Management and Conservation Note

Variation in Breeding Season Survival of Female Harlequin Ducks

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ABSTRACT Quantifying sources of variation in demographic rates can provide insight into processes underlying population dynamics and subsequently direct wildlife conservation. In the context of avian life history, understanding patterns of variation in survival rates of breeding females is particularly relevant because this cohort often has a disproportionately large effect on population dynamics. We estimated survival probability for 144 adult female harlequin ducks (*Histrionicus histrionicus*) that we marked with radiotransmitters and tracked at 4 breeding areas in western North America. Model selection results indicated both regional and temporal variation in survival rates, with most mortality attributed to predation. Cumulative survival probability ($\pm$SE) during the 100-day study period was lower at 2 sites in the Rocky Mountains of Alberta, Canada (AB1 and AB2: 0.75 ± 0.11) than in the Coast Mountains of British Columbia, Canada (BC: 0.88 ± 0.08) or the Cascade Mountains of Oregon, USA (OR: 0.89 ± 0.08). Survival also was lower during incubation than nest-initiation or brood-rearing stages at all 4 study areas. In comparison to other annual cycle stages and locations, harlequin duck mortality rates were highest on the breeding grounds, suggesting that management actions designed to reduce mortality during breeding would achieve meaningful population-level benefits. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):965–972; 2009)

In ecology and wildlife management, quantifying sources of variation in demographic rates is important for identifying mechanisms underlying changes in abundance and distribution, as well as gauging population health (Lebreton et al. 1992, Sæther and Bakke 2000). Generation of population-specific fecundity and survival estimates also can lead to a better understanding of constraints on population growth and indicate when and where conservation efforts would be most effective (Schmutz et al. 1997; Hoekman et al. 2002, 2006; Sillett and Holmes 2002).

Survival rates are key parameters in species' demographics and advances in statistical theory and software have greatly improved our capacity to test biological hypotheses and draw inferences about sources of variation in survival rates (Lebreton et al. 1992, White and Burnham 1999). For Anatinae (hereafter, ducks), understanding patterns of variation in female survival is particularly important because most species exhibit male-biased sex ratios, making breeding-age females a limiting factor from a population growth perspective (Johnson et al. 1992). Male-biased sex ratios among ducks are thought to result from females being more vulnerable than males during the breeding season, due to the higher predation rates females face when incubating and providing parental care (Johnson and Sargeant 1977, Sargeant et al. 1984). However, few studies provide mortality rate estimates during the breeding season, and

no estimates exist for most species in most areas (Sargeant and Raveling 1992).

Available breeding-season survival estimates for female ducks suggest considerable variation among species and populations and across breeding stages (e.g., Kirby and Cowardin 1986, Devries et al. 2003, Brook and Clark 2005, Richkus et al. 2005, Safine 2005). Notably, Kirby and Cowardin (1986) reported lower survival for female mallards (*Anas platyrhychos*) in Minnesota, USA, during the breeding season, with the lowest survival rates documented during the incubation period. Also, in a geographically extensive comparison of female mallard survival rates across multiple study areas in the Prairie Pothole Region of Canada, Devries et al. (2003) reported considerable spatial and temporal variation, characterized by lower survival during nesting and in relation to wetland habitat such that survival was lowest at western sites with low wetland densities. However, most of the published studies deal with Anatini (hereafter, dabbling ducks), and it is unclear the degree to which the patterns that have been described apply to other taxa.

We investigated breeding-season survival rates of female harlequin ducks (*Histrionicus histrionicus*) from locations in Alberta (Canada), British Columbia (Canada), and Oregon (USA). We drew our dataset from several independent research teams using similar radiotelemetry approaches, thereby allowing for the first broad and direct consideration of breeding-season survival rates for the species. Harlequin ducks are Mergini (hereafter, sea ducks), and compared to dabbling ducks, sea duck life histories tend to be

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characterized by longer life spans, delayed reproductive maturity, and lower annual fecundity (Goudie et al. 1994). Harlequin ducks are among the best-studied sea duck species from a demographic perspective, and estimates of both annual (Cooke et al. 2000, Regehr 2003) and stage-specific overwinter (Esler et al. 2000) and postbreeding (Iverson and Esler 2007) female survival have been reported. However, there are no published estimates of female survival during the breeding season, when harlequin ducks leave coastal areas and migrate to inland freshwater streams to breed. Given conservation concerns raised for Pacific populations in North America (Robertson and Goudie 1999, Smith et al. 2001, Rodway et al. 2003) and the listing of the eastern population in Atlantic Canada and Quebec as a species of Special Concern (Environment Canada 2006), it is important to develop a fuller understanding of harlequin duck demography, which in turn will lead to better management. Our objectives were to address this gap in the understanding of harlequin duck demography by 1) estimating female harlequin duck breeding-season survival rates at 4 western North America study areas, 2) evaluating geographic and temporal variation in breeding-season survival rates, including differences during nest initiation, incubation, and brood rearing, and 3) comparing breeding-season survival rates to estimates derived during other annual cycle stages to determine the degree to which the breeding stage acts as a constraint on populations.

STUDY AREA

We studied harlequin duck breeding ecology at nesting areas around 1) Banff National Park, Alberta (AB1; 1997–1999), 2) the foothills of west-central Alberta (AB2; 1997–1999, 2004), 3) the southern Coast Mountains of British Columbia (BC; 2003–2004), and 4) the central Cascade Mountains of Oregon (OR; 1994–1995; Fig. 1). Harlequin duck breeding habitat in all 4 areas was characterized by fast-flowing rivers and streams, where harlequin ducks nest cryptically in low densities (Roberston and Goudie 1999).

We conducted research in AB1 on the Bow River in Banff National Park (51°26′N, 116°11′W) and the Kananaskis River (50°55′N, 115°7′W) and the Elbow River in the Kananaskis Country Recreation Area (50°51′N, 114°45′W). We conducted research in AB2 on the McLeod River and its tributaries including Whitehorse Creek (53°1′N, 117°19′W). We conducted research in BC on 7 streams around Pemberton (50°19′N, 122°48′W) and Lillooet (50°41′N, 121°56′W), including Bridge River, Seton River, Cayoosh Creek, Yalakom River, Ryan River, Rutherford Creek, and Brandywine Creek. We conducted research in OR on tributaries of the Willamette River between Salem and Eugene (43°52′N, 121°15′W).

METHODS

We captured female harlequin ducks shortly after their arrival in the breeding area using mist nets suspended over streams. We aged captured ducks based on plumage characteristics (Smith et al. 1998) and bursal depth (Mather and Esler 1999) and attached transmitters only to after-
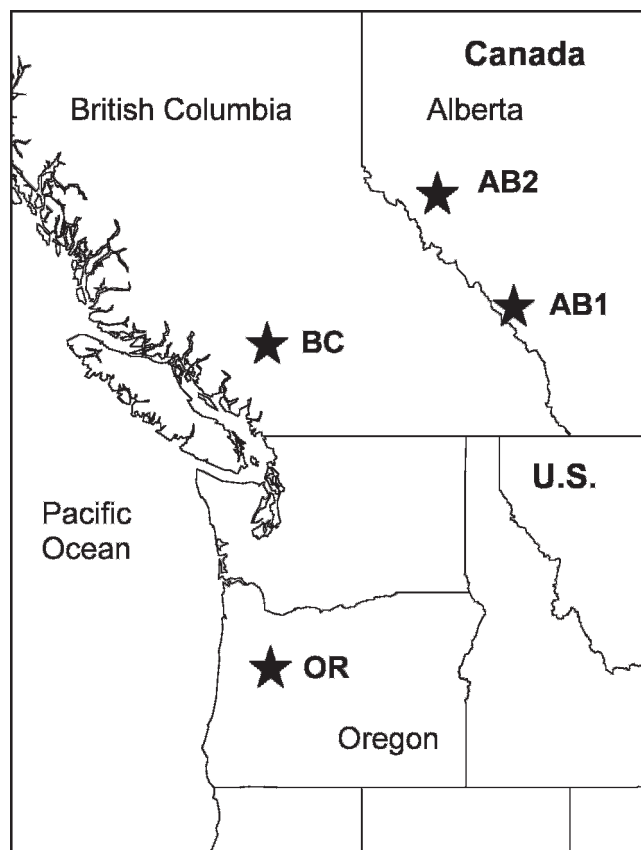

Figure 1. Map of western North America indicating locations of the 4 harlequin duck study areas. We studied harlequin duck breeding ecology at nesting areas around 1) Banff National Park, Alberta, Canada (AB1; 1997–1999), 2) the foothills of west-central Alberta (AB2; 1997–1999, 2004), 3) the southern Coast Mountains of British Columbia, Canada (BC; 2003–2004), and 4) the central Cascade Mountains of Oregon, USA (OR; 1994–1995).

third-year females. In AB1, we used 2 types of transmitters: 20-g cylindrical coelomic implants with external antennae (Korschgen et al. 1996; $n = 15$; hereafter, implants) and 4-g external transmitters attached mid-dorsally with a subcutaneous prong and suture (Mauser and Jarvis 1991, Pietz et al. 1995; $n = 10$; hereafter, back-mounts). In AB2 and OR, we tied and glued 6-g external transmitters to the underside of the central tail feathers ($n = 52$ and 34, respectively; hereafter, tail-mounts). In BC, we attached 6-g back-mounts mid-dorsally using a subcutaneous prong and glue (Pietz et al. 1995; $n = 34$). Surgeries for the implants in AB1 were performed by a licensed veterinarian and all field procedures followed approved Simon Fraser University (permit no. 668B-033; 478B), Canadian Wildlife Service (permit no. 1165-36/C255), or United States Fish and Wildlife Service Animal Care Committee procedures.

We determined location, signal strength, and survival status every 1–10 days by traveling on foot using handheld receivers and antennae. We confirmed evidence of mortality by location of carcasses or other evidence of predation, including strewn feathers, a transmitter in a predator's den, or discovery of leg bands. We monitored all radiomarked birds throughout the breeding season and distinguished transmitters for which signals were temporarily undetected

(i.e., located during one encounter interval, but not located during the next, and then located again) from those that were permanently lost due to the transmitter being shed, transmitter failure, undetected mortality, or permanent emigration. We restricted our analyses to the period from 29 April to 7 August and summarized individual fates over 10-day intervals to ensure adequate encounter histories were available for survival estimation.

We used the Known-Fate modeling procedure in Program MARK (White and Burnham 1999) to evaluate survival in relation to potential explanatory variables. The procedure is derived from the Kaplan–Meier estimator (Kaplan and Meier 1958), with modifications to allow for staggered entry of subjects into the study population (Pollock et al. 1989) and likelihood inference based on binomial probabilities (White and Burnham 1999). Bunck and Pollock (1993) summarize the key assumptions of known-fate models to include 1) radiomarked animals are representative of the population; 2) survival is independent among individuals; 3) censoring of animals for which signals are lost is independent of the fate of those individuals (i.e., undetected signals are no more or less likely to be dead than animals for which fate is known); and 4) radiomarking does not affect survival during the study period. We felt that the first 3 assumptions were likely to have been met based on our marking and tracking methods, and we conducted a diagnostic analysis to evaluate the final assumption.

Among waterfowl, deleterious effects have been associated with some transmitter types, particularly during the period immediately following transmitter attachment (Dzus and Clark 1996, Mulcahy and Esler 1999). Therefore, we followed recommendations by Esler et al. (2000) and Iverson et al. (2006a) and applied a 14-day postsurgery censoring period to all data collected from implanted birds. Although the surgery required for implants is more invasive than that required for external mounts, sea duck mortality rates have proven to be similar for different transmitter types (Iverson et al. 2006a). To explicitly test for biases associated with transmitter type, we compared survival rates using a null model, in which we assumed no variation in survival probability, to an alternate model, in which we assumed different survival rates for birds given implants and externally mounted transmitters.

We designed our principal analysis to evaluate survival rates in relation to geographic location and breeding stage. To facilitate our analysis, we organized the data for comparison at 4 spatial scales (i.e., study area, province, region, pooled) and at 4 temporal levels (i.e., 10-day intervals, 3-stage, 2-stage, time invariant). We then evaluated all additive (+) and interactive (×) combinations of this 4 × 4 parameter space, which resulted in a candidate set that included 25 models. The province categorization included 3 variables and distinguished between study areas in Alberta, British Columbia, and Oregon, whereas the region categorization included 2 variables and distinguished between Rocky Mountain study areas (AB1 and AB2) and Coast or Cascade Mountain study areas (BC and OR). With respect to temporal variation, the 10-day interval

parameterization assumed unique survival probabilities for each encounter interval, whereas the 3-stage parameterization divided the breeding season into nest-initiation, incubating, and brood-rearing stages and assumed constant survival rates within periods. The 2-stage parameterization assumed different survival probabilities during the incubation versus the nest-initiation and brood-rearing stages combined. We based these categorizations on median egg laying and hatch dates within the respective study areas that were derived during the same years in which we collected the telemetry data. In Alberta, the median start date for incubation was 15 June and the median hatch date was 13 July (Smith 2000). Thus, the nest-initiation period survival for AB1 and AB2 encompassed the first 5 10-day encounter-history intervals, incubation encompassed intervals 6–8, and brood rearing was during intervals 9–10. In BC, median incubation initiation and hatch dates were 25 May and 22 June, respectively (J. Bond, Simon Fraser University, unpublished data). The nest-initiation period survival for BC was, therefore, encompassed by intervals 1–2, incubation by intervals 3–5, and brood rearing by intervals 6–10. In OR, median incubation initiation date was 15 May and hatch date 12 June (Bruner 1997), yielding nest initiation during interval 1, incubation during intervals 2–4, and brood rearing during intervals 5–10.

All models were run in Program MARK using a logit link function. We ranked competing models using the change in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c).We used Akaike weights (w_i), calculated as a model's likelihood proportional to all models included in the candidate set, to evaluate relative support for each. We considered the model with lowest AIC_c to be the best-approximating model and were primarily interested in models within 2 AIC_c units of the most parsimonious model (Burnham and Anderson 2002). Multi-model inference provides a formal means of addressing inherent uncertainty in selecting one best model (Burnham and Anderson 2002); therefore, we generated 10-day survival estimates from all models in our candidate set and used model-averaging to derive parameter estimates. To determine the importance of individual explanatory variables, we summed Akaike weights for all candidate models containing the variable under consideration, thus providing a combined Akaike weight. Combined Akaike weights were particularly useful for quantifying relative support for individual variables when several models had similar ΔAIC_c scores.

Goodness-of-fit statistics are currently unavailable for known-fate models; therefore, we evaluated potential effects of overdispersion on model selection by adjusting the variance inflation factor in Program MARK from 1 (no overdispersion) to 3 (extreme overdispersion) in increments of 0.5 and examining the effect of this change on model rankings. We chose not to evaluate year as an explanatory variable in our primary analysis because there were few instances where we could compare multiple study areas during the same year and with sufficient sample size. We did, however, conduct a series of diagnostic evaluations to investigate annual variation within study areas, in which we
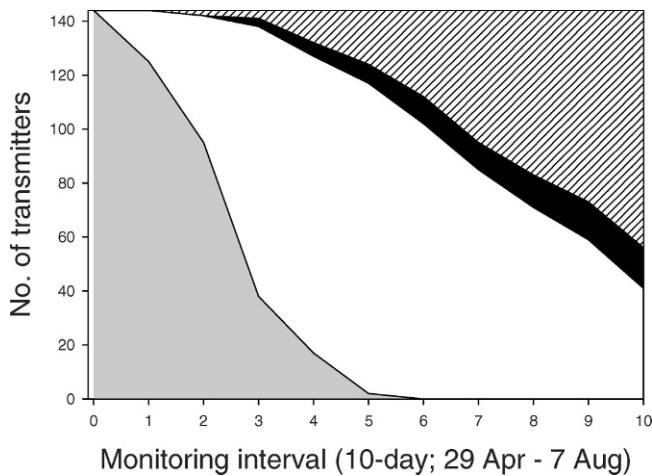
Figure 2. Number of radiomarked female harlequin ducks available (out of 144) for survival estimation at the start of each 10-day monitoring interval (29 Apr–7 Aug) for our research conducted in British Columbia and Alberta, Canada, and Oregon, USA, between 1994 and 2004. Grey area represents left-censored data (before transmitter was deployed); white area represents the number of active transmitters; black area represents the number of dead birds; and white area with diagonal stripes represents right-censored data (due to transmitter loss, transmitter failure, undetected mortality, or emigration from the study areas).

compared a null model that assumed no effects to an alternate model that included year of capture (YOC) as an explanatory variable.

RESULTS

Model-fitting results indicated that transmitter type had little effect on harlequin duck survival probability. The null model had a lower AIC_c score and higher weight (AIC_c = 147.57; $\Delta AIC_c = 0.00$; $w_i = 0.82$; $k = 1$) than the alternate model, which included transmitter type as an explanatory variable ($AIC_c = 150.71$; $\Delta AIC_c = 3.14$; $w_i = 0.17$; $k = 2$). Model-averaged survival probabilities ($\pm$SE) for the 10-day encounter intervals were indistinguishable for implant (0.976 ± 0.011) and externally mounted (0.979 ± 0.006) transmitters after application of a standard 14-day censor period on the data for implanted birds. During the immediate postrelease period, 1 of the 15 coelomically implanted birds died, whereas none of the 140 birds with externally mounted transmitters died.

Among the 144 monitored harlequin ducks, 15 died during the 29 April–7 August study period. Although causes of mortality were sometimes difficult to determine, we attributed most to predators. Evidence from 11 of 15 mortalities suggested mustelid predators, such as mink (*Neovison vison*) or marten (*Martes americana*), and the remaining 4 mortalities suggested avian predators. However, it was not possible to distinguish kills from scavenging events that may have occurred after mortality. With respect to transmitter detection rates, we estimated that we located 93.2% of all active transmitters during each encounter interval. We right-censored 58 birds from the dataset before the 7 August end date (Fig. 2); however, the reduction in sample size that occurred over the course of the study was gradual and most likely related to the shedding of externally

Table 1. Akaike's Information Criterion scores (AIC_c; the subscript denotes adjustment for small sample sizes) and Akaike weights (w_i) of candidate models explaining differences in harlequin duck survival during the breeding season at 4 study areas in the Oregon, USA (1994–1995), British Columbia, Canada (2003–2004), and Alberta, Canada (1997–1999, 2004). The province categorization included 3 variables and distinguished between study areas in Alberta, British Columbia, and Oregon, whereas the region categorization included 2 variables and distinguished between Rocky Mountain study areas (Alberta) and Coast or Cascade Mountain study areas (British Columbia and Oregon). The 10-day intervals parameterization assumed unique survival probabilities for each encounter interval, whereas the 3-stage parameterization divided the breeding season into nest-initiation, incubating, and brood-rearing stages and assumed constant survival rates within periods. The 2-stage parameterization assumed different survival probabilities during the incubation versus the nest-initiation and brood-rearing stages combined.

Model[a]	AIC_c	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
Region	146.16	0.00	0.21	2	21.20
Region + 2-stage	146.84	0.68	0.15	3	19.87
Null	147.57	1.42	0.10	1	24.63
Province	147.91	1.75	0.09	3	20.94
Region × 2-stage	148.19	2.03	0.08	4	19.20
2-stage	148.51	2.35	0.06	2	23.56
Province + 2-stage	148.55	2.40	0.06	4	19.56
Region + 3-stage	148.84	2.68	0.05	4	19.84
Region × 10-day	149.26	3.10	0.04	10	8.01
Study area	149.92	3.76	0.03	4	20.92
3-stage	150.24	4.08	0.03	3	23.27
Province + 3-stage	150.56	4.40	0.02	5	19.54
Study area + 2-stage	150.58	4.42	0.02	5	19.56
Province × 2-stage	151.34	5.18	0.02	6	18.28
Region × 3-stage	151.73	5.57	0.01	6	18.67
Study area + 3-stage	152.59	6.43	0.01	6	19.53
Study area × 2-stage	155.27	9.11	0.00	8	18.13
Province × 3-stage	156.92	10.76	0.00	9	17.72
10-day	158.72	12.57	0.00	10	17.47
Province + 10-day	160.07	13.91	0.00	12	14.69
Region + 10-day	160.89	14.73	0.00	11	17.57
Study area + 10-day	162.13	15.97	0.00	13	14.67
Study area × 3-stage	162.68	16.52	0.00	12	17.30
Province × 10-day	190.33	44.17	0.00	30	6.67
Study area × 10-day	205.81	59.65	0.00	40	0.00

[a] Model structure.
[b] Difference between AIC_c of the current model vs. the best-supported model.
[c] Relative likelihood of a model among the 25 tested.
[d] No. of parameters.

mounted transmitters. Overall, detection rates remained sufficiently high for robust survival estimation in all 4 study areas throughout the study.

The most parsimonious model explaining variation in adult female harlequin duck survival recognized differences between the Rocky Mountain and Coastal and Cascade Mountain ranges combined [S(Region)] and had an Akaike weight of 0.21 (Table 1). Support also was evident for the region-specific model that included 2-stage temporal variation as an additive effect [S(Region + 2 stage); ΔAIC_c = 0.68; $w_i = 0.15$]. The third-ranked model was the null model ($\Delta AIC_c = 1.42$; $w_i = 0.10$), which treated survival rate as a constant across locations and encounter intervals. Combined Akaike weights for models considering area-specific differences in survival probability were 0.07, 0.19, 0.55, and 0.20 at the study area, province, region, and no spatial-variation levels, respectively. Combined Akaike weights for models considering 10-day, 3-stage, 2-stage,
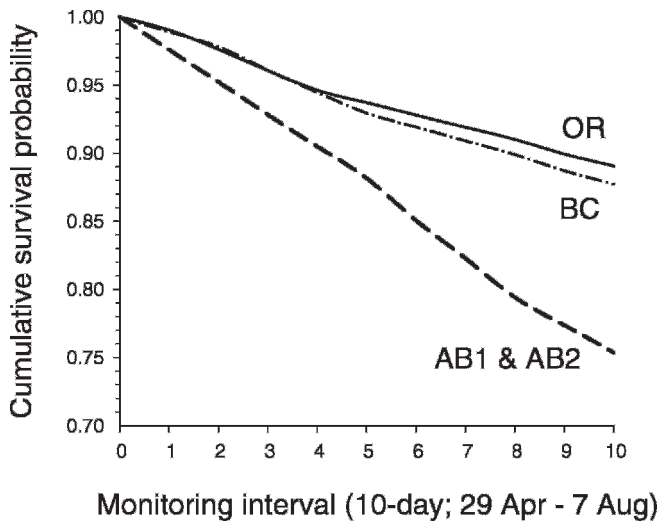
Figure 3. Model-averaged cumulative survival probability estimates (29 Apr–7 Aug) for adult female harlequin ducks breeding at 4 study areas in Oregon, USA (OR; 1994–1995), British Columbia, Canada (BC; 2003–2004), and Alberta, Canada (AB1 and AB2; 1997–1999, 2004).

and time-invariant variation were 0.05, 0.13, 0.39, and 0.43, respectively. These results suggest strong support for region as a predictor of spatial variation and similar degrees of support for survival differences during incubation versus time-invariant survival during the breeding season.

Model-averaged survival estimates were higher in BC and OR than they were in AB1 and AB2 (Fig. 3). The cumulative survival rate of adult females averaged 0.809 ± 0.052 for the full study period, and study-area–specific estimates were 0.754 ± 0.110 at AB1, 0.753 ± 0.109 at AB2, 0.877 ± 0.076 at BC, and 0.891 ± 0.077 at OR. With respect to breeding stage, parameter estimates were slightly lower during the incubation period than during the nest-initiation or brood-rearing stages in all 4 study areas (Table 2).

Known-fates models assume that individuals have independent survival probabilities and our results were robust to moderate levels of overdispersion. We found that model ranks did not change until adjustments of $\hat{c}$ exceeded 2.5, after which the null model was the most parsimonious in the candidate set. With respect to year effects and potential interactions between YOC and study area, our results were equivocal. We used separate diagnostic models to compare year-specific breeding-season survival rates within study areas and determined that model fit was best for the null model in 2 areas (AB1 and OR) and best for the YOC model in the others (AB2 and BC). In all cases ΔAIC_c between models was <2. Further analysis indicated that the coefficient of variation across study areas (CV = 1.32; n = 4) was larger than across years (CV = 1.19; n = 7) and a plot of year-specific breeding-season survival rates supported our known-fates model conclusions, namely that although annual effects may be present, geographic region remains as a driving factor underlying variation in survival rates among individuals (Fig. 4).

DISCUSSION

Survival of adult female harlequin ducks during the 100-day breeding season averaged 0.81 ± 0.05 across all areas and years and was lower in the Rocky Mountains of Alberta than the Coast Mountains of British Columbia or the Cascade Mountains of Oregon. Our estimate is higher than has been reported for most dabbling duck species (Kirby and Cowardin 1986, Devries et al. 2003) and similar to the rate reported for lesser scaup (*Aythya affinis*), a diving duck, in the Northwest Territories (Brook and Clark 2005), as well as other sea ducks, including white-winged scoters (*Melanitta fusca*) in Alaska, USA (Safine 2005). No other estimates of female harlequin duck breeding survival exist, but apparent annual survival of females was estimated at 0.74 ± 0.04 for harlequin ducks wintering in the Strait of Georgia, British Columbia (Cooke et al. 2000), where at least some of the birds from our study areas are known to winter. Cooke et al. (2000) based this estimate on resighting of marked individuals and it does not distinguish mortality from permanent emigration; however, harlequin ducks homing rates to molting and wintering areas tend to be very high (Cooke et al. 2000, Iverson et al. 2004), and we view this apparent survival rate as a close, if slightly underestimated, approximation of true annual survival. Thus, combining estimates across studies to obtain a gross estimate for survival during the nonbreeding season, our data indicate a nonbreeding survival rate of >0.90 would be necessary to result in the reported annual rate, where $S_{annual} = S_{breeding} \times S_{nonbreeding}$.

Survival estimates from other annual cycle stages are few, but available data corroborate the expectation that mortality rates are in fact higher during the breeding season but may not be uniform across wintering areas. Iverson and Esler

Table 2. Model-averaged parameter estimates ($\hat{s}$) for adult female harlequin duck survival during the nest-initiation, incubating, and brood-rearing stages of the breeding season. We studied harlequin duck breeding ecology at nesting areas around 1) Banff National Park, Alberta, Canada (AB1; 1997–1999), 2) the foothills of west-central Alberta (AB2; 1997–1999, 2004), 3) the southern Coast Mountains of British Columbia, Canada (BC; 2003–2004), and 4) the central Cascade Mountains of Oregon, USA (OR; 1994–1995). Observations collected from 29 April to 7 August.

Study area	Nest-initiation stage		Median incubation date[b]	Incubation stage		Median hatch date[b]	Rearing stage	
	$\hat{s}$[a]	SE		$\hat{s}$[a]	SE		$\hat{s}$[a]	SE
AB1	0.975	0.011	15 Jun	0.966	0.017	13 Jul	0.974	0.013
AB2	0.975	0.011	15 Jun	0.966	0.016	13 Jul	0.974	0.013
BC	0.989	0.008	25 May	0.983	0.011	22 Jun	0.988	0.011
OR	0.990	0.008	15 May	0.985	0.011	12 Jun	0.989	0.009

[a] Survival-rate estimates are the probability of remaining alive for a 10-day interval during each respective stage.
[b] Median incubation and hatch dates denote starting point of each new stage.
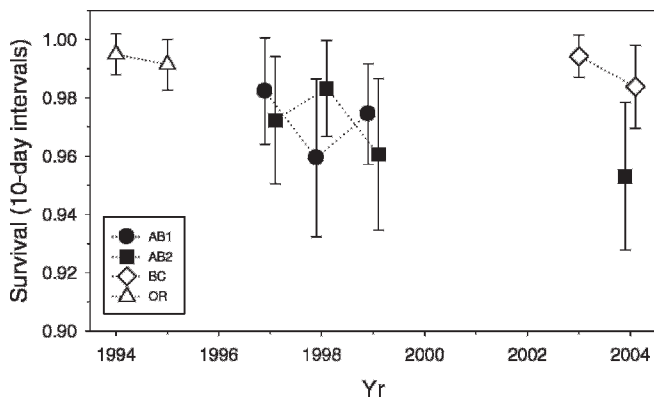
Figure 4. Location and year-specific breeding-season survival estimates for female harlequin ducks. Black fills represent model-averaged survival rates for study areas in the Rocky Mountain Region (squares represent AB1; circles represent AB2 [Canada]). White fills represent model-averaged survival rates for study areas in the Coast or Cascade Mountain Region (diamonds represent BC [Canada]; triangles represent OR [USA]). Points on the x-axis are offset slightly to allow standard error bars to be visible for all estimates.

(2007) reported a cumulative survival rate (CSR) of 0.99 ± 0.02 for radiomarked female harlequin ducks during the postbreeding period (20 Aug–15 Oct; 56 days) in Prince William Sound, Alaska. In a separate study, Esler et al. (2000) estimated a CSR of 0.84 ± 0.03 during winter (1 Oct–31 Mar; 183 days) for a subsample of the same radiomarked birds when monitored in unoiled control areas of Prince William Sound following the *Exxon Valdez* oil spill. Prince William Sound is at the northern extent of the harlequin duck Pacific Coast winter range and Esler et al. (2000) also found that winter survival rates were lowest during mid-winter when climatic conditions were most adverse. When combined, the Prince William Sound studies indicate a daily survival rate (DSR) of approximately 0.999 averaged across the 226-day nonbreeding period, where $CSR = DSR^n$. It is not known if overwinter survival rates in the southern portion of the harlequin duck Pacific range are higher than those estimated in Prince William Sound; however, irrespective of differences among wintering populations, our CSR for breeding females in Alberta, British Columbia, and Oregon corresponds to a lower DSR during the breeding season of 0.998 when averaged across locations, with a range of values between 0.997 and 0.999 for the study-area–specific estimates we derived in Alberta and Oregon.

Within the breeding season, our model-averaged parameter estimates indicate that survival rates are lowest during incubation. However, the similarity of model likelihoods for our S(region) and S(region + 2-stage) models suggests some uncertainty in the strength of the temporal effect. We speculate that the similarity in model fit is related in part to a lack of statistical power, given the relatively small sample size and lack of breeding-status categorizations for each individual. In lieu of direct daily categorizations of breeding status, we relied on median laying and hatching dates to categorize breeding stages and assigned individual status within 10-day encounter intervals. Although these estimates were study-area–specific and derived during the same years in which we collected telemetry data, they do not offer the same resolution as would be possible if we could evaluate individual covariates. Thus, we conclude our breeding-stage survival estimates are best viewed as a rough measure, which are consistent with those estimates from other studies that also have reported that females are more vulnerable to mortality while incubating nests (Kirby and Cowardin 1986, Devries et al. 2003, Richkus et al. 2005). If biased, our estimates would tend to underemphasize fine-scale differences among stages. Harlequin ducks are cryptic, solitary nesters that breed in low densities and often locate their nest on cliff ledges or on small islands within streams, which may reduce their susceptibility to predation during incubation; however, like other birds they are forced to remain sedentary and face a direct trade-off between maximizing their own survival versus the survival of their young.

With respect to geographic variation in breeding-season survival rates, we speculate that regional variation in female breeding survival was due primarily to differences in predator communities. Most mortalities appeared to result from mustelid predation, and the proportion of mortalities caused by these predators was similar in all regions. This suggests that mustelid predators may have been more abundant or that the number of breeding sites that provided adequate cover from mustelids were more limited in the Alberta sites. Devries et al. (2003) also proposed that geographic differences in duck survival could be related to predators concentrating in desirable habitats, which would impact duck survival in those areas. Similarly, Heath et al. (2006) suggested that differences in abundance of raptors on streams in Labrador influenced demographic characteristics of eastern population harlequin ducks. However, it also must be noted that we were not able to distinguish predator kills from scavenging so cannot be conclusive about the precise cause of mortality. For example, we could not distinguish a bird that had starved to death and been scavenged before it was located by researchers from a healthy bird that was predated. Another possibility for survival differing by geographic location is that females migrating to Alberta are incurring higher flight costs than those migrating to breeding sites closer to their wintering areas, such as British Columbia and Oregon. Cross-seasonal effects are known to play a role in nutrient-reserve dynamics of harlequin ducks (Bond and Esler 2006, Bond et al. 2007) and these higher energetic costs may reduce the females' condition such that they would be more susceptible to predation, starvation, or stochastic events. We did not collect differences in habitat and female condition attributes in a manner across study areas that we could readily incorporate into our survival analyses, and such detailed studies remain open to future investigation.

One of the strengths of our study was use of data collected by several research teams over a large geographic area and over a number of years to infer broad-scale patterns. However, the potential for biases resulting from methodological differences, namely the use of different transmitter types and attachment methods, as well as the potential for

year effects on breeding-season survival rates, also must be considered. With respect to transmitter type, although surgical implantation of transmitters requires use of anesthesia and opening of the coelomic cavity, recent studies suggest implants may actually have fewer negative effects than externally mounted transmitters (Hupp et al. 2003, Iverson et al. 2006a). We found no evidence for negative effects and no difference in survival rates among harlequin ducks fitted with different transmitter packages. For example, if transmitter type was influencing the study area effects that we observed, then survival rates in AB1 and BC, where we used back-mounted transmitters, should have been similar (with some added variation in AB1 due to implants), whereas AB2 and OR would be similar due to tail-mounted transmitters. This was clearly not the case.

With respect to potential year effects, our study design did not permit us to evaluate annual variation with replicated study areas. Each location had data collected over several years resulting in survival estimates averaged over a longer period than just one season. Our diagnostic analyses suggest that geographic region was a prime determinant of survival rate, but annual differences may also be important from a demographic standpoint. Available data from harlequin duck wintering areas suggest that the species exhibits little annual variation in abundance and adult to young ratios (Smith et al. 2001, Rodway et al. 2003, Rosenberg et al. 2005, Iverson et al. 2006b), which is evidence that the species does not experience pronounced boom and bust cycles. Population models indicate that harlequin duck population growth rates are most sensitive to adult female survival (Goudie et al. 1994; S. A. Iverson and D. Esler, Simon Fraser University, unpublished data); however, these models employed a deterministic structure and the magnitude of annual, decadal, or longer time-scale fluctuations is unknown. Based on these findings, we conclude that the primary contribution of our study is confirmation of female survival during the breeding season as a likely constraint on harlequin duck population growth and stability, for which causal mechanisms underlying observed patterns of geographic and breeding-stage–specific variation remain unknown and are recommended priority areas for further research.

Management Implications

Population dynamics of harlequin ducks are particularly sensitive to variation in adult female survival, and management action directed at increasing female survival during the breeding season would be particularly effective for influencing population trends. This could take the form of maintenance of appropriate nesting habitat, measuring predator numbers and trends, management of food availability, or reduction in additive mortality from anthropogenic sources. Further research into causes of mortality for adult female harlequin ducks during the breeding season is important for directing management action. In addition, a directed study designed to contrast finer scale habitat attributes in regions where breeding-season survival rates were high (e.g., Coast Mountains of BC) and areas where breeding-season survival was low (e.g., Rocky Mountains of AB) could offer valuable insights about how best to enhance populations of conservation concern.

LITERATURE CITED

Bond, J. C., and D. Esler. 2006. Nutrient acquisition by female harlequin ducks prior to migration and reproduction: evidence for body mass optimization. Canadian Journal of Zoology 84:1223–1229.

Bond, J. C., D. Esler, and K. A. Hobson. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by harlequin ducks. Condor 109:698–704.

Brook, R. W., and R. G. Clark. 2005. Breeding season survival of female lesser scaup in the northern boreal forest. Arctic 58:16–20.

Bruner, H. J. 1997. Habitat use and productivity of harlequin ducks in the central Cascade Region of Oregon. Thesis, Oregon State University, Corvallis, USA.

Bunck, C. M., and K. H. Pollock. 1993. Estimating survival of radio-tagged animals. Pages 51–63 in J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhauser Verlag, Basal, Switzerland.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cooke, F., G. J. Robertson, and C. M. Smith. 2000. Survival, emigration, and winter population structure of harlequin ducks. Condor 102:137–144.

Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. Journal of Wildlife Management 67:551–563.

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

Environment Canada. 2006. Management plan for the harlequin duck (Histrionicus histrionicus) eastern population, in Atlantic Canada and Québec [Proposed]. Environment Canada, Ottawa, Canada.

Esler, D., J. A. Schmutz, R. L. Jarvis, and D. M. Mulcahy. 2000. Winter survival of adult female harlequin ducks in relation to history of contamination by the Exxon Valdez oil spill. Journal of Wildlife Management 64:839–847.

Goudie, R. I., S. Brault, B. Conant, A. V. Kondratyev, M. R. Peterson, and K. Vermeer. 1994. The status of sea ducks in the North Pacific Rim: toward their conservation and management. Transactions of the 59th North American Wildlife and Natural Resources Conference 59:27–49.

Heath, J. P., G. J. Robertson, and W. A. Montevecchi. 2006. Population structure of breeding harlequin ducks and the influence of predation risk. Canadian Journal of Zoology 84:855–864.

Hoekman, S. T., T. S. Gabor, R. Maher, H. R. Murkin, and M. S. Lindberg. 2006. Demographics of breeding female mallards in southern Ontario, Canada. Journal of Wildlife Management 70:111–120.

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

Hupp, J. W., G. A. Ruhl, J. M. Pearce, D. M. Mulcahy, and M. A. Tomeo. 2003. Effects of implanted radiotransmitters with percutaneous antennas on the behavior of Canada geese. Journal of Field Ornithology 74:250–256.

Iverson, S. A., W. S. Boyd, D. Esler, D. M. Mulcahy, and T. D. Bowman. 2006a. Comparison of the effects and performance of four radiotransmitter types for use with scoters. Wildlife Society Bulletin 34:656–663.

Iverson, S. A., W. S. Boyd, H. M. Regehr, and M. S. Rodway. 2006b. Sex and age-specific distributions of seaducks wintering in the Strait of Georgia, British Columbia: implications for the use of age ratios as an index of recruitment. Canadian Wildlife Service, Technical Report Series, Pacific and Yukon Region, Canada.

Iverson, S. A., and D. Esler. 2007. Survival of female harlequin ducks during wing molt. Journal of Wildlife Management 71:1220–1224.

Iverson, S. A., D. Esler, and D. J. Rizzolo. 2004. Winter philopatry of harlequin ducks in Prince William Sound, Alaska. Condor 106:711–715.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446–485 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

Johnson, D. H., and A. B. Sargeant. 1977. Impact of red fox predation on the sex ratio of prairie mallards. U.S. Fish and Wildlife Service Research Report 6, Washington, D.C., USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of American Statistical Association 53:457–481.

Kirby, R. E., and L. M. Cowardin. 1986. Spring and summer survival of female mallards from northcentral Minnesota. Journal of Wildlife Management 50:38–43.

Korschgen, C. E., K. P. Kenow, A. Gendron-Fitzpatrick, W. L. Green, and F. J. Dein. 1996. Implanting intra-abdominal radiotransmitters with external whip antennas in ducks. Journal of Wildlife Management 60:132–137.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Mather, D. D., and D. Esler. 1999. Evaluation of bursal depth as and indicator of age class of harlequin ducks. Journal of Field Ornithology 70:200–205.

Mauser, D. M., and R. L. Jarvis. 1991. Attaching radiotransmitters to 1-day-old mallard ducklings. Journal of Wildlife Management 55:488–491.

Mulcahy, D. M., and D. Esler. 1999. Surgical and immediate postrelease mortality of harlequin ducks implanted with abdominal radiotransmitters with percutaneous antennae. Journal of Zoo and Wildlife Medicine 30:397–401.

Pietz, P. J., D. A. Brandt, G. L. Krapu, and D. A. Buhl. 1995. Modified transmitter attachment method for adult ducks. Journal of Field Ornithology 66:408–417.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Regehr, H. M. 2003. Movement patterns and population structure of harlequin ducks wintering in the Strait of Georgia, British Columbia. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Richkus, K. D., F. C. Rohwer, and M. J. Chamberlain. 2005. Survival and cause-specific mortality of female northern pintails in southern Saskatchewan. Journal of Wildlife Management 69:574–581.

Robertson, G. J., and R. I. Goudie. 1999. Harlequin duck (*Histrionicus histrionicus*). Account 466 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Rodway, M. S., H. M. Regehr, and F. Cooke. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering harlequin ducks: implications for conservation and estimating recruitment rates. Canadian Journal of Zoology 81:492–503.

Rosenberg, D. H., M. J. Petrula, D. D. Hill, and A. M. Christ. 2005. Harlequin duck population dynamics: measuring recovery from the *Exxon Valdez* oil spill. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 040407). Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, USA.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Safine, D. E. 2005. Breeding ecology of white-winged scoter on Yukon-Flats, Alaska. Thesis, University of Alaska-Fairbanks, USA.

Sargeant, A. B., S. H. Allen, and R. T. Eberhardt. 1984. Red fox predation on breeding ducks in midcontinent North America. Wildlife Monographs 89.

Sargeant, A. B., and D. G. Raveling. 1992. Mortality during the breeding season. Pages 396–422 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

Schmutz, J. A., R. F. Rockwell, and M. R. Petersen. 1997. Relative effects of survival and reproduction on population dynamics of emperor geese. Journal of Wildlife Management 61:191–201.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smith, C. M. 2000. Survival and recruitment of juvenile harlequin ducks. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Smith, C. M., F. Cooke, and R. I. Goudie. 1998. Ageing harlequin duck *Histrionicus histrionicus* drakes using plumage characteristics. Wildfowl 49:245–248.

Smith, C. M., R. I. Goudie, and F. Cooke. 2001. Winter age ratios and the assessment of recruitment of harlequin ducks. Waterbirds 24:39–44.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (supplement):120–139.

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