

1 **Effects of hunting season structure, weather, and body condition on overwintering mallard**
2 **survival**

3

4 JOSHUA L. DOOLEY, *Department of Fish, Wildlife, and Conservation Biology and the*
5 *Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins,*
6 *CO 80523, USA – phone: 405-274-3454; email: jdooley48@gmail.com*

7 TODD A. SANDERS, *Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, CO*
8 *80526, USA – phone: 503-231-2384; email: Todd_Sanders@fws.gov*

9 PAUL F. DOHERTY, JR., *Department of Fish, Wildlife, and Conservation Biology, Colorado*
10 *State University, Fort Collins, CO 80523, USA – phone: 970-491-6597; email:*
11 *paul.doherty@colostate.edu*

12

13 Key Words: *Anas platyrhynchos*, body condition, hunting regulations, mallard, split hunting
14 season, survival, winter

15

16 Corresponding author: Joshua L. Dooley

17 Current address: 103 Oakwood Drive, Tuttle, OK 73089

18

19

20

21

22

23

24

25 **ABSTRACT**

26

27 Information on waterfowl survival during the overwintering season (i.e., autumn and winter),
28 when hunting seasons occur, is important for making harvest management decisions. However,
29 the relationship of overwintering survival to hunting season structure, weather, and body
30 condition are not well understood. We measured survival of 235 radio-marked adult female and
31 male mallards *Anas platyrhynchos* along the South Platte River corridor in northeastern Colorado
32 during the overwintering seasons of 2005–2006 (pilot year), 2006–2007, and 2007–2008, and we
33 determined the primary factors affecting survival. Hunting was the most important factor
34 affecting survival. Sixty-seven percent of mortality was a direct result of hunting, and survival
35 was lower during hunting periods compared to non-hunting periods. Within hunting periods,
36 survival was lowest during the first 2–3 weekends of hunting periods. During 2006–2007 and
37 2007–2008, survival of radio-marked mallards was monitored September–February, and
38 estimated survival was 0.65 (95% CI = 0.50–0.78) for females and 0.54 (95% CI = 0.39–0.68)
39 for males during 2006–2007 and 0.55 (95% CI = 0.40–0.69) for females and 0.42 (95% CI =
40 0.28–0.58) for males during 2007–2008. We did not observe a strong correlation between body
41 condition index and survival ($\tilde{\beta} = 0.36$, SE = 0.43). Accumulated snowfall and daily minimum
42 temperature were unimportant variables for predicting survival. Eighty-nine percent of hunting
43 recoveries occurred in the study area, and 15% and 18% of radio-marked mallards went missing
44 during 2006–2007 and 2007–2008. Our results suggest split hunting seasons are an effective
45 management tool to increase hunter harvest and affect overwintering survival. Given a set bag
46 limit and season length, managers may be able to increase hunter harvest by: (1) having hunting

47 periods of at least 3 weeks in length, (2) including as many weekend days (i.e., Saturdays and
48 Sundays) within hunting periods as possible, and (3) interspersing hunting periods with non-
49 hunting periods of at least 2–3 weeks.

50

51 **Introduction**

52

53 Waterfowl managers rely upon estimates of survival to aid in assessing waterfowl population
54 status and to guide management decision-making (Nichols et al. 1995, Johnson et al. 1997).

55 Overwintering survival (i.e., autumn and winter) is important to managers because hunter harvest
56 during regulated hunting seasons occurs during this period (Anderson 1975, Nichols et al. 2007),

57 and hunter harvest and survival can be influenced by hunting regulations (Smith & Reynolds
58 1992, Menu et al. 2002, Otis 2004, U.S. Fish and Wildlife Service 2008). One regulation

59 available to U.S. states is split hunting seasons, where the hunting season is divided into 2 or
60 more segments (Ladd et al. 1989). The U.S. Fish and Wildlife Service first offered the split-

61 season option to all U.S. states in 1948 (Ladd et al. 1989), and, by the mid-1980s, approximately
62 half of the states in the U.S. adopted split hunting seasons (Baldassarre & Bolen 2006). The

63 intention of split hunting seasons is to increase hunter success and opportunity by better
64 allocating hunting days to match waterfowl migrations through an area and by restoring

65 waterfowl naivety to hunting pressure during non-hunting periods (Baldassarre & Bolen 2006).

66 However, the efficacy of split hunting seasons has been little investigated, and the relationship of
67 overwintering waterfowl survival to time periods within the hunting season is little known.

68 Previous studies have found hunting to be the main cause of waterfowl mortality during
69 the overwintering season (Migoya & Baldassarre 1995, Cox et al. 1998, Fleskes et al. 2002,

70 Fleskes et al. 2007), and lower survival has been documented during hunting periods compared
71 to non-hunting periods (Cox et al. 1998, Fleskes et al. 2002, Moon & Haukos 2006).
72 Additionally, Fleskes et al. (2007) found an inverse relationship between overwintering survival
73 of female mallards *Anas platyrhynchos* in central California and the number of hunting days.
74 Hunting decreases survival directly through hunter harvest and crippling, and indirectly through
75 disturbance, which increases energy usage and causes waterfowl to avoid more preferred feeding
76 and roosting areas (Fox & Madsen 1997). With regard to waterfowl survival within hunting
77 periods, waterfowl mortality has been documented to be higher at the onset of hunting periods
78 (Longcore et al. 2000, Davis 2007, Fleskes et al. 2007) likely due to waterfowl naivety to
79 hunting pressure and increased hunter participation. Other studies, however, have found
80 mortality from hunting to be lower, or similar, to other causes of mortality (Bergan & Smith
81 1993, Bielefeld & Cox 2006, Moon & Haukos 2006) and have observed similar (Miller et al.
82 1995, Lee et al. 2007), or lower (Davis 2007), survival during non-hunting periods than hunting
83 periods.

84 Overwintering waterfowl survival is additionally affected by environmental factors and
85 body condition. Higher overwintering survival has been documented during years of increased
86 precipitation and better habitat conditions (Migoya & Baldassarre 1995, Moon & Haukos 2006,
87 Fleskes et al. 2007). Bergan & Smith (1993) found that survival of female mallards in the Playa
88 Lakes Region of northwestern Texas decreased following severe weather conditions (i.e., 5 days
89 of 0 °C with snow cover) as did Jeske (1991) for female mallards in the San Luis Valley of
90 Colorado, particularly after snow accumulation which reduced food availability. The relationship
91 of body condition to overwintering survival has also received much attention, but patterns are
92 less general. Some studies have supported the hypothesis that better body condition increases

93 overwintering survival and decreases susceptibility to harvest (Hepp et al. 1986, Dufour et al.
94 1993, Heitmeyer et al. 1993, Robb 2002) while other studies have not found this relationship
95 (Jeske et al. 1994, Cox et al. 1998, Lee et al. 2007). Individuals in poor body condition may be
96 more likely to be unpaired and thus more easily attracted to decoys, more susceptible to disease,
97 forced to use habitats with greater hunting pressure, and less focused on predator and hunter
98 avoidance due to spending more time searching for food (Hepp et al. 1986, Fleskes et al. 2002).
99 Body condition of mallards has been shown to decrease during cold weather events (Whyte &
100 Bolen 1984, Robb et al. 2001). Colorado mallards may be more vulnerable to mortality after
101 severe weather because of low endogenous energy stores (Jeske 1991, Dugger et al. 1994).

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

113

114 **Materials and methods**

115

116 **Study area**

117 We conducted our study on the South Platte River corridor (i.e., • 10 km buffer surrounding the
118 South Platte River) in Logan, Morgan, Sedgwick, and Washington counties in northeastern
119 Colorado. Most wetlands and bodies of water in these counties are within the South Platte River
120 corridor. During 2005–2006, the pilot study year, the study area included the South Platte River
121 corridor from Fort Morgan east to the Colorado-Nebraska state line, approximately 150
122 contiguous km. During 2006–2007 and 2007–2008, two smaller study areas within the 2005–
123 2006 study area were used. The eastern study area extended from the town of Sedgwick west to
124 the town of Iliff, approximately 56 km. The western study area extended from the town of
125 Sterling west to Snyder, approximately 48 km. Natural vegetation is shortgrass prairie,
126 dominantly *Bouteloua* and *Buchloe* spp. with cottonwoods *Populus* spp. occurring along
127 wetlands (Ringelman et al. 1989). Primary use of the landscape is cattle production and farming,
128 primarily corn.

129 **Trapping and tracking**

130 We radio-marked 235 adult (after-hatch year) mallards during the overwintering seasons of
131 2005–2006 (pilot year), 2006–2007, and 2007–2008: 14 females and 24 males in 2005–2006, 35
132 females and 60 males in 2006–2007, and 54 females and 48 males in 2007–2008. Mallards were
133 trapped with baited swim-in or walk-in funnel traps during September–January, except that
134 trapping started in late November during the 2005–2006 season. We measured body weight (g)
135 and wing length (mm) upon capture, except during 2005–2006 (N=38), to calculate body
136 condition index (BCI = body weight / wing length; Ringelman & Szynczak 1985). We used
137 backpack VHF radiotags, which weighed approximately 25g (model A1820 manufactured by
138 Advanced Telemetry Systems [ATS]). Battery life was approximately 9 months. Radio-marked

139 mallards were located with vehicle mounted Yagi antennas. Overwintering survival was
140 monitored from 1 December–21 February during 2005–2006, 15 September–10 February during
141 2006–2007, and 9 September–13 February during 2007–2008.

142 During 2005–2006, radio-marked mallards were located on average 3 (range = 1–15)
143 times per day for 3–7 consecutive days separated by 1–15 days of no monitoring. During 2006–
144 2007 and 2007–2008, radio-marked mallards were located 2–3 times per day for approximately 2
145 weeks separated by 3–19 days of no monitoring. Radiotags sending a mortality signal (i.e., signal
146 doubled in frequency after 4 hours of inactivity) were recovered as soon as possible to determine
147 cause of death. Carcasses, when available, were inspected for signs of predation and hunter
148 crippling (i.e., shotgun pellet wounds and shattered bones). We recorded mallards found dead
149 from apparent crippling and those reported harvested by hunters as hunting mortalities. All other
150 mortalities were recorded as non-hunting mortalities (also known as natural mortalities; see
151 Bergan & Smith 1993, Moon & Haukos 2006, Davis 2007).

152

153 **Statistical Analysis**

154 We used the nest survival model (Dinsmore et al. 2002, Rotella et al. 2004) in Program MARK
155 (White & Burnham 1999) to estimate daily survival rates. The nest survival model can be
156 extended to other known-fate data such as radio-telemetry data when marked animals are not
157 monitored at regular intervals of time (Schwartz et al. 2006, Mong & Sandercock 2007), as were
158 our data. We excluded all data from the first 4 days after radiotag attachment to protect against
159 mortality and emigration biases associated with capture, handling, and radiotag effects (Cox &
160 Afton 1998). Radio-marked mallards with no detectable signal within the study area or those that

161 were recovered dead outside the study area were censored from the survival analysis at the last
162 time they were located alive within the study area.

163 Based upon previous research, preliminary modeling, and to keep the size of our model
164 set manageable, we included sex and a parameter designating hunting periods from non-hunting
165 periods in all models. We considered other variables to examine variation in mallard survival
166 relative to year (2005–2006, 2006–2007, 2007–2008), different hunting periods (H), different
167 non-hunting periods (NH), time intervals within hunting periods (opening effect for 1, 2, or 3
168 weeks [1WK, 2WK, 3WK]; holiday effect [HOL]; quadratic trend across time[T²]), body
169 condition index (BCI), and environmental factors (accumulated snowfall [SNOW] and daily
170 minimum temperature [TEMP]; see Table 1 for descriptions). Temperature and precipitation data
171 were taken from the Akron 4 E, Colorado weather station (National Climatic Data Center 2008),
172 the weather station nearest the study area.

173 During the pilot study year, 2005–2006, mallards were captured later and hunting season
174 structure was different than the following years (Table 2). We expected survival would be higher
175 in 2005–2006 because mallards were not exposed to as many hunting days. We included data
176 from this year in analysis because we wanted to explore effects of weather on survival and were
177 interested in post-hunting survival rates, for which this sample was representative. Weather
178 conditions between 2006–2007 and 2007–2008 were similar and more severe compared to 2005–
179 2006. During the autumn (September–November) and winter (December–February), 86.1 cm of
180 snowfall fell in 2006–2007 and 81.0 cm of snowfall fell in 2007–2008, compared to 18.0 cm in
181 2005–2006. Average autumn and winter snowfall in this area was 51.5 cm (Akron 4 E, CO,
182 1948–present; High Plains Regional Climate Center 2008). Regarding average winter
183 temperature, 2006–2007 (-4.9 °C) and 2007–2008 (-4.5 °C) had lower averages than 2005–2006

184 (0.0 °C). Average winter temperature in this area was -2.2 °C (Akron 4 E, CO, 1948–present;
185 High Plains Regional Climate Center).

186 We used Akaike’s Information Criterion with small sample size adjustment (AIC_c) and
187 AIC_c weights to evaluate our candidate model set (Burnham & Anderson 2002). We used a
188 balanced model set so that predictor variables were included equally and used cumulative
189 variable weights to determine relative importance of predictor variables (Burnham & Anderson
190 2002). We model-averaged daily survival estimates and β estimates of interest using all models
191 with AIC_c weight (Burnham & Anderson 2002). Cumulative survival rates for males and females
192 for each study year were calculated from the daily survival estimates. Cumulative survival rate is
193 the overall survival rate for the entire time period radio-marked mallards were monitored each
194 year. Goodness-of-fit tests were not possible with the nest survival model (Dinsmore et al. 2002,
195 Schwartz et al. 2006), and we suspected little dependence in our sample because of the small
196 number of individuals radio-marked at the same location during the same trapping occasion (i.e.,
197 average and median = 3, range = 1–8). Thus, no adjustment for overdispersion was made.

198

199 **RESULTS**

200

201 **Mortalities and missing radio-marked mallards**

202 Of the 235 radio-marked mallards, sixty-four (28%) died, 130 (57%) survived, 1 (<1%) shed its
203 radiotag, and 33 (14%) went missing within the study area during the same study year of radio-
204 marking. Seven radio-marked male mallards were censored from analysis due to mortality
205 (N=3), never being located (N=3), or known radiotag malfunction (N=1) within 4 days after
206 radiotag attachment. Forty-three of the 64 (67%) mortalities were hunting mortalities (i.e., we

207 classified 4 of the 43 as hunting mortality based upon carcass inspection in the field; the other 39
208 were reported by hunters). The percentage of hunting mortality compared to non-hunting
209 mortality was higher for males, 75% (27 of 36), compared to females, 57% (16 of 28). The exact
210 location of mortality was known (i.e., talked to hunter or personally retrieved radiotag) for 42 of
211 the 43 hunting mortalities. Eighteen (43%) radio-marked mallards were shot on public lands, and
212 24 (57%) radio-marked mallards were shot on private lands.

213 Three additional hunting mortalities occurred during the same study year of radio-
214 marking but outside the study area, and 9 mortalities occurred after the year of radio-marking,
215 either inside (N=6) or outside (N=3) the study areas. Thus, 89% (49 of 55) of all known hunting
216 mortality of radio-marked mallards occurred in the study area. Hunting mortalities outside of the
217 study area occurred in Colorado, Alberta, Kansas, Nebraska (N=1, respectively) and Texas
218 (N=2).

219

220 **Radio-marked mallard survival**

221 There was strong support for survival differing among the 3 years (YR; cumulative variable
222 weight = 0.92; Table 3). Differences in survival among different non-hunting periods (NH;
223 cumulative variable weight = 0.16) and among different hunting periods (H; cumulative variable
224 weight = 0.24) were less supported (Table 3). For the opening week(s) effect of hunting periods,
225 3 week (3WK; cumulative variable weight = 0.28) and 2 week (2WK; cumulative variable
226 weight = 0.24) effects were more supported than a 1 week effect (1WK; cumulative variable
227 weight = 0.08). There was little support that the opening week(s) effect differed among hunting
228 periods (Table 3). Of the individual and environmental covariates considered, body condition
229 index (BCI; cumulative variable weight = 0.47) was better supported than accumulated snowfall

230 (SNOW; cumulative variable weight = 0.19) and daily minimum temperature (TEMP;
231 cumulative variable weight = 0.10; Table 3). There was little support for a holiday effect (HOL;
232 cumulative variable weight = 0.09) or a quadratic trend on survival during hunting periods after
233 the opening week(s) effect (T^2 ; cumulative variable weight = 0.05; Table 3).

234 During 2006–2007 and 2007–2008, survival was lower during hunting periods compared
235 to non-hunting periods (Fig. 1). Within hunting periods, survival was lowest for the first 2–3
236 weekends (Fig. 1). Survival during the weekdays for the first 3 weeks was comparable to the
237 survival rate observed during the remainder of the second hunting period (Fig. 1). Twenty-one of
238 43 (49%) hunting mortalities occurred during the first 3 weeks of hunting periods, with 16 (37%)
239 hunting mortalities occurring during the first 3 weekends. All hunting mortalities and 16 of the
240 21 (76%) non-hunting mortalities occurred during hunting periods. Male survival was slightly
241 lower than female survival, particularly during hunting periods. However, the variance of the
242 estimates was large, and a sex effect was not strongly detected with our sample size (Fig. 1).
243 Cumulative female and male survival was 0.65 (95% CI = 0.50–0.78) and 0.54 (95% CI =
244 0.39–0.68) during 2006–2007, respectively, and 0.55 (95% CI = 0.40–0.69) and 0.42 (95% CI =
245 0.28–0.58) during 2007–2008. There was no radio-marked mallard mortality during 2005–2006.
246 Thus, cumulative survival during 2005–2006 was 1.00.

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

252

253 **DISCUSSION**

254

255 Hunting (67%) was the primary cause of radio-marked mallard mortality. The percent of hunting
256 mortality is mostly likely an underestimate because dead radio-marked mallards without visible
257 signs of hunter kill were classified as non-hunting mortalities, and hunter killed carcasses were
258 nearly always depredated before being recovered. Of the 25 mortalities we recovered, 4 were
259 classified as hunter kill, and it is likely that more of these mortalities were mallards shot but not
260 retrieved by hunters. Norton & Thomas (1994) suggest that hunter crippling losses range from
261 20–40%. Misclassification of radio-marked mallards crippled by hunters may also explain why a
262 high proportion (76%) of non-hunting mortality occurred during hunting periods. However,
263 hunting is known to indirectly decrease survival by increasing levels of disturbance and by
264 causing waterfowl to avoid more preferred feeding and roosting areas (Fox & Madsen 1997).
265 Other studies have similarly documented hunting mortality as the primary cause of overwintering
266 mortality for waterfowl populations (Migoya & Baldassarre 1995, Cox et al. 1998, Fleskes et al.
267 2002, Fleskes et al. 2007) and lower survival during hunting periods compared to non-hunting
268 periods (Cox et al. 1998, Fleskes et al. 2002, Moon & Haukos 2006).

269 Survival of radio-marked mallards was similar between different hunting periods and was
270 lower during the first 3 weekends of hunting periods. Lower survival at the beginning of hunting
271 periods was likely related to mallard naivety to hunting pressure and increased hunter
272 participation, particularly on weekends. Other studies have similarly reported lower survival at
273 the beginning of hunting periods (Longcore et al. 2000, Davis 2007, Fleskes et al. 2007). A
274 noticeable drop in survival at 3 weekends after the beginning of hunting periods suggests that
275 waterfowl take longer than the onset of hunting to adjust patterns, although hunting pressure also

276 likely decreased during this time (T. A. Sanders, unpubl. data). The opening effect of hunting on
277 survival was similar between the first and second hunting periods and suggests that a non-
278 hunting period as little as 18–25 days between hunting periods may be adequate to restore
279 mallard naivety to hunting pressure. We observed little difference in mallard survival during
280 holiday weeks, when hunter participation was assumed to be high from field observation,
281 compared to non-holiday weeks within hunting periods after the opening weekends. This
282 suggests increased hunter participation alone may not directly influence survival, but it may
283 largely depend on the timing within the overwintering season.

284 Year was an important predictor variable of survival because no mortality occurred
285 during 2005–2006, whereas survival was lower and similar between 2006–2007 and 2007–2008.
286 No mortality during 2005–2006 was likely a result of our late radio-marking, which resulted in
287 the majority of exposure days occurring after the hunting season. Survival was found to be high
288 during this time period (i.e., POST) in the subsequent 2 years as well. Also, in 2005–2006,
289 hunting season structure was different and weather was more benign than 2006–2007 and 2007–
290 2008, and these factors may have contributed to the observed high survival rate. Our results are
291 consistent with Dugger et al. (1994), who radio-marked immature and adult female mallards
292 after the 1988 and 1989 hunting seasons in east central Arkansas and observed no mortality
293 either year.

294 Hunting mortality was higher for males (75%) than females (57%), and sex-specific
295 differences in mortality were likely a result of sex-specific bag limits (U.S. Fish and Wildlife
296 Service 2008) and possibly hunter preference for males. During the study period, Colorado
297 allowed a daily bag limit of 5 mallards of which only 2 could be female. Additionally, females,
298 perhaps because of lower body mass, may be more susceptible to non-hunting mortality during

299 the overwintering season than males, but this effect has been little evaluated. Other studies have
300 documented the proportion of mortality attributed to hunting for female mallards (Bergan &
301 Smith 1993, Davis 2007, Fleskes et al. 2007), but no such estimate was reported for male
302 mallards. Additionally, we were unable to find any published report of male mallard survival
303 during the overwintering season. Our cumulative female overwintering survival estimates during
304 2006–2007 and 2007–2008 were lower than other reported overwintering adult female survival
305 estimates (see Fleskes et al. 2007). However, we note that the duration which survival was
306 monitored differed among studies, and survival rates are not directly comparable. Also, survival
307 is a function of site- and temporal-specific conditions, which varied greatly between the studies.

308 Body condition index was the second highest ranking variable by cumulative AIC_c
309 weight, which suggests body condition index was an important predictor of survival relative to
310 the other variables examined. However, given the large variance surrounding our estimate, we
311 have little confidence in the effect size. Thus, we do not conclude any strong support for a
312 positive association between body condition index and survival. We do note that we recorded
313 body condition index in 2006–2007 and 2007–2008, when weather was relatively severe, and
314 body condition index may be less related to survival in years with less severe weather. We also
315 note that body condition index was measured at the time of capture and may serve as a poor
316 proxy for body condition index at the time of death.

317 Accumulated snowfall and daily minimum temperature were unimportant variables
318 predicting survival, even though winter weather during 2006–2007 and 2007–2008 was more
319 severe than normal. However, most mortality took place at the beginning of hunting periods
320 when weather conditions were generally snow free and temperatures were benign. Also, the
321 effects of weather may compound over the entire duration of the overwintering season, and

322 mortality may lag the original onset of weather events. Additionally, daily minimum temperature
323 and accumulated snowfall were highly correlated (-0.60). Modeling these variables to represent
324 their true effect poses challenges. Adverse effects on survival in this area may only become
325 realized at certain threshold values, such as cumulative days with high levels of accumulated
326 snowfall and/or low daily temperatures (Dooley 2008). Jeske (1991) and Bergan & Smith (1993)
327 observed lower survival for female mallards after severe winter weather, particularly snow cover
328 which reduces foraging ability. In our study area, radio-marked mallards preferred feeding in
329 corn fields grazed by cattle due to more available spare grain (T. A. Sanders, unpubl. data), a
330 pattern that has been previously documented (Jorde et al. 1983). Waterfowl may be little affected
331 by low accumulations of snow when livestock are present because livestock expose sufficient
332 amounts of grain (Jorde et al. 1983).

333 Negative effects from radiotags may have contributed to the survival rates observed
334 during 2006–2007 and 2007–2008, but we believe this bias was minimal since all radio-marked
335 mallards survived during 2005–2006 and we excluded the first 4 days after radiotag attachment
336 for our analysis. Jeske (1991) suspected that radiotags caused low survival rates of female
337 mallards in Colorado, and other studies focusing on mallard breeding biology have documented
338 negative effects from radiotags (Pietz et al. 1993, Dzus & Clark 1996, Paquette et al. 1997).
339 Regardless of whether radiotag effects were present or not, we believe the pattern of survival we
340 recorded (i.e., the opening weekend effect of hunting periods and lower survival during hunting
341 periods than non-hunting periods) would be little affected by radiotags, unless radio-marking
342 strongly affected mallard susceptibility to hunter harvest. Evidence from Longcore et al. (2000),
343 who surveyed hunters who shot radio-marked black ducks *Anas rubripes*, suggests this bias is

344 minimal. They found that 96% of hunters stated the flight of the radio-marked duck was not
345 affected, and 93% of hunters did not see the radiotag before shooting the duck.

346 Low percentages (3%, 15% and 18%) of radio-marked mallards went missing from the
347 study area each year and a high percentage (89%) of hunting mortality occurred in the study
348 area. Radio-marking may have affected migratory behavior of individuals, but we believe this
349 bias is negligible since we did have some recoveries well outside the study area and in
350 subsequent years after the year of radio-marking. Additionally, recovery information from
351 banded individuals during the same time period showed a similar pattern (Dooley 2008). Our
352 trapping protocol, though, may have skewed our sample toward more resident individuals. In
353 2005–2006, radio-marking did not begin until late November, and this may have been after most
354 migratory mallards passed through the area. In 2006–2007 and 2007–2008, we radio-marked
355 most of our mallards early in the year (i.e., the percent of mallards radio-marked each month,
356 September–January, was 43%, 37%, 4%, 11%, and 5%, respectively), and the majority of
357 individuals radio-marked could have been resident mallards rather than migrants.

358 For our analysis, we evaluated the importance of our predictor variables using cumulative
359 variable weights, and model averaged over our entire model set to derive our real estimates as
360 outlined in Burnham and Anderson (2002). We believe this approach has less bias for evaluating
361 the relative importance of predictor variables since variables are included equally in the model
362 set and less bias on the real estimates since all models in the model set are used in deriving
363 estimates (Doherty et al., provisionally accepted). However, this approach resulted in a large
364 model set with models that did not drastically differ from one another, and there was additional
365 uncertainty around estimates due to the incorporation of model set uncertainty, which made the
366 effect size of some of the variables vague. Also, we made no adjustment to account for possible

367 overdispersion (i.e., $c\text{-hat}$), so the precision of our estimates may actually be biased low,
368 although, as we stated, we expected that this bias was minimal.

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

380

381 *Acknowledgements* - funding was provided by the Colorado Division of Wildlife (CDOW). We
382 thank K. Burnham and G. White for analysis assistance and M. Manfredo for comments on
383 previous drafts. We thank C. Bishop, V. Drietz, J. Gammonley, P. Lukacs, L. Olton, and J.
384 Runge at the CDOW and other CDOW field personnel for project assistance and comments on
385 previous drafts. We appreciate the effort of M. Brekke, A. Dinges, J. Hess, N. Jerstad, and C.
386 Yarbrough in collecting data and the cooperation of countless private landowners.

387

388 **References**

389

390 Anderson, D. R. 1975: Optimal exploitation strategies for an animal population in a Markovian
391 environment - theory and an example. - *Ecology* 56:1281-1297.

392 Baldassarre, G. & Bolen, E. 2006: *Waterfowl Ecology and Management*. - Krieger Publishing,
393 Malabar, Florida, 609 pp.

394 Bergan, J. F. & Smith, L. M. 1993: Survival rates of female mallards wintering in the Playa
395 Lakes Region. - *Journal of Wildlife Management* 57:570-577.

396 Bielefeld, R. R. & Cox, R. R. 2006: Survival and cause-specific mortality of adult female
397 mottled ducks in east-central Florida. - *Wildlife Society Bulletin* 34:388-394.

398 Burnham, K. P. & Anderson, D. R. 2002: *Model selection and multimodel inference: a practical*
399 *information-theoretical approach*. Second edition. - Springer-Verlag, New York, 488 pp.

400 Cox, R. R. & Afton, A. D. 1998: Effects of capture and handling on survival of female Northern
401 Pintails. - *Journal of Field Ornithology* 69:276-287.

402 Cox, R. R., Afton, A. D. & Pace, R. M. 1998: Survival of female northern pintails wintering in
403 southwestern Louisiana. - *Journal of Wildlife Management* 62:1512-1521.

404 Davis, B. E. 2007: *Habitat use, movements, and survival of radio-marked female mallards in the*
405 *Lower Mississippi Alluvial Valley*. - Thesis, Louisiana State University, Baton Rouge,
406 USA.

407 Dinsmore, S. J., White, G. C. & Knopf, F. L. 2002: Advanced techniques for modeling avian
408 nest survival. - *Ecology* 83:3476-3488.

409 Doherty Jr., P.F., White, G. C. & Burnham, K. P. Provisionally accepted. Comparison of model
410 building and selection strategies - *Journal of Ornithology*.

411 Dooley, J. L. 2008: Mallard response to experimental human disturbance and non-breeding
412 survival along the South Platte River in Colorado. - Thesis, Colorado State University,
413 Fort Collins, USA.

414 Dufour, K. W., Ankney, C. D. & Weatherhead, P. J. 1993: Condition and vulnerability to
415 hunting among mallards staging at Lake St. Clair, Ontario. - *Journal of Wildlife*
416 *Management* 57:209-215.

417 Dugger, B. D., Reinecke, K. J. & Fredrickson, L. H. 1994: Late winter survival of female
418 mallards in Arkansas. - *Journal of Wildlife Management* 58:94-99.

419 Dzus, E. H. & Clark, R. G. 1996: Effects of harness-style and abdominally implanted
420 transmitters on survival and return rates of mallards. - *Journal of Field Ornithology*
421 67:549-557.

422 Fleskes, J. P., Jarvis, R. L. & Gilmer, D. S. 2002: September-March survival of female northern
423 pintails radiotagged in San Joaquin Valley, California. - *Journal of Wildlife Management*
424 66:901-911.

425 Fleskes, J. P., Yee, J. L., Yarris, G. S., Miller, M. R. & Casazza, M. L. 2007: Pintail and mallard
426 survival in California relative to habitat, abundance, and hunting. - *Journal of Wildlife*
427 *Management* 71:2238-2248.

428 Fox, A. D. & Madsen, J. 1997: Behavioural and distributional effects of hunting disturbance on
429 waterbirds in Europe: Implications for refuge design. - *Journal of Applied Ecology* 34:1-
430 13.

431 Heitmeyer, M. E., Fredrickson, L. H. & Humburg, D. D. 1993: Further evidence of biases
432 associated with hunter-killed mallards. - *Journal of Wildlife Management* 57:733-740.

433 Hepp, G. R., Blohm, R. J., Reynolds, R. E., Hines, J. E. & Nichols, J. D. 1986: Physiological
434 condition of autumn-banded mallards and its relationship to hunting vulnerability. -
435 Journal of Wildlife Management 50:177-183.

436 High Plains Regional Climate Center. 2008. University of Nebraska-Lincoln. Weather
437 information for Akron, Colorado. Available at: <<http://www.hprcc.unl.edu/>>. Last
438 accessed on 15-09-2008.

439 Jeske, C. W. 1991: Condition, survival, and management of mallards wintering in the San Luis
440 Valley, Colorado. - Dissertation, Colorado State University, Fort Collins, USA.

441 Jeske, C. W., Szymczak, M. R., Anderson, D. R., Ringelman, J. K. & Armstrong, J. A. 1994:
442 Relationship of body condition to survival of mallards in San Luis Valley, Colorado. -
443 Journal of Wildlife Management 58:787-793.

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

447 Jorde, D. G., Krapu, G. L. & Crawford, R. D. 1983: Feeding ecology of mallards wintering in
448 Nebraska. - Journal of Wildlife Management 47:1044-1053.

449 Ladd, W. N., Jr., Bartonek, J. C., Gamble, K. E. & Serie, J. R. 1989: Experiences with special
450 harvest management strategies for ducks. - Transactions of the North American Wildlife
451 and Natural Resources Conference 54:552-565.

452 Lee, C. K., Taylor, J. P., Haukos, D. A. & Andersen, M. C. 2007: Winter survival of northern
453 pintails in the Middle Rio Grande Valley, New Mexico. - Western North American
454 Naturalist 67:79-85.

455 Longcore, J. R., McAuley, D. G., Clugston, D. A., Bunck, C. M., Giroux, J. F., Ouellet, C.,
456 Parker, G. R., Dupuis, P., Stotts, D. B. & Goldsberry, J. R. 2000: Survival of American
457 black ducks radiomarked in Quebec, Nova Scotia, and Vermont. - *Journal of Wildlife*
458 *Management* 64:238-252.

459 Menu, S., Gauthier, G. & Reed, A. 2002: Changes in survival rates and population dynamics of
460 greater snow geese over a 30-year period: implications for hunting regulations. - *Journal*
461 *of Applied Ecology* 39:91-102.

462 Migoya, R., & Baldassarre, G. A. 1995: Winter survival of female northern pintails in Sinaloa,
463 Mexico. - *Journal of Wildlife Management* 59:16-22.

464 Miller, M. R., Fleskes, J. P., Orthmeyer, D. L., Newton, W. E. & Gilmer, D. S. 1995: Survival of
465 adult female northern pintails in Sacramento Valley, California. - *Journal of Wildlife*
466 *Management* 59:478-486.

467 Mong, T. W., & Sandercock, B. K. 2007: Optimizing radio retention and minimizing radio
468 impacts in a field study of upland sandpipers. - *Journal of Wildlife Management* 71:971-
469 980.

470 Moon, J. A., & Haukos, D. A. 2006: Survival of female northern pintails wintering in the Playa
471 Lakes Region of northwestern Texas. - *Journal of Wildlife Management* 70:777-783.

472 National Climatic Data Center. 2008. U.S. Department of Commerce. Weather information for
473 Akron, Colorado. Available at: <<http://www.ncdc.noaa.gov/oa/ncdc.html>>. Last
474 accessed on 15-09-2008.

475 Nichols, J. D., Johnson, F. A. & Williams, B. K. 1995: Managing North American waterfowl in
476 the face of uncertainty. - *Annual Review of Ecology and Systematics* 26:177-199.

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

480 Norton, M., & Thomas, V. 1994: Economic analyses of crippling losses of North American
481 waterfowl and their policy implications for management. - *Environmental Conservation*
482 21.4: 347-353.

483 Otis, D. L. 2004: Mallard harvest distributions in the Atlantic and Mississippi flyways during
484 periods of restrictive and liberal hunting regulations. - *Journal of Wildlife Management*
485 68:351-359.

486 Paquette, G. A., Devries, J. H., Emery, R. B., Howerter, D. W., Joynt, B. L. & Sankowski, T. P.
487 1997: Effects of transmitters on reproduction and survival of wild mallards. - *Journal of*
488 *Wildlife Management* 61:953-961.

489 Pietz, P. J., Krapu, G. L., Greenwood, R. J. & Lokemoen, J. T. 1993: Effects of harness
490 transmitters on behavior and reproduction of wild mallards. - *Journal of Wildlife*
491 *Management* 57:696-703.

492 Ringelman, J. K., Eddleman, W. R. & Miller, H. W. 1989: High Plains Reservoirs and Sloughs. -
493 In: Pederson, R. L. (Ed). *Habitat management for migrating and wintering waterfowl in*
494 *North America*, Texas Tech Press, Lubbock, USA: 311-340.

495 Ringelman, J. K., & Szymczak, M. R. 1985: A physiological condition index for wintering
496 mallards - *Journal of Wildlife Management* 49:564-568.

497 Robb, J. R. 2002: Band recovery and recapture rates of American black ducks and mallards. -
498 *Journal of Wildlife Management* 66:153-161.

499 Robb, J. R., Tori, G. M. & Kroll, R. W. 2001: Condition indices of live-trapped American black
500 ducks and mallards. - *Journal of Wildlife Management* 65:755-764.

501 Rotella, J. J., Dinsmore, S. J. & Shaffer, T. L. 2004: Modeling nest-survival data: a comparison
502 of recently developed methods that can be implemented in MARK and SAS. - *Animal*
503 *Biodiversity and Conservation* 27:187-205.

504 Schwartz, C. C., Haroldson, M. A., White, G. C., Harris, R. B., Cherry, S., Keating, K. A.,
505 Moody, D. & Servheen, C. 2006: Temporal, spatial, and environmental influences on the
506 demographics of grizzly bears in the Greater Yellowstone Ecosystem. - *Wildlife*
507 *Monographs*:1-68.

508 Smith, G. W., & Reynolds, R. E. 1992: Hunting and mallard survival, 1979-88. - *Journal of*
509 *Wildlife Management* 56:306-316.

510 U.S. Fish and Wildlife Service. 2008: Adaptive Harvest Management: 2008 Hunting Season.
511 U.S. Dept. Interior, Washington, D.C. 54pp. Available at:
512 <http://www.fws.gov/migratorybirds/mgmt/AHM/AHM-intro.html>. Last accessed on 15-
513 12-2008.

514 White, G. C., & Burnham, K. P. 1999: Program MARK: survival estimation from populations of
515 marked animals. - *Bird Study* 46:120-139.

516 Whyte, R. J., & Bolen, E. G. 1984: Impact of winter stress on mallard body composition. -
517 *Condor* 86:477-482.

518

519

Table 1. Variables used in overwintering (9 September–21 February) survival analysis of radio-marked mallards *Anas platyrhynchos* along the South Platte River in northeastern Colorado. Sex and a parameter designating non-hunting periods from hunting periods were included in every model.

Variable	Description
1WK, 2WK, 3WK ^a	Opening week effect lasting 1–3 weeks after the beginning of a hunting period
BCI ^b	Body condition index (body mass [g] wing length [mm])
HOL	Holiday weeks (Monday through Monday surrounding Thanksgiving and 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

^a 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., 1WK*H, 2WK*H, and 3WK*H).

^b Body condition index was not recorded during 2005–2006.

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 September 2005–February 2008. Colorado changed from three hunting periods in 2005–2006 to two hunting periods in 2006–2007. Mallards were first radio-marked at the end of the second hunting period in 2005–2006 (i.e., survival period began December 1).

Year	PRE	H1	BTW	H2	BTW	H3	POST
2005–2006	—	— ^a	—	1 Dec–4 Dec ^a	5 Dec–10 Dec	11 Dec–22 Jan	23 Jan–22 Feb
2006–2007	15 Sep–29 Sep	30 Sep–8 Oct	9 Oct–2 Nov	3 Nov–28 Jan	—	—	29 Jan–10 Feb
2007–2008	9 Sep–5 Oct	6 Oct–22 Oct	23 Oct–9 Nov	10 Nov–27 Jan	—	—	28 Jan–13 Feb

^a H1 and H2 for 2005–2006 were 1 Oct–23 Sep and 5 Nov–4 Dec, respectively.

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 *Anas platyrhynchos* along the South Platte River in northeastern Colorado. Cumulative variable weight is the summation of AIC_c model weights in which the variable appears. 1WK, 2WK, 3WK = opening week(s) effect after the beginning of hunting periods; 1WK*H, 2WK*H, 3WK*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
3WK	0.28
2WK	0.24
H	0.24
SNOW	0.19
NH	0.16
TEMP	0.10
HOL	0.09
1WK	0.08
3WK*H	0.07
2WK*H	0.05
T ²	0.05
1WK*H	0.02

Figure 1. Model-averaged daily survival rates and standard error ($\hat{S}\hat{E}$) for radio-marked mallards *Anas platyrhynchos* along the South Platte River in northeastern Colorado through the overwintering season (9 September–21 February) for A) 2006–2007 and B) 2007–2008. The overwintering season is partitioned into three non-hunting periods (PRE = pre-hunting period; BTW = between hunting periods; POST = post-hunting period) and two hunting periods (H1 = first hunting period; 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 through Monday surrounding Thanksgiving and the Friday before Christmas through the day after New Year’s day.

Figure 1A

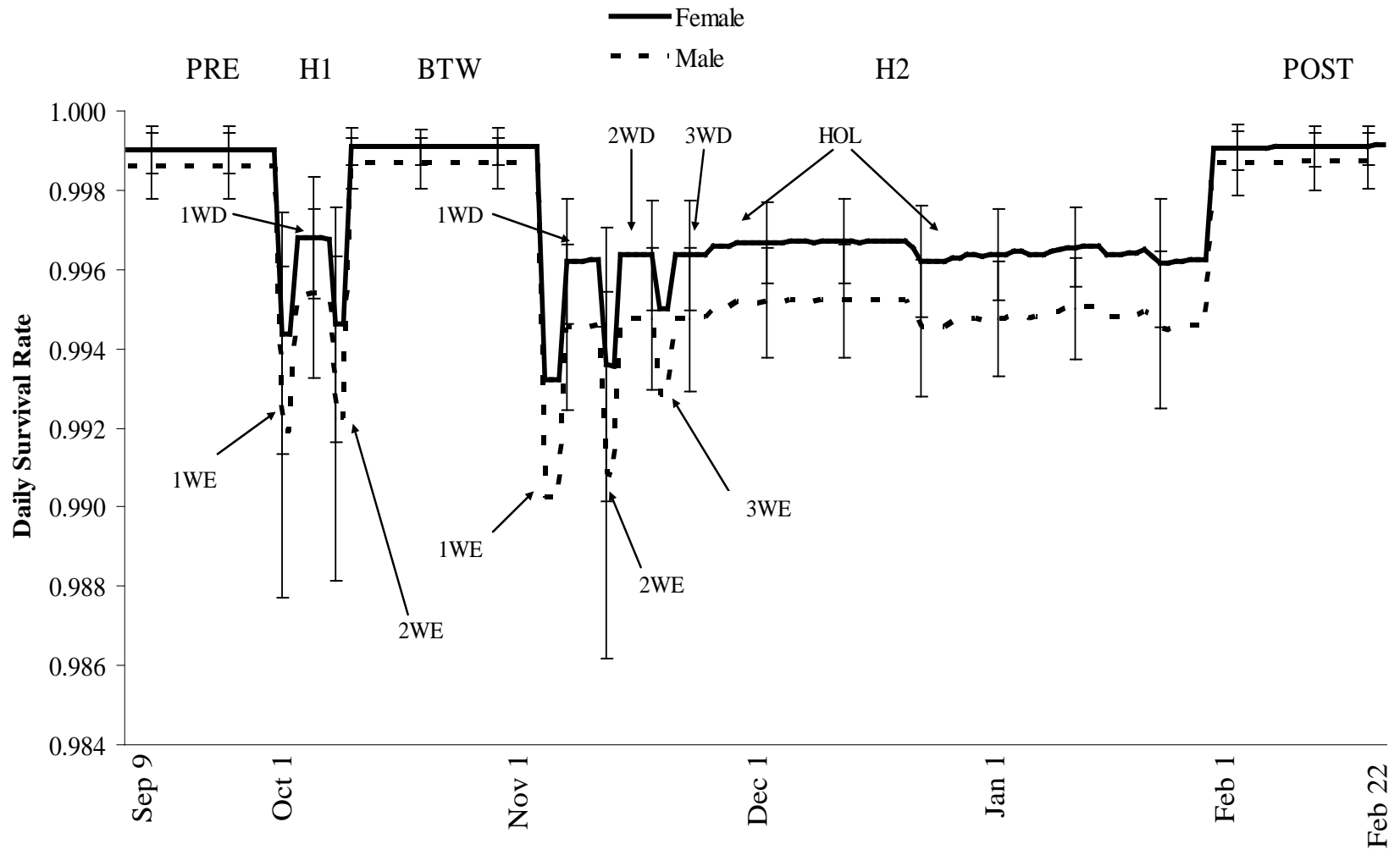


Figure 1B

