

ANNUAL SURVIVAL AND SITE FIDELITY OF NORTHERN PINTAILS BANDED ON THE YUKON-KUSKOKWIM DELTA, ALASKA

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Abstract: We banded northern pintails (*Anas acuta*; $n = 13,645$) at a single site on the Yukon-Kuskokwim Delta (YKD), Alaska, USA, from 1990 to 2001. We used recaptures from our site in combination with hunter recoveries to model annual survival, recovery rates, and fidelity to our capture location. Most recoveries (>90%) occurred in the Pacific Flyway with 64% reported from California's Central Valley. Our top candidate models allowed survival to vary by sex but not by age or year. Estimated annual survival was 77.6% (95% CI: 73.9–81.0%) for males and 60.2% (95% CI: 53.2–67.0%) for females. Reporting rates varied by age, sex, and year; estimates for adult males exceeded those for adult females by 3.5 times. Within sexes, reporting rates of hatch-year pintails exceeded those of adults. Estimated recovery rates were considerably lower than those estimated during the 1950s–1970s for winter banded pintails (Hestbeck 1993b), but there were no differences in survival rates. This suggests that changes in harvest regulations may not have influenced annual survival in this population. The propensity of banded pintails to return to our capture site (fidelity rate) varied between sexes and was positively correlated with water conditions in prairie Canada. Our estimates of fidelity rates varied from 77.4% to 87.2% for males and 89.8% to 94.3% for females. Our fidelity estimates suggest that some level of subpopulation structuring may exist for northern pintails. Additionally, our estimates of fidelity support previous observations of northern pintails overflying poor wetland habitat conditions on the Canadian prairies.

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Unlike other duck species, northern pintail (hereafter pintail) populations have not increased in response to an increase in the number of May ponds in prairie Canada during the mid to late 1990s (U.S. Fish and Wildlife Service 2002). Other species of dabbling ducks have shown substantial increases in population size that are correlated with wetland conditions. However, the number of pintails counted in Alaska has remained relatively constant through the long term (1955–2002), whereas the population nesting in the Prairie-Pothole Region is well below its long-term population average (U.S. Fish and Wildlife Service 2002, Bethke and Nudds 1995, Miller and Duncan 1999). The failure of pintail populations to respond to improved wetland conditions on the prairies has been related to poor recruitment rather than survival (Miller and Duncan 1999). However, Flint et al. (1998) developed a population model for pintails nesting on the YKD that demonstrated that annual survival of adult (after hatch year [AHY]) females had a relatively

greater effect on population dynamics than did any other demographic parameter (e.g., recruitment rate). Therefore, accurate annual survival rate estimates are critical to developing management strategies. Further, because harvest is a management tool and may represent a potential impact on population dynamics, estimates of recovery rate are important for assessing the impact of harvest on population dynamics.

Our primary objective was to estimate annual survival, recovery rates, and fidelity rates for pintails banded on YKD. We utilized a statistical technique that also allowed us to examine if these rates vary between ages, sexes, and years. We compare our estimates of survival and recovery rates with historic estimates from the Pacific Flyway and from other regions.

METHODS

We trapped pintails in a 5-km² area along the northwest shore of Kgun Lake (61°35'N, 165°55'W; elevation 2 m), located 145 km northwest of Bethel, Alaska, USA, on the YKD (Fig. 1). We positioned traps along shorelines of small (0.5 ha) to medium-sized (100 ha) soft-bottomed ponds connected to Kgun Lake by a network of sloughs. We selected the study area because of

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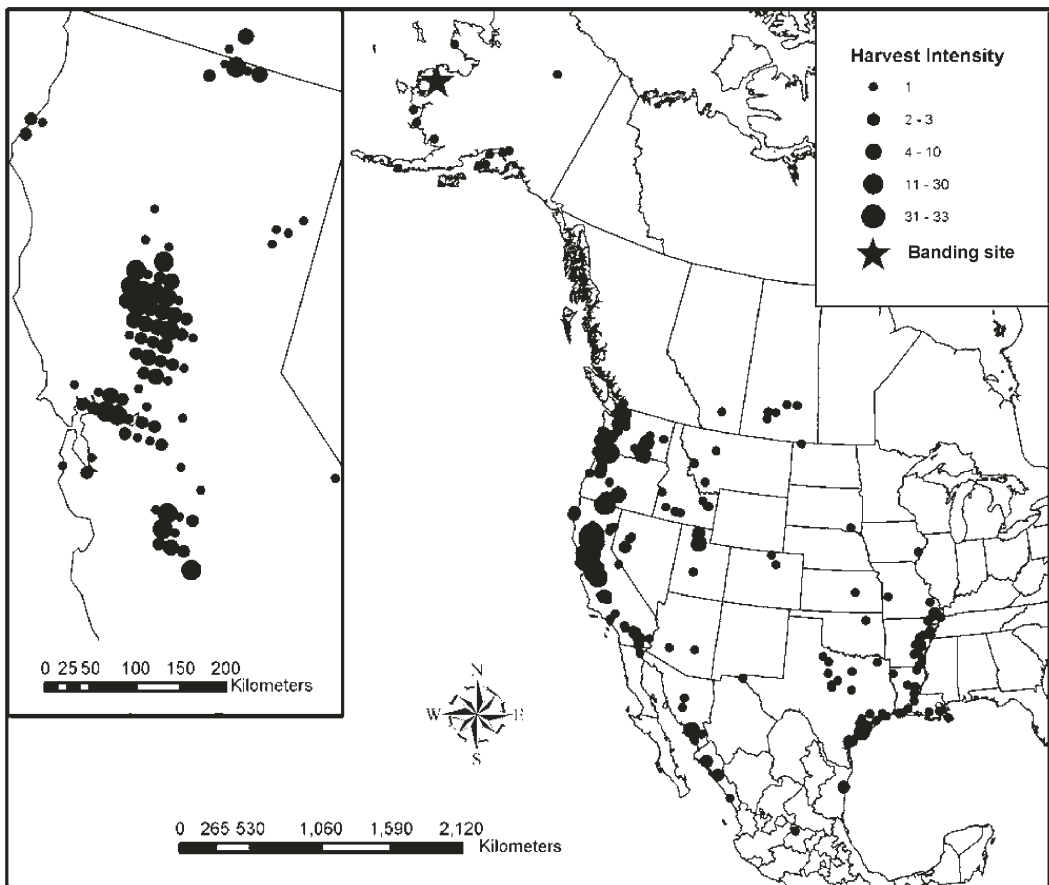


Fig. 1. Recovery locations of northern pintails banded on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

assured access to large concentrations of pintails (>10,000 pintails seen regularly during early Aug) and logistical feasibility. Vegetation consisted of heterogeneous communities of graminoid-dwarf shrub peatland (mostly *Salix*, *Carex*, *Poa*, and *Eriophorum* species) and graminoid marsh/meadows (mostly *Carex*, *Poa*, and *Hipperus* species; Tande and Jennings 1986).

Trapping began between 23 July–12 August and ended during 22–31 August and totaled 13–37 trapping days annually. We utilized 1–12 traps at each of 4–14 sites. We captured pintails during 1990–1997 in baited, swim-in, box traps measuring $1.8 \times 1.2 \times 0.6$ m and constructed of 5.1×6.4 -cm mesh, plasticized welded wire. The bottom was constructed of 0.6-cm mesh, galvanized hardware cloth. A 30.5-cm-wide funnel-shaped entrance that reduced to 10.2 cm was placed at the midpoint of 1 long side. We replaced box traps with cloverleaf traps measuring 6.1 m in diameter beginning in 1998. We constructed the sides of these traps using

2.5×5.1 -cm mesh, welded wire; these measured either 0.6- or 1.2-m high, and we used 2.5-cm mesh, nylon netting for the tops. We baited trap entrances with whole corn and checked traps daily. We marked all pintails with standard U.S. Fish and Wildlife Service AVISE metal leg-bands throughout our study; we did not use 1-800 style bands. We classified pintails to age by examining retrices, penis size, and presence/absence of a bursa. We determined sex by color of the secondaries and bill markings. Additionally, we recorded all recaptures of pintails.

Analysis

We constructed capture histories incorporating marking occasions, live recaptures (including pintails that died upon recapture), and hunter recoveries (Table 1). We classified birds by age at banding (i.e., AHY or hatch-year [HY]), and we excluded data pertaining to flightless young (locals) due to small sample size ($n = 11$). We

Table 1. Number of northern pintails captured by age and sex on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

Year	Adult		Hatch year		Total	Recaptures ^a	Recoveries ^b
	Males	Females	Males	Females			
1990	122	97	61	45	325	–	1
1991	386	564	287	301	1,538	7	17
1992	509	411	277	331	1,528	29	52
1993	668	331	180	185	1,364	38	62
1994	801	213	207	197	1,418	51	58
1995	311	290	200	269	1,070	48	70
1996	331	233	77	75	716	45	46
1997	217	182	190	229	818	14	59
1998	875	403	147	106	1,531	61	92
1999	641	150	58	64	913	15	106
2000	246	198	371	395	1,210	29	95
2001	743	370	50	51	1,214	45	73
Total	5,850	3,442	2,105	2,248	13,645	382	731

^a Recaptures are defined as the number of unique individuals banded on our study area in previous years.

^b Recoveries are defined as unique individuals shot or found dead and reported for the current year.

obtained band recovery data from the U.S. Geological Survey Bird Banding Laboratory in Laurel, Maryland, USA. We defined recoveries as reported bands from pintails shot or found dead. Because pintails are important to subsistence harvest on the YKD (Wentworth 1998), we included recoveries during subsistence (nontypical sport) harvest periods (i.e., Feb through Jul). Years began with the initiation of the marking period.

We used program MARK (White and Burnham 1999) and the model developed by Burnham (1993) to estimate survival probability, live recapture probability, reporting probability, and capture location fidelity (Arnold et al. 2002, Blums et al. 2002, Doherty et al. 2002). Estimation of fidelity removed bias from survival estimates resulting from permanent emigration. Reporting rate was defined as the probability that a marked individual was found dead and reported, given that it died during the period between banding occasions (Burnham 1993). This model assumes recaptures of live birds occur over a relatively short period (banding), whereas recoveries of dead birds occurred between banding operations.

The general model ($S[age + sex + year] p[sex + year] r[age + sex + year] F[age + sex + year]$) assumed that survival rates, reporting rates, and fidelity were a function of sex, age (HY or AHY), and year, and that recapture rates were sex- and year-specific. We assumed no age-specificity in recapture probabilities because all pintails were recaptured as adults. Our recapture and recoveries

were too sparse to estimate parameters from models with interaction terms; therefore, we only considered additive models. In addition, survival and fidelity rates were autocorrelated in likelihood estimates due to low recapture and reporting rates for pintails, and we only considered models in which variation was the same in the survival and fidelity rates (i.e., if survival was allowed to vary by age and sex, then fidelity was constrained to vary by age and sex). We followed methods pre-

sented by Doherty et al. (2002) to examine a series of reduced parameter models in a systematic fashion using Akaike's Information Criterion (AIC) to identify models that best described our data (Burnham and Anderson 1999).

We assessed goodness-of-fit to the global model using the parametric bootstrap procedure available in program MARK. We divided deviance from the global model by the mean deviance for 500 simulated data sets to estimate a variance inflation factor. Model selection was based on comparison of the quasi-likelihood Akaike's Information Criterion (QAIC_c), which incorporated lack-of-fit (Burnham and Anderson 1998). We estimated model parameters as a weighted average by using normalized Akaike weights and the parameter estimates from each model (Burnham and Anderson 1998).

Because pintails are believed to disperse from prairie areas during drought years (Smith 1970, Hochbaum and Bossenmaier 1972, Derksen and Eldridge 1980), they might have entered our Alaskan sample in higher proportion during those years. Therefore, we included the number of Canadian ponds surveyed annually in May (USFWS 2002) as a cohort group covariate for fidelity rates. We added this covariate only to the best model identified by AIC. Use of this covariate was similar to transient models used to correct for capture of individuals that temporarily immigrated from other populations (Loery et al. 1997). We transformed our reporting rate (r) to a recovery rate (f) of $f = r * (1 - \text{survival rate})$

Table 2. Models used to estimate survival of northern pintails banded on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

Model ^a	QAIC _c	ΔQAIC _c	MW ^b	NP ^c
$S_s P_{s+y} r_{a+s+y} F_{s+WB}$	9,393.35	0.00	0.63	31
$S_s P_{s+y} r_{a+s+y} F_s$	9,394.76	1.41	0.31	30
$S_{a+s} P_{s+y} r_{a+s+y} F_{a+s}$	9,398.34	4.99	0.05	32
$S_{a+y} P_{s+y} r_{a+s+y} F_{s+y}$	9,406.46	13.11	0.00	51
$S_{a+s+y} P_{s+y} r_{a+s+y} F_{a+s+y}$	9,409.88	16.53	0.00	53

^a Notation follows Lebreton et al. (1992) where a letter indicates that a given parameter varies by that factor. The following designations apply: *S* = survival, *p* = recapture probability, *r* = reporting probability, and *F* = fidelity to the study area. Subscripts are defined as: *a* = age, *s* = sex, *y* = year, *WB* = number of Canadian May ponds in year banded. Additive models are designated by + between factors.

^b MW = model weights generated by program MARK.

^c NP = number of model parameters.

(Brownie et al. 1985). This allowed direct comparison to previous recovery rate estimates based on a Brownie model (Rienecker 1987a).

RESULTS

We captured 5,850 AHY males, 3,442 AHY females, 2,105 HY males, and 2,248 HY females (Table 1). Most recoveries (>90%) occurred in the Pacific Flyway (Fig. 1). California had the largest number of recoveries (64%), with 57% reported from the Central Valley region. One pintail was recaptured in northern Japan, indicating that the YKD population may mix with Asian waterfowl populations. Only 2 bands were reported from the spring subsistence harvest on the YKD.

We estimated the variance inflation factor as 1.28. The most parsimonious model assumed adult survival varied by sex; recapture probability varied by sex and year; recovery probability varied by age, sex, and year; and fidelity rates varied by sex and were correlated with Canadian May Pond indices during the year of initial banding (Table 2).

Model selection favored models in which survival was a function of sex. Models that contained age and/or variation in time explained little variation in survival (parameter likelihoods = 0.05 for age and 0.00 for year). Annual survival of males (77.6%, 95% CI:73.9–81.0%) exceeded rates of females (60.2%, 95% CI:53.2–67.0%). Reporting rate model selection favored models that contained effects of age, sex, and year. For adults, reporting rates of males exceeded those of females (Fig. 2). Within sexes, reporting rates of HY pintails exceeded those of AHY pintails (Fig. 2). Reporting rates of HY males were typically twice those of AHY males, and the relative difference between sexes was greater for HY birds (Fig. 2). We were able to estimate year-specific recovery

rates by transforming reporting rates and by the variance decomposition procedure described by Burnham et al. (1987). Recovery rates averaged 0.019 (0.002 SE) for AHY males, 0.009 (0.001 SE) for AHY females, 0.043 (0.005 SE) for HY males, and 0.023 (0.003 SE) for HY females (Table 3). Because these are transformed values

based on constant annual survival, patterns of annual variation and standard errors mirror those for reporting rates (Fig. 2). Recapture rate model selection favored models in which recapture probability varied by sex and year and were quite low (<0.06; Table 3). Because we constrained our candidate model set so that survival and fidelity were modeled with the same variables, fidelity in our candidate models also varied only by sex. Fidelity rates were positively correlated with numbers of Canadian May Ponds in the year of banding (Fig. 3) as a cohort effect and reflected the probability that an individual would ever return to our capture location again. Females returned to the banding site at higher rates (0.899 in capture years with low May pond numbers and 0.943 in capture years with high May pond numbers) than did males (0.774 in capture years with low May pond numbers and 0.872 in capture years with high May pond numbers).

DISCUSSION

Because we combined live recaptures and recoveries of dead birds, we were able to model emigration directly, so our estimates of survival were free of this potential bias. Our survival estimates for adults were very similar to those reported by Rienecker (1987a) and Hestbeck (1993b) from winter-banded pintails across North America prior to 1979. However, it is likely that these estimates based on winter-banded birds represented subsamples of birds from a variety of breeding locations. Accordingly, we caution that comparison with data from a single breeding area may be misleading.

The reporting rate for HY males was 3 times higher than for HY females. Certainly, this is partially explained by higher harvest rates of HY male pintails (Cox et al. 1998). However, this does not

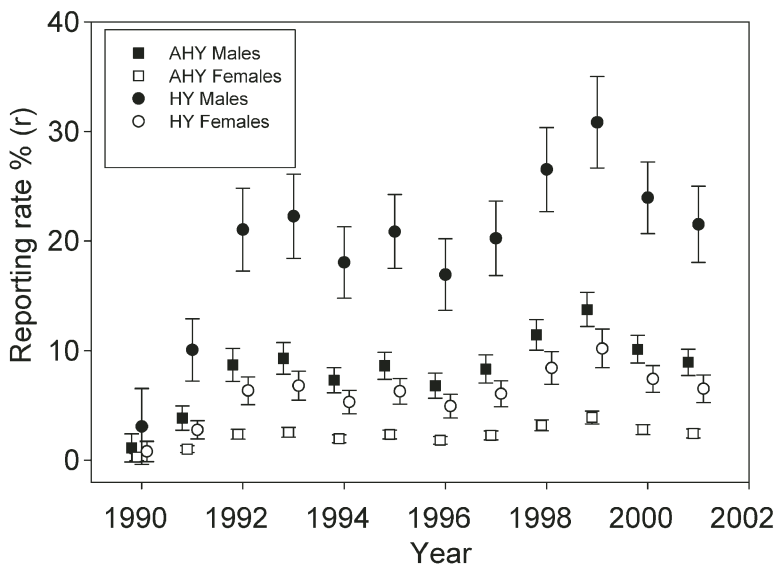


Fig. 2. Reporting rates (\pm SE) for northern pintails banded on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

explain all of the variation between sexes because reporting rate was 3 times higher for HY males relative to HY females, whereas the recovery rate for males was only about twice as high as females. The interpretation of these reporting rates is the proportional contribution of mortality associated with band reporting (i.e., harvest) to overall annual mortality. In a comparative sense, reporting rates increase as nonharvest mortality rates decline relative to harvest rates. Therefore, part of the difference in reporting rates between HY males and HY females is related to lower non-hunting mortality rates for males. We conclude that harvest is an important mortality factor for

HY males; but other factors, likely associated with their first breeding season, are dominant mortality factors for HY females (Johnson et al. 1992).

Recovery rates estimated by Rienecker (1987a) during the 1960–1980s exceeded those for our summer-banded sample. There are 2 possible explanations for this difference in recovery rates. First, harvest rates may have declined in response to more restrictive harvest regulations. If so, this apparent reduction in harvest rate did not result in subsequent increases in annual survival. This

suggests that harvest mortality was not additive. Alternatively, we suggest that recovery rates for Alaskan breeding pintails could be lower than for other pintails wintering in California. Rienecker (1987a) marked his pre-season sample in August and September well before most Alaskan birds would be present. Fleskes et al. (2002a) noted that HY pintails arrived in California later than AHY birds, implying that timing of migration depended upon reproductive status. Further, a significant number of pintails staged in Alaska in late October when hunting seasons in California were open, thereby reducing exposure of Alaskan birds to harvest. Additionally, our estimates of recovery rate

Table 3. Recapture and recovery rates^a of northern pintails banded on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

Year	Recapture estimate				Recovery estimate							
	Males	SE	Females	SE	AHY-M	SE	AHY-F	SE	HY-M	SE	HY-F	SE
1990	—	—	—	—	0.003	0.003	0.001	0.001	0.007	0.008	0.003	0.004
1991	0.024	0.011	0.056	0.024	0.009	0.003	0.004	0.001	0.023	0.006	0.011	0.003
1992	0.017	0.004	0.041	0.008	0.020	0.003	0.009	0.002	0.047	0.008	0.025	0.005
1993	0.016	0.004	0.038	0.008	0.021	0.003	0.010	0.002	0.050	0.009	0.027	0.005
1994	0.020	0.004	0.048	0.008	0.016	0.003	0.008	0.001	0.040	0.007	0.021	0.004
1995	0.018	0.004	0.043	0.009	0.019	0.003	0.009	0.002	0.047	0.008	0.025	0.005
1996	0.017	0.004	0.040	0.008	0.015	0.003	0.007	0.001	0.038	0.007	0.020	0.004
1997	0.006	0.002	0.015	0.005	0.019	0.003	0.009	0.002	0.045	0.008	0.024	0.005
1998	0.028	0.006	0.063	0.012	0.026	0.003	0.013	0.002	0.059	0.009	0.034	0.006
1999	0.006	0.002	0.014	0.004	0.031	0.003	0.015	0.002	0.069	0.009	0.041	0.007
2000	0.012	0.003	0.029	0.007	0.023	0.003	0.011	0.002	0.054	0.007	0.030	0.005
2001	0.018	0.004	0.042	0.009	0.020	0.003	0.010	0.002	0.048	0.008	0.026	0.005

^aRecovery rates (*f*) are transformed from our model averaged estimates of reporting rate (*r*, see Fig. 2).

may potentially be biased low due to low reporting rates of subsistence-harvest-killed pintails. We acknowledge that prairie originating pintails may not be subjected to the same subsistence harvest pressure as YKD pintails. However, this source of harvest on the YKD is believed to be low; thus, it cannot fully explain the disparity between our recovery estimates and those of Rienecker (1987a). Because harvest regulations varied, we cannot discriminate between effects of harvest regulation changes and differential harvest susceptibility.

Recovery rates of males exceeded those of females and likely reflected hunter selectivity as suggested by Rienecker (1987a) and Metz and Ankney (1991). Also, recovery rates of HY pintails exceeded those of adults, suggesting that HY pintails have higher vulnerability to hunting like other ducks (Haramis et al. 1993, Pace and Afton 1993).

The Central Valley region of California was the primary wintering area for pintails we banded, and the geographic distribution of recoveries appears to fit the fidelity rates we estimated. For example, <10% of the recoveries occurred outside the Pacific Flyway. These may have been birds that emigrated to Alaska and entered our sample during drought years on the Canadian prairies and subsequently returned to prairie nesting regions under better water conditions. Our estimated fidelity rates for AHY females were similar to fidelity rates estimated by Hestbeck (1993a) for pintails wintering in California. Therefore, there is a relatively strong fidelity between Alaskan breeding grounds and associated Californian wintering areas.

Female pintails prefer ephemeral wetlands (Smith 1968) and regularly pioneer new areas to adapt to annual variation in habitat conditions (Johnson and Grier 1988). Our estimates of female site fidelity are considerably higher than those recorded for most other duck species (Anderson et

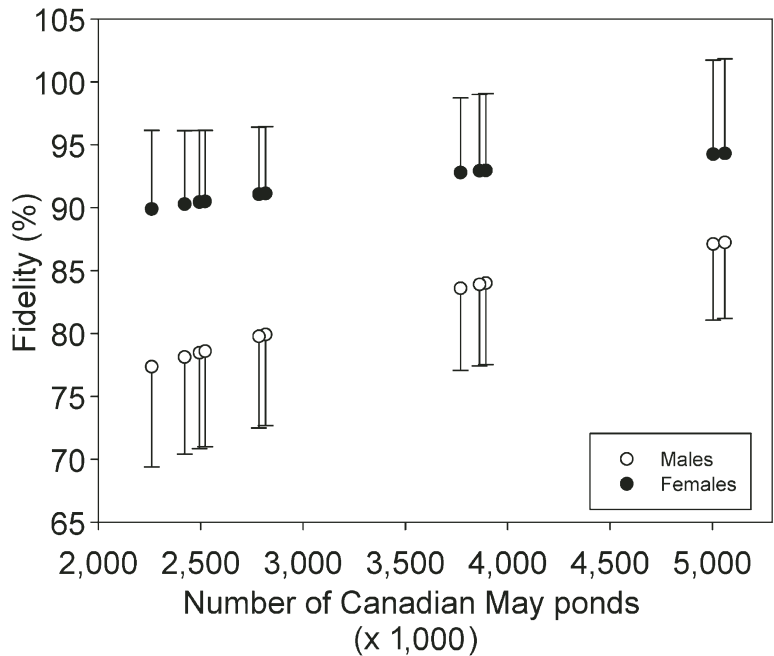


Fig. 3. Fidelity rates (\pm SE) for northern pintails banded on the Yukon-Kuskokwim Delta, Alaska, USA, 1990–2001.

al. 1992). It may be advantageous for female pintails to show high fidelity to the YKD because the relative consistency of wetland conditions results in breeding habitat that varies little between years. However, in our analyses, temporary emigration was confounded with our recapture rate, and we could not detect short term displacement associated with water conditions. We predict that, while rates of temporary emigration away from the prairies are highly variable, true female fidelity rates to prairie areas are likely similar to what we measured for YKD birds because transients apparently returned to the prairies in subsequent years (i.e., they showed fidelity to the prairies).

Our results are also unusual in that male and female fidelity rates differed by <13%, regardless of age. Other studies suggest females have substantially higher return rates to nesting areas than males (Rohwer and Anderson 1988, Anderson et al. 1992). Rienecker (1987b) reported that female pintails also had higher fidelity rates to wintering areas than males. If breeding populations mix on wintering areas and random pair formation occurs, we would expect large differences in fidelity rates between sexes as found in other waterfowl (Lindberg et al. 1998). One explanation for the high fidelity rate of YKD male pintails is that pair formation may not occur ran-

domly. Nonrandom mate selection would require that YKD wintering populations be relatively segregated from other subpopulations during pair formation. However, Fleskes et al. (2002b) described low levels of subpopulation segregation on wintering areas. Alternatively, males may undertake a molt migration to consistent areas regardless of the breeding location of their mate. Accordingly, the fidelity rate we document for male pintails may not be indicative of breeding site fidelity.

Some of the adult females we banded could have been molt migrants. However, we assume that the HY birds we captured most likely came from the local breeding area. Median hatch dates for pintails nesting on the YKD were in late June (Flint and Grand 1996), and we captured birds shortly after fledging. We assume it is unlikely that HY birds from other breeding areas would have migrated to the YKD during our capture periods. Flint et al. (1998) suggested that pintails breeding on the YKD fledged only 0.16 young females per breeding female annually. Under the assumption that we captured a random sample of birds with respect to age and sex, the age ratio of our banded sample (i.e., 0.65 HY females per AHY female) implies that there were not an excess of adult females present on our study area. If our banding location consistently attracted a large number of molt migrants, we would expect this ratio to be considerably lower. Accordingly, we assume that our fidelity rates for females reflect breeding site fidelity to the YKD.

The May ponds covariate in the fidelity estimate supports the presence of transients during years with prairie drought. Therefore, when May Pond numbers were high, few birds from the prairies were available on the YKD to be banded in our study. Conversely, when May Pond numbers were low, prairie pintails dispersed from the prairies, and were more likely to be banded on our study area. Thus, the true fidelity rate (i.e., in the absence of transients) for YKD pintails is likely greater than 95% for females and greater than 87% for males. We tested for an age effect in fidelity, but we found little evidence ($\Delta QAIC_c = 4.99$; Table 2) for this effect, which implies higher natal philopatry than anticipated. Cronin et al. (1996) reported no genetic differentiation among breeding populations in Alaska and the Prairie Pothole region. Our fidelity rates support this assessment, as our dispersal rates would easily support sufficient gene flow to eliminate genetic differences between these populations. Howev-

er, the combination of adult female site fidelity and natal philopatry are 2 key pieces for the development of subpopulation structure. Therefore, even if genetic differences do not exist, the YKD supports a relatively distinct subpopulation.

MANAGEMENT IMPLICATIONS

Our data suggest that movement in addition to local survival and recruitment must be considered when assessing local population dynamics because 5–10% of females disperse in any given year. Perhaps pintails are best viewed as a metapopulation. Rates and patterns of movements among segments of this metapopulation deserve further study.

Flint et al. (1998) demonstrated that population dynamics were most sensitive to adult female survival. We recommend that future studies focus on partitioning of annual survival into key parts of the pintail annual life cycle so that future management options can focus on more pressing population bottlenecks. The relatively low recovery rate of pintails in our sample, especially adult females (<1%), indicates that harvest does not have a major impact on YKD pintail populations. Given low harvest rates, other management options focused on non-hunting mortality or recruitment would likely be more effective than further harvest restrictions. We recommend replication of pre- and post-season banding studies within California (Rienecker 1987a) to directly assess temporal changes in survival associated with harvest and nonharvest sources of mortality.

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LITERATURE CITED

- ANDERSON, M. G., J. M. RHYMER, AND F. C. ROHWER. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 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.
- ARNOLD, T. W., M. G. ANDERSON, C. D. SORENSON, AND R. B. EMERY. 2002. Survival and philopatry of female redheads breeding in Southwestern Manitoba. *Journal of Wildlife Management* 66:162–169.
- BETHKE, R. W., AND T. D. NUDDS. 1995. Effects of climate change and land use on duck abundance in Canadian prairie-parklands. *Ecological Adaptations* 5:588–600.
- BLUMS, P., J. D. NICHOLS, J. E. HINES, AND A. MEDNIS. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. *Journal of Animal Ecology* 71:438–450.
- BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1985. Statistical inference from band recovery data—a handbook. Second edition. U.S. Fish and Wildlife Service, Resource Publication 156.
- BURNHAM, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 in J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhauser Verlag, Basel, Switzerland.
- , AND D. R. ANDERSON. 1998. Model selection and inference: a practical information—theoretic approach. Springer-Verlag New York, USA.
- , G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5.
- COX, R. R., JR., A. D. AFTON, AND R. M. PACE, III. 1998. Survival of female northern pintails wintering in southwestern Louisiana. *Journal of Wildlife Management* 62:1512–1521.
- CRONIN, M. A., J. B. GRAND, D. ESLER, D. V. DERKSEN, AND K. T. SCRIBNER. 1996. Breeding populations of northern pintails have similar mitochondrial DNA. *Canadian Journal of Zoology* 74:992–999.
- DERKSEN, D. V., AND W. D. ELDRIDGE. 1980. Drought-displacement of pintails to the arctic coastal plain, Alaska. *Journal of Wildlife Management* 44:224–229.
- DOHERTY, P. F., NICHOLS, J. D., J. TAUTIN, J. F. VOELZER, G. W. SMITH, D. S. BENNING, V. R. BENTLEY, J. K. BIDWELL, K. S. BOLLINGER, A. R. BRADZA, E. K. BUELNA, J. R. GOLDSBERRY, R. J. KING, F. H. ROETKER, J. W. SOLBERG, P. P. THORPE, AND J. S. WORTHAM. 2002. Sources of variation in breeding-ground fidelity of mallards (*Anas platyrhynchos*). *Behavioral Ecology* 13:543–550.
- DUFOUR, K. W., AND R. G. CLARK. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. *Condor* 104:297–308.
- FLESKES, J. P., R. L. JARVIS, AND D. S. GILMER. 2002. September–March survival of female northern pintails radiotagged in San Joaquin Valley, California. *Journal of Wildlife Management* 66:901–911.
- , ———, AND ———. 2002. Distribution and movements of female northern pintails radiotagged in San Joaquin Valley, California. *Journal of Wildlife Management* 66:138–152.
- FLINT, P. L., AND J. B. GRAND. 1996. Nesting success of Northern Pintails on the coastal Yukon-Kuskokwim Delta, Alaska. *Condor* 98:54–60.
- , ———, AND R. F. ROCKWELL. 1998. A model of northern pintail productivity and population growth rate. *Journal of Wildlife Management* 62:1110–1118.
- HARAMIS, G. M., D. G. JORDE, AND C. M. BUNCK. 1993. Survival of hatching-year female canvasbacks wintering on Chesapeake Bay. *Journal of Wildlife Management* 57:763–771.
- HESTBECK, J. B. 1993a. Overwinter distribution of northern pintail populations in North America. *Journal of Wildlife Management* 57:582–589.
- . 1993b. Survival of northern pintails banded during winter in North America, 1950–88. *Journal of Wildlife Management* 57:590–597.
- HOCHBAUM, G. S., AND E. F. BOSSENMAIER. 1972. Response of pintails to improved breeding habitat in southern Manitoba. *Canadian Field Naturalist* 86:79–81.
- JOHNSON, D. H., AND J. W. GRIER. 1988. Determinants of the breeding distributions of ducks. *Wildlife Monographs* 100.
- , 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, Minneapolis, USA.
- 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.
- LINDBERG, M. S., J. S. SEDINGER, D. V. DERKSEN, AND R. F. ROCKWELL. 1998. Natal and breeding philopatry in a black brant *Branta bernicla nigricans* metapopulation. *Ecology* 79:1893–1904.
- LOERY, G., J. D. NICHOLS, AND J. E. HINES. 1997. Capture-recapture analysis of a wintering black-capped chickadee population in Connecticut, 1958–1993. *Auk* 114:431–442.
- METZ, K. J., AND C. D. ANKNEY. 1991. Are brightly colored ducks selectively shot by duck hunters? *Canadian Journal of Zoology* 69:279–282.
- MILLER, M. R., AND D. C. DUNCAN. 1999. The northern pintail in North America: status and conservation needs of a struggling population. *Wildlife Society Bulletin* 27:788–800.
- PACE, III, R. M., AND A. D. AFTON. 1993. Direct recovery rates of lesser scaup banded in northwest Minnesota: sources of heterogeneity. *Journal of Wildlife Management* 63:389–395.
- RIENECKER, W. C. 1987. Survival and recovery rate estimation of northern pintail banded in California 1948–79. *California Fish and Game* 73:230–237.
- . 1987. Migration and distribution of northern pintail banded in California. *California Fish and Game* 73:139–155.
- ROHWER, F. C., AND M. G. ANDERSON. 1988. Female-biased philopatry, monogamy, and the timing of pair

- formation in migratory waterfowl. Pages 187–214 in R. F. Johnson, editor. *Current ornithology*. Volume 5. Plenum Press, New York, USA.
- SCHMUTZ, J. A., AND C. R. ELY. 1999. Survival of greater white-fronted geese: effects of year, season, sex, and body condition. *Journal of Wildlife Management* 63:1239–1249.
- SMITH, R. I. 1968. The social aspects of reproductive behavior in the pintail. *Auk* 85:381–396.
- . 1970. Response of pintail breeding population to drought. *Journal of Wildlife Management* 34:943–946.
- TANDE, G. F., AND T. W. JENNINGS. 1986. Classification and mapping of tundra near Hazen Bay, Yukon Delta National Wildlife Refuge, Alaska. U.S. Fish and Wildlife Service Report AI 87/01.
- U.S. FISH AND WILDLIFE SERVICE. 1990. Preseason pintail and mallard banding in Alaska–1990. Memo to field stations. Regional Directorate, Refuges and Wildlife, Anchorage, Alaska, USA.
- . 2002. Waterfowl population status, 2002. U.S. Department of the Interior, Washington, D.C., USA.
- WENTWORTH, C. 1998. Subsistence waterfowl harvest survey, Yukon-Kuskokwim Delta. Comprehensive report 1987–1997. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska, USA.
- WHITE, G. S., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked birds. *Bird Study (supplement)*:120–138.

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