

Management and Conservation Note

Variation in Breeding Season Survival of Female Harlequin Ducks

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-

(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 (3) 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 (DAIC_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

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 5 147.57; $DAIC_c$ 5 0.00;

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 $DAIC_c$ 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

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

(2007) reported a cumulative survival rate (CSR) of 0.99 ± 0.02 for radiomarked female harlequin ducks during the

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

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