Flightless and Post-molt Survival and Movements of Female Mallards Molting in Klamath Basin

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Abstract.—Flightless and post-molt survival and movements were studied during August-May, 2001-2002, 2002-2003 and 2006-2007 for 181 adult female Mallards (*Anas platyrhynchos*). Birds were radiotagged just before or early in their flightless period on four wetlands that differed in size on Klamath Basin (KB) National Wildlife Refuge complex. Flightless survival varied among years but was higher on two larger than two smaller wetlands; 30-day survival ranged from 11% (SE = 6.5%) on a small wetland in 2006 to 93% (SE = 6.5%) on a large wetland in 2001, and averaged 76.8% (SE = 6.1%). Most flightless mortality was from avian botulism (64%) and predation (26%). Of the 81 radiotagged Mallards that did not die in KB, 80% moved to the Central Valley of California (CVCA) before 31 January, 16% wintered in unknown areas, and 4% remained in KB through 31 January. Mallards departed KB 21 August-13 January (average: 11 Nov 2001, 25 Oct 2002, 19 Nov 2006). Post-molt survival during August-March in KB (20.7%, SE = 6.3%) was lower than in CVCA during this (62.9%, SE = 10.1%) and an earlier study. Survival in KB was consistently high only for females that molted in large permanent marshes, and although the impact of poor survival of molting females on Mallard population dynamics is unknown, KB water management plans should be developed that maintain these habitats. *Received 17 September 2009, accepted 21 February 2010.*

Key words.—*Anas platyrhynchos*, California, Klamath Basin, Mallard, molt, Oregon, survival.

Waterbirds 33(2): 208-220, 2010

Klamath Basin (KB) in southern Oregon and northeastern California is one of the most important waterfowl migration and breeding areas in North America (Bellrose 1980; Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986). In addition, about half of the Mallards (*Anas platyrhynchos*) that breed in California's Central Valley (Yarris *et al.* 1994; S. L. Oldenburger, California Department of Fish and Game, unpublished data), nearly all that breed in KB (Mauser 1991), and other ducks (Miller *et al.* 1992) use KB wetlands during late summer to undergo wing molt. Mallards seek out wetlands with emergent vegetation that provide concealment from predators and sources of disturbance (Ringelman 1990). During the flightless period, when old wing feathers are shed simultaneously and replaced by new ones, birds may be especially vulnerable to changing conditions of molting marshes and the surrounding landscape. Maintenance of KB molting habitats requires adequate water supplies (Mayer and Thomasson 2004), which are in short supply during late summer and fall, especially in drought years (Hathaway and Welch 2002). Wise allocation of the limited KB water supplies requires an understanding of the possible impacts of water supply allocations on wildlife, including molting Mallards (Jarvis 2002).

Demographic modeling indicates that the population growth rate of Mallards in California is highly sensitive to adult female survival during the non-breeding season (Oldenburger 2008); results similar to those Hoekman *et al.* (2006) reported for Mallards in eastern Canada but in contrast to midcontinent Mallard populations (Hoekman *et al.* 2002). However, timing and causes of mortality during the non-breeding season have not been extensively studied and there is much uncertainty about the relative importance of the molt vs. post-molt and other periods on waterfowl population dynamics. Fleskes *et al.* (2007) studied female Mallard non-breeding survival during September-March 1998-2000 in the Central Valley of California (CVCA) but most of their sample was captured in early fall in CVCA, before many of the Mallards that nested or molted in KB or other northern areas had arrived in CVCA. Little information is available on survival of molting waterfowl (Iverson and Esler 2007) and survival of female Mallards molting in KB has not been studied. To guide management of Mallards and their post-breeding habitats, survival and mortality causes of females that molted in KB were determined using radiotelemetry while they were flightless in KB and after they regained flight, in KB and en route to and in their primary wintering area, July-May 2001-2002, 2002-2003, and 2006-2007. Departure dates and winter destinations of female Mallards migrating from KB were also documented to better describe regional linkages.

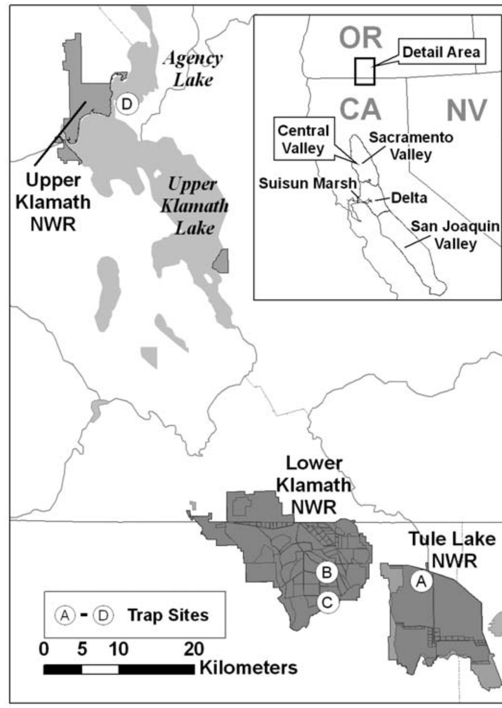

Figure 1. Wetland units of the Klamath Basin National Wildlife Refuge (NWR) complex where molting female Mallards (*Anas platyrhynchos*) were radiotagged (Tule Lake NWR sump 1-A [A], Lower Klamath NWR unit 8B [B] and 12C [C], and Upper Klamath NWR [D]) and the Central Valley of California where most went after regaining flight.

METHODS

Study Area

Klamath Basin, on the California-Oregon border is approximately 200 km north of CVCA (Fig. 1), the main wintering area for Pacific Flyway waterfowl (Bellrose 1980). Most waterfowl molting habitat in KB was on Lower Klamath, Tule Lake and Upper Klamath National Wildlife Refuges (NWRs) of the Klamath Basin NWR complex (Fig. 1). Marshes used by molting Mallards on these three NWRs were comprised of a mix of emergent marsh (i.e. cattail [*Typha* sp.], bulrush [*Scirpus* sp.] and other emergent vegetation interspersed with open water) and open water, and differed in size and hydrology. On Lower Klamath NWR, marsh units were <100 ha to several hundred hectares in size; molting Mallard survival was studied in units 8B (290 ha) and 12C (370 ha), both about half emergent marsh and open water. On Tule Lake NWR, the main molting habitat and where molting survival was studied was Sump 1-A (TL), a permanent wetland comprised of 870-ha of emergent marsh in the north and 3,760-ha of open water in the south. Upper Klamath (UK) molting habitat included the 5,800-ha emergent marsh unit of Upper Klamath NWR and other emergent cover and open water areas associated with Upper Klamath and Agency Lakes.

The amount of molting habitat varied among years. During 2001, severe drought and concerns of potential impacts of reduced Upper Klamath Lake levels on endangered suckers (*Deltistes luxatus, Chasmistes brevirostris*) that reside there resulted in greatly reduced summer water releases from Upper Klamath Lake into KB (Hathaway and Welch 2002). The reduced water releases resulted in more Lower Klamath NWR wetlands than usual becoming dry by late summer 2001, with 8B and 12C among the few that remained flooded. Endangered suckers reside in Tule Lake NWR Sump 1-A (California Department of Fish and Game 2008) and water levels there were better maintained all three years of the study. In 2002 and 2006, more normal precipitation and water releases from Upper Klamath Lake resulted in fewer wetlands on Lower Klamath NWR becoming dry in late summer than during 2001. The increased water releases from Upper Klamath Lake in 2002 reduced the lake level and dried some associated emergent cover that year.

Field Procedures

Night-lighting and swim-in traps were used to capture adult female Mallards on the main molting marshes at: 1) 8B and 12C during 8-30 August 2001, 18 July-15 August 2002, and 20 July-16 August 2006, 2) TL during 8-30 August 2001 and 18 July-15 August 2002, and 3) UK during 8-15 August 2002 (Fig. 1). Captured birds were sexed and females aged (Carney 1992; Dimmick and Pelton 1994). Adult females were weighed (±2.5g), measured (culmen [±0.05mm], tarsus [±0.05mm], ninth and tenth primary [±0.5mm]), and banded with a standard numbered metal leg band. Females with old wings (primaries worn and frayed) were classified as pre-molt, with new wings as post-molt, and as early-molt, mid-molt or late-molt based on primary feather length (early-molt: ninth or tenth primary <20 mm; mid-molt: ninth and tenth primary ≥20 mm and ninth or tenth primary <70 mm; late-molt: ninth and tenth primary ≥70 mm).

A 26-g (<3% of the body weight) backpack harness radiotag (Dwyer 1972) was attached to 181 female Mallards during the study. To obtain relatively precise survival estimates for each KB molting wetland studied, the sample was distributed about equally among wetlands studied each year rather than attempting to measure relative abundance of molters in each unit and distributing the sample proportionally. Thus, 20 Mallards were radiotagged each in 12C and TL, and 14 in 8B in 2001; 20 each in 12C, TL, and UK and 19 in 8B in 2002; and 22 in 12C and 26 in 8B in 2006. Half of the females radiotagged were early-molt, 23% were mid-molt, and 27% (2001: twelve of 20 in 12C, ten of 20 in 8B; 2002: 19 of 20 in UK; 2006: nine of 22 in 12C, four of 26 in 8B) were pre-molt. Late- or post-molt birds were not radiotagged. In 2001, the first pre-molt bird left the primary study area after release, so on all other pre-molt birds that year, a few primaries of one wing were trimmed to ensure that each molted in the same unit in which it had been captured. In 2002, no pre-molt birds were radiotagged in 12C, 8B, or TL and primaries were not trimmed on pre-molt birds that were radiotagged in UK. In 2006, pre-molt birds were radiotagged only if wing molt was imminent (as evidenced by primaries that fell out easily when gently tugged). Captured female Mallards were held until each was processed in uncrowded, shaded, plastic 32" × 24" × 11" cages and provided water. Females captured in swim-in traps (most entered traps at night) were processed at the capture site or nearby location and released back in the capture unit less than one to ten hours after being removed from traps. Night-lighted females were processed at a nearby location the next morning and released back in the capture unit three to 19 hours after capture.

Radiotags provided ≥200 day life, ≥3.2 km reception range from the ground (truck or handheld), ≥24 km range from aircraft, and (all but a few) included a mortality sensor (pulse rate doubles when no movement for six hours). Radiotags had a contact address and phone number embossed on the bottom. Information fliers were posted at hunter check stations requesting that hunters report radiotagged birds. Hand-held, truck-mounted and aircraft-mounted antennae (Gilmer *et al.* 1981) were used to monitor status (alive, dead) and location of each radiotagged Mallard in KB once a day during 2001 and 2002 and three times a day (early morning, afternoon and late evening) during 2006, from the time of radiotagging until it regained flight. Hand-held yagi antennae were used to walk or boat to Mallards and ascertain their status when a mortality signal or lack of signal fluctuation indicated possible death. Carcasses were recovered as quickly as possible (a few hours to seven days in 2001 and 2002; less than one to 23 hours in 2006) and sent to the National Wildlife Health Center for necropsy and follow-up laboratory analyses. If remains of the radiotagged duck were unsuitable for necropsy any other duck carcasses found nearby were collected and analyzed to help identify the likely cause of death of the radiotagged bird. Heart blood was assayed for botulinum toxin type C using the mouse cross protection test (Smith 1980). The location and survival of Mallards that survived the flightless period was monitored once a week (with a few exceptions) in KB and CVCA through 31 May 2002, 21 May 2003 and 6 January 2007. During 2001-2002 and 2002-2003, fixed-wing aircraft were used at least monthly to supplement ground tracking and to search CVCA and KB (and less frequently other northeastern California areas) for radiotagged Mallards. During 2006-2007, except for two aerial searches (26 Sep and 11 Oct) of KB, only ground tracking was used.

Analysis

The program MARK (White and Burnham 1999) and Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) (Akaike 1985; Burnham and Anderson 2002) were used to estimate flightless and post-molt survival and compare statistical support for models that included combinations of planned factors of interest. First, potential impact of how captured Mallards were handled was tested by modeling daily survival during the first 30 days after capture, with covariates for: 1) hours held before release (continuous), 2) capture method (night-lighting vs. bait trap), 3) radiotagging experience of the person that attached the radiotag, (most experienced vs. others), and 4) feather handling of pre-molt birds (primaries trimmed or tugged [i.e. manipulated] vs. not). The 30-day interval was used for this initial analysis because it was theorized that any handling effects would be most apparent within 30 days and a longer duration analysis could obscure weak effects (shorter duration models did not converge). In addition, to also maximize detection of any possible handling effects, data from 2006 were excluded because the extremely low survival in one unit that year would have confounded with any bird handling effects. For each covariate, ΔDeviance was calculated as the difference in deviance between models with and without the covariate (or, equivalently, negative two times the difference between their log likelihoods). The covariate provides: 1) no improvement to the model when ΔDeviance is zero, 2) barely enough improvement to offset the penalty of the additional covariate in the AIC_c value when ΔDeviance is two, and 3) substantial improvement when ΔDeviance is much greater than two.

Next, daily survival of flightless Mallards was modeled. The duration of each bird's flightless period was estimated by assuming each Mallard regained the capability to fly when their ninth primary reached 125 mm in length (Owen and King 1979; Panek and Majewski 1990), growing at 4.25 mm per day (Owen and King 1979). Thus, a 30-day (125/4.25 = 29.4 days rounded up) flightless period was assumed for female Mallards captured immediately after their primaries fell out, which is similar to female Mallard flightless periods reported by others (Balát 1970: 29-33 days; Owen and King 1979: 32 days; Klint 1982: 29.2 days; Leafloor 1989: 25-31 [$\bar{x}$ = 28.3] days). For pre-molt Mallards, based on lengths of primaries on carcasses and recaptures, and documented first-flight dates (J. P. Fleskes, U.S. Geological Survey, unpublished data), feather growth was assumed to begin the day after the bird was released if primaries fell out when they were gently tugged and on the eighth day after release for others. Survival models were tested that included handling method covariates identified in the initial analysis and effects of year, capture unit, capture date, capture body mass and capture molt stage (pre-molt, early-molt, mid-molt). Julian capture date (capdate) and capture body mass (capmass) were standardized so the range of their values (capture date: 18 Jul [199]-31 Aug [243]; mass: 655-1,210 g) were scaled to 0-1.

For Mallards that survived their estimated flightless period, weekly survival was modeled and, in addition to the covariates listed above, the region where Mallards were located (KB, not KB [mostly CVCA]) and the season (prehunt: from the earliest estimated date a radiotagged Mallard regained flight [24 Aug 2001, 17 Aug 2002, 22 Aug 2006] to start of the Oregon Youth Hunt season [22 Sep 2001, 21 Sep 2002, 23 Sep 2006], hunt: from the end of prehunt to the end of the California Youth Hunt in the Balance of the State zone [2 Feb 2002, 2 Feb 2003, 4 Feb 2007 but no data after 6 Jan 2007]; and posthunt: from end of hunt to the date radio-tracking ceased [31 May 2002, 21 May 2003, no posthunt data in 2007]) were tested. Radiotagged Mallards that could not be located were censored on the date they went missing.

Model averaging was used to estimate daily survival rates (DSR) during the flightless period, weekly survival rates for post-molt birds, and effects of covariates. Any of the models that had >1% AIC_c weight (Burnham and Anderson 2002) were included and rates were standardized to mean covariate values. Flightless survival for a 30-day interval (DSR^{30}) is also presented because 30 days is the approximate interval between when old primaries fall out and new primaries attain the 125 mm length that allows female Mallards to fly. Individuals may or may not fly immediately on the day their primaries reach 125 mm, but they do have the capability to fly to escape a predator or a molting marsh with poor conditions (e.g. lack of food or water). Model averaging was used to estimate survival rates and SEs, separately by wetland unit, year and season. Because the radiotagged sample was not distributed among molting units proportionally to abundance of molting female Mallards in each, for comparison with other regions, an overall KB flightless survival rate was calculated by weighting estimates for individual molting wetlands by the percentage of CVCA female Mallards that traveled to KB that molted in each wetland (i.e. 10/27 = 37% in UK, 10/27 = 37% in TL; 7/27 = 26% in 8B or 12C; Yarris *et al.* 1994; S. L. Oldenburger, California Department of Fish and Game, unpublished data). To compare seasonal postmolt survival of Mallards radiotagged during this study, while they were in KB or in other regions, wetland unit rates were averaged and SEs calculated by taking the square root of the variance divided by the number of rates. For comparison with August-March survival in the CVCA (Fleskes *et al.* 2007), August-May data from this study was used to determine seasonal rates, and the posthunt weekly rate was compounded through 31 March. For comparison with other non-breeding season (i.e. flightless and post-molt period combined) survival estimates, flightless and post-molt August-March estimates were multiplied. Estimates of covariate effects on daily (flightless) or weekly (post-molt) mortality are presented rather than survival because, although the models can estimate odds or probabilities of survival, the covariate parameters of the models only define effects on the odds. Also, since daily or weekly probability of mortality (1-p) is near zero, then it is almost equal to the odds of mortality ([1-p]/p). Therefore all effects on odds of mortality are approximately equal to effects on probability of mortality.

Weekly distribution and the approximate date of emigration from KB were summarized for radiotagged birds that survived molt. The date of emigration from KB was estimated as the mid-point between the date of the last KB location and the earliest of either the date first missing from KB or, if subsequently found in CVCA, the date first searched for in CVCA. General linear models in SAS (SAS Institute Inc. 2004) were used to investigate the relationship between date of emigration from KB and timing of molt (i.e. date regained flight-capability), study year, and capture body mass, and whether the lag (in days) between the date each Mallard regained flight-capability and the date of emigration from KB varied among years or was related to body mass.

RESULTS

Initial analysis to evaluate the importance of bird handling covariates on 30-day post-release survival indicated that holding time ($\Delta AIC_c = 2.01$, $\Delta Deviance = 0$), capture method ($\Delta AIC_c = 1.97$, $\Delta Deviance = 0.04$), and experience of the person attaching the radiotag ($\Delta AIC_c = 1.77$, $\Delta Deviance = 1.77$) did not improve the model. Thus, these were not retained in later analysis. Inclusion of the covariate for feather manipulation (hereafter "trimtug") did improve ($\Delta AIC_c = 1.67$, $\Delta Deviance = 3.68$) the model in one year (2001) and was included in later analysis to ensure any impact of feather manipulation was accounted for when estimating survival.

The highest-ranked ($AIC_c wt = 0.23$) daily survival model for flightless female Mallards included year x unit, trimtug, and capmass × capdate (Table 1). Two other models that included slightly different covariates were close to the best model (one without trimtug [$AIC_c wt = 0.14$] and one with moltstage instead of trimtug [$AIC_c wt = 0.12$]). Standardized to mean covariate values, 30-day flightless survival ranged from 11% (SE = 6.5%) in 12C in 2006 to 93% (SE = 6.5%) in TL in 2001 (Table 2). The wetland unit estimates, weighted by the percentage of CVCA adult Mallards molting in each (Yarris *et al.* 1994; S. L. Oldenburger, California Department of Fish and Game, unpublished data), averaged 76.8% (SE = 6.1%). Flightless survival averaged greater in TL and UK than in 12C or 8B but the difference varied among years and not all wetland units were studied every year (Table 2). Manipulation of primary feathers on pre-molt birds was associated with

Table 1. Numbers of parameters (k), Akaike Information Criterion (AIC_c) values adjusted for small sample size, ΔAIC_c, AIC_c weights (AIC_cwt), and deviance used to rank models containing factors (year [yr], and capture unit [unit], molt stage [moltstage], Julian date [capdate], and standardized mass [capmass]; trimtug refers to whether or not primaries on pre-molt birds were manipulated) hypothesized to impact flightless survival of female Mallards (*Anas platyrhynchos*) radiotagged just before or soon after molting wing feathers on Lower Klamath National Wildlife Refuge (NWR) wetland units 12C and 8B, Tule Lake NWR wetland unit 1-A, or Upper Klamath NWR and monitored during July-September 2001, 2002 and 2006. The global (yr*unit + trimtug + moltstage + capmass*yr + capdate*yr + capmass*capdate + capmass*unit + capdate*unit) and null (contains only the intercept) models are included for reference.

Model	k	AIC_c	ΔAIC_c	AIC_cwt	Deviance
yr*unit + trimtug +capmass*capdate	13	562.18	0	0.23	536.07
yr*unit + moltstage + capmass*capdate	14	563.22	1.04	0.14	535.10
yr*unit + capmass*capdate	12	563.54	1.36	0.12	539.45
yr*unit + trimtug + capmass*yr	13	564.10	1.92	0.09	538.00
yr*unit + trimtug + capmass	11	564.19	2.01	0.08	542.12
yr*unit + trimtug + capmass + capdate	12	564.54	2.36	0.07	540.45
yr*unit + trimtug	10	564.96	2.78	0.06	544.90
yr*unit + trimtug + capmass*yr + capdate	14	565.01	2.83	0.06	536.89
yr*unit + trimtug + capmass*yr + capmass*capdate	15	565.33	3.15	0.05	535.19
yr*unit + trimtug + capmass + capdate*unit	15	566.25	4.08	0.03	536.12
yr*unit + trimtug + capmass*yr + capdate*unit	17	566.61	4.43	0.03	532.44
yr + unit + trimtug	7	567.15	4.97	0.02	553.12
yr*unit + trimtug + capmass + capdate*yr	14	568.03	5.85	0.01	539.91
yr*unit + trimtug + capmass*yr + capdate*yr	16	568.44	6.26	0.01	536.29
yr*unit + trimtug + capmass*unit	14	569.89	7.71	<0.01	541.77
unit + trimtug	5	571.07	8.89	<0.01	561.05
Global model	24	575.49	13.31	<0.01	527.15
yr + trimtug	4	588.12	25.95	<0.01	580.11
Null model	1	594.27	32.09	<0.01	592.27
capmass	1	679.85	117.68	<0.01	677.85
capdate	1	1031.82	469.65	<0.01	1029.82

lower mortality (i.e. pre-molt birds whose primary feathers were trimmed or tugged survived better on average) but the difference was small and 95% confidence intervals overlapped (trimpul: daily mortality = 1.1%, SE = 0.4%, 95% CI = 0.32-1.88; not trimpul: daily mortality = 1.9%, SE = 0.7%, 95% CI = 0.53-3.26). The effect of capture date varied with capture mass; daily mortality of the lightest birds captured earliest was much lower (1.7%, SE = 0.5%) than for those captured latest (17.3%, SE = 3.9%) but daily mortality of the heaviest birds captured earliest (1.8%, SE = 0.7%) and latest (1.1%, SE = 0.4%) was similar.

Table 2. Estimated daily survival rate (DSR) and 30-day survival percentage (30d surv %) with SEs for flightless female Mallards (*Anas platyrhynchos*) radiotagged just before or soon after molting wing feathers on Lower Klamath National Wildlife Refuge (NWR) wetland units 12C and 8B, Tule Lake NWR wetland unit 1-A (TL), or Upper Klamath NWR (UK) and monitored during July-September 2001, 2002 and 2006.

	2001		2002		2006	
Unit	DSR or 30d surv %	SE	DSR or 30d surv %	SE	DSR or 30d surv %	SE
12C	0.99143	0.006218	0.97107	0.009258	0.92866	0.018396
8B	0.99124	0.005802	0.97902	0.014307	0.98818	0.004641
TL	0.99769	0.002314	0.99365	0.004133		
UK			0.99302	0.005994		
12C	77%	14.5%	41%	11.9%	11%	6.5%
8B	77%	13.5%	53%	23.4%	70%	9.9%
TL	93%	6.5%	83%	10.3%		
UK			81%	14.7%		

The most common causes of mortality among flightless female Mallards was type C avian botulism (64%) and predation (26%), but causes of mortality differed among molting wetlands (Table 3). Botulism was the main cause of mortality of Mallards in TL in 2002 and in 12C all three years based upon known botulism outbreaks and laboratory examinations of radiotagged (mostly in 2006) and other carcasses recovered near dead radiotagged birds (mostly in 2001 and 2002). Predation was the main cause of mortality in 8B based on lack of known botulism outbreaks, absence of other carcasses that would indicate a botulism outbreak, and the fact that remains were mostly consumed by predators even though radiotagged Mallards were recovered within a few hours after each died in 2006. Cause of death could not be determined for 10% of the mortalities. Also, necropsies showed that one Mallard from 8B in 2001 and two from 12C had elevated levels of lead, one showed signs of avian tuberculosis, and one tested positive for *Erysipelothrix* bacteria; indicating that other factors may have contributed to death of some that were classified as being killed by predators or botulinum intoxication.

Most female Mallards that molted in KB wintered in CVCA (Fig. 1), primarily in the northern part (i.e. Sacramento Valley), but with some late-winter locations for a few birds in the central (i.e. San Joaquin-Sacramento River Delta [Delta] and Suisun Marsh) and southern part (i.e. San Joaquin Valley). Of the 81 female Mallards that survived their flightless period and did not die in KB, 4% remained in KB through at least 31 January, 80% moved to CVCA before the end of January, and 16% wintered in unknown locations (likely not CVCA, KB, or the areas between which were all searched thoroughly) (Table 3). One of the 16% with unknown wintering location was located 100 km northeast of UK near Summer Lake, Oregon in late March, suggesting at least some of the missing birds wintered north of the KB in areas that were not searched (e.g. Columbia Basin, coastal Oregon).

Most surviving female Mallards left KB during October and November. Excluding the one each year that remained in KB

Table 3. Sample size and confirmed or suspected fate (see text) of female Mallards (*Anas platyrhynchos*) radiotagged on Lower Klamath National Wildlife Refuge (NWR) wetland units 12C and 8B, Tule Lake NWR wetland unit 1-A (TL), and Upper Klamath NWR (UK) in Klamath Basin (KB) and monitored July-May, 2001-2002, 2002-2003 and 2006-2007. Necropsies also showed elevated levels of lead in two birds, *Erysipelothrix* spp. bacteria in a third, and signs of avian tuberculosis in a fourth, that died of botulism in 12C in 2002; one killed by a predator in 8B in 2001 also had elevated levels of lead and one that died of avian botulism in 12C in 2001 showed presence of *Aspergillus* spp.

	2001-2002			2002-2003			2006-2007		
Sample size and fate	12C	8B	TL	12C	8B	TL	UK	12C	8B
Number marked as flightless	20	14	20	20	19	20	20	22	26
Died from avian botulism	6			12		4		18	
Killed by predator		4		1	5		1		5
Died from unknown cause			1		2		1		2
Radiotag shed or failed	1								1
Survived to become capable of flight	13	10	19	7	12	16	18	4	18
Died in KB from avian botulism	2							1	
Killed in KB by predator					1				2
Died in KB of unknown (unk) cause	2	1		1	3	1	6		
Shot in KB by hunter	4	3	2	1		1	1	1	3
Alive in KB through at least 31 Jan	1				1				1
Shot in or en route to Central Valley	1		2		2		1		
Died in Central Valley of unk cause				1			1		1
Flew to Central Valley and lived	3	5	14	3	2	12	9	2	6
Flew to unknown area		1	1	1	3	2			5

through February, the estimated date that females left KB ranged from 21 August to 13 January and differed among years ($F_{2,73}$ = 3.66, P = 0.03, Fig. 2), averaging 11 November 2001, 25 October 2002, and 19 November 2006 (Fig. 2). Overall, the average departure date was 4 November. By the end of October, 17.8% in 2001, 47.4% in 2002 and 33.4% in 2006 of the surviving female Mallards had left KB. By the end of November, the cumulative total that had left KB increased to 85.7% in 2001, 92.1% in 2002, but only 60.1% in 2006. The estimated date that female Mallards left KB was not related to the estimated date each regained flight capability ($F_{1,74}$ = 0.04, P = 0.83) or their body mass at capture ($F_{1,74}$ = 2.23, P = 0.14). The lag between when each female regained flight capability and when they left KB averaged 62 days. The lag was not related to body mass at capture ($F_{1,74}$ = 2.35, P = 0.13) but did

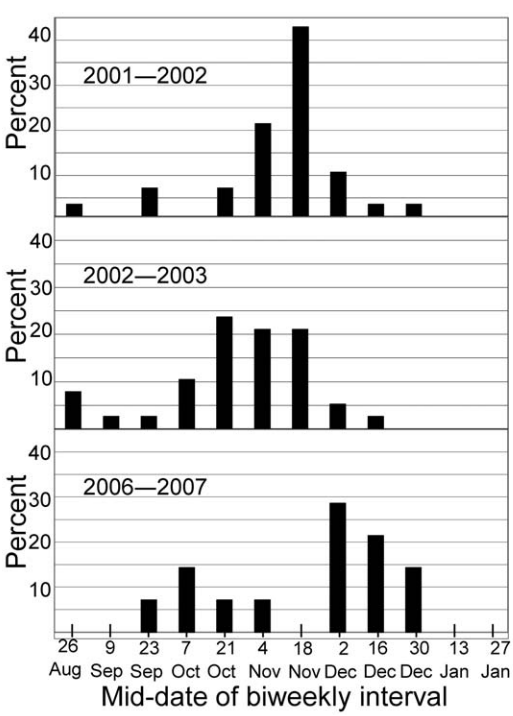

Figure 2. Percentage distribution across biweekly intervals (mid-date shown) when radiotagged female Mallards (*Anas platyrhynchos*) left Klamath Basin during 19 August-9 February 2001-2002 (*n* = 27), 2002-2003 (*n* = 37) and 2006-2007 (*n* = 14). (Excludes one each year that wintered in Klamath Basin).

vary among years ($F_{2,73}$ = 3.03, P = 0.05; 2001: 64d [SE = 6d], 2002: 54d [SE = 5d], 2006: 77d [SE = 8d]).

The highest-ranked (AIC_cwt = 0.50) post-molt survival model included season, region and unit; these factors were in all other models with AIC_cwt ≥0.01 (Table 4). The next best model included trimtug (AIC_cwt = 0.21) and models with capdate, capmass, or year each had AIC_cwt ≤0.08 (Table 3). Standardized to mean covariate values, weekly survival was lower during hunt than other seasons, lower for Mallards that molted in 12C or UK than in the other units, and lower in KB than outside KB (Table 5). Post-molt weekly mortality rates in KB were much higher than in CVCA (Table 6); post-molt survival during late August-late March averaged 20.7% (SE = 6.3%) in KB and 62.9% (SE = 10.1%) in CVCA. Capture covariates had no detectable relationship to post-molt survival; change in odds of weekly mortality due to feather manipulation (11%, SE = 55%), capture mass (heaviest relative to lightest: -1%, SE = 33%), or capture date (latest relative to earliest: -2%, SE = 34%) were not significant.

Hunting was the main cause of mortality for post-molt Mallards both within (16 of 37 deaths) and outside KB (six of nine deaths) (Table 3). Cause of death could not be determined for 14 in KB and three in CVCA due to lack of access to recover the carcass or because remains recovered were inadequate for analysis. In KB, seven died (three avian botulism, two predation, two unknown cause) in the same wetland unit as where they had molted within a few days after each was projected to regain flight capability.

With much lower post-molt survival in KB than in CVCA, non-breeding survival was higher for AHY female Mallards that migrated to CVCA. Overall, non-breeding season survival was 15.9% (SE = 5.0%) in KB (i.e., 76.8% flightless survival in KB x 20.7% post-molt survival in KB = 15.9%), 48.3% (SE = 8.7%) in CVCA (i.e., 76.8% flightless survival in KB × 62.9% post-molt survival in CVCA = 48.3%) and 29.8% (SE = 7.1%) overall (weighted by average seasonal distribution).

Table 4. Number of parameters (k), Akaike Information Criterion (AIC_c) values adjusted for small sample size, ΔAIC_c, AIC_c weights (AIC_cwt), and deviance used to rank models containing factors (season [seas], bird location region [reg], study year [yr], and capture unit [unit], Julian date [capdate], and standardized mass [capmass]; trimtug refers to whether or not primaries on pre-molt birds were manipulated) hypothesized to impact post-molt survival August-May, 2001-2002, 2002-2003 and 2006-2007, of female Mallards (*Anas platyrhynchos*) radiotagged just before or soon after molting wing feathers on Lower Klamath National Wildlife Refuge (NWR) wetland units 12C and 8B, Tule Lake NWR wetland unit 1-A, or Upper Klamath NWR and tracked in the Klamath Basin and Central Valley regions. The global (seas + reg + trimtug + capmass*capdate + unit + yr + yr*unit + yr*reg) and null (contains only the intercept) models are included for reference.

Model	k	AIC_c	ΔAIC_c	AIC_cwt	Deviance
seas + reg + unit	7	422.60	0	0.49	408.54
seas + reg + trimtug + unit	8	424.30	1.70	0.21	408.22
seas + reg + trimtug + capdate + unit	9	426.29	3.69	0.08	408.19
seas + reg + trimtug + capmass + unit	9	426.30	3.70	0.08	408.20
seas + reg + yr + unit	9	426.49	3.88	0.07	408.38
seas + reg + trimtug + capmass + capdate + unit	10	428.29	5.69	0.03	408.17
seas + reg + trimtug + yr + unit	10	428.32	5.71	0.03	408.19
seas + reg + unit + yr + yr*unit	12	432.43	9.83	<0.01	408.25
seas + reg + trimtug	5	433.82	11.22	<0.01	423.79
seas + reg + capdate	5	434.03	11.43	<0.01	423.99
seas + reg + trimtug + capmass*capdate + yr + unit	13	434.25	11.65	<0.01	408.05
seas + reg + trimtug + unit + yr + yr*unit	13	434.29	11.69	<0.01	408.08
seas + reg	4	434.77	12.16	<0.01	426.74
reg	2	435.61	13.01	<0.01	431.60
seas + reg + trimtug + yr	7	436.28	13.68	<0.01	422.22
seas + reg + trimtug + capdate + unit + yr + yr*unit	14	436.29	13.68	<0.01	408.05
seas + reg + trimtug + capmass + unit + yr + yr*unit	14	436.31	13.70	<0.01	408.07
seas + reg + capmass	5	436.73	14.12	<0.01	426.69
seas + yr + reg	6	438.11	15.50	<0.01	426.06
seas + reg + trimtug + capmass + capdate + unit + yr + yr*unit	15	438.31	15.70	<0.01	408.04
yr + reg	4	439.12	16.51	<0.01	431.09
seas + reg + trimtug + capmass*capdate + unit + yr + yr*unit	16	440.30	17.70	<0.01	407.99
seas + yr + reg + yr*reg	8	442.01	19.41	<0.01	425.93
yr + reg + yr*reg	6	442.52	19.92	<0.01	430.48
Global model	18	444.25	21.65	<0.01	407.87
seas	3	446.94	24.34	<0.01	440.93
seas + yr	5	450.15	27.55	<0.01	440.12
Null model	1	457.99	35.39	<0.01	455.99
yr	3	459.80	37.20	<0.01	453.79

DISCUSSION

Flightless female Mallard survival during this study (Table 2) was similar to survival of Mallards molting on eight large wetlands in the Canadian prairies during 1999-2001 (Evelsizer 2003, DSR range = 0.9025-0.9987, average = 0.9825). The lowest survival during both this and Evelsizer's (2003) study were in wetlands where avian botulism caused most or all of the mortality. Daily survival of Mallards during this and Evelsizer's (2003) study averaged lower than molting female Mallards in Minnesota (0.9979; Kirby and Cowardin 1986), female Northern Pintails (*Anas acuta*) in California (0.9934; Miller *et al.* 1992 [seven molted in CVCA, two in KB]), female Black Ducks (*Anas rubripes*) in Maine (0.9954; Ringelman and Longcore 1983), male Black Ducks in Labrador (0.9952; Bowman and Longcore 1989), and female Harlequin Ducks (*Histrionicus histrionicus*) in Alaska (0.999; Iverson and Esler 2007). Unlike during this and Evelsizer's (2003) study, no losses were attributed to avian botulism in those other studies, largely explaining the differences in survival. To model midcontinent Mallard populations, Koford *et al.* (1992) assumed a DSR of 0.9995 for post-breeding females but also included an addi-

Table 5. Estimated seasonal (prehunt, hunt, posthunt) weekly survival rate (WSR) with SE for post-molt adult female Mallards (*Anas platyrhynchos*) captured and radiotagged in 2001, 2002 or 2006 just before or soon after starting wing molt on Lower Klamath National Wildlife Refuge (NWR) wetland units 12C or 8B, Tule Lake NWR wetland unit 1-A (TL), or Upper Klamath NWR (UK) and located in the Klamath Basin (KB) or Central Valley of California (CVCA). Average (Avg) of unit estimates; SE for average = square root of (variance/number of units).

		Prehunt		Hunt		Posthunt	
Bird region	Capture unit	WSR	SE	WSR	SE	WSR	SE
KB	12C	0.9262	0.02742	0.9152	0.02147	0.9812	0.02009
	8B	0.9570	0.01520	0.9504	0.01407	0.9893	0.01159
	TL	0.9842	0.00748	0.9817	0.00740	0.9962	0.00430
	UK	0.9206	0.03894	0.9089	0.03218	0.9797	0.02224
	Avg	0.9470	0.01477	0.9391	0.01689	0.9866	0.00382
CVCA	12C	0.9778	0.01253	0.9742	0.01083	0.9946	0.00559
	8B	0.9873	0.00691	0.9853	0.00642	0.9969	0.00319
	TL	0.9954	0.00276	0.9947	0.00261	0.9989	0.00116
	UK	0.9760	0.01495	0.9722	0.01245	0.9941	0.00608
	Avg	0.9841	0.00452	0.9816	0.00523	0.9961	0.00111

tional 0.0007 daily mortality from avian botulism during July-September, resulting in a DSR of 0.9988.

Survival rates observed for flightless female Mallards during this study are likely representative of long-term rates in KB because losses to botulism in KB marshes (2001:649; 2002:1,042; 2006:12,000; average = 4,564) were similar to the long term (1990-2006 range = 0-14,000; average = 4,710; D. S. Blehert, U.S. Geological Survey and D. M. Mauser, U.S. Fish and Wildlife Service, unpublished data). Avian botulism is one of the most important waterfowl diseases in the world (Rocke 2006) and is most prevalent in North America during late June-early September (Samuel 1992). Certain wetland water quality characteristics have been found to be associated with frequency and severity of outbreaks but relations are complex (Rocke and Samuel 1999) and not consistent (Hernandez 2007). Hernandez (2007) reported that modeled botulism risk (Rocke and Samuel 1999) based on water quality measures during 2000 and 2001 was 3.3 times greater in 12C than in either 8B or TL. The fact that an extensive botulism outbreak killed most radiotagged Mallards in 12C in 2006, five years after the Hernandez (2007) study, suggests that the environmental characteristics causing elevated risk for botulism in 12C is persistent. Two of the wetland units (TL, UK) where survival of molting Mallards was high and botulism infrequent or absent were larger and associated with more permanent water than 12C. Thus, larger wetlands with more permanent water may have lower botulism risk than smaller, less permanent wetlands in KB.

Predation rates also may be related to molting marsh size. Predators killed a greater percentage of molting hens on the smaller than on the larger wetlands in this study (Table 3). Groups of molting waterfowl were

Table 6. Estimated seasonal (prehunt, hunt, posthunt) weekly mortality rate percentage (WMR%) with SE% for post-molt adult female Mallards (*Anas platyrhynchos*) radiotagged (Tag) in Klamath Basin (KB) during this 2001-2007 study and located (Loc) in KB or Central Valley of California (CVCA) compared with rates for adult female Mallards radiotagged and located in CVCA during Fleskes *et al.* (2007) 1998-2000 study.

	Region		Prehunt		Hunt		Posthunt	
Data source	Tag	Loc	WMR%	SE%	WMR%	SE%	WMR%	SE%
This study	KB	KB	5.30	1.81	6.09	1.14	1.34	1.41
This study	KB	CVCA	1.59	0.83	1.84	0.65	0.39	0.39
Fleskes *et al.*	CVCA	CVCA	0.10-0.12	0.06	1.89-2.22	0.66	0.10-0.12	0.06

frequently encountered and radiotagged molters were often on levees and roads at night surrounding the Lower Klamath NWR units, where they were likely very vulnerable to predators. Use of shorelines and roads may be more common around smaller molting marshes because they have more edge relative to wetland area than do larger marshes.

Other factors may have contributed to mortality that was attributed to disease or predation (Johnson *et al.* 1987). Although the elevated levels of lead in three Mallard carcasses recovered from Lower Klamath may be from lead ingested elsewhere, Mallards sampled during the 1990s in Lower Klamath NWR wetlands also had elevated levels of lead (D. M. Mauser, U.S. Fish and Wildlife Service, unpublished data). Elevated levels of lead may not only cause mortality directly but may also increase vulnerability to disease or predators (Friend and Franson 1999). Samuel (1992) estimated that if the 1991 lead shot ban reduced lead poisoning mortality rate by 75%, the proportion of mid-continent female Mallards with sublethal lead exposure would be reduced from 20.4% down to 5.5%, a rate similar to that during this study (three of 39 tested = 7.7%). Thus, although the 1991 national ban on lead shot for waterfowl hunting has not eliminated the lead shot hazard in KB to Mallards, it likely has reduced it. Presence of numerous dead and dying waterfowl from avian botulism may also attract predators and increase depredation of healthy birds after carcasses become less available. Increased daily mortality rates of light-weight birds that were captured late in the season during this study suggest some aspect of the molting marsh (e.g. food, water quality, sites safe from predators, predator density) deteriorated as the season progressed causing female Mallards in poor condition to be more susceptible to predation and disease.

Post-molt survival in August-March for radiotagged Mallards while they were in KB was not only much lower than outside KB (mostly in CVCA) during this study but also for Mallards radiotagged and wintering in CVCA during an earlier study (1998-1999: 74.4% SE = 7.7%, 1999-2000: 70.6% SE = 7.2%, Fleskes *et al.* 2007). Thus, either post-molt Mallards that remained in KB were less fit than those that left or conditions (e.g. hunting pressure, predator abundance, disease prevalence) for post-molt Mallards were less favorable in KB than in CVCA. The best KB post-molt survival model included wetland unit, reflecting that some Mallards during this study probably did not fly on the estimated date that they were capable; these remained in the molting wetland during prehunt where they were apparently more vulnerable to disease and predators than those that flew to other wetlands. Some of the Mallards that flew from their molting unit but remained in KB may also have been weakened by disease or were in poor body condition due to poor habitat conditions in the molting wetland unit (Pehrsson 1987), resulting in increased vulnerability to hunting and other factors (Greenwood *et al.* 1986). Further, Mallards in KB were exposed to hunting three to five weeks earlier than in CVCA, likely resulting in higher vulnerability to harvest (Hochbaum 1947) and contributing to their lower survival compared to Mallards that migrated to CVCA. Inclusion of some flightless birds in the prehunt estimate for KB does not explain why prehunt mortality was so much higher in KB than in CVCA during the Fleskes *et al.* (2007) study (Table 6), because 65% of Fleskes *et al.*'s (2007) CVCA sample was radiotagged as flightless molters (J. P. Fleskes, U.S. Geological Survey, unpublished data).

Oldenburger (2008) calculated non-breeding season (i.e. mid July-mid Mar) survival rates of 62.8%-67.3% for adult female Mallards nesting in CVCA during 2004 and 2005 by dividing band-derived annual survival (56.5%) by breeding season survival (84%-90%) which were determined with radiotelemetry. In KB, Mauser and Jarvis (1994) reported no mortality of 77 nesting radiotagged female Mallards and evidence of hen mortality at only three of 401 nests monitored, indicating very high (e.g. 95%) breeding season survival for female Mallards nesting in KB. Dividing annual survival of AHY female Mallards banded in KB (55%, SE = 1.3%; Rienecker 1990) by 95% breeding season survival results in a non-breeding season survival estimate of 57.9% for adult female Mallards nesting in KB. These band-derived non-breeding season survival estimates (i.e. CVCA nesters: 62.8%-67.3%, KB nesters: 57.9%) are similar to the radiotelemetry-derived estimate of non-breeding season survival during this study for adult female Mallards that molted in KB and went to CVCA (48.3%, SE = 8.7%) but are much higher than non-breeding survival for Mallards while in KB during this study (15.9%, SE = 5.0%). Several factors could cause differences in survival estimates among these studies. Large annual variation in KB survival mainly due to variation in botulism losses was observed during this study and if the band-derived estimates are mostly from years with few botulism losses then the band-derived non-breeding survival estimates would be higher. Alternatively, band-derived estimates may be biased high or radiotelemetry-derived estimates may be biased low. Band-derived survival estimates would be biased high if banding is terminated when botulism or other disease outbreaks occur at a trap site or if wetlands with consistent botulism outbreaks are avoided as band trap sites. Negative impacts of radiotagging have been reported on ducks during the nesting season (Pietz *et al.* 1993; Rotella *et al.* 1993) but not the flightless period. No indication was found during this study that field methods reduced flightless survival. The variable for feather manipulation was retained in the best model but manipulation was associated with increased (not decreased) survival. Thus, while the biological significance of the estimated increase in survival should be discounted because 95% CIs for the covariate estimates overlapped, it is safe to say that feather manipulation did not lower flightless survival. There is some evidence that flighted ducks adjust their body mass to compensate for the radiotag (Fleskes 2003) and this ability may have been impaired in disease-weakened and other poor-condition post-molt birds. Thus, radiotags may have contributed to the poor condition, and resulting increased vulnerability to hunting (Greenwood *et al.* 1986; Heitmeyer *et al.* 1993) or other mortality of some post-molt Mallards in KB, thus inflating the difference between KB and CVCA post-molt survival.

Our study indicates that survival of female Mallards that molt in KB may be less than for those that molt in CVCA. However, concurrent research in KB and CVCA is needed to better understand factors related to flightless and post-molt survival and their impact on Mallard population dynamics. The high mortality rate of molting female Mallards from avian botulism in some KB wetlands reinforces the need for research to better understand environmental factors that lead to botulism outbreaks. Providing secure loafing islands or other over-water loafing cover such as dense emergent vegetation, especially in small molting marshes, could reduce depredation losses. Molting Mallard survival was highest in large permanent marshes and potential negative impacts on survival that could result if water supplies for wetland habitats were reduced should be considered when developing KB water management plans.

ACKNOWLEDGMENTS

Funding and logistical support was provided by California Department of Fish and Game-Duck Stamp Program and Wildlife Program, California Waterfowl Association, U.S. Fish and Wildlife Service-Central Valley Joint Venture, U.S. Fish and Wildlife Service-Klamath Basin NWR and USGS-Western Ecological Research Center. We thank D. Thompson, J. Beckstrand, J. Kesling, D. Skalos and N. M. Smith for trapping and tracking Mallards and summarizing habitat information. We thank D. Yparraguirre, M. Weaver, E. Buelna and J. Hainline for aerial searches and D. Loughman and J. Laughlin for monitoring Mallards in CVCA. M. Samuel and K. Converse of USGS-National Wildlife Health Center coordinated and summarized necropsies. K. Ellsworth and L. Naylor entered data. W. Perry, J. Daugherty and L. Williams provided GIS support. S. Oldenburger, D. Yparraguirre, J. Ackerman and M. Casazza commented on the manuscript. An Animal Care and Use Committee reviewed and approved the methods to ensure compliance with the Animal Welfare Act and United States Government Principles for Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training policies. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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