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Original article

Effects of hunting season structure, weather and body condition on overwintering mallard *Anas platyrhynchos* survival

Joshua L. Dooley, Todd A. Sanders & Paul F. Doherty, Jr.

Information on waterfowl survival during the overwintering season (i.e. autumn and winter), when hunting seasons occur, is important for making harvest management decisions. However, the relationship of overwintering survival to hunting season structure, weather and body condition are not well understood. We measured survival of 235 radio-marked adult female and male mallards *Anas platyrhynchos* along the South Platte River corridor in northeastern Colorado, USA, during the overwintering seasons of 2005/06 (pilot year), 2006/07 and 2007/08, and we determined the primary factors affecting survival. Hunting was the most important factor affecting survival. Of mortality, 67% were direct results of hunting, and survival was lower during hunting periods compared to non-hunting periods. Within hunting periods, survival was lowest during the first 2-3 weekends of the hunting periods. During the seasons 2006/07 and 2007/08, survival of radio-marked mallards was monitored during September-February. The estimated survival was 0.65 (95% CI=0.50 - 0.78) for females and 0.54 (95% CI=0.39 - 0.68) for males during 2006/07, and 0.55 (95% CI= 0.40 - 0.69) for females and 0.42 (95% CI=0.28 - 0.58) for males during 2007/08. We did not observe a strong correlation between body condition index and survival ($\tilde{\beta} = 0.36$, SE = 0.43). Accumulated snowfall and daily minimum temperature were unimportant variables for predicting survival. Of hunting recoveries, 89% occurred in our study area, and 15% and 18% of radio-marked mallards went missing during 2006/07 and 2007/08, respectively. Our results suggest that split hunting seasons are an effective management tool to increase hunter harvest and affect overwintering survival. Given a set bag limit and season length, managers may be able to increase hunter harvest by: 1) having hunting periods of at least three weeks in length, 2) including as many weekend days (i.e. Saturdays and Sundays) within hunting periods as possible and 3) interspersing hunting periods with non-hunting periods of at least 2-3 weeks.

Key words: Anas platyrhynchos, body condition, hunting regulations, mallard, split hunting season, survival, winter

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Waterfowl managers rely upon estimates of survival to aid in assessing waterfowl population status and to guide management decision-making (Nichols et al. 1995, Johnson et al. 1997). Overwintering survival (i.e. autumn and winter) is important to managers because hunter harvest during regulated hunting seasons occurs during this period (Anderson 1975, Nichols et al. 2007) and hunter harvest and survival can be influenced by hunting regulations (Smith & Reynolds 1992, Menu et al. 2002, Otis 2004, U.S. Fish and Wildlife Service 2008). One regulation type available to U.S. states are split hunting seasons, where the hunting season is divided into two or more segments (Ladd et al.

1989). The U.S. Fish and Wildlife Service first offered the split-season option to all U.S. states in 1948 (Ladd et al. 1989), and by the mid-1980s, approximately half of the states in the U.S. adopted split hunting seasons (Baldassarre & Bolen 2006). The intention of split hunting seasons is to increase hunter success and opportunity by better allocating hunting days to match waterfowl migrations through an area and by restoring waterfowl naivety to hunting pressure during non-hunting periods (Baldassarre & Bolen 2006). However, the efficacy of split hunting seasons has only been investigated a little and the relationship of overwintering waterfowl survival to time periods within the hunting season is little known.

Previous studies have found hunting to be the main cause of waterfowl mortality during the overwintering season (Migoya & Baldassarre 1995, Cox et al. 1998, Fleskes et al. 2002, Fleskes et al. 2007), and lower survival has been documented during hunting periods compared to non-hunting periods (Cox et al. 1998, Fleskes et al. 2002, Moon & Haukos 2006). Additionally, Fleskes et al. (2007) found an inverse relationship between overwintering survival of female mallards *Anas platyrhynchos* in central California, USA, and the number of hunting days. Hunting decreases survival directly through hunter harvest and crippling, and indirectly through disturbance, which increases energy usage and causes waterfowl to avoid more preferred feeding and roosting areas (Fox & Madsen 1997). With regard to waterfowl survival within hunting periods, waterfowl mortality has been documented as being higher at the onset of hunting periods (Longcore et al. 2000, Davis 2007, Fleskes et al. 2007), likely due to waterfowl naivety to hunting pressure and increased hunter participation. Other studies, however, have found mortality from hunting to be lower than, or similar to, other causes of mortality (Bergan & Smith 1993, Bielefeld & Cox 2006, Moon & Haukos 2006) and have observed similar (Miller et al. 1995, Lee et al. 2007) or lower (Davis 2007) survival during non-hunting periods, than during hunting periods.

Overwintering waterfowl survival is additionally affected by environmental factors and body condition. Higher overwintering survival has been documented during years of increased precipitation and better habitat conditions (Migoya & Baldassarre 1995, Moon & Haukos 2006, Fleskes et al. 2007). Bergan & Smith (1993) found that survival of female mallards in the Playa Lakes Region of northwestern Texas, USA, decreased following severe weather conditions (i.e. five days of 0 °C with snow cover) as did Jeske (1991) for female mallards in the San Luis Valley of Colorado, USA, particularly after snow accumulation which reduced food availability. The relationship between body condition and overwintering survival has also received much attention, but patterns are less general. Some studies have supported the hypothesis that better body condition increases overwintering survival and decreases susceptibility to harvest (Hepp et al. 1986, Dufour et al. 1993, Heitmeyer et al. 1993, Robb 2002), while other studies have not found this relationship (Jeske et al. 1994, Cox et al. 1998, Lee et al. 2007). Individuals in poor body condition may be more likely to be unpaired and thus more easily attracted to decoys, more susceptible to disease, forced to use habitats with greater hunting pressure and less focused on predator and hunter avoidance due to spending more time searching for food (Hepp et al. 1986, Fleskes et al. 2002). Body condition of mallards has been shown to decrease during cold weather events (Whyte & Bolen 1984, Robb et al. 2001). Colorado mallards may be more vulnerable to mortality after severe weather because of low endogenous energy stores (Jeske 1991, Dugger et al. 1994).

Uncertainty exists for the factors affecting overwintering waterfowl survival, and no study, to our knowledge, has empirically tested for effects associated with the opening of hunting periods. Given this uncertainty and the widespread application of split hunting seasons in the USA, we estimated adult mallard daily survival rates along the South Platte River corridor in northeastern Colorado during September - February. We tested *a priori* hypotheses about differences in survival between years, sexes, different non-hunting and hunting periods and time intervals within hunting periods (i.e. beginning 1-3 weeks of hunting periods, weekends and holiday weeks), and determined the impact of body condition and environmental conditions (i.e. daily minimum temperature and accumulated snowfall) on overwintering survival. Based upon our findings, we provide recommendations that may be used by managers to affect overwintering survival.

Material and methods

Study area

We conducted our study on the South Platte River

corridor (i.e. ≈ 10 km buffer surrounding the South Platte River) in Logan, Morgan, Sedgwick and Washington counties in northeastern Colorado. Most wetlands and bodies of water in these counties are within the South Platte River corridor. During 2005/06, the pilot study year, our study area included the South Platte River corridor from Fort Morgan east to the Colorado-Nebraska state line, approximately 150 contiguous kilometres. During 2006/07 and 2007/08, two smaller study areas within the 2005/06 study area were used. The eastern study area extended from the town of Sedgwick west to the town of Iliff, approximately 56 km. The western study area extended from the town of Sterling west to Snyder, approximately 48 km. Natural vegetation is shortgrass prairie, dominantly grama species *Bouteloua* spp. and buffalograss *Buchloe dactyloides* with cottonwoods *Populus* spp. occurring along wetlands (Ringelman et al. 1989). Primary use of the landscape is cattle production and farming, primarily corn.

Trapping and tracking

We radio-marked 235 adult (after-hatch year) mallards during the overwintering seasons of 2005/06 (pilot year), 2006/07 and 2007/08: 14 females and 24 males in 2005/06, 35 females and 60 males in 2006/07 and 54 females and 48 males in 2007/08. Mallards were trapped with baited swim-in or walk-in funnel traps during September-January, except that trapping started in late November during the 2005/06 season. We measured body weight (g) and wing length (mm) upon capture, except during 2005/06 ($N = 38$), to calculate body condition index (BCI = body weight/wing length; Ringelman & Szymczak 1985). We used backpack VHF radio-tags, which weighed approximately 25 g (model A1820 manufactured by Advanced Telemetry Systems (ATS)). Battery life was approximately nine months. Radio-marked mallards were located with vehicle mounted Yagi antennas. Overwintering survival was monitored from 1 December - 21 February during 2005/06, 15 September - 10 February during 2006/07 and 9 September - 13 February during 2007/08.

During 2005/06, radio-marked mallards were located on average three times per day (range: 1-15) for 3-7 consecutive days separated by 1-15 days of no monitoring. During 2006/07 and 2007/08, radio-marked mallards were located 2-3 times per day for approximately two weeks separated by 3-19 days of no monitoring. Radio-tags sending a mortality signal (i.e. signal doubled in frequency after four hours of inactivity) were recovered as soon as possible to determine cause of death. Carcasses, when available, were inspected for signs of predation and hunter crippling (i.e. shotgun pellet wounds and shattered bones). We recorded mallards found dead from apparent crippling and those reported harvested by hunters as hunting mortalities. All other mortalities were recorded as non-hunting mortalities (also known as natural mortalities; see Bergan & Smith 1993, Moon & Haukos 2006, Davis 2007).

Statistical analysis

We used the nest survival model (Dinsmore et al. 2002, Rotella et al. 2004) in Program MARK (White & Burnham 1999) to estimate daily survival rates. The nest survival model can be extended to other known-fate data such as radio-telemetry data, when marked animals are not monitored at regular intervals of time (Schwartz et al. 2006, Mong & Sandercock 2007), as were our data. We excluded all data from the first four days after radio-tag attachment to avoid mortality and emigration biases associated with capture, handling and radio-tag effects (Cox & Afton 1998). Radio-marked mallards with no detectable signal within our study area or those that were recovered dead outside our study area were censored from the survival analysis at the last time they were located alive within our study area.

Based on previous research, preliminary modeling and to keep the size of our model set manageable, we included sex and a parameter designating hunting periods from non-hunting periods in all models. We considered other variables to examine variation in mallard survival relative to year (2005/06, 2006/07 and 2007/08), different hunting periods (H), different non-hunting periods (NH), time intervals within hunting periods (opening effect for one, two or three weeks (1 WK, 2 WK and 3 WK), holiday effect (HOL), quadratic trend across time (T^2), body condition index (BCI) and environmental factors (accumulated snowfall (SNOW) and daily minimum temperature (TEMP); see Table 1 for descriptions). Temperature and precipitation data were taken from the Akron 4 E, Colorado weather station (National Climatic Data Center 2008), the weather station closest to our study area.

During the pilot study year 2005/06, mallards were captured later and hunting season structure

Table 1. Variables used in overwintering (9 September - 21 February) survival analysis of radio-marked mallards along the South Platte River in northeastern Colorado, USA. Sex and a parameter designating non-hunting periods from hunting periods were included in every model. The opening week effect was modeled constant for the number of weeks specified and a weekend effect was always included to model weekends separately from weekdays. The first week was the opening day of a hunting period until the first Friday. All subsequent weeks were Saturday - Friday. In addition to a similar opening week(s) effect among hunting periods, we modeled an opening week(s) by hunting split interaction (i.e. 1 WK*H, 2 WK*H and 3 WK*H). Body condition index was not recorded during 2005/06.

Variable	Description
1 WK, 2 WK, 3 WK	Opening week effect lasting 1-3 weeks after the beginning of a hunting period
BCI	Body condition index (body mass (g)/wing length (mm))
HOL	Holiday weeks (Thanksgiving holiday: Monday before through Monday after Thanksgiving day and Christmas holiday: the Friday before Christmas through the day after New Year's day)
H	All three hunting periods different
NH	All three non-hunting periods different
SNOW	Accumulated snowfall
T^2	Quadratic trend on survival during hunting periods after the opening week(s) effect
TEMP	Daily minimum temperature
YR	All years different

was different than the following years (Table 2). We expected survival would be higher in 2005/06 because mallards were not exposed to as many hunting days. We included data from this year in our analysis because we wanted to explore effects of weather on survival and were interested in post-hunting survival rates, for which this sample was representative. Weather conditions between 2006/07 and 2007/08 were similar and more severe compared to 2005/06. During the autumn (September - November) and winter (December - February), 86.1 cm of snowfall fell in 2006/07 and 81.0 cm of snowfall fell in 2007/08, compared to 18.0 cm in 2005/06. Average autumn and winter snowfall in this area was 51.5 cm (Akron 4 E, Colorado, 1948 until present day; High Plains Regional Climate Center 2008). Regarding average winter temperature, 2006/07 (-4.9 °C) and 2007/08 (-4.5 °C) had lower average temperatures than 2005/06 (0.0 °C). Average winter temperature in this area was -2.2 °C (Akron 4 E, Colorado, 1948 until present day; High Plains Regional Climate Center 2008).

We used Akaike's Information Criterion with small sample size adjustment (AIC_c) and AIC_c weights to evaluate our candidate model set (Burnham & Anderson 2002). We used a balanced model set so that predictor variables were included equally and used cumulative variable weights to determine relative importance of predictor variables (Burnham & Anderson 2002). We model-averaged daily survival estimates and β estimates of interest using all models with AIC_c weight (Burnham & Anderson 2002). Cumulative survival rates for males and females for each study year were calculated from the daily survival estimates. Cumulative survival rate is the overall survival rate for the entire time period in which radio-marked mallards were monitored each year. Goodness-of-fit tests were not possible with the nest survival model (Dinsmore et al. 2002, Schwartz et al. 2006), and we suspected little dependence in our sample because of the small number of individuals radio-marked at the same location during the same trapping occasion (i.e. average and median = 3, range: 1 - 8). Thus, no adjustment for overdispersion was made.

Results

Mortalities and missing radio-marked mallards

Of the 235 radio-marked mallards, 64 (28%) died, 130 (57%) survived, 1 (< 1%) shed its radio-tag and 33 (14%) went missing within our study area during the same study year of radio-marking. Seven radio-marked male mallards were censored from analysis

Table 2. Timeline of the overwintering season divided by non-hunting periods (PRE = pre-hunting period, BTW = between hunting periods, POST = post-hunting period) and hunting periods (H1-H3) for the South Platte River in northeastern Colorado, USA, September 2005 - February 2008. Colorado changed from three hunting periods in 2005/06 to two hunting periods in 2006/07. Mallards were first radio-marked at the end of the second hunting period in 2005/06 (i.e. survival period began 1 December).

Year	PRE	H1	BTW	H2	BTW	H3	POST
2005/06	-	-[a]	-	1 - 4 Dec.[a]	5 - 10 Dec.	11 Dec. - 22 Jan.	23 Jan. - 22 Feb.
2006/07	15 - 29 Sep.	30 Sep. - 8 Oct.	9 Oct. - 2 Nov.	3 Nov. - 28 Jan.	-	-	29 Jan. - 10 Feb.
2007/08	9 Sep - 5 Oct.	6 - 22 Oct.	23 Oct. - 9 Nov.	10 Nov. - 27 Jan.	-	-	28 Jan. - 13 Feb.

[a] H1 and H2 for 2005/06 were 1 October - 23 September and 5 November - 4 December, respectively.

due to mortality (N = 3), never being located (N = 3) or known radio-tag malfunction (N = 1) within four days after radio-tag attachment. Of the 64 (67%) mortalities, 43 were hunting mortalities (i.e. we classified four of the 43 as hunting mortality based on carcass inspection in the field, while the other 39 were reported by hunters). The percentage of hunting mortality compared to non-hunting mortality was higher for males, 75% (27 of 36), compared to females, 57% (16 of 28). The exact location of mortality was known (i.e. talked to hunter or personally retrieved radio-tag) for 42 of the 43 hunting mortalities. Of the radio-marked mallards, 18 (43%) were shot on public lands and 24 (57%) radio-marked mallards were shot on private lands.

Three additional hunting mortalities occurred during the same study year of radio-marking, but outside our study area, and nine mortalities occurred after the year of radio-marking, either inside (N = 6) or outside (N = 3) our study area. Thus, 89% (49 of 55) of all known hunting mortality of radio-marked mallards occurred in our study area. Hunting mortalities outside our study area occurred in Colorado, Alberta, Kansas, Nebraska (N = 1, respectively) and Texas (N = 2).

Radio-marked mallard survival

There was strong support for survival differing among the three years (YR; cumulative variable weight = 0.92; Table 3). Differences in survival among different non-hunting periods (NH; cumulative variable weight = 0.16) and among different hunting periods (H; cumulative variable weight = 0.24) were less supported (see Table 3). For the opening week(s) effect of hunting periods, three weeks (3 WK; cumulative variable weight = 0.28) and two weeks (2 WK; cumulative variable weight = 0.24) effects were more supported than a one week effect (1 WK; cumulative variable weight = 0.08). There was little support that the opening week(s) effect differed among hunting periods (see Table 3). Of the individual and environmental covariates considered, body condition index (BCI; cumulative variable weight = 0.47) was better supported than accumulated snowfall (SNOW; cumulative variable weight = 0.19) and daily minimum temperature (TEMP; cumulative variable weight = 0.10; see Table 3). There was little support for a holiday effect (HOL; cumulative variable weight = 0.09) or a quadratic trend on survival during hunting periods after the opening week(s) effect (T^2; cumulative variable weight = 0.05; see Table 3).

Table 3. Cumulative variable weights for variables used in a balanced model set to evaluate overwintering (9 September - 21 February) survival of radio-marked mallards along the South Platte River in northeastern Colorado, USA. Cumulative variable weight is the summation of AIC_c model weights in which the variable appears. 1 WK, 2 WK, 3 WK = opening week(s) effect after the beginning of hunting periods, 1 WK*H, 2 WK*H, 3 WK*H = opening week(s) effect by hunting split interaction, BCI = body condition index, H = all hunting periods different, HOL = holiday weeks, NH = all non-hunting periods different, SNOW = accumulated snowfall, TEMP = daily minimum temperature, YR = all years different.

Variable	Weight
YR	0.92
BCI	0.47
3 WK	0.28
2 WK	0.24
H	0.24
SNOW	0.19
NH	0.16
TEMP	0.10
HOL	0.09
1 WK	0.08
3 WK*H	0.07
2 WK*H	0.05
T^2	0.05
1 WK*H	0.02

During the periods 2006/07 and 2007/08, survival was lower during hunting periods compared to non-hunting periods (Fig. 1). Within hunting periods, survival was lowest for the first 2-3 weekends (see Fig. 1). Survival during the weekdays for the first three weeks was comparable to the survival rate observed during the remainder of the second hunting period (see Fig. 1). Of 43 (49%) hunting mortalities, 21 occurred during the first three weeks of hunting periods, with 16 (37%) hunting mortalities occurring during the first three weekends. All hunting mortalities and 16 of the 21 (76%) non-hunting mortalities occurred during hunting periods. Male survival was slightly lower than female survival, particularly during hunting periods. However, the variance of the estimates was large, and a sex effect was not strongly detected with our sample size (see Fig. 1). Cumulative female and male survival was 0.65 (95% CI = 0.50 - 0.78) and 0.54 (95% CI = 0.39 - 0.68) during 2006/07, respectively, and 0.55 (95% CI = 0.40 - 0.69) and 0.42 (95% CI = 0.28 - 0.58) during 2007/08, respectively. There was no radio-marked mallard mortality during 2005/06. Thus, cumulative survival during 2005/06 was 1.00.

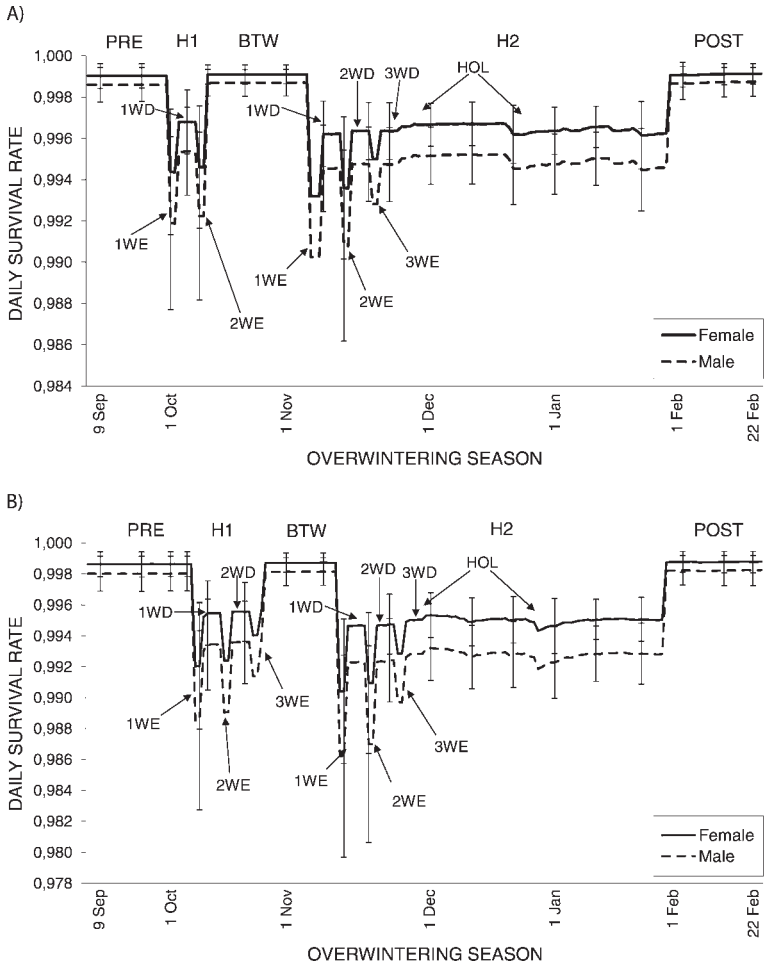

Figure 1. Model-averaged daily survival rates and standard error (SE) for radio-marked mallards along the South Platte River in northeastern Colorado, USA, during the overwintering season (9 September - 21 February) for A) 2006/07 and B) 2007/08. The overwintering season is partitioned into three non-hunting periods (PRE = pre-hunting period, BTW = between hunting periods and POST = post-hunting period) and two hunting periods (H1 = first hunting period and H2 = second hunting period). The first three weeks of hunting periods are divided into weekends (WE: Saturday and Sunday) and weekdays (WD: Monday - Friday). Holiday weeks (HOL) are the Monday before through the Monday after Thanksgiving day and the Friday before Christmas through the day after New Year's day.

There was no difference in survival between holiday and non-holiday weeks (see Fig. 1). Body condition index and survival had a slight positive correlation ($\bar{\beta} = 0.36$, SE = 0.43), but the variance around this estimate was large. Thus, we found little evidence for a body condition index effect with our sample size. Daily minimum temperature and accumulated snowfall had little predictive power ($\bar{\beta}$s were < 0.01).

Discussion

Hunting (67%) was the primary cause of radio-marked mallard mortality. The percent of hunting mortality is most likely an underestimate because dead radio-marked mallards without visible signs of being shot were classified as non-hunting mortalities and hunter-killed carcasses were nearly always depredated before being recovered. Of the 25 mortalities we recovered, four were classified as hunter kill, and it is likely that more of these mortalities were mallards shot but not retrieved by hunters. Norton & Thomas (1994) suggest that hunter crippling loses range from 20-40%. Misclassification of radio-marked mallards crippled by hunters may also explain why a high proportion (76%) of non-hunting mortality occurred during hunting periods. However, hunting is known to indirectly decrease survival by increasing levels of disturbance and by causing waterfowl to avoid more preferred feeding and roosting areas (Fox & Madsen 1997). Similarly, other studies have documented hunting mortality as the primary cause of overwintering mortality for waterfowl populations (Migoya & Baldassarre 1995, Cox et al. 1998, Fleskes et al. 2002, Fleskes et al. 2007), and lower survival during hunting periods compared to non-hunting periods (Cox et al. 1998, Fleskes et al. 2002, Moon & Haukos 2006).

Survival of radio-marked mallards was similar between different hunting periods and was lower during the first three weekends of the hunting periods. Lower survival at the beginning of hunting periods was likely related to mallard naivety to hunting pressure and increased hunter participation, particularly on weekends. Other studies have similarly reported lower survival at the beginning of hunting periods (Longcore et al. 2000, Davis 2007, Fleskes et al. 2007). A noticeable drop in survival three weekends after the beginning of hunting periods suggests that waterfowl take longer than the original onset of hunting (i.e. the first weekend) to adjust their patterns (T.A. Sanders, unpubl. data). The opening effect of hunting on survival was similar between the first and second hunting periods and suggests that a non-hunting period as little as 18-25 days between hunting periods may be adequate to restore mallard naivety to hunting pressure. Within hunting periods after the opening weekends, we observed that there was little difference in mallard survival during holiday weeks, compared to non-holiday weeks, although, according to field observation, hunter participation was assumed to be high during holidays. This suggests increased hunter participation alone may not directly influence survival, but it may largely depend on the timing within the overwintering season.

Year was an important predictor variable of survival because no mortality occurred during 2005/06, whereas survival was lower and similar between 2006/07 and 2007/08. No mortality during 2005/06 was likely a result of our late radio-marking, which resulted in the majority of exposure days occurring after the hunting season. Survival was found to be high during this time period (i.e. POST) in the subsequent two years as well. Also, in 2005/06, hunting season structure was different and weather was more benign than 2006/07 and 2007/08, and these factors may have contributed to the observed high survival rate. Our results are consistent with Dugger et al. (1994), who radio-marked immature and adult female mallards after the 1988 and 1989 hunting seasons in east central Arkansas, USA, and observed no mortality either year.

Hunting mortality was higher for males (75%) than females (57%), and sex-specific differences in mortality were likely a result of sex-specific bag limits (U.S. Fish and Wildlife Service 2008), and possibly hunter preference for males. During the study period, Colorado allowed a daily bag limit of five mallards of which only two could be female. Additionally, females, perhaps because of lower body mass, may be more susceptible to non-hunting mortality during the overwintering season than males, but this effect has been little evaluated. Other studies have documented the proportion of mortality attributed to hunting for female mallards (Bergan & Smith 1993, Davis 2007, Fleskes et al. 2007), but no such estimate was reported for male mallards. Additionally, we were unable to find any published report of male mallard survival during the overwintering season. Our cumulative female overwintering survival estimates during 2006/07 and 2007/08 were lower than other reported overwintering adult female survival estimates (see Fleskes et al. 2007). However, we note that the duration which survival was monitored differed among studies, and survival rates were not directly comparable. Also, survival is a function of site- and temporal-specific conditions, which varied greatly between the studies.

Body condition index was the second highest ranking variable by cumulative AIC_c weight, which suggests body condition index was an important predictor of survival relative to the other variables examined. However, given the large variance surrounding our estimate, we have little confidence in the effect size. Thus, we do not conclude any strong support for a positive association between body condition index and survival. We do note that we recorded body condition index in 2006/07 and 2007/08, when weather was relatively severe, and body condition index may be less related to survival in years with less severe weather. We also note that body condition index was measured at the time of capture and may serve as a poor proxy for body condition index at the time of death.

Accumulated snowfall and daily minimum temperature were unimportant variables predicting survival, even though winter weather during 2006/07 and 2007/08 was more severe than normal. However, most mortality took place at the beginning of hunting periods when weather conditions were generally snow free and temperatures were benign. Also, the effects of weather may compound over the entire duration of the overwintering season, and mortality may lag the original onset of weather events. Additionally, daily minimum temperature and accumulated snowfall were highly correlated (Pearson's correlation: $r = -0.60$). Modeling these variables to represent their true effect poses challenges. Adverse weather effects on survival in this area may only become realized at certain

threshold values, such as cumulative days with high levels of accumulated snowfall and/or low daily temperatures (Dooley 2008). Jeske (1991) and Bergan & Smith (1993) observed lower survival for female mallards after severe winter weather, particularly snow cover which reduces foraging ability. In our study area, radio-marked mallards preferred feeding in corn fields grazed by cattle due to more available spare grain (T.A. Sanders, unpubl. data), a pattern that has been previously documented (Jorde et al. 1983). Waterfowl may be little affected by low accumulations of snow when livestock are present because livestock expose sufficient amounts of grain (Jorde et al. 1983).

Negative effects of radio-tags may have contributed to the survival rates observed during 2006/07 and 2007/08, but we believe this bias was minimal since all radio-marked mallards survived during 2005/06 and we excluded the first four days after radio-tag attachment from our analysis. Jeske (1991) suspected that radio-tags caused low survival rates of female mallards in Colorado, and other studies focusing on mallard breeding biology have documented negative effects from radio-tags (Pietz et al. 1993, Dzus & Clark 1996, Paquette et al. 1997). Regardless of whether radio-tag effects were present or not, we believe the pattern of survival we recorded (i.e. the opening weekend effect of hunting periods and lower survival during hunting periods than non-hunting periods) would be little affected by radio-tags, unless radio-marking strongly affected mallard susceptibility to hunter harvest. Evidence from Longcore et al. (2000), who surveyed hunters who shot radio-marked black ducks *Anas rubripes,* suggests this bias is minimal. They found that 96% of hunters stated the flight of the radio-marked duck was not affected and 93% of hunters did not see the radio-tag before shooting the duck.

Low percentages (3%, 15% and 18%) of radio-marked mallards went missing from our study area each year and a high percentage (89%) of hunting mortality occurred in our study area. Radio-marking may have affected migratory behaviour of individuals, but we believe this bias was negligible since we had some recoveries well outside our study area and in subsequent years after the year of radio-marking. Additionally, recovery information from banded individuals during the same time period showed a similar pattern (Dooley 2008). Though, our trapping protocol may have skewed our sample towards more resident individuals. In 2005/06, radio-marking did not begin until late November, and this may have been after most migratory mallards had passed through the area. In 2006/07 and 2007/08, we radio-marked most of our mallards early in the year (i.e. the percent of mallards radio-marked each month during September - January was 43, 37, 4, 11 and 5%, respectively), and the majority of individuals radio-marked could have been resident mallards rather than migrants.

For our analysis, we evaluated the importance of our predictor variables using cumulative variable weights, and model averaged over our entire model set to derive our real estimates as outlined in Burnham & Anderson (2002). We believe that this approach has less bias for evaluating the relative importance of predictor variables since variables are included equally in the model set and less bias on the real estimates, since all models in the model set are used in deriving estimates (Doherty et al. in press). However, this approach resulted in a large model set with models that did not drastically differ from one another and there was additional uncertainty around estimates due to the incorporation of model set uncertainty, which made the effect size of some of the variables vague. Also, we made no adjustment to account for possible overdispersion (i.e. c-hat), so the precision of our estimates may actually be biased low, although, as we stated, we expected that this bias was minimal.

Our results suggest split hunting seasons are an effective management tool to increase hunter harvest and affect overwintering survival. Experimental studies comparing different hunting season structures (i.e. number of hunting periods and length of hunting and non-hunting periods) with regard to survival and hunter harvest are needed. However, based on our results and given a set bag limit and season length, we suggest managers may be able to increase hunter harvest through altering season structure by: 1) interspersing hunting periods with non-hunting periods of at least 2-3 weeks since we observed a similar opening week effect during the second hunting period, 2) having hunting periods at least three weeks in duration since we observed lower survival during this time compared to the remainder of the hunting period and 3) including as many weekend days (i.e. Saturdays and Sundays) within hunting periods as possible, since we observed lower survival for these days.

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