

SURVIVAL AND MOVEMENT OF POSTFLEDGING JUVENILE HARLEQUIN DUCKS

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ABSTRACT.—Age specific survival and movement are important components of demography and population structure, and quantification of these rates is useful for management and conservation. However, information on the postfledging ecology of waterfowl species frequently is unavailable to managers. I studied postfledging survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia, using radio marking and capture-mark-recapture analysis of banded birds captured at coastal wintering areas. Survival of juvenile females was high, providing evidence that female winter survival may be similar among age groups. Radio-marked juvenile males were more likely to die than juvenile females, and juvenile males had lowest local survival rates of all sex-age classes. Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and at least 25% ($n = 9$) of radio-marked females moved >30 km from their capture location. These results were unexpected, based on previous evidence for female philopatry and theories of male-biased dispersal in waterfowl, and suggest that males and females both likely contribute to gene flow and demographic connection among populations. Received 14 March 2003, accepted 15 November 2003.

The immature stage has been shown to play an important role in population dynamics in some waterfowl species (Coulson 1984, Cooch and Cooke 1991). However, information on postfledging survival and movement patterns frequently are unavailable to managers. Although age ratios may provide a measure of production for hunted species (Bellrose 1980) and for species with visually identifiable first-year plumage (Smith et al. 2001, Iverson et al. 2003, Rodway et al. 2003a), age specific survival rates are needed to estimate recruitment into the breeding population (Cooch and Cooke 1991, Perrins 1991, Anderson et al. 2001). Survival rates of juveniles generally are difficult to estimate. Juveniles can be difficult to identify or capture, frequently resulting in small sample sizes. Also, survival rates often are confounded by juvenile dispersal from study areas, and dispersal can be difficult to assess without simultaneous sampling of neighboring populations (Clobert and Lebreton 1991). Thus, information on dispersal is needed to separate mortality from emigration (Lebreton et al. 1992), which is an important distinction for large scale management of populations. In addition, although much emphasis has been placed on philopatry of waterfowl to breeding areas (Anderson et al. 1992), little attention has been paid to win-

ter philopatry and dispersal (Robertson and Cooke 1999). Because many waterfowl pair during winter, it is the movements of unpaired individuals among wintering areas that largely influence the degree of genetic structuring among populations for many species (Rockwell and Barrowclough 1987). Information on movement patterns during winter also are important to the understanding of demographic connection among wintering populations (Esler 2000).

I investigated survival and movements of juvenile Harlequin Ducks (*Histrionicus histrionicus*) captured at wintering areas. Harlequin Ducks breed at inland streams, winter at coastal areas, show delayed maturation, pair during winter, and form long term pair bonds (Robertson and Goudie 1999). Previous analysis for a small wintering population indicated that local (or apparent) survival (the probability of surviving and returning to the study area; Lebreton et al. 1992) of juvenile and subadult males was lower than that of adults, but that local survival rates of females did not differ among age groups (Cooke et al. 2000). Assuming that differences in local survival rates of young males and females were due to differences in emigration rates and not death, these results supported theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992), and suggested that dispersal of males resulted in a considerable amount of gene flow among populations.

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My objectives were to use radio marking to estimate survival and movement of juveniles during their first winter and to allow separation of mortality from emigration, to use capture-mark-recapture (CMR) analysis to compare local survival among sex-age classes, to determine whether age specific mortality rates should be incorporated into estimates of recruitment, and to test predictions of male-biased dispersal. I chose the juvenile age class because survival and movement rates during the first year of life likely differ most from that of mature birds and because information on postfledging ecology is lacking almost entirely, not only for Harlequin Ducks, but also for other sea ducks and many waterfowl species.

METHODS

Researchers captured juvenile Harlequin Ducks at coastal wintering areas using two methods. We captured 15 juveniles among older birds in drive traps designed to capture flightless molting adults from mid-August through mid-September, 1995–1998. In addition, we specifically searched for juveniles and captured 19 of them using mist nets and decoys during the first half of September in 1999 and 2000. We captured juveniles on Hornby Island (49° 32' N, 124° 40' W) and on the eastern coast of Vancouver Island between Comox (49° 42' N, 124° 52' W) and Campbell River (49° 58' N, 125° 12' W) in the northern Strait of Georgia (Fig. 1), and at White Rock (49° 02' N, 122° 51' W) in the Lower Mainland, British Columbia. We identified juveniles by the finely vermiculated plumage on their breast, belly, and vent, their mottled yellowish legs and feet, and their dusky faces, full primaries, and notched tail feathers (Regehr et al. 2001), and sexed them by cloacal examination. We marked all captured juveniles with a U.S. Fish and Wildlife Service band on the left tarsus, and a colored, laminated plastic band uniquely engraved with two alpha numeric digits on the right tarsus. During September 2000, we also marked 15 juveniles (nine females, six males) with external radio transmitters attached mid-dorsally with subdermal wire anchors. We captured radio-marked juveniles at Hornby Island, Comox, and Willow Point (Fig. 1). Nine radios weighed 9 g each and had 2-cm wide wire

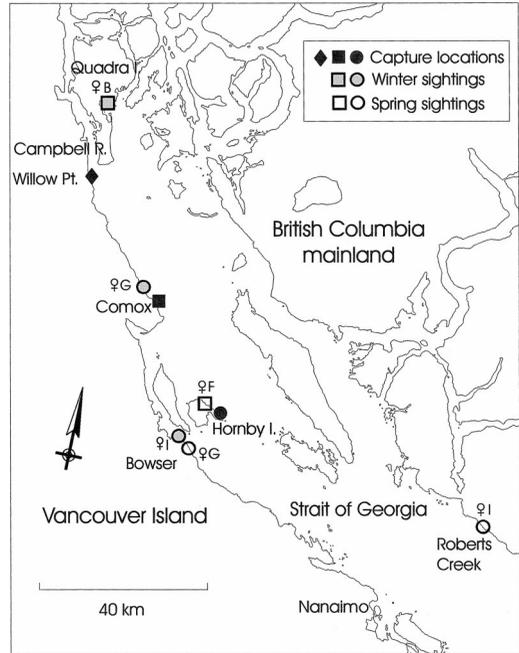


FIG. 1. Four of eight juvenile female Harlequin Ducks marked with external radio transmitters moved >10 km from their capture location in the northern Strait of Georgia, British Columbia, Canada, 2000–2001. Capture locations are shown as solid symbols; winter (mid-October through February) and spring (March) sighting locations of females that moved >10 km are shown as partially filled and unfilled symbols, respectively, with the type of symbol indicating the capture location from which the individual originated. Individual females are identified with letters (see also Table 2).

anchors; six weighed 3 g each with 1-cm wire anchors. We distributed radio types equally between the sexes. Radio transmitters weighed a maximum of 2% of body mass for all juveniles and were assumed not to affect behavior.

Researchers reported sightings of individuals marked with colored bands from 1995–2001 during the fall (August to October), when postjuvenile birds molt, and during spring (March), when many Harlequin Ducks aggregate at Pacific herring (*Clupea pallasii*) spawning sites (Rodway et al. 2003b). At these times birds spend less time feeding than during winter and frequently haul out on shoreline rocks. Two to several observers typically searched for marked birds for a number of days approximately equivalent to 1–6

weeks during fall, and 1–4 weeks during spring. From September to December 2000, I located juveniles with radio transmitters from land, or with fixed-wing aircraft. I conducted three telemetry flights in October and November and covered the northern Strait of Georgia, from the northern end of Quadra Island to Nanaimo (Fig. 1) at least once, and most areas at least twice. I determined distances individuals had moved from capture locations using a handheld GPS unit or from measurements taken from marine charts. I report records during winter (mid-October through February) separately from those during spring (March) because movement during spring can be associated with aggregation at herring spawning sites (Rodway et al. 2003b). I could not compare movement distances between radio-marked males and females due to small sample size of surviving males (see results). However, I was able to compare philopatry between the sexes by comparing proportions of all marked juveniles (captured before 2000) observed at their capture location during their second winter at the coast.

I was able to monitor survival of most juveniles carrying transmitters from September through November, until batteries failed or transmitters were lost, after which juveniles were resighted opportunistically. I confirmed the death of radio-marked juveniles by pinpointing their transmitters to small areas (several m²) of dense shoreline vegetation (two cases), or by retrieving the carcass (one case).

I estimated local survival rates and tested hypotheses that they differed by sex and by age (juvenile and postjuvenile) using sightings of all juveniles marked with bands (21 females, 13 males) and the CMR program MARK (White and Burnham 1999). I developed a candidate model set that included the models containing effects necessary to test my hypotheses and that were based on *a priori* biological and sampling information (Lebreton et al. 1992, Anderson and Burnham 1999). Because sightings were recorded biannually (fall and spring), I estimated survival rates for 6-month periods, with the juvenile age class considered to last for one year (two 6-month periods). Biannual sightings permitted estimation of season specific survival and sighting rates, the inclusion of which I expected would improve model fit. Juveniles remain at

the coast during their first summer and likely gain experience over time, suggesting that survival may be lower during winter (fall to spring) than summer (spring to fall); postjuvenile females incur costs of breeding during summer suggesting that their survival is likely higher during winter than summer (Robertson and Goudie 1999, Cooke et al. 2000). I also expected sighting rates to differ between fall and spring due to seasonal differences in observer effort and bird behavior. Models in the candidate model set therefore included those with and without the effects of age, sex, and season on survival, and with and without the effect of season on sighting rates (Table 1). I assumed that sighting probabilities did not differ by sex or age. Models with time dependence had too many parameters for the data to be fit properly. Competing models were ranked using Akaike's Information Criterion (AIC), which is based on the concept of statistical parsimony and is calculated as the best compromise between minimizing the number of parameters and maximizing model fit (Lebreton et al. 1992, Anderson and Burnham 1999, Cooch and White 2001).

I evaluated model fit and overdispersion with bootstrap goodness-of-fit testing (Cooch and White 2001). In this method, encounter histories are simulated using model parameters, generating simulated data sets that exactly meet model assumptions that individuals behave independently and that their rates are identical within classes (Lebreton et al. 1992). Comparison of observed and simulated model deviances then allows evaluation of model fit and estimation of the variance inflation factor, \hat{c} , a measure of the magnitude of overdispersion. I adjusted model fit for overdispersion and used the Quasi Akaike's Information Criterion (QAICc) to indicate models substantially supported by the data. I determined relative model support by the ratio of QAICc weights. Effects of band wear (Regehr and Rodway 2003) were unlikely to bias estimates of juvenile survival rates because bands wear little during their first year; however, band wear likely caused the survival rates of the postjuvenile age class to be underestimated slightly.

I used Fisher's exact test to compare proportions of juveniles dying to those remaining

TABLE 1. Candidate models ranked in order of increasing QAIC_c indicate that survival rate differs by age (juvenile versus postjuvenile) and resighting rate differs by season (fall versus spring) for banded Harlequin Ducks, captured as juveniles, in the northern Strait of Georgia, British Columbia, 1995–2000. AIC_c values were adjusted for \hat{c} of 1.24.

Model description	Number of parameters	QAIC _c	Delta QAIC _c	QAIC _c weight
Survival rate differs by age, sighting rate differs by season	4	114.26	0.00	0.4552
Survival rate differs by sex, sighting rate differs by season	4	115.28	1.02	0.2728
Survival rate differs by age and sex, sighting rate differs by season	6	115.88	1.62	0.2020
Survival rate differs by age, sex, and season for the juvenile age class, sighting rate differs by season	8	119.21	4.95	0.0382
Survival rate differs by age, sex, and season for the juvenile age class and for postjuvenile females, sighting rate differs by season	9	120.17	5.91	0.0237
Survival rate differs by age, sex, and season for both age classes, sighting rate differs by season (general model)	10	122.32	8.06	0.0081
Survival and sighting rates are constant	2	138.56	24.30	0.0000
Survival rate differs by age, sighting rate is constant	3	139.65	25.39	0.0000
Survival rate differs by sex, sighting rate is constant	3	140.21	25.95	0.0000
Survival rate differs by sex and age, sighting rate is constant	5	142.07	27.81	0.0000

in their capture location. I set type I error rate at 0.05.

RESULTS

Among radio-marked juveniles, a greater proportion of males died (50%, $n = 6$) than did females (0%, $n = 9$; Fisher's exact test, $P = 0.044$). All deaths occurred within 46 days after capture. Two of the males that died were unusually light at capture (males N and O, Table 2). The death of the third male 46 days after capture (male K, Table 2) most likely was due to predation; four days earlier he had been observed 2 km from his capture location, feeding alongside two juvenile females. Based on sightings during and after the study period, I determined that ≥ 8 of the 9 radio-marked females survived the winter.

I contrasted 10 models in CMR analysis to test hypotheses that local survival rates differed by sex and age, and to estimate sex and age specific local survival rates (Table 1). Bootstrap goodness-of-fit testing with 1,000 simulations revealed adequate model fit; the probability of a deviance as great or greater than that of the most general model was 0.12, and the variance inflation factor, \hat{c} , was estimated at 1.24. Three models had similar QAIC_cs (differing by < 2), thus they were fairly similar in their abilities to describe the data in a parsimonious manner and I drew in-

ferences from this subset of models (Lebreton et al. 1992, Anderson and Burnham 1999). The most saturated of the three models estimated separate 6-month local survival rates for juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31–0.80), postjuvenile males (0.94 ± 0.09 SE; 95% CI = 0.44–1.00), juvenile females (0.84 ± 0.08 SE; 95% CI = 0.61–0.95), and postjuvenile females (0.89 ± 0.06 SE; 95% CI = 0.71–0.96). Based on these rates I built an additional model in which survival of juvenile males was set different from all other sex-age classes (four parameters). This model was well supported by the data (QAIC_c = 111.84, with 3.4 times the support of the highest ranking model in Table 1), indicating that local survival of juvenile males (0.58 ± 0.14 SE; 95% CI = 0.31–0.81) was different from all other sex-age classes, and that I was unable to detect differences in local survival among juvenile females, postjuvenile females, and postjuvenile males (0.88 ± 0.04 SE; 95% CI = 0.77–0.94). Models were improved consistently by including the effect of season on sighting rates (fall: 0.31 ± 0.09 SE; 95% CI = 0.16–0.51; spring: 0.95 ± 0.05 SE; 95% CI = 0.72–0.99), but inclusion of season specific survival rates did not improve model fit.

Of the three potentially surviving radio-marked males (Table 2), one may have left the study area (male L). I last detected his radio

TABLE 2. Maximum movement distances from the capture sites of radio-marked juvenile female (f) and male (m) Harlequin Ducks during winter (mid-October through February) and during the herring spawning period in spring (March) in the northern Strait of Georgia, British Columbia, 2000–2001. At least 25% of females moved >30 km from their capture sites during winter and spring. Three of six radio-marked males died (marked with an asterisk). Locations are given in parentheses (see Fig. 1) for movement distances >10 km.

Identity code	Sex	Mass at capture (g)	Capture location ^a	Winter location			Spring location	
				Maximum movement distance (km)	Months recorded ^b	Number of records ^c	Maximum movement distance (km)	Number of records ^c
A	f	580	Comox	unknown ^d	—	—	unknown	—
B	f	570	Comox	48 (Quadra)	Oct.–Nov.	4	unknown ^e	—
C	f	515	Comox	3	Oct.–Feb.	9	4	4
D	f	500	Comox	7	Oct.–Jan.	7	3	1
E	f	485	Comox	3	Oct.–Feb.	8	1	1
F	f	610	Comox	2	Oct.–Feb.	7	35 (Hornby I.)	8
G	f	530	Hornby I.	36 (Comox)	Jan.–Feb.	3	11 ^f (Bowser)	1
H	f	460	Hornby I.	1	Nov.–Jan.	3	4	4
I	f	535	Hornby I.	12 (Bowser)	Oct.	3	35 (Roberts Creek)	1
J	m	605	Willow Pt.	unknown ^g	—	—	unknown	—
K*	m	590	Comox	2	Oct.	1	—	—
L	m	565	Comox	15 ^h	Nov.	1	unknown	—
M	m	485	Hornby I.	unknown	—	—	2	6
N*	m	415	Hornby I.	—	—	—	—	—
O*	m	410	Hornby I.	—	—	—	—	—

^a Juveniles were captured 3–14 September 2000.

^b Range of months during which records were obtained for winter location.

^c Number of sightings and detections of radio frequency at winter or spring location, with maximum of 1/day.

^d Radio lost 7 km from capture location on tidal shelf; individual sighted during spring 2002.

^e Winter location could not be surveyed during spring.

^f Also seen once at Hornby Island, 2 km from capture location.

^g Located four days following capture, then probably lost radio.

^h Radio signal last indicated a location about 15 km south of capture site on 11 Nov.

signal about 15 km south of his capture site, possibly over open water, 64 days after capture. Although I conducted a telemetry flight over the entire study area six days later, he was never found again. I could not locate the second male (male M) during winter but sighted him close to his capture location on Hornby Island during March, suggesting a lost or malfunctioning radio during winter. The third male (male J) was observed 10 km north of his Campbell River capture location four days after capture but was never sighted again. This male received a 3-g transmitter with a small subcutaneous anchor which he probably lost shortly after this sighting.

Of nine radio-marked females, I was able to determine the locations of eight during winter, and of seven during both winter and spring (Table 2, Fig. 1). I could not relocate one female (female A) because she lost her radio 7 km from her capture site soon after capture; she was confirmed alive during spring 2002. Female B was not resighted during spring; however, her wintering location at Quadra Is-

land could not be revisited at that time. The mean maximum distances females were found from their capture locations were 14.0 km \pm 6.3 SE ($n = 8$) and 13.2 km \pm 5.7 SE ($n = 7$) during winter and spring, respectively.

I detected no significant difference between the sexes in the proportion of marked juveniles resighted at their capture location during their second winter (males: 29%, $n = 7$; females: 25%, $n = 12$; Fisher's exact test, $P > 0.99$).

DISCUSSION

Results of this study provide new information important to understanding the post-fledging ecology and population dynamics of Harlequin Ducks. First, radio marking of juvenile females indicated that, contrary to previous evidence for philopatry (Robertson and Goudie 1999, Cooke et al. 2000), some juvenile females moved substantial distances during winter. Second, contrary to predictions from theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and An-

derson 1988, Anderson et al. 1992), and assumptions of male-biased dispersal in young Harlequin Ducks (Cooke et al. 2000), proportions of banded male and female juveniles resighted at their capture locations during their second winter did not differ, suggesting equal dispersal rates. Third, radio marking in combination with CMR analysis indicated that first-winter survival of juvenile Harlequin Duck females was high, providing further evidence that female winter survival may be similar among age groups. Conclusions pertaining to female survival rates must, however, be treated with caution due to sample size limitations.

Results of this study also suggest that juvenile male Harlequin Ducks may be more likely to die than juvenile females. However, inferences regarding differences in survival between the sexes are weak due to small sample sizes of radio-marked birds. Although lower survival of juvenile males relative to the other sex-age classes also was supported by CMR analyses, the local survival rates estimated by CMR analysis reflect a combination of mortality and emigration, and large confidence intervals surrounding point estimates limit confidence in apparent differences. The reason for a higher death rate of male than female juveniles is not clear, but might be related to differences in vulnerability to predation resulting from differences in conspicuousness of plumage, or to differences in susceptibility to the effects of food shortage due to larger size and higher growth rate of males (Clutton-Brock 1986, Cooch et al. 1997). My results suggest that the assumption that low local survival of juvenile and subadult males reflects emigration and not mortality (Cooke et al. 2000) should be re-assessed.

Juvenile survival rates generally are lower than those of adults in waterfowl (Johnson et al. 1992). However, most juvenile mortality occurs during the pre fledging and migration periods (Nichols and Hines 1987, Francis et al. 1992, Johnson et al. 1992), and hunting mortality tends to be juvenile biased (Bellrose 1980). The high winter survival observed for juvenile Harlequin Duck females in this study therefore may at least partly reflect the fact that juveniles were captured after migrating to wintering areas and that hunting mortality is low for Harlequin Ducks on the western coast

of North America (Robertson and Goudie 1999). Results of this study, in combination with that of Cooke et al. (2000), who primarily included subadult (second and third year) and adult (after third year) females in CMR analyses, suggest little difference in winter survival rates of female Harlequin Ducks of different ages, provided that juveniles have completed their first migration, and that these rates likely can be set equal for estimates of recruitment into the breeding population. However, the possibility remains that the similar adult and subadult female local survival rates observed by Cooke et al. (2000) were due to subadults having lower death rates balanced by higher emigration rates (Cooke et al. 2000). Also, conclusions pertaining to juvenile females remain tentative due to sample size limitations in this study. Clearly, size of the study area also may affect conclusions. Considering movement rates and distances observed in this study, reduced juvenile female local survival due to emigration would be more likely if the study area were small. Summer survival rates of juvenile and subadult females might be expected to be somewhat higher than those of adult females because at least some immature females do not breed and hence do not incur associated mortality (Robertson and Goudie 1999, Cooke et al. 2000).

Proportions of banded juveniles found at their capture location during their second winter did not differ significantly between males and females, suggesting equal dispersal rates, and $\geq 25\%$ of radio-marked females moved >30 km from their capture location. These results were unexpected, based on previous evidence for juvenile female philopatry (Robertson and Goudie 1999, Cooke et al. 2000), and theories of male-biased dispersal in waterfowl (Greenwood 1980, Rohwer and Anderson 1988, Anderson et al. 1992). However, I was unable to compare movement distances between sexes. Dispersing juvenile male Harlequin Ducks may move greater distances than dispersing juvenile females, as has been observed for some other waterfowl species (Kirby 1976, Rienecker 1987, Baldassarre et al. 1988). One of three surviving radio-marked males may have left the study area, whereas no female did. Individuals that disperse greater distances are less likely to be resighted than those moving smaller distances. Thus, greater

male dispersal distances, possibly in combination with higher death rates, could account for lower local survival of male than female juveniles.

Results of this study have implications for genetic and demographic population structure of Harlequin Ducks. Juvenile Harlequin Ducks are believed to leave inland breeding areas and arrive at coastal wintering areas in family groups accompanied by their mothers, at least when families are intact at the time of fledging (Regehr et al. 2001). In this study, juveniles of both sexes dispersed from their coastal capture locations, suggesting that both sexes likely contribute to gene flow among populations. Also, dispersal of females in addition to males increases the potential for demographic connection among populations because successful recolonization or rescue of extinct or reduced populations are dependent upon female movement (Avisé 1995). Further study is required to test the idea that low local survival rates of juvenile males may be partly due to higher death rates, to resolve potential sex differences in juvenile dispersal distances, and to investigate what factors affect differences in dispersal strategies among individuals of the same sex. Exceptions to patterns of sex-bias in subsets of populations can aid in our overall understanding of the evolutionary forces shaping dispersal patterns.

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LITERATURE CITED

- ANDERSON, D. R. AND K. P. BURNHAM. 1999. General strategies for the analysis of ringing data. *Bird Study* 46S:261–270.
- ANDERSON, M. G., M. S. LINDBERG, AND R. B. EMERY. 2001. Probability of survival and breeding for juvenile female Canvasbacks. *J. Wildl. Manage.* 65:385–397.
- ANDERSON, M. G., J. M. RHYMER, AND F. C. RÖHWER. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pp. 365–395 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Univ. of Minnesota Press, Minneapolis.
- AVISÉ, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. *Conserv. Biol.* 9:686–690.
- BALDASSARRE, G. A., E. E. QUINLAN, AND E. G. BOLEN. 1988. Mobility and site fidelity of Green-winged Teal wintering on the Southern High Plains of Texas. Pp. 483–493 in *Waterfowl in winter* (M. W. Weller, Ed.). Univ. of Minnesota Press, Minneapolis.
- BELLROSE, F. C. 1980. *Ducks, geese and swans of North America*. Stackpole Books, Harrisburg, Pennsylvania.
- CLOBERT, J. AND J.-D. LEBRETON. 1991. Estimation of demographic parameters in bird populations. Pp. 75–104 in *Bird population studies: relevance to conservation and management* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford Univ. Press, Oxford, United Kingdom.
- CLUTTON-BROCK, T. H. 1986. Sex-ratio variation in birds. *Ibis* 128:317–329.
- COOCH, E. G. AND F. COOKE. 1991. Demographic changes in a Snow Goose population: biological and management implications. Pp. 168–189 in *Bird population studies: relevance to conservation and management* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford Univ. Press, Oxford, United Kingdom.
- COOCH, E. G., D. LANK, R. ROBERTSON, AND F. COOKE. 1997. Effects of parental age and environmental change on offspring sex ratio in a precocial bird. *J. Anim. Ecol.* 66:189–202.
- COOCH, E. G. AND G. C. WHITE. 2001. Program MARK: a gentle introduction. <http://www.phidot.org/software/mark/docs/book> (27 February 2003).
- COOKE, F., G. J. ROBERTSON, C. M. SMITH, R. I. GOUDIE, AND W. S. BOYD. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. *Condor* 102:137–144.
- COULSON, J. C. 1984. The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adults. *Ibis* 126:525–543.
- ESLER, D. 2000. Applying metapopulation theory to conservation of migratory birds. *Conserv. Biol.* 14:366–372.
- FRANCIS, C. M., M. H. RICHARDS, F. COOKE, AND R. F. ROCKWELL. 1992. Changes in survival rates of

- Lesser Snow Geese with age and breeding status. *Auk* 109:731–747.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- IVERSON, S. A., D. ESLER, AND W. S. BOYD. 2003. Plumage characteristics as an indicator of age class in the Surf Scoter. *Waterbirds* 26:56–61.
- JOHNSON, D. H., J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl. Pp. 446–485 in *Ecology and management of breeding waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Univ. of Minnesota Press, Minneapolis.
- KIRBY, R. E. 1976. Fall movements, behavior, and habitat use of young Mallards and Wood Ducks in north-central Minnesota. Ph.D. diss., Univ. of Minnesota, Minneapolis.
- 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. *Ecol. Monogr.* 62:67–118.
- NICHOLS, J. D. AND J. E. HINES. 1987. Population ecology of the Mallard, VIII: winter distribution patterns and survival rates of winter-banded Mallards. Resource Publication 162. U.S. Fish and Wildlife Service, Washington, D.C.
- PERRINS, C. M. 1991. Constraints on the demographic parameters of bird populations. Pp. 190–206 in *Bird population studies: relevance to conservation and management* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, Eds.). Oxford Univ. Press, Oxford, United Kingdom.
- REGEHR, H. M. AND M. S. RODWAY. 2003. Evaluation of nasal discs and colored leg bands as markers for Harlequin Ducks. *J. Field Ornithol.* 74:129–135.
- REGEHR, H. M., C. M. SMITH, B. ARQUILLA, AND F. COOKE. 2001. Post-fledging broods of migratory Harlequin Ducks accompany females to wintering areas. *Condor* 103:408–412.
- RIENECKER, W. C. 1987. Migration and distribution of Northern Pintails banded in California. *Calif. Fish Game* 73:139–155.
- ROBERTSON, G. J. AND F. COOKE. 1999. Winter philopatry in migratory waterfowl. *Auk* 116:20–34.
- ROBERTSON, G. J. AND R. I. GOUDIE. 1999. Harlequin Duck (*Histrionicus histrionicus*). No. 466 in *The birds of North America* (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- ROCKWELL, R. F. AND G. F. BARROWCLOUGH. 1987. Gene flow and the genetic structure of populations. Pp. 223–255 in *Avian genetics: a population and ecological approach* (F. Cooke and P. A. Buckley, Ed.). Academic Press, London, United Kingdom.
- RODWAY, M. S., H. M. REGEHR, J. ASHLEY, P. V. CLARKSON, R. I. GOUDIE, D. E. HAY, C. M. SMITH, AND K. G. WRIGHT. 2003a. Aggregative response of Harlequin Ducks to herring spawn in the Strait of Georgia, British Columbia. *Can. J. Zool.* 81:504–514.
- RODWAY, M. S., H. M. REGEHR, AND F. COOKE. 2003b. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment. *Can. J. Zool.* 81:492–503.
- ROHWER, F. C. AND M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Curr. Ornithol.* 5:187–221.
- 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* 46S:120–139.