class: a) robust individuals are more susceptible to harvest, and b) frail individuals are more susceptible to harvest. Both scenarios vary across hypothetical heterogeneity strength in survival and population composition of quality classes. Density-dependent harvest effects are fixed at $b = 1$. Heterogeneity strength is the deviation from natural survival (S_o) of 0.5 for each quality class where robust is above and frail is below (i.e., heterogeneity strength = 0.1 indicates $S_{o\text{ Frail}} = 0.4$ and $S_{o\text{ Robust}} = 0.6$). Heterogeneity slope coefficient is the slope parameter linking survival to harvest and in the face of heterogeneity is formulated as $b_b = \frac{S_a - S_o b}{S_o K_{\bar{x}}}$, where S_a is survival adjusted for harvest and heterogeneity and $K_{\bar{x}}$ is the population's mean harvest rate.

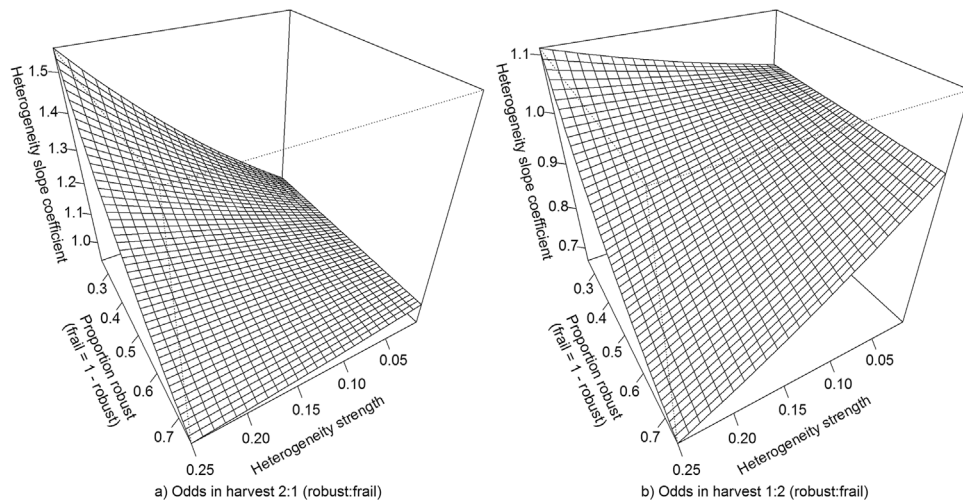


Figure 3. Projected survival effect of harvest where the populations mean harvest rate is constant ($K_{\bar{x}} = 0.1$) and the heterogeneity in harvest risk between quality classes is constant under 2 differing scenarios. Both scenarios vary across hypothetical heterogeneity strength in survival and population composition of quality classes. Density-dependent harvest effects are fixed at $b = 1$. Heterogeneity strength is the deviation from natural survival (S_o) of 0.5 for each quality class where robust is above and frail is below (i.e., heterogeneity strength = 0.1 indicates $S_o_{Frail} = 0.4$ and $S_o_{Robust} = 0.6$). Heterogeneity slope coefficient is the slope parameter linking survival to harvest and in the face of heterogeneity is formulated as $b_b = \frac{S_o - S_a}{S_o K_{\bar{x}}}$, where S_a is survival adjusted for harvest and heterogeneity.

$$b_{rv} = \frac{\sum_{i=1}^n w_i v_i b_i}{\sum_{i=1}^n w_i v_i}$$

Thus, the slope coefficient respective of reproductive value would be calculated as:

$$b_{rv} = \frac{b_{rv}}{b}$$

where w_i is the proportion of the population in i th quality class, b_i is the harvest rate of the i th quality class, and v_i is the reproductive value of the i th quality class. We again consider a hypothetical grouse population that consists of 2 quality classes (frail and robust) that are equally represented in the population ($w_{(i)} = 0.5$ for both frail and robust) for the sake of clarity. Let the robust class' reproductive value equal 0.8 and the frail class' equal 0.2. First consider a scenario where the frail class is more susceptible to harvest ($b_{frail} = 10\%$ and $b_{robust} = 2\%$; note $K_{\bar{x}} = 6\%$). In this instance $b_{rv} = 0.6$, and harvest is partially compensated through heterogeneity. Alternatively consider a scenario where the robust class is more susceptible to harvest ($b_{frail} = 2\%$ and $b_{robust} = 10\%$; note $K_{\bar{x}} = 6\%$) as has been suggested for sage-grouse (Connelly et al. 2000; Reese and Connelly 2011; Caudill et al. 2014a,b) and blue grouse (Mussehl 1960, Bendell and Elliot 1967, Redfield 1975). When the robust class is more susceptible, $b_{rv} = 1.4$ and the effect of harvest in the presence of individual heterogeneity in reproductive value is depensatory. From the heterogeneity perspective, whenever the robust class is more susceptible to harvest, the resulting effect will be depensatory. Conversely when the frail class is more susceptible, some level of compensation will exist (Figs. 1 and 2).

INDIVIDUAL HETEROGENEITY IN SAGE-GROUSE DEMOGRAPHY

Heterogeneity between individuals is a fundamental aspect of ecology. Trade-offs between current reproduction and future survival and reproduction are central to life-history theory and have received considerable attention (Williams 1966, Reznick 1985, Røskaft 1985, Stearns 1989, Erikstad et al. 1998). Although in many instances negative correlations, a cost of reproduction, are expected (Williams 1966, Reznick 1985, Erikstad et al. 1998), positive correlations can also exist (van Noordwijk and de Jong 1986; Cam et al. 1998, 2002; Barbraud and Weimerskirch 2005; Cam et al. 2013). Positive correlations could arise when variation in individual quality or ability to garner resources exists (van Noordwijk and de Jong 1986; Cam et al. 1998, 2013). In sage-grouse, reproduction has been reported to negatively affect subsequent survival (Blomberg et al. 2013) and future reproduction (Caudill et al. 2014a). However, individual heterogeneity could lessen the cost of reproduction for higher quality individuals (Caudill et al. 2014a). Evaluations of individual heterogeneity in sage-grouse are largely lacking, and we are aware of only 2 studies that have explicitly accounted for individual heterogeneity (i.e., explicitly accounted for latent or hidden individual variation) while evaluating reproduction (Caudill et al. 2014a, 2016a) and none for survival. Hence additional investigation of individual heterogeneity is needed and we provide an evaluation regarding survival on the Parker Mountain sage-grouse population.

The Parker Mountain sage-grouse population is well studied (Dahlgren et al. 2010; Caudill et al. 2013, 2014a, 2016a; Guttery et al. 2013), and consequently we only consider a small number of covariates that these studies have

Table 1. Candidate models (generalized linear mixed model) evaluating the effects of climate on annual survival of female greater sage-grouse on Parker Mountain, Utah, USA, 1998–2010. We present models and Akaike’s Information Criterion adjusted for sample size (AIC_c), difference in AIC_c values between each model and the best model (ΔAIC_c), AIC_c weight (ω_i), number of parameters (K), and random individual intercept variance (σ_R^2).

Model ^{a,b}	AIC_c	ΔAIC_c	ω_i	Deviance	K	σ_R^2
Winter PZ _{<i>t-1</i>}	324.86	0.00	0.93	318.76	3	0.486
Summer PZ _{<i>t</i>}	330.63	5.77	0.05	324.53	3	0.512
Intercept only	332.23	7.37	0.02	328.18	2	0.031

^a Models with $\Delta AIC_c >$ intercept only; models not shown: winter PZ_{*t*} and Apr PZ_{*t*}.

^b Winter = 1 Nov–31 Mar, Summer = 1 May–31 Aug, PZ = Palmer Z index of drought, *t* = current year, *t* – 1 = previous year.

previously identified as important to sage-grouse demography. To evaluate survival we used covariates regarding previous reproductive success (Caudill et al. 2014a) and drought indices (Gutteny et al. 2013, Caudill et al. 2014a). We captured female grouse (Giesen et al. 1982) in spring 1998–2009 and fitted them with necklace-style very high frequency (VHF) radio transmitters (Advanced Telemetry Systems, Isanti, MN, USA and Holohil Systems, Ontario, Canada). Capture and transmitter attachment procedures were approved by the Utah State University Institutional Animal Use and Care Committee (IACUC Numbers 945, 945R, 942, and 942R). We monitored survival and reproductive success annually 1998–2010 (Gutteny et al. 2013, Caudill et al. 2014a, Dahlgren et al. 2016). We estimated annual survival using a generalized linear mixed model with a random intercept for each individual, the equivalent of a known-fate model with a random effect, using the glmer function from the lme4 package (Bates et al. 2014) in R 3.1.1 (R Core Team 2014). We fit models with a binomial distribution, a logit link, and an adaptive Gaussian Hermite approximation. We used a sequential approach where we first evaluated climatic parameters (Table 1), and then added reproduction parameters to a final candidate model set (Table 2). We ranked models using Akaike’s Information Criterion (Akaike 1973) adjusted for sample size (AIC_c ; Burnham and Anderson 2002), and we counted parameters as the number of fixed effects plus an additional parameter for the random individual intercept. Models with $\Delta AIC_c \leq 2$ were considered competitive model structures. Our modeling approach intentionally led to nested models,

which we further evaluated using likelihood ratio tests (Table 3) in addition to our information-theoretic approach.

Our survival models were based on 247 observations of 184 individuals. The previous winter’s drought index was the best climatic predictor of survival (Table 1), where increased winter precipitation increased survival ($\beta = 0.31$, $SE = 0.12$). The addition of previous reproductive effort seemed to explain overall variation in our data (i.e., ΔAIC_c and LRT; Tables 2 and 3) and variation among individuals (i.e., σ_R^2 ; Table 2), where attempting to reproduce (initiating a nest) and successfully raising a brood increased the probability of female survival ($\beta = 0.55$, $SE = 0.29$; $\beta = 0.46$, $SE = 0.31$, respectively). Female age did not appear to affect survival, but our comparison was between juveniles and adults (i.e., second year and after second year), which could obscure the effect of age on survival (Caudill et al. 2016a).

In our study species and system, individual heterogeneity appeared to lessen the cost of reproduction for some individuals (Caudill et al. 2014a) and predict higher quality individuals because reproduction appears to be correlated with increased survivorship ($\beta_{\text{nest initiation}} = 0.55$, $SE_{\text{nest initiation}} = 0.29$; $\beta_{\text{brood success}} = 0.46$, $SE_{\text{brood success}} = 0.31$). The apparent positive correlation between reproduction and survival could also support the frailty hypothesis (Vaupel et al. 1979, Vaupel and Yashin 1985; see also selection hypothesis, Forslund and Pärt 1995), which supports previous findings in sage-grouse (Caudill et al. 2016a). Consequently, our results seem to support the hypothesis that nonbreeding individuals tend to be lower quality individuals (Cam et al. 1998), whereby the recommendation to avoid harvesting reproductively successful females seems prudent (Caudill et al. 2014a,b). Even small changes in harvest timing (delaying harvest by 1 or 2 weeks) could significantly influence the susceptibility to harvest of successful females, because the distribution of juveniles and successful females is rapidly changing during this period (Caudill et al. 2016b). Hence the heterogeneity trade-off associated with later harvest (as previously outlined) likely outweighs the temporal compensation potential (i.e., density dependence) on these short time scales. Moreover, when harvest is additive, from the density-dependent perspective, delaying harvest does not have a larger effect size (under a proportional harvest strategy), but the potential for heterogeneity to induce some level of compensation does exist.

Table 2. Final candidate model set (generalized linear mixed model) evaluating annual survival of female greater sage-grouse on Parker Mountain, Utah, USA, 1998–2010. We present models and Akaike’s Information Criterion adjusted for sample size (AIC_c), difference in AIC_c values between each model and the best model (ΔAIC_c), AIC_c weight (ω_i), number of parameters (K), and random individual intercept variance (σ_R^2).

Model ^{a,b}	AIC_c	ΔAIC_c	ω_i	Deviance	K	σ_R^2
Winter PZ _{<i>t-1</i>} + initiation _{<i>t</i>}	323.40	0.00	0.50	315.24	4	0.131
Winter PZ _{<i>t-1</i>} + brood _{<i>t</i>}	324.77	1.37	0.25	316.60	4	0.144
Winter PZ _{<i>t-1</i>}	324.86	1.45	0.24	318.76	3	0.486
Intercept only	332.23	8.83	0.01	328.18	2	0.031

^a Models with pretending variables (Anderson 2008; see also uninformative parameters, Arnold 2010) not shown: winter PZ_{*t*} + age_{*t*} and winter PZ_{*t*} + nest_{*t*}.

^b Winter = 1 Nov–31 Mar, PZ = Palmer Z index of drought, initiation = whether a nest was initiated, brood = brood success, nest = nest success, age = adult or yearling, *t* = current year, *t* – 1 = previous year.

Table 3. Likelihood ratio test of 4 models evaluated for annual female survival (S) of greater sage-grouse on Parker Mountain, Utah, USA, 1998–2010.

General model ^a	Reduced model ^a	X^2	df	P	Hypothesis tested
$S \sim (1 ID) + \text{winter PZ}$	$S \sim (1 ID)$	9.42	1	0.002	Previous winter drought affects survival
$S \sim (1 ID) + \text{winter PZ} + \text{initiation}$	$S \sim (1 ID) + \text{winter PZ}$	3.52	1	0.061	Breeding status affects survival
$S \sim (1 ID) + \text{winter PZ} + \text{brood}$	$S \sim (1 ID) + \text{winter PZ}$	2.15	1	0.142	Brood status affects survival

^a (1|ID) = random intercept by individual, winter PZ = previous winters (1 Nov–31 Mar) drought index, initiation = whether an individual attempted reproduction, brood = brood success in the year.

DISCUSSION

Individual heterogeneity has been recognized as potentially important in harvest effects (Lebreton 2005, Lindberg et al. 2013, Guillemain et al. 2014) but could complicate traditional harvest strategies (Caudill et al. 2014a). For example, Caudill et al. (2014a,b) hypothesized that delaying harvest, even by a short period, could result in harvest becoming less selective of demographic groups important to population persistence and growth (e.g., successful adult F, juvenile F). Implicit in this argument is that multiple alternate mechanisms for population responses exist; compensation could occur via heterogeneity in reproductive potential and evolutionary implications of harvest could outweigh short-term effects. Conversely, Blomberg (2015) strongly criticized delaying harvest, but in doing so assumed that harvest was evenly distributed across groups, both within the population and across time, and therefore failed to recognize that a fundamental assumption of the analysis could be violated if early harvest biases the effect of harvest toward critical groups, as previously suggested (Caudill et al. 2014a,b, 2016b). For example, Blomberg's (2015) assumed population-level harvest rate ($K=0.1$; generally the target harvest rate for sage-grouse; Reese and Connelly 2011) is exceeded by nearly 2-fold for juveniles in several systems (Wik 2002, Beck et al. 2006, Caudill et al. 2014b), and year-specific estimates of nearly 3–4 times greater exist (37.5%, Wik 2002; 26.9%, Caudill et al. 2014b). Moreover, crippling loss is common in harvested populations (Braun and Beck 1985, Hoffman 1985, Small et al. 1991, Caudill et al. 2014b), and is implicitly ignored by many studies, which thereby underestimate the effect size of harvest. Hence harvest rates can vary through time and across groups, and these dynamics along with crippling losses are vital to accurate conceptualization of harvest effects. We conclude, as has been previously shown (Lebreton 2005, Lindberg et al. 2013, Guillemain et al. 2014), that heterogeneity can play a larger role in harvest effects than traditionally thought. Furthermore, our findings support previous reports that when heterogeneity induces compensation in harvest mortality, the assumption that compensation occurs only after harvest (Kokko 2001, Blomberg 2015) appears incorrect (Sedinger and Herzog 2012).

Differential susceptibility to harvest could arise as a consequence of intentional harvest paradigms and social factors (Coltman et al. 2003, Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014) or as inadvertent byproducts (Bendell and Elliot 1967, Redfield 1975, Zwickel

1982, Connelly et al. 2000). Regardless, selective harvest has potential evolutionary ramifications for species (Coltman et al. 2003, 2005; Law and Salick 2005; Garel et al. 2007; Swain et al. 2007) that can manifest even at low harvest rates (Coltman 2008) and in short timescales (Coltman et al. 2003, Jørgenson et al. 2007, Darimont et al. 2009). Interestingly, despite the relatively early pervasive view of predation acting upon natural selection (Sumner 1935; Isley 1938; Dice 1949; Kettlewell 1955, 1956), human harvest as a potential evolutionary force received relatively little attention until recently (Coltman et al. 2003, Law and Salick 2005, Allendorf and Hard 2009, Bonenfant et al. 2009, Festa-Bianchet et al. 2014). In some instances harvest may be biased towards poor-quality individuals, notably in waterfowl (Hepp et al. 1986, Dufour et al. 1993, Heitmeyer et al. 1993, Pace and Afton 1999), which could provide some compensation for harvest mortality (Lebreton 2005, Lindberg et al. 2013, Guillemain et al. 2014). However, in other instances harvest regimes could be selective of higher quality individuals, which we demonstrate can cause the short-term effect of harvest to become compensatory. Nonetheless, selective harvest could also cause artificial selection and potentially shift phenotypes (Coltman et al. 2003, Garel et al. 2007, Bonenfant et al. 2009, Hengeveld and Festa-Bianchet 2011, Festa-Bianchet et al. 2014); however, evolution in harvested populations is complex because the relative strength of natural and artificial selection act in combination to affect trait change (Edeline et al. 2007). When traits that confer little fitness advantage are selected, artificial selection on the phenotype is unlikely (Rughetti and Festa-Bianchet 2010), and accordingly altering harvest regimes to be more selective of frail individuals could be advantageous to confer partial compensation and reduce the risk of artificial selection.

Identification of traits related to individual quality is imperative when managing harvest in relation to the heterogeneity tradeoff. Individual morphometric traits related to individual quality are readily identifiable prior to harvesting in some instances (Festa-Bianchet 2003, 2017; Kuparinen and Festa-Bianchet 2017); for example, horn size in some mammals (Coltman et al. 2003, Garel et al. 2007, Festa-Bianchet et al. 2014, Douhard et al. 2016, Pigeon et al. 2016) and body size in some fish (Conover and Munch 2002, Edeline et al. 2007, Jørgenson et al. 2007, Kuparinen and Merilä 2007, Swain et al. 2007). In other instances behavioral traits associated with individual quality could be less readily apparent and require research to identify; for example, variability in space use in some grouse populations

(Mussehl 1960; Redfield 1975; Connelly et al. 2000; Caudill et al. 2014*b*, 2016*b*). Conversely, the linkages between traits (e.g., behavioral, morphometric) and individual quality are unknown in many instances. Further study regarding the potential links between individual traits and individual quality will aid in optimizing harvest strategies, in relation to the heterogeneity tradeoff, across taxa.

MANAGEMENT IMPLICATIONS

When faced with uncertainty in harvest effects, we recommend a conservative approach whereby managers assume harvest is mostly additive to natural mortality, as has been previously articulated (Lebreton 2005), but recognize alternate mechanisms for compensation could occur (e.g., compensatory natality, immigration, individual heterogeneity). We recommend researchers investigate and managers employ harvest paradigms that best fit species- and site-specific goals. For example, Blomberg (2015) suggested altering bag limits and season lengths to achieve variable harvest rates in grouse. However, previous research has demonstrated that these could have little bearing on overall harvest rate (Braun and Beck 1985, Hoffman 1985), although some reports of numerical increases in harvest exist (Crawford 1982). Conversely, habitat (Autenrieth 1981, Brøseth and Pedersen 2010), entry points (Fischer and Keith 1974, Brøseth and Pedersen 2000), and landownership (Small et al. 1991) can influence grouse harvest rates, and accordingly should be incorporated into management. Timing of harvest could be used to mitigate or exploit spatiotemporal characteristics of populations and alter harvest mortality structures (i.e., additive–compensatory harvest continuum), contrary to previous claims (Blomberg 2015).

Harvest strategies that decrease harvest rates on higher quality demographic groups could help mitigate the potential for artificial selection (Kuparinen and Festa-Bianchet 2017). Our findings show that selective harvest of higher quality individuals can also induce compensatory population effects. Conversely, shifting the heterogeneity tradeoff to lower quality individuals can induce a partially compensatory effect. Hence evaluating and managing the heterogeneity tradeoff has both short- and long-term consequences for wild populations. We echo previous recommendations that evaluating and minimizing impact of selective harvest should become a management priority (Festa-Bianchet 2003, Allendorf and Hard 2009, Bonenfant et al. 2009, Myserud and Bischof 2010), thus ensuring the long-term viability of harvest and reducing the possibility of incurring large Darwinian debts for future generations (Loder 2005).

ACKNOWLEDGMENTS

M. S. Lindberg, J.-D. Lebreton, and J. H. Schmidt provided valuable discussion on individual heterogeneity and harvest effects. Comments from R. A. Merizon, J. R. Caikoski, J. W. Merickel, L. S. Parrett, and 2 anonymous reviewers provided valuable commentary that improved the manuscript. This research was supported in part by Alaska Department of Fish and Game, Tall Timbers Research Station and Land

Conservancy, Utah State University, University of Georgia, and Florida Fish and Wildlife Conservation Commission.

LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and B. F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest.
- Allen, D. L. 1947. Hunting as a limitation to a Michigan pheasant population. *Journal of Wildlife Management* 11:232–243.
- Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest on wild animals. *Proceedings of the National Academy of Sciences* 106:9987–9994.
- Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA.
- Anderson, D. R., and K. P. Burnham. 1976. Population of the mallard: VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service Publication 128, Washington, D.C., USA.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. *Biological Conservation* 111:115–123.
- Aubry, L. M., E. Cam, J.-Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology* 80:375–383.
- Aubry, L. M., D. N. Koons, J.-Y. Monnat, and E. Cam. 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived sea bird. *Ecology* 90:2491–2502.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game, Wildlife Bulletin 9, Boise, USA.
- Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86:682–692.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7, <<http://CRAN.R-project.org/package=lme4>>. Accessed 7 May 2015.
- Beck, D. I., and C. E. Braun. 1978. Weights of Colorado sage grouse. *Condor* 80:241–243.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* 34:1070–1078.
- Bendell, J. F., and P. W. Elliot. 1967. Behavior and the regulation of numbers in blue grouse. Canadian Wildlife Service Report Series, No. 4, Ottawa, Canada.
- Bergerud, A. T. 1985. The additive effect of hunting mortality on the natural mortality rates of grouse. Pages 345–366 in S. L. Beasom and S. F. Roberson, editors. Game harvest management. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Bergerud, A. T. 1988*a*. Population ecology of grouse. Pages 578–685 in A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, USA.
- Bergerud, A. T. 1988*b*. Increasing the numbers of grouse. Pages 686–731 in A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, USA.
- Blomberg, E. J. 2015. The influence of harvest timing on greater sage-grouse survival: a cautionary perspective. *Journal of Wildlife Management* 79:695–703.
- Blomberg, E. J., J. S. Sedinger, D. V. Nonne, and M. T. Atamian. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. *Journal of Avian Biology* 44:149–158.
- Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009. Age-dependent relationship between horn growth and survival in wild sheep. *Journal of Animal Ecology* 78:161–171.
- Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. *Oikos* 87:419–426.
- Braun, C. E., and T. D. I. Beck. 1985. Effects of changes in hunting regulations on sage grouse harvest populations. Pages 335–343 in S. L.

- Beasom, and S. F. Roberson, editors. Game harvest management. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory *vs.* additive hypotheses of mortality in mallards. *Ecology* 65:105–112.
- Burnham K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Brøseth, H., and H. C. Pedersen. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *Journal of Applied Ecology* 37: 182–190.
- Brøseth, H., and H. C. Pedersen. 2010. Disturbance effects of hunting activity in a willow ptarmigan *Lagopus lagopus* population. *Wildlife Biology* 16:241–248.
- Cam, E., O. Gimenez, R. Alpizar-Jara, L. M. Aubry, M. Authier, E. G. Cooch, D. N. Koons, W. A. Link, J.-Y. Monnat, J. D. Nichols, J. J. Rotella, J. A. Royle, and R. Pradel. 2013. Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population. *Oikos* 122:739–753.
- Cam, E., J. E. Hines, J.-Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? The kittiwake model. *Ecology* 79:2917–2930.
- Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Cam, E., and J.-Y. Monnat. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology* 69:380–394.
- Caudill, D., M. R. Guttery, B. Bibles, T. A. Messmer, G. Caudill, E. Leone, D. K. Dahlgren, and R. Chi. 2014a. Effects of climatic variation and reproductive trade-offs vary by measure of reproductive effort in greater sage-grouse. *Ecosphere* 5:art154.
- Caudill, D., M. R. Guttery, E. Leone, G. Caudill, and T. A. Messmer. 2016a. Age-dependence and individual heterogeneity in reproductive success of greater sage-grouse. *Journal of Avian Biology* 47:719–723.
- Caudill, D., T. A. Messmer, B. Bibles, and M. R. Guttery. 2013. Winter habitat use by juvenile greater sage-grouse on Parker Mountain, Utah: implications for sagebrush management. *Human-Wildlife Interactions* 7:250–259.
- Caudill, D., T. A. Messmer, B. Bibles, and M. R. Guttery. 2014b. Greater sage-grouse juvenile survival in Utah. *Journal of Wildlife Management* 78:808–817.
- Caudill, D., T. M. Terhune, B. Bibles, and T. A. Messmer. 2016b. Factors affecting seasonal movements of juvenile greater sage-grouse: a reconceptualized nest survival model. *Condor* 118:139–147.
- Coltman, D. W. 2008. Evolutionary rebound from selective harvesting. *Trends in Ecology and Evolution* 23:117–118.
- Coltman, D. W., P. O'Donoghue, J. T. Hogg, and M. Festa-Bianchet. 2005. Selection and genetic (co)variation in bighorn sheep. *Evolution* 59:1372–1382.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. *Wildlife Biology* 6:227–232.
- Connelly, J. W., J. H. Gammonley, and T. W. Keegan. 2012. Harvest management. Pages 202–231 in N. J. Silvy, editor. *The wildlife techniques manual: management (volume 2)*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Connelly, J. W., K. P. Reese, E. O. Garton, and M. L. Commons-Kemner. 2003. Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. *Wildlife Biology* 9:335–340.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96.
- Conroy, M. J., C. J. Fonnnessbeck, and N. L. Zimper. 2005. Modeling regional waterfowl harvest rates using Markov chain Monte Carlo. *Journal of Wildlife Management* 69:77–90.
- Cooly, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of compensatory mortality hypothesis. *Ecology* 90:2913–2921.
- Crawford, J. A. 1982. Factors affecting sage grouse harvest in Oregon. *Wildlife Society Bulletin* 10:374–377.
- Dahlgren, D. K., M. R. Guttery, T. A. Messmer, D. Caudill, R. D. Elmore, R. Chi, and D. N. Koons. 2016. Evaluating vital-rate contributions to greater sage-grouse population dynamics to inform conservation. *Ecosphere* 7:e01249.
- Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving better estimates of greater sage-grouse chick survival in Utah. *Journal of Wildlife Management* 74:1286–1294.
- Darimont, C. T., C. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmsers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* 106:952–954.
- Dice, L. R. 1949. The selection index and its test of significance. *Evolution* 3:262–265.
- Douhard, M., M. Festa-Bianchet, F. Pelletier, J.-M. Gaillard, and C. Bonenfant. 2016. Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecological Applications* 26:309–321.
- Dufour, K. W., C. D. Ankney, and P. J. Weatherhead. 1993. Condition and vulnerability to hunting among mallards staging at lake St. Clair, Ontario. *Journal of Wildlife Management* 57:209–215.
- Edeline, E., S. M. Carlson, L. C. Stige, I. J. Winfield, J. M. Fletcher, J. B. James, T. O. Haugen, L. A. Vøllestad, and N. C. Stenseth. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences* 104:15799–15804.
- Engen, S., R. Lande, and B.-E. Sæther. 2014. Evolutionary consequences of nonselective harvesting in density-dependent populations. *American Naturalist* 184:714–726.
- Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.
- Errington, P. L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. *Ecological Monographs* 15:1–34.
- Errington, P. L. 1956. Factors limiting higher vertebrate populations. *Science* 124:304–307.
- Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191–207 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C., USA.
- Festa-Bianchet, M. 2017. When does selective hunting select, how can we tell, and what should we do about it? *Mammal Review* 47:79–81.
- Festa-Bianchet, M., F. Pelletier, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Decrease in horn size and increase in age of trophy sheep in Alberta over 37 years. *Journal of Wildlife Management* 78:133–141.
- Fischer, C. A., and L. B. Keith. 1974. Population responses of central Alberta ruffed grouse to hunting. *Journal of Wildlife Management* 38:585–600.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, United Kingdom.
- Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypotheses and tests. *Trends in Ecology and Evolution* 10:374–378.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 2000:367–393.
- Gaillard, J.-M. and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Garel, M., J. Cugnasse, D. Maillard, J. Gaillard, A. J. M. Hewison, and D. Dubray. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Adaptations* 17:1607–1618.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224–231.
- Guillemain M. R. Pradel, O. Devineau, G. Simon, and M. Gauthier-Clerc. 2014. Demographic heterogeneity among individuals can explain the discrepancy between capture-mark-recapture and waterfowl count results. *Condor* 116:293–302.
- Guttery, M. R., D. K. Dahlgren, T. A. Messmer, J. W. Connelly, K. P. Reese, P. A. Terletzky, N. Burkepile, and D. N. Koons. 2013. Effects of

- landscape-scale environmental variation on greater sage-grouse chick survival. *PLoS ONE* 8:e65582.
- Hamel, S., S. D. Côté, J. Gaillard, and M. Festa-Bianchet. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology* 78:143–151.
- Hamel, S., S. D. Côté, K. G. Smith, and M. Festa-Bianchet. 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. *Journal of Wildlife Management* 70:1044–1053.
- Heitmeyer, M. E., L. H. Fredrickson, and D. D. Humburg. 1993. Further evidence of biases associated with hunter-killed mallards. *Journal of Wildlife Management* 57:733–740.
- Hengeveld, P. M., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. *Journal of Wildlife Management* 75:189–197.
- Hepp, G. R., R. J. Blohm, R. E. Reynolds, J. E. Hines, and J. D. Nichols. 1986. Physiological condition of autumn-banded mallards and its relationship to hunting vulnerability. *Journal of Wildlife Management* 50:177–183.
- Hoffman, R. W. 1985. Effects of changes in hunting regulations on blue grouse populations. Pages 327–334 in S. L. Beason, and S. F. Roberson, editors. *Game harvest management*. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Hudson, P. J. 1985. Harvesting red grouse in the North of England. Pages 319–326 in S. L. Beason and S. F. Roberson, editors. *Game harvest management*. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Isley, F. B. 1938. Survival of acridian protective coloration. *Ecology* 19:370–389.
- Jørgenson, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Erande, A. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp. 2007. Managing evolving fish stocks. *Science* 318:1247–1252.
- Kettlewell, H. B. D. 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity* 9:323–342.
- Kettlewell, H. B. D. 1956. Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* 10:287–301.
- Kokko, H. 2001. Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildlife Biology* 7:141–150.
- Kokko, H., and J. Lindström. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecological Modelling* 110:293–304.
- Koons, D. N., R. F. Rockwell, and L. M. Aubry. 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. *Journal of Animal Ecology* 83:365–374.
- Kuparinen, A., and M. Festa-Bianchet. 2017. Harvest-induced evolution: insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B* 372:20160036.
- Kuparinen, A., and J. Merilä. 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution* 22:652–659.
- Kvalnes, T., B.-E. Sæther, H. Haanes, K. H. Røed, S. Engen, and E. J. Solberg. 2016. Harvest-induced phenotypic selection in an island population of moose, *Alces alces*. *Evolution* 70:1486–1500.
- Lack, D. 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford, United Kingdom.
- Law, W., and J. Salick. 2005. Human-induced dwarfing of Himalayan snow lotus, *Saussurea laniceps* (Asteraceae). *Proceedings of the National Academy of Sciences* 102:10218–10220.
- Lebreton, J.-D. 2005. Dynamical and statistical models for exploited populations. *Australian & New Zealand Journal of Statistics* 47:49–63.
- Lindberg, M. S., J. S. Sedinger, and J.-D. Lebreton. 2013. Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. *Ecology and Evolution* 3:4045–4056.
- Loder, N. 2005. Point of no return. *Conservation in Practice* 6:124–129.
- Mussehl, T. W. 1960. Blue grouse production, movements, and populations in the Bridger Mountains, Montana. *Journal of Wildlife Management* 24:60–68.
- Mysterud, A., and R. Bischof. 2010. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? *Journal of Animal Ecology* 79:148–160.
- Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. *Annual Review of Ecology and Systematics* 26:117–199.
- Pace, R. M. III, and A. D. Afton. 1999. Direct recovery rates of lesser scaup banded in northwest Minnesota: sources of heterogeneity. *Journal of Wildlife Management* 63:389–395.
- Pendergast, B. A., and D. A. Boag. 1973. Seasonal changes in the internal anatomy of spruce grouse in Alberta. *Auk* 90:307–317.
- Péron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *Journal of Animal Ecology* 82:408–417.
- Péron, G., J.-M. Gaillard, C. Barbraud, C. Bonenfant, A. Charmantier, R. Choquet, T. Coulson, V. Grosbois, A. Loison, G. Marzolin, N. Owen-Smith, D. Pardo, F. Plard, R. Pradel, C. Toigo, and O. Gimenez. 2016. Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution* 70:2909–2914.
- Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- Pollock, K. H., C. T. Moore, W. R. Davidson, F. E. Kellog, and G. L. Doster. 1989. Survival rates of bobwhite quail based on band recovery analyses. *Journal of Wildlife Management* 53:1–6.
- R Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Redfield, J. A. 1973. Variations in weight of blue grouse (*Dendragapus obscurus*). *Condor* 75:312–321.
- Redfield, J. A. 1975. Comparative demography of increasing and stable populations of blue grouse (*Dendragapus obscurus*). *Canadian Journal of Zoology* 53:1–11.
- Reese, K. P., J. W. Connelly, E. O. Garton, and M. L. Commons-Kemner. 2005. Exploitation and greater sage-grouse *Centrocercus urophasianus*: a response to Seding and Rotella. *Wildlife Biology* 11:377–381.
- Reese, K. P., and J. W. Connelly. 2011. Harvest management for greater sage-grouse: a changing paradigm for game bird management. Pages 101–112 in S. T. Knicks, and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Published for the Cooper Ornithological Society. *Studies in Avian Biology* vol. 38, University of California Press, Berkeley, USA.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44:257–267.
- Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. *Journal of Wildlife Management* 45:293–313.
- Roseberry, J. L. 1979. Bobwhite population response to exploitation: real and stimulated. *Journal of Wildlife Management* 43:285–305.
- Røskaft, E. 1985. The effect of enlarged brood size on the future reproductive potential of the Rook. *Journal of Animal Ecology* 54:255–260.
- Rughetti, M., and M. Festa-Bianchet. 2010. Compensatory growth limits opportunities for artificial selection in alpine chamois. *Journal of Wildlife Management* 74:1024–1029.
- Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology* 80:244–258.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Second edition. Macmillan, New York, New York, USA.
- Sedinger, J. S., N. D. Chelgren, D. H. Ward, and M. S. Lindberg. 2008. Fidelity and breeding probability related to population density and individual quality in black brant geese *Branta bernicla nigricans*. *Journal of Animal Ecology* 77:702–712.
- Sedinger, J. S., and M. P. Herzog. 2012. Harvest and dynamics of duck populations. *Journal of Wildlife Management* 76:1108–1116.
- Sedinger, J. S., C. A. Nicolai, C. J. Lensink, C. Wentworth, and B. Conant. 2007. Black brant harvest, density dependence, and survival: a record of population dynamics. *Journal of Wildlife Management* 71:496–506.
- Sedinger, J. S., and J. J. Rotella. 2005. Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data? *Wildlife Biology* 11:371–375.
- Servanty, S. R., R. Choquet, E. Baubet, J. Gaillard, M. Schaub, C. Toigo, J.-D. Lebreton, M. Buoro, and O. Gimenez. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state-space modeling approach. *Ecology* 91:1916–1923.
- Small, R. J., J. C. Holzgart, and D. H. Rusch. 1991. Predation and hunting mortality of ruffed grouse in central Wisconsin. *Journal of Wildlife Management* 55:512–520.

- Smith, G. W., and R. E. Reynolds. 1992. Hunting and mallard survival, 1979–88. *Journal of Wildlife Management* 56:306–316.
- Souchay, G., G. Gauthier, J. Lefebvre, and R. Pradel. 2015. Absence of difference in survival between two distant breeding sites of greater snow geese. *Journal of Wildlife Management* 79:570–578.
- Souchay, G., G. Gauthier, and R. Pradel. 2013. Temporal variation of juvenile survival in a long-lived species: the role of parasites and body condition. *Oecologia* 173:151–160.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Sumner, F. B. 1935. Evidence for the protective value of changeable coloration in fishes. *American Naturalist* 69:245–266.
- Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B: Biological Sciences* 274:1015–1022.
- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* 128:137–142.
- Vaupel, J. W., M. G. Manton, and R. Stallard. 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16:439–454.
- Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity's ruse: some surprising effects of selection on population dynamics. *American Statistician* 39:176–185.
- Wik, P. 2002. Ecology of greater sage-grouse in south-central Owyhee county, Idaho. Thesis, University of Idaho, Moscow, USA.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687–690.
- Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* 25:207–214.
- Wing, L. W. 1951. Practice of wildlife conservation. John Wiley and Sons, New York, New York, USA.
- Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. *Biological Conservation* 182:187–196.
- Zwicker, F. C. 1982. Demographic composition of hunter-harvested blue grouse in east central Vancouver Island, British Columbia. *Journal of Wildlife Management* 46:1057–1061.

Associate Editor: Timothy Fulbright.