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Commentary

Harvest and Dynamics of Duck Populations

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ABSTRACT The role of harvest in the dynamics of waterfowl populations continues to be debated among scientists and managers. Our perception is that interested members of the public and some managers believe that harvest influences North American duck populations based on calls for more conservative harvest regulations. A recent review of harvest and population dynamics of North American mallard (*Anas platyrhynchos*) populations (Pöysä et al. 2004) reached similar conclusions. Because of the importance of this issue, we reviewed the evidence for an impact of harvest on duck populations. Our understanding of the effects of harvest is limited because harvest effects are typically confounded with those of population density; regulations are typically most liberal when populations are greatest. This problem also exists in the current Adaptive Harvest Management Program (Conn and Kendall 2004). Consequently, even where harvest appears additive to other mortality, this may be an artifact of ignoring effects of population density. Overall, we found no compelling evidence for strong additive effects of harvest on survival in duck populations that could not be explained by other factors. © 2012 The Wildlife Society.

KEY WORDS additive harvest, compensation, density dependence, heterogeneity, mallard, population dynamics.

The role of human harvest in the regulation of waterfowl populations in North America has been of interest for more than 3 decades (Nichols et al. 1995). An early central focus in this effort was to determine the extent to which harvest mortality is either compensatory or additive to other forms of mortality (Anderson and Burnham 1976, Burnham and Anderson 1984, Nichols et al. 1984, Nichols 1991). When harvest mortality is completely compensatory to other sources of mortality, we observe no change in annual survival rate at the population level in response to changes in harvest mortality rate (the proportion of individuals in a population shot by hunters), at least below some threshold of harvest rate (Anderson and Burnham 1976). In contrast, when harvest mortality is additive to other sources of mortality, we observe a direct negative relationship between survival at the population level and harvest rate (Anderson and Burnham 1976). The extent to which harvest affects survival was historically important because the effects of harvest on waterfowl population dynamics were thought to operate primarily, if not exclusively, through the effects of harvest on the mortality process (e.g., Anderson and Burnham 1976, Nichols et al. 1984, Krementz et al. 1988). Much of the original work to distinguish between these hypotheses failed to find strong evidence in favor of the additive mortality hypothesis and could not reject the compensatory hypothesis (review in Nichols 1991).

More recently, adaptive management approaches (Walters 1986) have played a role in interpreting the effects of harvest on the dynamics of waterfowl populations (Johnson et al. 1997, Nichols et al. 2007). Adaptive management provides a mechanism for evaluating the relative performance of competing mathematical models to explain the dynamics of ecological systems (Walters 1986). Such approaches have been employed in several management regimes to attempt to better understand system dynamics under different management actions. Adaptive management approaches are generally divided into 2 classes: passive and active. Active adaptive management relies on management actions as experiments or "deliberate probing for information," intended to improve understanding of system dynamics (Walters 1986:232). In contrast, passive adaptive management relies "just on parameter revision" or fitting models in the absence of probing (Walters 1986:232). An example of active adaptive management in the management of waterfowl harvest might be implementation of liberal harvest regulations when populations are low and restrictive harvest regulations when populations are high. The current adaptive harvest management (AHM) program for ducks in the United States is an example of passive adaptive management (Johnson et al. 1997, Williams et al. 2001).

Understanding the role of harvest in regulation of North American duck populations has become more important in the past 2 decades because some populations (northern pintails [*Anas acuta*], lesser scaup [*Aythya affinis*]) did not respond to improved habitat conditions in the mid-1990s on the primary breeding areas of the mid-continent of North America (Hestbeck 1996, Afton and Anderson 2001, United States Fish and Wildlife Service [USFWS] 2004). Conservative harvest regulations were promulgated to address these low population levels, despite the absence of a clear linkage between such management action and population response (e.g., Lynch 1984, Ankney 1996, Rice et al.

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2010). Maybe as importantly, some hunters attribute changes in their hunting experience and by association, population dynamics of duck populations to overharvest (e.g., http://www.madduck.org/, http://www.michaelfurtman.com/pdf/Conservative%20Duck.pdf). A group of European waterfowl scientists also recently suggested that the paradigm has changed and, "something fundamental has happened in the response of the North American mallard population to harvesting," such that evidence in favor of the additive mortality has increased (Pöysä et al. 2004:614).

Use of harvest regulations as a tool for the management of populations that are below their North American Waterfowl Management Plan (NAWMP) goal, perception by some hunters that harvest rates were too high, and recent interpretation by some scientists that North American harvest of mallards (*Anas platyrhynchos*) have become an additive source of mortality, prompted us to evaluate the historical relationships among harvest regulations and population dynamics of North American ducks. We comment on the conclusions of Pöysä et al. (2004) because of the potential influence of their analysis on international scientists. We assess the evidence for the competing hypotheses of compensatory versus additive harvest mortality. We also review historical relationships between populations and harvest regulations, especially confounding between density-dependent processes and harvest mortality. We accept the possibility that a gradient in additivity of harvest mortality may exist across species varying in life histories. For example, additivity of harvest is widely accepted for geese (*Branta* spp.) (Rexstad 1992, Sedinger et al. 2007), and canvasbacks (*Aythya valisineria*) may occupy an intermediate position (Anderson et al. 2001). We focus primarily on harvest management of dabbling ducks (genus *Anas*). Our goal was to critically evaluate evidence for the additive versus compensatory harvest mortality hypotheses, not to criticize the general trend toward application of AHM (Nichols et al. 2007) in management of waterfowl harvest, which we believe is a positive development that should be encouraged.

HARVEST, DENSITY-DEPENDENCE, AND MORTALITY PROCESSES

The most prominent hypothesis explaining compensation for harvest in the dynamics of wildlife populations requires density-dependent feedbacks in demography. That is, when individuals are removed from the population by harvest, either fecundity or survival of remaining individuals is expected to increase under the hypothesis (Boyce et al. 1999). In North American duck populations, detecting such density dependence directly has been difficult for several reasons, including: 1) environmental conditions are extremely variable on both the breeding and wintering grounds; 2) harvest regulations, and consequently harvest, have tended to track environmental conditions, confounding the 2 potential sources of population regulation; 3) studies required to assess the role of harvest in overall mortality have not been conducted; 4) the phase of the annual cycle (breeding, molt, migration, winter, etc.), when density dependence might occur is unknown and potentially variable; and 5) surveys of waterfowl during winter, when density-dependent mortality may occur, are extremely imprecise.

Harvest rates for waterfowl are typically estimated using band recovery rates estimated from Brownie models of band recoveries (Brownie et al. 1985), because such rates are directly related to harvest rates by the proportion of bands reported to the United States Geological Survey Bird Banding Laboratory by hunters. Band recovery rates represent the probability that a banded bird alive and in the population is shot by a hunter, retrieved, and the band reported to the Bird Banding Lab. Thus, except for the bias associated with unretrieved kill, estimates of the proportion of retrieved and reported bands provide a mechanism for estimating harvest rate, as long as band reporting rate is also estimated (Nichols et al. 1995). Several studies have estimated band reporting rate (Nichols et al. 1995) and band recovery rates provide a reliable index of harvest rate as long as band reporting rates do not vary too much.

Fluctuation in numbers of ducks in North America historically has been driven primarily by variation in number of wetlands in the prairie-parkland of the mid-continent (Batt et al. 1989), although both northern pintails (USFWS 2004) and lesser scaup (*Aythya affinis*; Afton and Anderson 2001) failed to respond to the last wet cycle in the 1990s. Numbers of mallards counted during the breeding surveys in May have fluctuated between 4.9 and 11.2 million since 1955, while number of May ponds counted have varied between 2.1 and 8.1 million over the same period (Wilkins and Otto 2003). Number of breeding mallards closely tracks the number of May ponds (Crissey 1969, Kaminski and Gluesing 1986). Similarly, wetland conditions on wintering areas also fluctuate dramatically (Heitmeyer and Fredrickson 1981). In the context of such dramatic variation, it is not clear how to assess density dependence directly (Williams et al. 2001). Clearly, we cannot view density dependence in relation to some fixed carrying capacity. Nonetheless, several studies have detected density dependence in the reproductive process (Kaminski and Gluesing 1986, USFWS 2003[Q1]). As Pöysä et al. (2004) point out, density dependence in reproduction is sufficient to support a sustainable harvest program. Numerous mechanisms could contribute to density dependence in recruitment, including carryover effects from wintering areas (Heitmeyer and Fredrickson 1981), behavioral spacing mechanisms on breeding areas (Dzubin 1969, Johnson and Grier 1988), or density-related mortality of nests or ducklings (Elmberg 2003, Amundson and Arnold 2011). Presently, the influence of these mechanisms is poorly understood at the continental scale.

Density dependence in the mortality process, however, provides 1 mechanism for compensation for harvest mortality. For populations that exceed carrying capacity during the late, or post-hunting season period, individuals could be harvested up to a level equaling the difference between population size and carrying capacity and would not result in an effect on survival (Errington 1945). Under this scenario, harvest mortality would be completely compensatory for a proportion of the population and population size in spring would be identical whether harvest occurred or not (Boyce et al. 1999). This contrasts with Lebreton's (2005) conclusion that potential for compensation of harvest mortality is modest under density-dependent mortality. The differences between the conclusions of Errington (1945) and Lebreton (2005) could result from differences in assumptions about the strength of selection on individual survival. Under Errington's (1945) threshold of security hypothesis, the mortality rate in the absence of harvest is 1.0 for a proportion of the population above carrying capacity, whereas in Lebreton's (2005) assessment, mortality rates in the absence of harvest are <1.0.

One modification in our thinking about temporal patterns of density-dependent mortality is important if we are to make progress in understanding the potential for compensation of harvest. Compensation for harvest mortality was historically thought to occur following the hunting season, because the most limiting portion of the year occurred in winter (Errington 1945); this is an important assumption in some modern harvest strategies (e.g., USFWS 2011). Numerous more recent studies suggest that waterfowl face nutritional or energetic challenges in December and January (Delnicki and Reinecke 1986, Miller and Newton 1999, Rhodes et al. 2006, Stafford et al. 2007). Therefore, the potential exists for nutrition-related mortality to occur during these months, which coincide with the late hunting season in North America. In addition, waterfowl diseases cause substantial mortality between September and late spring (Wobeser et al. 1983, Botzler 1991), much of which occurs when hunting season is open. To the extent that either nutrient- or disease-related mortality is a function of population density, these mortality processes could produce density-dependent mortality during the waterfowl hunting season.

Anderson and Burnham's (1976) pioneering study found essentially no change in annual survival across a broad range of harvest rates for mallards banded and harvested between 1961 and 1970 and they rejected a fully additive harvest hypothesis. Burnham and Anderson (1984), using a larger data set for mallards, rejected the fully additive harvest mortality hypothesis and concluded, "The results were very similar to those expected if the data sets all came from a completely compensatory process," although they cautioned that more data were needed for female mallards.

Examining the linkage between harvest and survival has been complicated by the covariance among population size, harvest, and survival. Harvest rates have tended to track population size in North American duck harvest (Raveling and Heitmeyer 1987; Fig. 1). Thus, even if survival rates decline at greater harvest rates, one cannot determine whether a lower survival rate resulted from harvest or density-dependent mortality (Fig. 2). As an illustration, consider a case in which no causal relationship exists between annual survival and harvest (Fig. 2a); that is, harvest mortality is completely compensatory. Assume that annual survival is negatively density-dependent, creating a negative relationship between population size and annual survival (Fig. 2c). Because harvest has generally been managed so that harvest rates are greater when population size is greater (Fig. 2b), one will observe a negative relationship between annual survival and harvest (Fig. 2d) unless population size is explicitly controlled for in such analyses. In fact, survival estimates produced by Trost (1987) declined significantly with increasing numbers of mallards in North America (Fig. 3). Thus, the covariance among harvest, survival, and population size precludes the indirect assessment of density-dependent mortality by examining the performance of compensatory harvest mortality models. This point appears to be the source of substantial confusion among biologists and managers with whom we have spoken. Although compensatory harvest mortality may be explained by the presence of density dependence in the mortality process, the lack of support for compensatory harvest models does not imply absence of

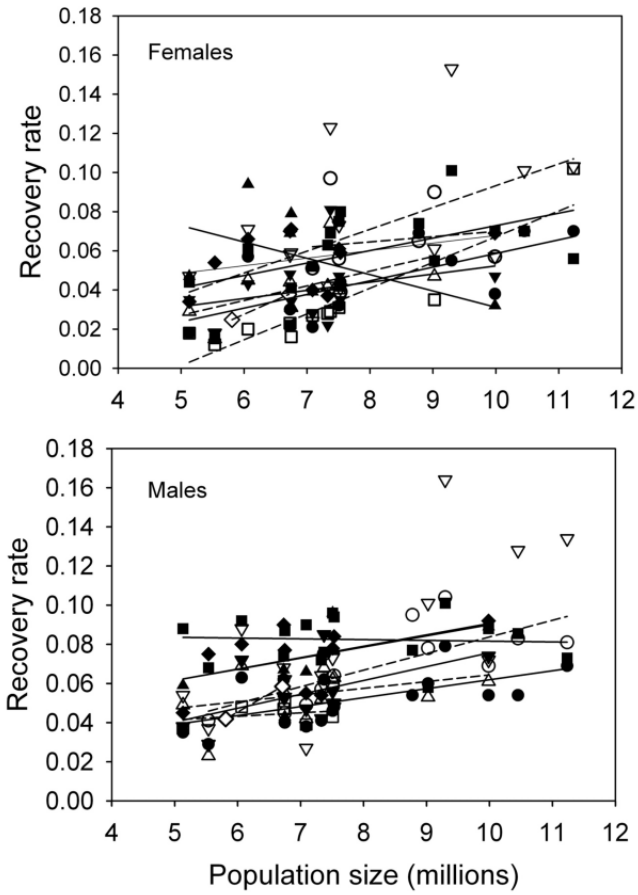

Figure 1. Band recovery rates from mallards shot by hunters in North America between 1955 and 1985 in relation to breeding population indices based on aerial surveys the previous spring. Recovery rates were estimated using Brownie (Brownie et al. 1985) models. Band recovery rates are related to harvest rates through the expression: $h = f/\lambda$; where h is harvest rate, f is band recovery rate, and λ is band reporting rate (Nichols et al. 1995). We have ignored unretrieved kill in this equation because it is difficult to estimate and is typically assumed to be constant (e.g., United States Fish and Wildlife Service 2011). Each line represents a different banding reference area. Recovery rates increased with population size in all but 2 areas (from Anderson 1975[Q2]). Band recovery rates varied among areas (PROC GLM, $F_{8,186} = 3.26$, $P = 0.0017$; SAS Institute 2001) and between sexes ($F_{1,186} = 30.06$, $P \leq 0.001$). Band recovery rates generally increased with increasing breeding population ($F_{1,186} = 38.37$, $P \leq 0.001$), although a significant interaction between areas and breeding population ($F_{8,186} = 3.09$, $P = 0.0027$) was consistent with deviation from this overall pattern in 1 geographic region for each sex.

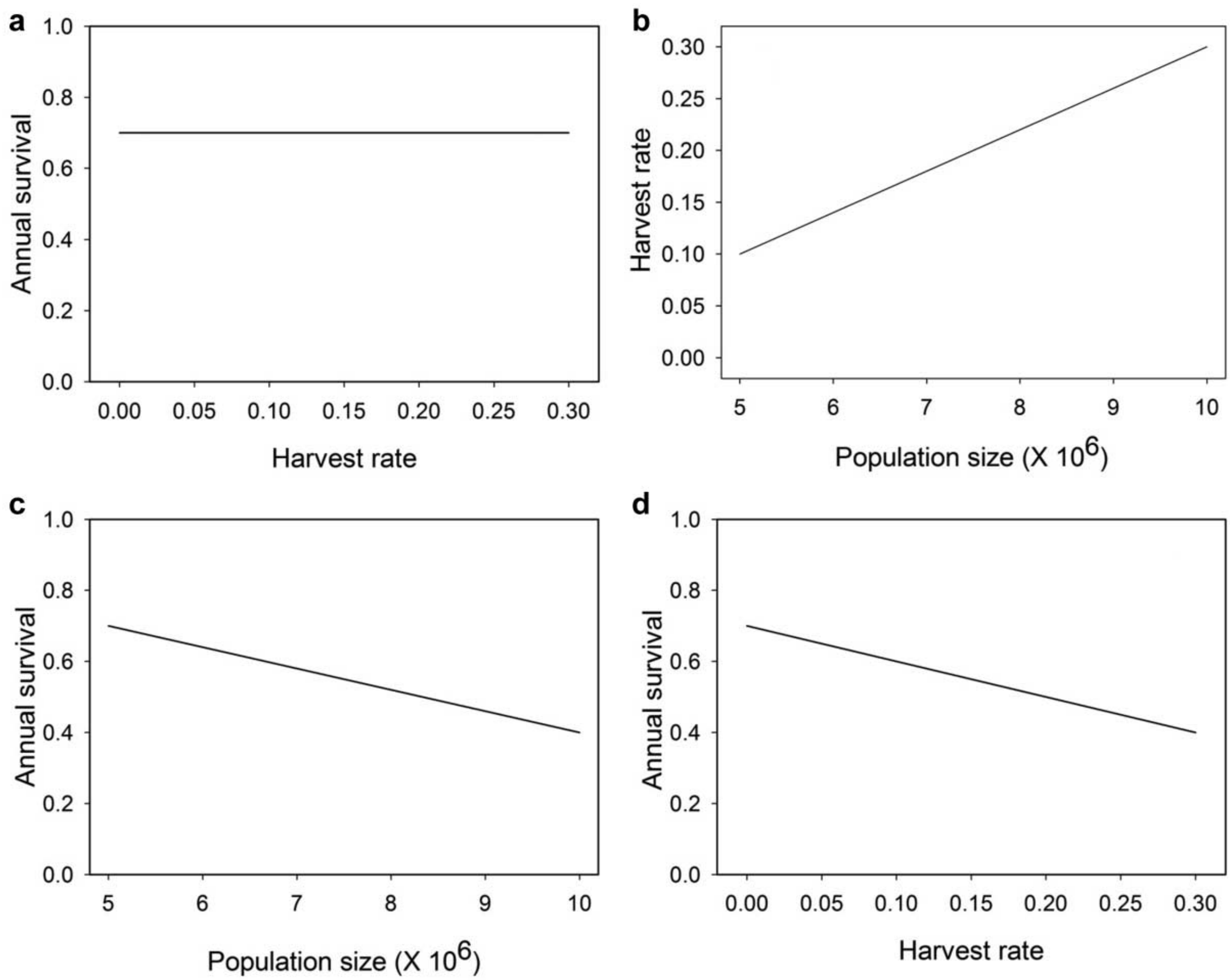

Figure 2. Graphical examples of how failure to account for population density (or size) can lead to the conclusion that harvest is additive to other forms of mortality even in the case where harvest mortality is completely compensated. (a) The relationship between total annual survival and harvest rate in this hypothetical population under the assumption that harvest mortality is fully compensated by reduction in natural mortality. Scales on axes approximate the typical range of variation for mallards. (b) The general long-term relationship between harvest rate and population size. (c) The relationship between annual survival and population size under the hypothesis of negatively density-dependent mortality. (d) The expected statistical relationship between annual survival and harvest, if population size is not explicitly accounted for, which will be observed even in the absence of additive harvest mortality, given patterns in b and c. We are not implying that a and c are biologically correct, which is currently unknown. However, analyses of the relationship between annual survival and harvest will incorrectly detect additive harvest mortality in the presence of density-dependent annual survival unless population size is accounted for.

density dependence. In fact, as we show here, density-dependent mortality, combined with compensatory harvest mortality and a positive correlation between harvest rate and population density, will favor additive harvest mortality models when contrasted against compensatory harvest models, even in the absence of additive harvest mortality.

This problem applies to Smith and Reynolds's (1992) analysis of survival and harvest rates for the 1980s (Sedinger and Rexstad 1994). Population size was declining (Sedinger and Rexstad 1994) over the period considered by Smith and Reynolds (1992) and harvest was more restrictive later in the study period, resulting in lower harvest rates during the second half of the period considered by Smith and Reynolds (1992; Fig. 3). Sedinger and Rexstad (1994) pointed out that models of density-dependent mortality performed nearly as well as those relating survival to harvest, despite much poorer estimates of population density than harvest rate. Imprecise estimates of population size during winter increase the difficulty of directly assessing the role of population density in the mortality process, especially given the covariance between population size and harvest in current data. We note that the same general covariance among harvest rate, population size, and annual survival of black ducks (Krementz et al. 1988, Wilkins and Otto 2006[Q3]) confounds analysis of the relationship between harvest and survival in this species. Consequently, we conclude that no past studies of the relationship between harvest and survival provide unambiguous evidence that harvest is additive to other sources of mortality.

INDIVIDUAL HETEROGENITY AS A MECHANISM FOR COMPENSATION

Variation among individuals in inherent mortality risk, frailty, is now well established in natural populations (Cam et al.

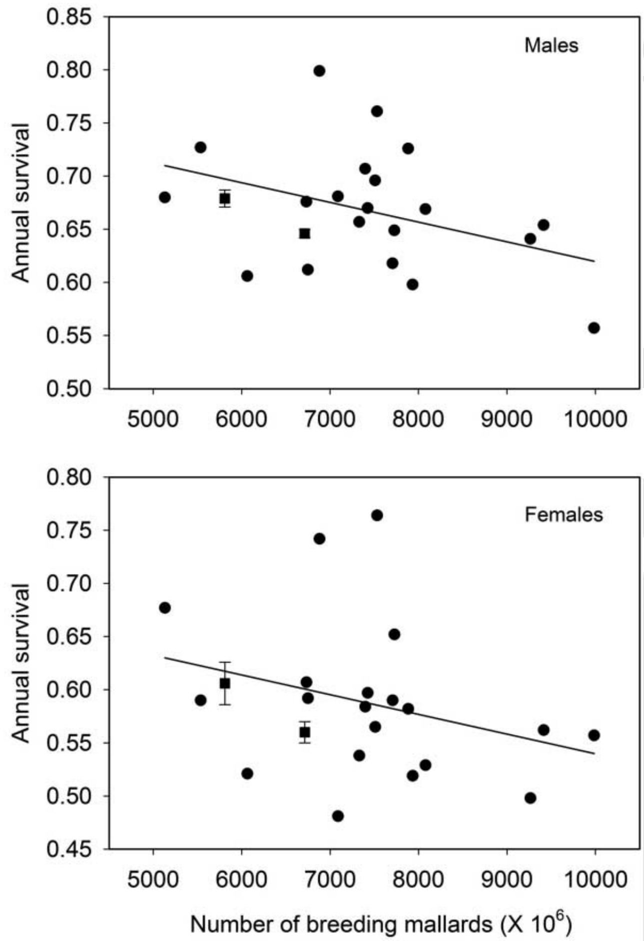

Figure 3. Relationship between annual survival and population size in North American mallards. Circles represent data from Trost (1987), squares (±SEs) are from Smith and Reynolds (1992). Continental estimates of survival probability were significantly negatively related to breeding population ($F_{1,37} = 4.48$, $P = 0.041$; SAS Institute 2001) for data from the Trost (1987) study.

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2002), including waterfowl (Francis et al. 1992, Rexstad and Anderson 1992, Sedinger and Chelgren 2007). If individuals with greater inherent mortality probability are also more vulnerable to harvest, this could provide 1 mechanism for compensation of harvest mortality because individuals shot by hunters had a low probability of surviving even in the absence of harvest. This idea was first explored by Lebreton (2005), who showed that differential vulnerability to harvest by individuals with high frailty had to be substantial if heterogeneity was to produce compensatory harvest mortality. Heterogeneity in vulnerability to harvest has not been explicitly examined in natural populations, specifically with respect to the hypothesis of compensatory harvest mortality, but greater vulnerability to harvest of individuals in poor nutritional condition (Greenwood et al. 1986, Dufour et al. 1993) is consistent with the hypothesis that inherent frailty is associated with harvest risk. Lower survival probability and greater harvest risk for individuals to which artificial markers (e.g., neck collars) have been affixed (Schmutz and Morse 2000, Alisauskas et al. 2006) provide experimental (albeit inadvertent) support for a linkage between frailty and harvest risk.

To the extent that variation in frailty explains compensation for harvest mortality, the requirement for density dependence as a necessary condition for compensatory harvest mortality might be relaxed. We are unaware of studies that specifically address the interaction between population density and individual heterogeneity. Two studies, however, suggest that heterogeneity in frailty exists across a range of population densities. Sedinger and Chelgren (2007) showed that gosling size had the same relationship to first-year survival across 12 cohorts of black brant (*Branta bernicla nigricans*) for which population density and mean survival varied substantially. Coulson et al. (1998) did not detect an interaction between population density and correlates of first-year survival in red deer (*Cervus elaphus*), suggesting that variation in frailty was consistent across population densities. Although neither Sedinger and Chelgren (2007) nor Coulson et al. (1998) detected an interaction between frailty and population density, such interactions seem probable. Selection against frail individuals should increase at greater population densities. Nevertheless, the existence of individual heterogeneity may reduce the effect of density dependence in the biological mechanism underlying compensation for harvest mortality.

To the extent that compensatory harvest mortality is explained by heterogeneity in survival risk, compensation may occur during the hunting season. Combined with the potential that more traditional density-dependent mortality processes may also occur during the hunting season (see above), the assumption that compensatory mortality occurs only after the hunting season (e.g., Errington 1945, Runge and Boomer 2005) may not be correct.

DOES THE AHM PROGRAM FOR MIDCONTINENT MALLARDS PROVIDE SUPPORT FOR AN ADDITIVE MODEL?

The AHM program in the United States, is used to annually establish hunting regulations for mallards and, indirectly for other species (Johnson et al. 2002). Each year 4 population models (2 each for additive and compensatory mortality hypotheses) within AHM are used to predict population size the next year (Johnson et al. 1997). A probability distribution is generated for each model centered on the prediction and with variance representing various uncertainties and sampling errors in parameter estimates used in the models. The position of the estimated population size the next year, based on the May Breeding Population Survey (Cowardin and Blohm 1992), in the probability distribution for a given model then provides an estimate of the probability that model is correct. These weights are updated each year using a Bayesian process, in which the previous year's model probabilities (weights) serve as prior probabilities. Recent model weights were 0.4 for the compensatory models and 0.6 for the additive models (USFWS 2007).

The current AHM process applies a penalty on harvest, when the mallard population is below the North American Waterfowl Management Plan goal. This penalty results in more restrictive harvests when populations are low, as in past practice. Density-dependent mortality is not explicitly modeled in current AHM, creating a potential bias within AHM toward additive models for reasons discussed earlier (Fig. 2). Conn and Kendall (2004) recently showed in a simulation study that AHM tended to favor additive harvest models even when the population was regulated entirely by density-dependent processes. Conn and Kendall (2004) used the AHM regulations packages current at the time, which retained a positive correlation between harvest regulations and population size (Conn and Kendall 2004). Because density dependence in the mortality process is not explicitly modeled in the AHM process, spurious correlations (Fig. 2) provide a reasonable hypothesis explaining this result. We, thus, predict that using a regulatory framework that was neutral to population size (as would be produced if the North American Waterfowl Management Plan Goal was removed from the current AHM objective function) would favor compensatory harvest mortality models in the Conn and Kendall (2004) simulations. Most importantly, however, Conn and Kendall (2004) demonstrate the potential for the current AHM program to support additive harvest models, even when populations are governed entirely by density-dependent processes.

AHM MODELS FOR NORTHERN PINTAILS

Adaptive management has been implemented for northern pintails and formal modeling approaches have been employed for management of eastern and western mallard stocks and lesser scaup (USFWS 2011). Currently, only the management of northern pintails and mallards considers competing additive and compensatory harvest mortality models (USFWS 2011) so we do not consider models for other species or stocks here.

For northern pintails, harvest is assumed to be fully additive in additive harvest models. The compensatory harvest model assumes all compensation occurs after the hunting season. Performance of compensatory versus additive harvest models in predicting the size of the breeding population the next year is the basis for evaluating additive versus compensatory harvest mortality (Runge and Boomer 2005, USFWS 2011). Currently, the additive harvest mortality model is receiving greater model weights than the compensatory model (USFWS 2011), apparently providing support for the additive harvest mortality model. In our view, 3 problems are associated with this interpretation. First, adding harvest mortality to a model containing only population size only marginally improved prediction of population size the next year. A model containing only population size in year t explained 78% of population size in year $t + 1$, whereas a model containing both population size and harvest explained 82% of the variation in population size in year $t + 1$ (Runge and Boomer 2005). The fact that adding harvest increased model r^2 only from 0.78 to 0.82 indicates that the variable harvest had little effect on population dynamics. Second, the model allowing for compensation predicted a smaller population the next year than a model lacking compensation (Runge and Boomer 2005). We cannot envision a biologically realistic mechanism by which compensatory mortality could reduce population size below that occurring when harvest mortality is entirely additive. Predictions of the additive and compensatory harvest models for northern pintails suggest that the current compensatory mortality model does not correctly capture the biological mechanism by which harvest mortality is compensated.

The third piece of evidence that population dynamics of northern pintails do not support the hypothesis of additive harvest mortality is that annual survival has been relatively invariant over the past 50 years, despite substantial variation in harvest rates (Rice et al. 2010). Rice et al. (2010) failed to detect an effect of harvest regulations on annual survival in northern pintails, nor did they detect an increase in survival in response to substantially reduced harvest rates (indexed by band recovery rates) that resulted from implementation of restrictive harvest regulations for northern pintails in the 1980s. Rice et al. (2010) noted that low population levels coincided with restrictive harvest regulations, so effects of these 2 factors cannot be separated. Both low population size and restrictive harvest should be expected to increase survival under hypotheses of either density-dependent mortality or additive harvest mortality. Failure of annual survival to increase when both harvest mortality and population size declined, however, suggests that additive harvest mortality has little influence on annual survival in northern pintails.

NORTH AMERICAN MALLARD HARVEST AS INTERPRETED BY PÖYSÄ ET AL.

Pöysä et al. (2004) reviewed studies of harvest and survival in North American mallards and reached the conclusion that shifts in the ecology of North American mallards have caused harvest mortality to change from compensatory to additive over the last 3 decades. Pöysä et al. (2004) updated Nichol's (1991: Table 24.1) analysis by including the study of Smith and Reynolds (1992). Pöysä et al. categorized each study by the date of publication into 4 time intervals (1976–1980, 1981–1985, 1986–1990, 1991–1995) and tallied the number of tests that provided support for either the compensatory or additive hypothesis in each interval. Their Figure 1 suggests multiple tests of the relationship between harvest and survival within each time interval and indicates that the proportional support for the additive model has changed from 0% in 1976–1980 to 75% in 1991–1995. The sample size for each of the 4 time periods ($n = 16$, 14, 12, 8) gives the impression that a large number of independent tests have been conducted.

We believe this analysis is somewhat misleading for 3 reasons. First, the tests tallied in Pöysä et al. (2004: Fig. 1 and Table 1) are not independent. Many of the studies examine approximately the same series of years, albeit with different analytical procedures. Hence, the different studies do not necessarily use independent data sets. More importantly, in several studies considered by Pöysä et al. (2004), the data are analyzed multiple ways in a single study. For example, Smith and Reynolds (1992) analyzed the same data set using 2 different methods to estimate survival:

model H_{02} of Brownie et al. (1985), which assumes that survival during each period of comparison was constant, versus models H_1 or H_2 of Brownie et al. (1985), wherein survival was estimated annually and subsequently averaged for each period of comparison. Similarly, Trost (1987) tested for a relationship between harvest and survival for each age and sex class using several analyses, including: 1) correlation of continental survival rate and harvest rate, and 2) using partitioned data sets to estimate survival rate and harvest rate independently (as per Nichols and Hines 1983), and conducting subsequent analyses comparing survival and harvest among years within areas, between years of high and low harvest, and among areas. Hence, although these studies are notable for their thoroughness in examining the same data using a variety of approaches, they do not constitute independent tests per se.

Second, when harvest regulations are changed in North America, they are changed in a similar direction for all age and sex classes. For example, when harvest is restricted for adult males, it is also restricted for the other 3 age and sex classes, although not always the same magnitude. All age and sex classes experience the same length of hunting season but bag limits may differ for the sexes. Thus, patterns for the 4 age and sex classes do not provide independent assessments of the effect of harvest on survival.

Also, Pöysä et al. (2004) tallied studies with reference to the year of publication, not the years for which the data were collected. An ideal analysis would partition the data into the 4 time intervals and ask whether the relationship between harvest rate and survival varied among those intervals. Pöysä et al. (2004) ask instead whether studies published in the different time intervals—often using many or all of the same years of data—vary in their support for either hypothesis. This is more problematic, especially when one considers the number of studies rather than the number of tests as the sample size. For example, the interval 1986–1990 is represented by only a single study, that of Trost (1987). Pöysä et al. (2004) indicate in Figure 1 that the sample size for this interval is 12, yet these are all variants of the tests performed by Trost (1987), of which 10 of the 12 used the same partitioned data set of mallards banded and recovered during 1975–1985. Based on his extensive analysis, Trost (1987) concluded that the relationship between harvest and survival remained ambiguous.

Likewise, the interval of 1991–1995 is represented by only a single study, that of Smith and Reynolds (1992). Again, although the sample size is listed as 8 tests, these represent analyses for each of the 4 age–sex classes and using 2 methods of estimating survival (see above). Smith and Reynolds's (1992) study is notable because it is 1 of the few that provide evidence that survival rates increased when harvest rates declined (Caswell et al. 1985 present similar evidence for 1 region in SW Manitoba). Using a composite test statistic and 1 method of estimating survival (H_{02} of Brownie et al. 1985), Smith and Reynolds (1992) found evidence consistent with an additive mortality hypothesis for 3 of 4 age–sex classes and marginally for the fourth (Smith and Reynolds 1992: Table 4); using a second method of estimating survival (H_1 and H_2 of Brownie et al. 1985), the composite test statistic was significant for 2 of 4 age–sex classes (Smith and Reynolds 1992: Table 5). When all tests were summed, Pöysä et al. (2004) estimated that 75% (6 of 8) supported the additive mortality hypothesis. Smith and Reynolds's (1992) study constitutes the entire evidence that the additive mortality paradigm has shifted in the 1990s.

We note several difficulties with this interpretation. First, Smith and Reynolds (1992) reported considerable geographic variation in analyses that detected a change in survival consistent with the additive harvest mortality hypothesis; 10 of 26 tests (each age, sex, and region) were significant at $P < 0.10$ using method H_{02} and 8 of 32 tests were significant using test H_1 and H_2. Hence, support for the additive mortality hypothesis did not apply to all, or even the majority, of banding reference areas (see also Trost 1987, Nichols 1991 for discussion of geographic variation in harvest relationships). Second, an alternative hypothesis based on density-dependent mortality can account nearly equally well for Smith and Reynolds's (1992) results, indicating that the conclusion of additive mortality may be premature (Sedinger and Rexstad 1994, but see Smith and Reynolds 1994). Finally, even assuming that Smith and Reynolds's (1992) results hold, the evidence for a shift in the mortality paradigm reported by Pöysä et al. (2004) relied essentially on a single study that was published 2 decades ago. No new data were presented and as we discuss earlier, other evidence from the AHM model cited in support of the paradigm shift was incorrect. Hence, although the ideas of Pöysä et al. (2004) are provocative and merit further investigation, we question whether they provide evidence that harvest has become increasingly additive in recent decades for North American mallards.

CONCLUSIONS

We argue that there is no convincing evidence that harvest mortality of North American dabbling ducks is currently additive to other sources of mortality. We acknowledge that current tests of the relationship between harvest and survival are relatively weak because of the confounding of population size, harvest rate, and survival. We believe 1 approach that could improve our understanding of the relationship between harvest and survival involves stabilizing harvest regulations. Producing less variable harvest rates would decouple the correlation between harvest rate and population size, improving our ability to assess the role of harvest in the annual survival process. This strategy has little risk because of the weak relationship between harvest and survival at current harvest rates. Furthermore, duck populations are highly prolific under good wetland conditions and have the capacity for rapid increase even if harvest rates were too high for a short period. We note that using stabilized regulations to improve our understanding of the mortality process in ducks was advocated >30 years ago and led to the harvest regulations in place during the first half of the Smith and Reynolds (1992) study (e.g., Nichols et al. 1984). Rice et al. (2010) also note the potential for "experimental harvest regulations" to improve our understanding of the relationship between harvest and annual survival in North American ducks.

Releasing individuals throughout the year may allow us to better understand seasonal variation in survival. Because most duck banding occurs in the few weeks or months before the hunting season begins, partitioning mortality into time periods less than 1 year is not possible. Use of pre- and post-season banding represents a simple version of this approach (e.g., Reynolds et al. 1995). We recognize several technical and biological issues (e.g., stock identification) associated with this approach, but the potential to better understand the mortality process at finer temporal scales suggests that effort devoted to understanding these issues might bear fruit in the context of improving harvest management.

In summary, we agree with Pöysä et al. (2004) that the relationship between harvest and annual survival is an important issue for managers. We do not, however, believe there is currently good evidence that harvest mortality is additive to other forms of mortality in dabbling ducks. In fact, we see no new evidence that would favor a shift from the conclusion of Anderson and Burnham (1976) over 3 decades ago that harvest mortality was primarily compensatory to other mortality in North American mallards.

MANAGEMENT IMPLICATIONS

Our uncertainty about the role of harvest in the mortality process for North American duck populations has 3 potential management implications. First, if regulations are established under an additive harvest mortality scenario, when in fact harvest mortality is compensatory, harvest opportunity will have been lost and harvest rates will not be optimum. Restrictive harvest regulations have been cited as 1 factor leading to reduced numbers of hunters; consequently, overly restrictive harvest regulations may have sociological consequences. Second, the historical pattern of harvest regulations tracking population size, which rests on an implicit assumption that harvest mortality is additive, reinforces the natural belief in additivity of harvest among managers and the public. This belief, in turn, may be manifested in pressure for more restrictive harvest regulations through public input and the political process. Finally, to the extent that harvest is viewed as a principal regulator of duck populations, emphasis may be shifted away from habitat programs.

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LITERATURE CITED

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65:781–796.

Alisauskas, R. T., K. L. Drake, S. M. Slattery, and D. K. Kellett. 2006. Neckbands, harvest, and survival of Ross's geese from Canada's central arctic. Journal of Wildlife Management 70:89–100.

Amundson, C. L., and T. W. Arnold. 2011. The role of predator removal, density-dependence, and environmental factors on mallard duckling survival in North Dakota. Journal of Wildlife Management 75:1330–1339.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publication 128, Washington D.C., USA.

Anderson, M. G., M. S. Lindberg, and R. B. Emery. 2001. Probability of survival and breeding for juvenile canvasbacks. 2001. Journal of Wildlife Management 65:385–397.

Ankney, C. D. 1996. Why did the ducks come back in 1994 and 1995: was Johnny Lynch right? Proceedings of the International Waterfowl Symposium 7:40–44.

Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. Pages 204–227 *in* A. van der Valk, editor. Northern prairie wetlands. Iowa State University Press, Ames, USA.

~~Boomer~~[Q4]~~, G. S., and F. A. Johnson. 2007. A proposed assessment and decision-making framework to inform scaup harvest management. Report, Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Laurel, Maryland, USA.~~

Botzler, R. G. 1991. Epizootiology of avian cholera in wildfowl. Journal of Wildlife Diseases 27:367–395.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data—a handbook. Second edition. U.S. Fish Wildlife Service Resource Publication 15, Washington, D.C., USA.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

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.

Caswell, F. D., G. S. Hochbaum, and R. K. Brace. 1985. The effect of restrictive regional hunting regulations on survival rates and local harvests of southern Manitoba mallards. Transactions of the North American Wildlife and Natural Resources Conference 50:549–556.

Conn, P. B., and W. L. Kendall. 2004. Evaluating mallard adaptive management models with time series. Journal of Wildlife Management 68:1065–1081.

Conroy, M. J., and W. W. Blandin. 1984. Geographic and temporal differences in band reporting rates for American black ducks. Journal of Wildlife Management 48:23–36.

Coulson, T. N., S. D. Albon, J. M. Pemberton, J. Slate, F. E. Guiness, and T. H. Clutton-Brock. 1998. Genotype by environment interactions in winter survival in red deer. Journal of Animal Ecology 67:434–445.

Cowardin, L. M., and R. J. Blohm. 1992. Breeding population inventories and measures of recruitment. Pages 423–445 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

Crissey, W. F. 1969. Prairie potholes from a continental viewpoint. Pages 161–171 *in* Saskatoon wetlands seminar. Canadian Wildlife Service Report Series 6, Ottawa, Canada.

Delnicki, D., and K. J. Reinecke. 1986. Mid-winter food use and body weights of mallards and wood ducks in Mississippi. Journal of Wildlife Management 50:43–51.

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.

Dzubin, A. 1969. Comments on carrying capacity of small ponds for ducks and possible effects of density on mallard production. Pages 138–160 *in* Saskatoon wetlands seminar. Canadian Wildlife Service Report Series 6, Ottawa, Canada.

Elmberg, J. 2003. Density dependent breeding success in mallards *Anas platyrhynchos* on a eutrophic lake. Wildlife Biology 9:67–73.

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.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Changes in survival rates of lesser snow geese with age and breeding status. Auk 109:731–747.

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Greenwood, H., R. G. Clark, and P. J. Weatherhead. 1986. Condition bias of hunter-shot mallards (*Anas platyrhynchos*). Canadian Journal of Zoology 64:599–601.

Heitmeyer, M. E., and L. H. Fredrickson. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence mallard recruitment? Transactions of the North American Wildlife and Natural Resources Conference 46:44–57.

Hestbeck, J. B. 1996. Northern pintails: have the paradigms changed? Proceedings of the International Waterfowl Symposium 7:45–49.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883–900.

Johnson, D. H., and J. W. Grier. 1988. Determinants of breeding distributions of ducks. Wildlife Monographs 100.

Johnson, F. A., W. L. Kendall, and J. A. Dubovsky. 2002. Conditions and limitations on learning in the adaptive management of mallard harvests. Wildlife Society Bulletin 30:176–185.

Johnson, F. A., C. T. Moore, W. L. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Kelley, Jr., and B. K. Williams. 1997. Uncertainty and the management of mallard harvests. Journal of Wildlife Management 61:202–216.

Kaminski, R. M., and E. A. Gluesing. 1986. Density- and habitat-related recruitment in mallards. Journal of Wildlife Management 51:141–148.

Krementz, D. G., M. J. Conroy, J. E. Hines, and H. F. Percival. 1988. The effects of hunting on survival rates of American black ducks. Journal of Wildlife Management 52:214–226.

Lebreton, J.-D. 2005. Dynamical and statistical models for exploited populations. Australian New Zealand Journal of Statistics 47:49–63.

Lynch, J. J. 1984. Escape from mediocrity: a new approach to American waterfowl hunting regulations. Wildfowl 35:5–13.

Miller, M. R., and W. E. Newton. 1999. Population energetics of northern pintails wintering in the Sacramento Valley, California. Journal of Wildlife Management 63:1222–1238.

Nichols, J. D. 1991. Responses of North American duck populations to exploitation. Pages 498–521 *in* C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, United Kingdom.

Nichols, J. D., R. J. Blohm, R. E. Reynolds, R. E. Trost, J. E. Hines, and J. P. Bladen. 1991. Band reporting rates for mallards with reward bands of different dollar values. Journal of Wildlife Management 55:119–126.

Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of the North American Wildlife and Natural Resources Conference 49:535–554.

Nichols, J. D., and J. E. Hines. 1983. The relationship[Q5] between harvest and survival rates of mallards: a straightforward approach with partitioned data sets. Journal of Wildlife Management 334–348.

Nichols, J. D., R. E. Reynolds, R. J. Blohm, R. E. Trost, J. E. Hines, and J. P. Bladen. 1995. Geographic variation in band reporting rates for mallards based on reward banding. Journal of Wildlife Management 59:697–708.

Nichols, J. D., M. C. Runge, F. A. Johnson, and B. K. Williams. 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. Journal of Ornithology 148:S343–S349.

Pöysä, H., J. Elmberg, G. Gunnarsson, P. Nummi, G. G. Sjöberg, and K. Sjöberg. 2004. Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? Oikos 104:612–615.

Raveling, D. G., and M. E. Heitmeyer. 1987. Relationships of population size and recruitment of pintails to habitat conditions and harvest. Journal of Wildlife Management 53:1088–1103.

Rexstad, E. A. 1992. Effect of hunting on annual survival of Canada geese in Utah. Journal of Wildlife Management 56:297–305.

Rexstad, E. A., and D. R. Anderson. 1992. Heterogeneous survival rates of mallards (*Anas platyrhynchos*). Canadian Journal of Zoology 70:1878–1885.

Reynolds, R. E., R. J. Blohm, J. D. Nichols, and J. E. Hines. 1995. Spring-summer survival rates of yearling versus adult mallard females. Journal of Wildlife Management 59:691–696.

Rhodes, O. E., T. L. DeVault, and L. M. Smith. 2006. Seasonal variation in carcass composition of American widgeon wintering in the southern High Plains. Journal of Field Ornithology 77:220–228.

Rice, M. B., D. A. Haukos, J. A. Dubovsky, and M. C. Runge. 2010. Continental survival and recovery rates of northern pintails using band-recovery data. Journal of Wildlife Management 74:778–787.

Runge, M. C., and G. S. Boomer. 2005. Population dynamics and harvest management of the continental northern pintail population. Final Report, Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

SAS Institute. 2001. The SAS System for Windows, version 8.2. SAS Institute, Inc., Cary, North Carolina, USA.

Schmutz, J. A., and J. A. Morse. 2000. Effects of neck collars and radio transmitters on survival and reproduction of emperor geese. Journal of Wildlife Management 64:231–237.

Sedinger, J. S., and N. D. Chelgren. 2007. Survival and breeding advantages of larger black brant (*Branta bernicla nigricans*) goslings: within- and among-cohort variation. Auk 124:1281–1293.

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 E. R. Rexstad. 1994. Do restrictive harvest regulations result in higher survival rates in mallards? A comment. Journal of Wildlife Management 58:571–577.

Smith, G. W., and R. E. Reynolds. 1992. Hunting and mallard survival, 1979–88. Journal of Wildlife Management 56:306–316.

Smith, G. W., and R. E. Reynolds. 1994. Hunting and mallard survival: a reply. Journal of Wildlife Management 58:578–581.

Stafford, J. D., R. M. Kaminski, K. J. Reinecke, and S. W. Manley. 2007. Waste rice for waterfowl in the Mississippi Alluvial Valley. Journal of Wildlife Management 70:61–69.

Trost, R. E. 1987. Mallard survival and harvest rates: a reexamination of relationships. Transactions of the North American Wildlife and Natural Resources Conference 52:264–284.

United States Fish and Wildlife Service [USFWS]. 2004. Waterfowl population status, 2004. U.S. Department of the Interior, Washington, D.C., USA.

United States Fish and Wildlife Service [USFWS]. 2007. Adaptive harvest management: 2007 duck hunting season. U.S. Department of the Interior, Washington, D.C., USA.

United States Fish and Wildlife Service [USFWS]. 2010. Northern pintail harvest strategy 2010. U.S. Department of the Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Washington, D.C., USA.

United States Fish and Wildlife Service [USFWS]. 2011. Adaptive harvest management: 2010 hunting season. U.S. Department of the Interior, Washington, D.C., USA.

Walters, C. 1986. Adaptive management of renewable resources. Caldwell Press, Caldwell, New Jersey, USA.

Wilkins, K. A., and M. C. Otto. 2003. Trends in duck breeding populations, 1955–2003. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Administrative Report, Washington, D.C., USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wobeser, G., D. J. Rainnie, T. B. Smith-Windsor, and G. Bogdan. 1983. Avian botulism during late autumn and early spring in Saskatchewan. Journal of Wildlife Diseases 19:90–94.

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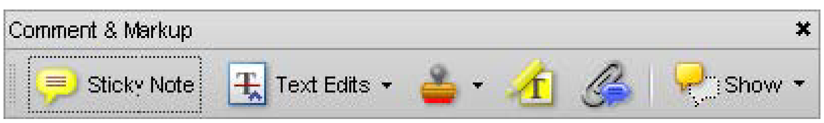

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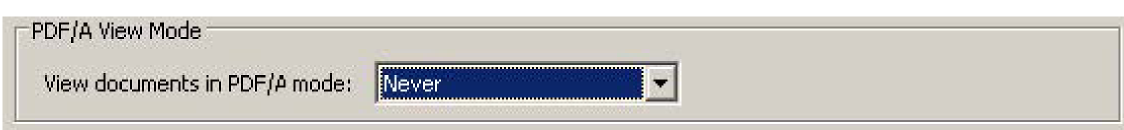

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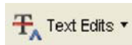
Click the ‘Text Edits’ 

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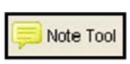
Click on the ‘Note Tool’ 

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