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AGE-SPECIFIC SURVIVAL AND PHILOPATRY IN THREE SPECIES OF EUROPEAN DUCKS: A LONG-TERM STUDY[1]

PETER BLUMS,[2] AIVARS MEDNIS, ILMARS BAUGA
Institute of Biology, Latvian Academy of Sciences, Miera 3, LV-2169, Salaspils, Latvia

JAMES D. NICHOLS AND JAMES E. HINES
Patuxent Environmental Science Center, National Biological Service, Laurel, MD 20708

Abstract. Capture-recapture and band recovery models were used to estimate age-specific survival probabilities for female Northern Shovelers (*Anas clypeata*), Common Pochards (*Aythya ferina*), and Tufted Ducks (*Aythya fuligula*) at Engure Marsh, Latvia, in 1964–1993. We banded more than 65,100 day-old ducklings of both sexes and captured 10,211 incubating females (3,713 new bandings and 6,498 recaptures). We developed a set of 3-age capture-recapture models to estimate annual survival rates for female ducklings, yearlings (SY), and adults (ASY) using programs SURGE and SURVIV and selected parsimonious models using a method developed by Akaike (1973). Survival rates of SY and ASY females were highest for Tufted Ducks intermediate for Common Pochards, and lowest for Northern Shovelers. Survival rates of SY and ASY females varied in parallel for shovelers and pochards. We believe that much of the difference in survival estimates between SY and ASY birds was caused by mortality rather than permanent emigration. Estimates of day-old duckling survival, reflecting both mortality and permanent emigration, were 0.12 for shoveler, 0.06 for pochard, and 0.03 for Tufted Duck. For all species, duckling survival varied over years, but the pattern of variation was not similar to that of the other age classes. Estimates of survival using band recovery data for SY + ASY female pochards and Tufted Ducks were similar to the capture-recapture estimates, suggesting that surviving females returned to the breeding marsh with probabilities approaching 1.

Key words: age-specific female survival; Anatidae; Anas clypeata; Aythya ferina; Aythya fuligula; *breeding philopatry; permanent emigration; Latvia.*

INTRODUCTION

Capture-recapture and band recovery models are becoming increasingly important for estimation of survival rates of birds, including waterfowl. Traditionally, band recovery models have been used extensively to estimate survival rates of ducks and geese (reviewed by Johnson et al. 1992), but capture-recapture models have received little attention, primarily because of the lack of long-term studies with marked birds. There have been few long-term capture-recapture studies of breeding ducks that estimated survival probabilities based on modern statistical methods. Most of these have focused on box-nesting species such as Wood Duck, *Aix sponsa* (Hepp et al. 1987, Dugger 1991, Hepp and Kennamer 1993) and Common Goldeneye, *Bucephala clangula* (Dow and Fredga 1984) or island nesting Common Eider, *Somateria mollissima* (Coulson 1984), all of which are relatively easy to capture.

Most evidence on breeding philopatry in female waterfowl comes from estimates of return rate, however, this statistic incorporates three probabilities and can be only used to draw tentative inferences about homing (Anderson et al. 1992, Johnson et al. 1992). If both band recovery and capture-recapture survival estimates can be obtained for breeding females banded in a particular location then it is possible to directly estimate unconfounded homing probability (see Methods). Because of the lack of adequate data no such estimates are currently available (but see Hepp et al. 1987).

In this paper we use 27 years of band recovery and 18 years of capture-recapture data to estimate survival and breeding probabilities of female ground-nesting and over-water nesting ducks on a single study area in Latvia. Aging of breeding females and banding of day-old ducklings with special oval bands (Blums et al. 1994),

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[2] Present address: Gaylord Memorial Laboratory, The School of Natural Resources, University of Missouri–Columbia, Puxico, MO 63960, USA.

permitted inferences that have not been possible using previous methods (i.e., we estimated survival probabilities for females of three age classes). To determine whether females are philopatric, we compared survival estimates from band recovery and capture-recapture models, and also evaluated band recovery locations of females captured on the nests.

METHODS

STUDY AREA AND BREEDING POPULATIONS OF DUCKS

A long-term capture-recapture study of Northern Shoveler (*Anas clypeata,* hereafter shoveler), Common Pochard (*Aythya ferina,* hereafter pochard), and Tufted Duck (*Aythya fuligula*) was conducted from 1958 to 1993 on Engure Marsh, Latvia, Eastern Europe. The 35-km^2 Engure Marsh is a shallow, permanently-flooded palustrine marsh (Cowardin et al. 1979) on the east coast of the Baltic Sea (57°15′N, 23°07′E). The marsh has gradually changed from an open to a hemi-marsh (Weller and Spatcher 1965) dominated by tall, robust hydrophytes such as Common Reed (*Phragmites australis*) and cattail (*Typha* spp.). Human activities are prohibited on islands and areas of emergent vegetation during the breeding season but most of the marsh is open to waterfowl hunting during early August through early November. Different management activities (such as construction of artificial islands, vegetation and predator control, and attraction of gulls and terns) were conducted on all sampling areas throughout the study that prevented the decline of carrying capacity of breeding habitats (Mihelsons et al. 1976, Blums and Viksne 1990, Blums and Mednis 1991). Predators were systematically controlled for two to three months beginning with the break-up of ice, and an average of 11 (range 1–17) American Minks (*Mustela vison*), 83 (44–144) Marsh Harriers (*Circus aeruginosus*), 21 (0–63) Ravens (*Corvus corax*), 17 (6–34) Hooded Crows (*Corvus corone*), 14 (2–25) Herring Gulls (*Larus argentatus*), etc., were removed or relocated out of the marsh during each breeding season (records from 1978 through 1993).

Permanent sampling areas included five natural islands with a total surface area at low water of approximately 20 ha, from 1958 to 1981. Large portions of these islands were flooded during high water conditions and were not always suitable for nesting. To maintain stable breeding conditions, many artificial elevated islands were constructed on the flooded sections of two natural islands during 1981–1983 (Blums and Mednis 1991). Beginning in 1984, 82 islands totaling 14.3 ha in area were available for nesting within the previous island territory. We believe that fragmentation of large islands increased the carrying capacity of island breeding habitats despite the substantial decrease in total surface area. This was confirmed by the highest ever number of duck nests recorded on all islands in the early 1990s (Blums et al. 1993).

In addition to the natural and artificial islands, nest searches were expanded to three isolated areas of persistent emergent marsh in 1972, totaling approximately 111 ha of reed-beds and cattail stands, excluding open water. Thus, permanent sampling areas included natural and artificial islands, 1958–1993, and emergent marshes, 1972–1992.

During the last 20 years, the marsh supported about 2,000 breeding pairs of ducks, with about 60% consisting of pochards, Tufted Ducks, and shovelers. The average numbers of breeding pairs on the entire marsh during 1977–1993 were as follows (Blums et al. 1993): Common Pochard 900 (range 560–1640), Tufted Duck 280 (160–360), and Northern Shoveler 33 (range 19–59). Of these numbers 99% of shovelers, 42% of Tufted Ducks, and 23% of pochards nested within permanent sampling areas. Shovelers nested almost exclusively on the islands within permanent sampling areas, thus the entire breeding population was monitored each year during routine nest searches. The breeding populations of Tufted Ducks and shovelers were fairly stable throughout the study period however, the number of shovelers increased substantially during the last five years (Blums et al. 1993). Pochards increased during the last 16 years.

FIELD METHODS

We conducted two to three complete searches for duck nests on the permanent sampling areas from mid-May to mid-June. All breeding habitats within permanent sampling areas were systematically searched to locate nests by walking parallel transects. We adjusted the distance between transects from 1.5 to 3.0 m in relation to vegetation density and height. Additional intensive efforts were made each breeding season to locate new nests by flushing females and watching lone individuals of both sexes. We believe the effectiveness of nest searches was high because certain sampling areas were assigned to the biologists who worked on the same areas for 10–30 consecutive field seasons and knew potential nest sites. That knowledge was especially important for finding nests in reed-beds. Experimental burns on islands, after the last nests hatched, verified that more than 95% of all nests were found each year. We captured incubating females on nests during the last week of incubation using drop-door traps (Blums et al. 1983) or dip nets; unmarked females were banded with conventional legbands.

Beginning in 1976, we obtained a sample of known-age females using two different methods. First, more than 65,000 day-old ducklings were individually marked using plasticine-filled legbands (Blums et al. 1994). Subsequent recaptures of these birds as breeding females allowed us to assign them an exact age. Second, unmarked incubating females were aged as either yearlings (1-year-old, SY) or adults (≥2-years-old, ASY) using wing feather characteristics. There were a relatively small fraction of unmarked birds (no plasticine-filled or conventional bands) in the sample of females that were used for capture-recapture analyses (24, 25, and 32% of Tufted Ducks, shovelers, and pochards, respectively).

The shape and coloration of greater secondary coverts (GSC) were key identification characters used singly or in combination for all three species (see Boyd et al. 1975, Palmer 1976). The 11th or 12th, rather than 13th or 14th, GSC were better indicators for both diving ducks because these coverts usually had not been molted during the breeding season. The age-specific pattern in shape (Tufted Duck, pochard) of GSC was similar to that described by Dane and Johnson (1975) for Redheads (*Aythya americana*), and vermiculation of upper wing feathers (pochard), to that described by Serie et al. (1982) for Canvasbacks (*Aythya valisineria*), respectively, in North America. The coloration of first GSC and distal parts of middle and lesser secondary coverts were the best indicators for shovelers. Eye color also was used to age female Tufted Ducks (see Trauger 1974), although there was some overlap in color between SY and ASY females. The iris color of SY females was brownish-yellow or dull-yellow, or rarely yellow with a blurred brownish inner zone adjacent to the pupil. The iris color of ASY females was typically orange-yellow or yellow, or rarely with scattered brownish markings or a narrow brownish ring at the inner part of iris.

Newly hatched ducklings were captured by hand at nests and banded with plasticine-filled oval aluminum bands (Blums et al. 1994) rather than with the web tags commonly used by American biologists (Grice and Rogers 1965, Haramis and Nice 1980). Band loss for ducklings was estimated to be extremely low, <0.5% (Blums et al. 1994). Oval bands were replaced with conventional round bands at the first recapture when birds returned to breed.

STATISTICAL METHODS

Birds marked in this study were reobserved in two different ways. First, some birds were recovered after having been shot or found dead and their band numbers reported by investigators or the general public. Resulting banding and recovery data were analyzed using band recovery models of Brownie et al. (1985). These models permit estimation of annual survival rates and band recovery rates. Annual survival rates reflect the proportion of birds alive at the time of banding in one year that are still alive at the time of banding in the subsequent year. The complement of survival rate estimates obtained from band recovery data and models ($1 - \hat{S}$, where $\hat{S}$ is a survival estimate) typically reflects only mortality.

Second, many females were recaptured at nests during the breeding season each year by investigators. Resulting data were analyzed using capture-recapture models for open populations, defined as populations in which birds can enter or leave the population between sampling period (Seber 1982, Pollock et al. 1990, Lebreton et al. 1992). Unlike band recovery data in which a banded bird can be recovered as dead only once, a single bird may be recaptured in multiple years.

Band recoveries can occur over a broad geographic area, but recapture data typically come from restricted study areas (in our case the Engure Marsh). As a result, the complement of "survival" estimates from capture-recapture models includes both death and permanent emigration, since marked birds may depart the study area and go to different breeding areas in subsequent years. This difference in the survival estimates computed from band recovery and capture-recapture data and models permits inference about homing and permanent emigration (Hepp et al. 1987). If all birds home back to the breeding marsh each year, then survival estimates hased on band recovery and capture-recapture data should be similar, as they estimate the same quantity. Conversely, if many birds do not return to the breeding marsh but shift breeding locations, then the survival estimate from band recovery data will be larger than the estimate from capture-recapture data, with the difference reflecting the amount of permanent emigration (Hepp et al. 1987).

Band recovery models. Survival rates were estimated from band recovery data using the models described by Brownie et al. (1985). Band recovery data were limited, and numbers of bandings and recoveries of female ducks were fewer than those typically used in banding studies from North America. Northern Shoveler data were insufficient for reasonable use with these models but numbers of bandings and recoveries were adequate for pochards and Tufted Ducks, so we estimated survival rates because of the virtual absence of other survival estimates for these diving ducks. For the Common Pochard, there were enough data for SY and ASY females to compare model H0 (year-specific survival and recovery rates; no age-specificity) against H1 (year- and age-specific survival and recovery rates) using the contingency table test of Brownie et al. (1985) for age-specificity of survival and recovery rates. We conducted this test for two separate time periods, 1974–1982 and 1984–1991 (data were scarce for 1983), and summed the resulting χ^2 values (and their associated degrees of freedom) to obtain an overall test of the null hypothesis of no difference between the two age classes of pochards. Tests for age-specificity of survival and recovery rates of pochards did not indicate that the null hypothesis should be rejected ($\chi^2_{34} = 35.9$, $P = 0.38$).

Band recovery analyses were therefore conducted on combined SY and ASY females for pochards (1974–1992) and Tufted Ducks (1964–1991). We used single-age models of program ESTIMATE, selecting a parsimonious model using likelihood ratio and goodness-of-fit tests. Likelihood ratio tests were conducted between a more general model (representing the alternative hypothesis) with more parameters and a simpler model (representing the null hypothesis) with fewer parameters. A significant (e.g., $P < 0.10$) likelihood ratio χ^2 test statistic provides evidence that the additional parameters of the more general model are required to adequately model the data, whereas a nonsignificant test statistic indicates that the more general model is not needed to explain the data. Goodness-of-fit tests provide evidence about the adequacy of a particular model to describe the variation in the data set. A significant χ^2 goodness-of-fit test statistic indicates lack of fit of the model to the data, whereas a nonsignificant test statistic provides no evidence of lack of fit. After obtaining these estimates, we compared the two species using program CONTRAST (Sauer and Williams 1989, Hines and Sauer 1989).

Capture-recapture models. Capture-recapture data from the permanent sampling areas at Engure Marsh were available for all three species. Because ducklings were banded with legbands (Blums et al. 1994) and because older birds could be identified as SY (1-year-old) or ASY (≥2-year-old), we were able to consider models in which survival and capture probabilities differed among three age classes of ducks (Pollock 1981). The only complication in this modeling was that not all ducklings were sexed. We dealt with this by assuming 50% females among banded ducklings. Preliminary analysis revealed no significant deviation from a 50:50 sex ratio (6,495 day-old ducklings sexed) at hatching for all three species (Blums and Mednis 1996). So if n_t is the total number of ducklings banded and released in year t and r_t is the number of these that are recaptured as SY or ASY females in subsequent years, then we computed the number of female ducklings released but never recaptured as: $(n_t/2) - r_t$.

We developed three-age capture-recapture models for each species using programs SURGE (Pradel et al. 1990) and SURVIV (White 1983). Our approach was to use SURGE in some of the initial screening of models and then to use SURVIV in the final analyses. We developed the models to investigate two possible sources of variation in survival and capture probabilities, age and time (calendar year). Model parameters included survival probability, ϕ_{at}, the probability that an animal of age a (day-old duckling, SY, ASY) in the breeding season of year t survived until the breeding season of year $t + 1$ and did not permanently emigrate from Engure Marsh, and capture probability, p_{at}, the probability that an animal of age a in the breeding season of year t was captured in that season.

Different models are defined by the subscripts on survival and capture probability parameters.

The presence or absence of a subscript indicates that the source of variation (age or time) does or does not apply to the parameter, respectively. With respect to age, we considered models with all three age classes (denoted by subscript a) and models with only two age classes, ducklings and SY + ASY (these models are denoted by subscript a'). Thus model ($\phi_{a \cdot t}$, $p_{a \cdot t}$) indicates the general 3-age model with temporal and age-specific variation in both survival and capture probabilities. This model contains separate parameters for each age-time combination for both survival and capture probability. Capture probability cannot be estimated for the initial age class, so model ($\phi_{a \cdot t}$, $p_{a \cdot t}$) has the following age-specific parameters: ϕ_{1t}, ϕ_{2t}, ϕ_{3t}, p_{2t} and p_{3t}. Model ($\phi_{a'}$, p) indicates a model in which survival differs for the two age classes (ducklings, SY + ASY), capture probability applies to the combined SY + ASY class, and neither capture nor survival probabilities vary over time (they are constants for all years of the study).

In instances where both age and time were important sources of variation in model parameters, we tested models in which age-specific parameters exhibited "parallelism" (sensu Lebreton et al. 1992) over time. For example, in model ($\phi_{a \cdot t}$, p_{a+t}), where the subscript $a+t$ denotes parallelism, capture probability for SY females at time t is modeled as $p_{2t} = \gamma'' p_{3t}$. So capture probability varies by age but the pattern of temporal variation is similar for the two age classes. For survival, subscript $a+t$ denotes full parallelism ($\phi_{1t} = \gamma\phi_{3t}$, $\phi_{2t} = \gamma'\phi_{3t}$, ϕ_{3t}), whereas subscript $(a+t)'$ denotes parallelism between SY and ASY survival probabilities but not with duckling survival (ϕ_{1t}, $\phi_{2t} = \gamma'\phi_{3t}$, ϕ_{3t}). We used likelihood ratio tests to test for specific sources of variation using nested models. Two models are nested if one model can be obtained by constraining the parameters of the other.

We used Akaike's Information Criterion (AIC, Akaike 1973) as a means of selecting the most parsimonious model for each data set. The Principle of Parsimony (see Burnham and Anderson 1992) is based on the idea that our model should reflect a compromise between "overfitting" and "underfitting" our data. Variances of estimates increase as the number of model parameters increases, so if our model contains more parameters than are needed, we will sacrifice precision needlessly, by having larger than necessary variance estimates. Conversely, if we do not include enough parameters to adequately describe the variation in the data, then estimates are likely to be biased. AIC can be computed for all models under consideration for a given data set. The model with the lowest AIC is optimal with respect to this tradeoff between adequate fit and precision.

We used the Pearson goodness-of-fit test with the cell pooling algorithm of SURVIV to assess the fit of each model to the data. Simulations, however, indicated that the pooled Pearson fit statistic rejected the null hypothesis of reasonable model fit more frequently than the nominal level when the null hypothesis was true. Thus, in cases where the goodness-of-fit statistic for the low-AIC model indicated lack of fit ($P < 0.05$), we investigated model fit in more detail via Monte Carlo simulation. We generated 500 data sets using the actual sample sizes and model parameter values set equal to the actual estimates. For the simulated data sets, we computed the distribution of the goodness-of-fit statistics divided by their degrees of freedom, χ^2/df, and then noted the location of the actual χ^2/df relative to this distribution.

Although our capture-recapture modeling was directed at making inferences about survival (ϕ), we also used an approach based on the reasoning of Clobert et al. (1990, 1994) to investigate age-specific breeding proportions. Clobert et al. (1990, 1994) have noted that in species for which individuals are only available for capture in years when they attempt breeding, age-specific differences in capture probability can often be attributed to differences in age-specific breeding proportions. Specifically, if SY and ASY females that nest in a given year are equally likely to be captured (a reasonable assumption in this study), then the ratio of SY to ASY capture probabilities, p_{2t}/p_{3t}, should estimate the ratio of SY to ASY breeding probabilities. When the breeding probability for ASY approaches 1 (i.e., when virtually all ASY females breed), then the ratio of capture probabilities estimates the proportion of SY females that breed (Clobert et al. 1990, 1994).

We chose to estimate the ratio of capture probabilities directly using models with age-specific parallelism in capture probabilities, i.e., the p_{a+t} models. The estimates of $\hat{\gamma}''$ from such models directly estimate the ratio of SY to ASY breeding proportions and, if all ASY females breed, the proportion of SY females that breed. We compared the age-specific ratios of breeding propor-

TABLE 1. Band recovery model goodness-of-fit and likelihood ratio tests for SY and ASY female Common Pochards and Tufted Ducks banded at Engure Marsh, Latvia.

Type of test	Model(s)	Common Pochard, 1974–1992 χ^2	df	P	Tufted Duck, 1964–1991 χ^2	df	P
Goodness-of-fit	Model 1	30.9	24	0.16	19.5	8	0.01
	Model 2	39.9	37	0.34	46.2	33	0.06
	Model 3	96.8	63	<0.01	85.6	61	0.02
Likelihood ratio	Model 3 vs. 1	65.3	35	<0.01	82.3	53	<0.01
	Model 2 vs. 1	18.0	17	0.39	36.0	26	0.09

tion, $\hat{\gamma}''$, as well as survival rates, $\hat{\phi}$, among species using program CONTRAST (Sauer and Williams 1989, Hines and Sauer 1989).

RESULTS

BANDING AND CAPTURE DATA

A sample of 65,122 day-old ducklings of both sexes was banded and 10,211 incubating females were captured (3,713 new bandings and 6,498 recaptures) at the marsh during the study, but data were broken down by periods and species for analyses. Samples of 17,802 (748), 1,351 (668), and 3,783 (2,229) releases (recaptures) of duckling, SY, and ASY females, respectively, were used for estimation of age-specific survival probabilities with programs SURGE and SURVIV for the periods 1976–1993 (shoveler) and 1976–1992 (pochard, Tufted Duck). New bandings (n = 4,064) of incubating females and associated band recoveries (n = 515) provided data for estimation of survival probabilities for diving ducks with program ESTIMATE for the periods 1964–1992 (Tufted Duck), and 1974–1993 (pochard).

BAND RECOVERY MODELS

Common Pochard and Tufted Duck. Results of goodness-of-fit and likelihood ratio tests (Table 1) led us to select Model 2 (Brownie et al. 1985) for both species of diving ducks. Model 2 contains a single time-constant survival parameter and year-specific recovery rates. The estimated survival rate for female pochards ($\hat{S}$ = 0.59; $\widehat{SE}[\hat{S}]$ = 0.022), and Tufted Ducks ($\hat{S}$ = 0.71; $\widehat{SE}[\hat{S}]$ = 0.020) were different (χ^2_1 = 15.4, P < 0.01). Average estimated recovery rates for the two species were $\hat{f}$ = 0.046 ($\widehat{SE}[\hat{f}]$ = 0.003) for pochards and $\hat{f}$ = 0.056 ($\widehat{SE}[\hat{f}]$ = 0.005) for Tufted Ducks. There was some evidence of different recovery rates for the two species, but test results were equivocal (χ^2_1 = 3.3, P = 0.07).

CAPTURE-RECAPTURE MODELS

Northern Shoveler. The model with the lowest AIC for female shovelers was model ($\phi_{(a+t)'}$, p_a) (Table 2). The pooled goodness-of-fit statistics from program SURVIV indicated poor fit of this model to the data (P = 0.03; Table 2); the simulation-based estimate, however, indicated an acceptable fit (P = 0.09). Under model ($\phi_{(a+t)'}$, p_a) capture probability varied by age (SY and ASY) but not by time. Estimated capture probability for ASY (0.80) was higher than that for SY females (0.51; Table 3). We used model ($\phi_{(a+t)'}$, p_{a+t}) to directly estimate the ratio of SY to ASY breeding proportions as $\hat{\gamma}''$ = 0.70 ($\widehat{SE}$ = 0.081).

Annual survival probability varied by age and time. Temporal variation in survival probabilities of SY females paralleled that of ASY females, but variation in duckling survival probabilities did not parallel that of the other two age classes. Thus the same factors probably are responsible for year-to-year variation in survival probabilities of the two older age classes, but other factors are responsible for temporal variation in survival during the first year of life. The mean annual survival probability for ASY females was 0.58. The estimate of $\hat{\gamma}'$ = 0.65 for SY females indicates that average SY survival probabilities $\hat{\phi}_2$ were about 0.38 (Table 3). The average survival estimate for ducklings was 0.12 and reflects the probability that a newly-hatched duckling survived the subsequent year and returned to the study area on Engure Marsh the following breeding season (i.e., did not permanently emigrate to another breeding area).

Common Pochard. Numbers of pochard captures exceeded those of shovelers and Tufted Ducks, and required a general (i.e., incorporating many sources of variation) model ($\phi_{(a+t)'}$, $p_{a \cdot t}$; Table 4). Capture probabilities varied by both age and time, and the pattern of temporal vari-

TABLE 2. AIC values, goodness-of-fit test statistics and likelihood ratio (LR) test statistics for female Northern Shovelers captured and recaptured at Engure Marsh, Latvia, 1976–1993.

Model	NP**	AIC	Goodness-of-fit			LR test with $(\phi_{(a+t)'}, p_a)$*			Source of variation tested by LR
			χ^2	df	P	χ^2	df	P	
$(\phi_{(a+t)'}, p_a)$*	37	422.9	33.3	20	0.03	—	—	—	—
$(\phi_{(a+t)'}, p_{a\cdot t})$	67	434.3	—	—	—	48.6	30	0.02	Full temporal variation in p_a
$(\phi_{(a+t)'}, p_{a+t})$	52	428.8	28.5	7	<0.01	24.0	15	0.06	Parallel temporal variation in p_a
$(\phi_{(a+t)'}, p)$	36	440.0	42.3	21	<0.01	19.2	1	<0.01	Age-specific variation in p
(ϕ_a, p_a)	5	441.9	116.7	54	<0.01	83.0	32	<0.01	Temporal variation in ϕ_a
(ϕ_{a+t}, p_a)	21	449.0	94.8	38	<0.01	58.2	16	<0.01	Parallel temporal variation in ϕ_1, ϕ_2 and ϕ_3
$(\phi_{a\cdot t}, p_a)$	53	428.4	13.7	4	<0.01	26.5	16	0.05	Full temporal variation in ϕ_a
(ϕ_t, p_a)	19	605.2	276.7	48	<0.01	218.4	18	<0.01	Age-specific variation in ϕ_t

* Model selected for use in estimation.
** Number of parameters estimated.

ation was not parallel for SY and ASY females. Average capture probability was higher for ASY ($\hat{p}_3 = 0.69$) than for SY females ($\hat{p}_2 = 0.54$; Table 5). We used model $(\phi_{(a+t)'}, p_{a+t})$ to directly estimate the ratio of SY to ASY breeding proportions as $\hat{\gamma}'' = 0.70$ ($\widehat{SE} = 0.045$).

Survival probabilities also varied by age and time (Table 4). Parallel temporal variation was observed in survival probabilities of SY and ASY birds, but variation in duckling survival was not parallel to that of the other two age classes. Mean annual probability of surviving and not permanently emigrating was estimated at 0.06 for ducklings and 0.65 for ASY females (Table 5). The estimated $\hat{\gamma}'$ of 0.85 indicates an average survival rate for SY females of about 0.55.

TABLE 3. Parameter estimates under model $(\phi_{(a+t)'}, p_a)$* for female Northern Shovelers captured and recaptured at Engure Marsh, Latvia, 1976–1993.

Year (t)	Duckling survival $\hat{\phi}_{1t}(\widehat{SE}[\hat{\phi}_{1t}])$	ASY survival $\hat{\phi}_{3t}(\widehat{SE}[\hat{\phi}_{3t}])$
1976	0.11 (0.039)	0.61 (0.128)
1977	0.11 (0.043)	0.52 (0.124)
1978	0.21 (0.054)	0.38 (0.105)
1979	0.04 (0.021)	0.48 (0.105)
1980	0.22 (0.059)	0.30 (0.107)
1981	0.04 (0.022)	0.49 (0.126)
1982	0.05 (0.028)	0.57 (0.124)
1983	0.08 (0.040)	0.66 (0.145)
1984	0.07 (0.032)	0.78 (0.130)
1985	0.03 (0.024)	0.63 (0.132)
1986	0.15 (0.051)	0.59 (0.131)
1987	0.23 (0.058)	0.47 (0.124)
1988	0.18 (0.053)	0.79 (0.131)
1989	0.07 (0.027)	0.62 (0.107)
1990	0.23 (0.046)	0.54 (0.092)
1991	0.10 (0.026)	0.69 (0.094)
1992	0.09 (0.030)	0.72 (0.098)
Means	0.12 (0.013)	0.58 (0.030)

* Other parameter estimates under this model are: ratio of SY to ASY survival ($\gamma' = \phi_{2t}/\phi_{3t}$), $\hat{\gamma}' = 0.65$, $\widehat{SE}(\hat{\gamma}') = 0.076$; SY capture probability, $\hat{p}_{2t} = 0.51$, $\widehat{SE}(\hat{p}_{2t}) = 0.054$; ASY capture probability, $\hat{p}_{3t} = 0.80$, $\widehat{SE}(\hat{p}_{3t}) = 0.034$.

Tufted Duck. Tufted Ducks were best modeled using model $(\phi_{(a' \cdot t)}, p_a)$ in which capture probabilities varied by age but not time (Table 6). Estimated capture probability for ASY females (0.80) was higher than that for SY (0.73; Table 7). We used model $(\phi_{(a' \cdot t)}, p_{a+t})$ to directly estimate the ratio of SY to ASY breeding proportions as $\hat{\gamma}'' = 0.89$ ($\widehat{SE} = 0.047$).

The mean estimated probability that a duckling survived until the next breeding season and did not permanently emigrate from Engure Marsh was 0.032, the lowest value for the three species. There was no evidence of a difference in annual survival rate between SY and ASY Tufted Ducks (Table 6), and the average annual survival rate estimate (0.71) for these birds was very high (Table 7).

INTERSPECIFIC COMPARISONS

The ratios of SY to ASY breeding proportions varied among the three species ($\chi^2_2 = 9.6$, $P < 0.01$), being large for Tufted Ducks and smaller, but nearly identical, for shovelers and pochards (Table 8). Survival rates of ducklings varied among the three species ($\chi^2_2 = 76.1$, $P < 0.01$), with estimates for shovelers being largest and estimates for Tufted Ducks being smallest. Survival estimates also varied among species for SY

TABLE 4. AIC values, goodness-of-fit test statistics and likelihood ratio (LR) test statistics for female Common Pochards captured and recaptured at Engure Marsh, Latvia, 1976–1992.

Model	NP**	AIC	Goodness-of-fit			LR test with model $(\phi_{(a+t)'}, p_{a\cdot t})^*$			Source of variation tested by LR
			χ^2	df	P	χ^2	df	P	
$(\phi_{(a+t)'}, p_{a\cdot t})^*$	63	816.8	46.2	41	0.27	—	—	—	—
$(\phi_{(a+t)'}, p_{a})$	35	828.9	114.3	72	<0.01	68.1	28	<0.01	Full temporal variation in p_a
$(\phi_{(a+t)'}, p_{a+t})$	49	822.5	79.0	55	0.02	33.7	14	<0.01	Parallel temporal variation in p_a
$(\phi_{(a+t)'}, p_{t})$	48	858.4	131.3	57	<0.01	71.6	15	<0.01	Age-specific variation in p_t
$(\phi_{a}, p_{a\cdot t})$	35	888.4	171.3	72	<0.01	127.5	28	<0.01	Temporal variation in ϕ_a
$(\phi_{a+t}, p_{a\cdot t})$	49	869.6	127.4	54	<0.01	80.8	14	<0.01	Parallel temporal variation in ϕ_1, ϕ_2 and ϕ_3
$(\phi_{a\cdot t}, p_{a\cdot t})$	78	835.0	35.3	27	0.13	11.9	15	0.69	Full temporal variation in ϕ_a
$(\phi_{t}, p_{a\cdot t})$	47	2,567.9	1,706.0	46	<0.01	1,783.1	16	<0.01	Age-specific variation in ϕ_t

* Model selected for use in estimation.
** Number of parameters estimated.

(χ^2_2 = 71.0, $P < 0.01$) and ASY females (χ^2_2 = 23.1, $P < 0.01$), but the ordering was opposite that for duckling survival, with the largest estimates for Tufted Ducks and the smallest for shovelers (Table 8).

INFERENCES ABOUT PHILOPATRY

We were interested in the null hypothesis that the conditional probability of a breeding female duck returning to the same breeding area, given that the bird is alive, equals 1. The capture-recapture survival estimate (0.71) for ASY female Tufted Ducks was identical to the band recovery survival estimate (0.71), providing no evidence to reject the null hypothesis. The ratio of the two estimates was 1.0, indicating that the estimated probability of permanent emigration was zero. This means that the capture-recapture survival estimate reflects the true survival for female Tufted Ducks.

The capture-recapture survival estimates for pochards were clearly age-specific. To obtain a single survival estimate for pooled age groups (SY + ASY) we weighted both values for their relative importance in the population (SY/ASY = 0.26/0.74) and calculated the weighted mean survival rate estimate, 0.62. The single capture-recapture estimate for pochards (0.62) was slight-

TABLE 5. Parameter estimates under model $(\phi_{(a+t)'}, p_{a\cdot t})^*$ for female Common Pochards captured and recaptured at Engure Marsh, Latvia, 1976–1992.

Year (t)	Duckling survival $\hat{\phi}_{1t}(\widehat{SE}[\hat{\phi}_{1t}])$	ASY survival $\hat{\phi}_{3t}(\widehat{SE}[\hat{\phi}_{3t}])$	SY capture probability $\hat{p}_{2t}(\widehat{SE}[\hat{p}_{2t}])$	ASY capture probability $\hat{p}_{3t}(\widehat{SE}[\hat{p}_{3t}])$
1976	0.10 (0.018)	0.54 (0.056)	—	—
1977	0.03 (0.011)	0.64 (0.060)	0.57 (0.096)	0.63 (0.068)
1978	0.04 (0.013)	0.55 (0.058)	0.43 (0.152)	0.58 (0.057)
1979	0.05 (0.014)	0.64 (0.055)	0.63 (0.156)	0.55 (0.058)
1980	0.06 (0.016)	0.72 (0.061)	0.71 (0.161)	0.81 (0.049)
1981	0.07 (0.016)	0.54 (0.052)	0.43 (0.118)	0.61 (0.058)
1982	0.05 (0.015)	0.70 (0.061)	0.68 (0.121)	0.77 (0.053)
1983	0.05 (0.015)	0.59 (0.059)	0.37 (0.127)	0.63 (0.058)
1984	0.06 (0.014)	0.65 (0.049)	0.40 (0.131)	0.67 (0.059)
1985	0.14 (0.020)	0.60 (0.049)	0.57 (0.117)	0.79 (0.048)
1986	0.04 (0.009)	0.62 (0.046)	0.46 (0.071)	0.73 (0.052)
1987	0.04 (0.009)	0.73 (0.048)	0.54 (0.115)	0.66 (0.045)
1988	0.06 (0.012)	0.78 (0.046)	0.72 (0.130)	0.63 (0.044)
1989	0.11 (0.017)	0.75 (0.041)	0.58 (0.103)	0.68 (0.043)
1990	0.03 (0.007)	0.72 (0.043)	0.25 (0.056)	0.81 (0.037)
1991	—	—	0.76 (0.138)	0.78 (0.041)
Means	0.06 (0.004)	0.65 (0.014)	0.54 (0.033)	0.69 (0.014)

* Ratio of SY to ASY survival $\gamma' = \phi_{2t}/\phi_{3t}$ under this model is $\hat{\gamma}' = 0.85$ ($\widehat{SE}[\hat{\gamma}'] = 0.036$).

TABLE 6. AIC values, goodness-of-fit test statistics and likelihood ratio (LR) test statistics for female Tufted Ducks captured and recaptured at Engure Marsh, Latvia, 1976–1992.

Model	NP**	AIC	Goodness-of-fit			LR test with $(\phi_{a'\cdot t}, p_a)$*			Source of variation tested by LR
			χ^2	df	P	χ^2	df	P	
$(\phi_{a'\cdot t}, p_a)$*	34	563.6	33.1	42	0.83	–	–	–	–
$(\phi_{a'\cdot t}, p_{a\cdot t})$	62	600.1	27.5	18	0.07	19.6	28	0.88	Full temporal variation in p_a
$(\phi_{a'\cdot t}, p_{a+t})$	48	579.8	32.1	32	0.46	11.8	14	0.62	Parallel tepmoral variation in p_a
$(\phi_{a'\cdot t}, p)$	33	566.0	35.1	42	0.76	4.3	1	0.04	Age-specific variation in p
$(\phi_{a'}, p_a)$	4	617.7	146.4	79	<0.01	114.1	30	<0.01	Full temporal variation in $\phi_{a'}$
(ϕ_{a+t}, p_a)	20	609.3	107.2	58	<0.01	73.6	14	<0.01	Parallel temporal variation in ϕ_1, ϕ_2 and ϕ_3
$(\phi_{(a+t)'}, p_a)$	18	613.8	114.1	58	<0.01	82.2	16	<0.01	Parallel temporal variation in ϕ_1 and ($\phi_2 = \phi_3$)
$(\phi_{a\cdot t}, p_a)$	50	585.9	24.1	28	0.68	9.8	16	0.88	Full age-specific variation in ϕ_t

* Model selected for use in estimation.
** Number of parameters estimated.

ly higher than the band recovery estimate (0.59), providing no evidence to reject the null hypothesis.

DISCUSSION

CAPTURE PROBABILITIES

Average capture probabilities of ASY females were relatively high (0.69–0.80) for all three duck species, suggesting that effectiveness of nest searches and capture rates of breeding females have been generally high despite the large territories and difficult terrain. Capture probabilities were similar or even higher than those estimated from long-term studies of box-nesting Wood Ducks in the United States (0.78, Hepp et al. 1987; 0.65, Dugger 1991).

TABLE 7. Parameter estimates under model $(\phi_{a'\cdot t}),p_a)$* for female Tufted Ducks captured and recaptured at Engur Marsh, Latvia, 1976–92.

Year (t)	Duckling survival $\hat{\phi}_{1t}(\widehat{SE}[\hat{\phi}_{1t}])$	SY + ASY survival $\hat{\phi}_{3t}(\widehat{SE}[\hat{\phi}_{3t}])$
1976	0.082 (0.0140)	0.69 (0.052)
1977	0.046 (0.0092)	0.84 (0.038)
1978	0.016 (0.0055)	0.70 (0.040)
1979	0.056 (0.0108)	0.75 (0.042)
1980	0.020 (0.0065)	0.73 (0.039)
1981	0.025 (0.0078)	0.76 (0.041)
1982	0.031 (0.0083)	0.72 (0.044)
1983	0.017 (0.0064)	0.70 (0.046)
1984	0.003 (0.0028)	0.59 (0.049)
1985	0.039 (0.0103)	0.60 (0.052)
1986	0.019 (0.0072)	0.72 (0.049)
1987	0.003 (0.0030)	0.79 (0.048)
1988	0.032 (0.0100)	0.67 (0.054)
1989	0.021 (0.0079)	0.67 (0.053)
1990	0.051 (0.0133)	0.69 (0.058)
1991	0.049 (0.0136)	0.71 (0.060)
Means	0.032 (0.0022)	0.71 (0.011)

* Other parameter estimates under this model are: SY capture probability, $\hat{p}_{2t} = 0.73$, $\widehat{SE}(\hat{p}_{2t}) = 0.037$; ASY capture probability, $\hat{p}_{3t} = 0.80$, $\widehat{SE}(\hat{p}_{3t}) = 0.013$.

Estimated average capture probability of ASY was higher than that of SY females for all three species. Because almost all females were captured on nests, differences in capture probabilities most likely reflect lower probabilities of nesting by SY females. Indeed, our estimates of SY to ASY breeding proportions were 0.70 for shoveler and pochard, and 0.89 for Tufted Duck. These estimates were based on the assumption that all ASY (≥2-year-old) females breed. However, as indicated by our previous research (Mihelsons et al. 1986) and some North American studies (Afton 1984), possibly not all 2-year-old females breed. Therefore, our estimates of breeding proportions of SY birds may have been biased slightly high.

The pattern of temporal variation of capture probabilities was not parallel for SY and ASY pochards. This may suggest heterogeneity in capture rates of females of different age classes in particular years. Possibly, SY and ASY females responded differentially to changes in breeding habitats, and different proportions from these two age classes may have temporarily emigrated to suitable areas outside permanent sampling areas.

Capture probabilities of pochards also varied over time. Potential explanations for this lack of uniformity in capture rates were: (1) pochards showed the most flexible nesting patterns and bred at a wide variety of different habitats within the marsh (e.g., in years with high water levels

TABLE 8. Interspecific comparisons of mean estimates for different age classes of females in three species of European ducks. See text for $\widehat{SE}$.

Species	Band recovery survival	Capture-recapture survival			Proportion of yearlings that breed
	SY + ASY	DU*	SY	ASY	
Northern Shoveler	—	0.12	0.38	0.58	0.70
Common Pochard	0.59	0.06	0.55	0.65	0.70
Tufted Duck	0.71	0.03	0.71	0.71	0.89

* Ducklings.

some females temporarily emigrated from permanent sampling areas and bred in adjacent flooded reed-beds that were seldom used in years with normal and low water levels), and (2) nest success of pochard was the lowest of all three species and exhibited the highest annual variation (Blums et al. 1993); this evidently resulted in lowered capture rates in some years.

Capture probabilities did not appear to vary by time for shovelers and Tufted Ducks. Both species had higher nest success than pochard, showed relatively conservative nesting patterns and were constrained to particular breeding habitats, such as grassy islands (shoveler, Tufted Duck) and Black-headed Gull (*Larus ridibundus*) colonies located on floating mats of emergent vegetation (Tufted Duck). As a result, capture probabilities of these two species were higher and relatively constant during the entire study period.

SURVIVAL OF ADULTS AND YEARLINGS

Our data provide some of the first estimates of survival rates for European ducks that were based on modern statistical models. Because our aging techniques permitted captured females to be identified as SY and ASY, we estimated age-specific survival probabilities for SY, a topic about which little is known.

Annual survival probabilities of SY and ASY females were the highest for Tufted Ducks (0.71 for both age classes), intermediate for Common Pochards (0.55 and 0.65), and lowest for Northern Shovelers (0.38 and 0.58). This pattern also was reflected in maximum longevity of breeding females recorded on Engure Marsh: Tufted Ducks and pochards reached ≥14 years, whereas shovelers only reached age 10.

Removal of predators increased nest success and it is possible that survival rates of female ducks at Engure Marsh were higher than those of ducks in other breeding areas. However, we found no evidence that annual variation in survival rates can be explained by differential predation on nesting females. Two major predators were known to kill nesting females at Engure Marsh; the American Mink (73% of all killings) and the Marsh Harrier (15%). We estimated that on average only 2.8% (range 0.0–13.6), 2.0% (0.0–4.6), and 1.3% (range 0.0–4.0) of female shovelers, pochards, and Tufted Ducks, respectively, were found dead each year from the number of available breeders at permanent sampling areas. We believe most dead females were found, and thus breeding-season mortality of these three duck species at Engure Marsh should have been much lower than the 20–40% reported for female Mallards in North American prairies (reviewed by Sargeant and Raveling 1992, Greenwood et al. 1995). Because predator control at Engure Marsh was consistently effective, apparent nest success was high (long-term average 0.81, 0.78, and 0.69 for Tufted Duck, shoveler, and pochard, respectively) and breeding-season mortality of female low.

The only direct comparison of annual survival estimates obtained in this study can be made with mark-resighting survival estimates of Northern Shoveler in Canada (Arnold and Clark, unpubl.), but this survival rate (0.51) included pooled age groups of breeding females. No estimates of Tufted Duck and pochard survival are available. A review by Johnson et al. (1992) and other recent studies (Hepp et al. 1987, Szymczak and Rexstad 1991, Anderson et al., unpubl., Arnold et al., unpubl., Arnold and Clark, unpubl.), provided survival estimates of the adult females (SY + ASY) for 11 species of North American ducks marked during either the breeding or preseason period. These estimates ranged from 0.47 to 0.70 and were derived from band recovery, capture-recapture, and mark-resighting data. Thus, average survival probability (0.71) of breeding female Tufted Ducks on Engure Marsh, Latvia, was among the highest ever recorded for female dabbling or diving ducks when estimates were based on modern statistical models.

Evidently some sea ducks exhibit even higher survival with estimates of 0.90 reported by Coulson (1984) for Common Eider in England. Another long-term eider study (Baillie and Milne 1982) from Scotland reported extremely high average life expectancy of 26 years that should also be associated with very high survival rate. Dow and Fredga (1984) obtained a high survival estimate (0.77) for female Common Goldeneyes in Sweden.

Survival probabilities varied significantly by age for pochards and shovelers ($P < 0.01$), but not for Tufted Ducks ($P = 0.88$). The only information on annual survival probabilities of SY and ASY females is from a long-term capture-recapture study of Wood Ducks in Missouri (Dugger and Fredrickson, unpubl.). Dugger and Fredrickson used program JOLLYAGE and found some evidence that SY females exhibit lower survival than ASY females (0.45 vs. 0.60), however, the overall contingency chi-square test was not significant. The test result may reflect low power because of small sample sizes rather than a true lack of age-dependence. Reynolds et al. (1995) found that SY female Mallards (*Anas platyrhynchos*) exhibited higher survival during spring-summer than did older females, but this inference pertained to season survival and most likely resulted from differences in reproductive behavior of the two age groups (a large portion of SY females do not breed and thus avoid mortality by nest predators). In North Dakota, ASY and ATY female Gadwalls (*Anas strepera*) had significantly higher return rates than SY females but the factors causing this difference were not identified (Lokemoen et al. 1990). Return rates include the probabilities of surviving, returning to the study area, and being recaptured or reobserved, and are thus not always easy to interpret.

There is no reason to suspect that permanent emigration within the Engure Marsh may have affected survival estimates for any age category of breeding female shovelers (see below). However, some SY and ASY female pochards did emigrate permanently out of sampling plots to other areas of the marsh, and, if this emigration is age-specific, survival probability estimates for SY birds may have been biased downwards. We examined 1,787 short-distance (< 10 km) breeding dispersal movements of female pochards within sampling areas and within all territory of the marsh and found no evidence that SY females moved significantly farther than ASY birds, either after successful or failed nesting. We concluded that much of the difference between survival estimates of SY vs. ASY females for shoveler and pochard in this study concerns mortality rather than emigration.

SURVIVAL OF DUCKLINGS

Survival estimates for ducklings, which reflect both survival and permanent emigration, were typically low, and averages ranged from 0.03 to 0.12. The species with the highest SY and ASY survival probability, the Tufted Duck, had the lowest duckling survival probability, and, conversely, the species with the lowest SY and ASY survival probability, the Northern Shoveler, had the highest duckling survival probability. Capture-recapture models for annual survival estimates of ducklings have not been used by other researchers, so comparable data are not available. There are two main reasons for these low survival probabilities of ducklings, (1) ducks exhibit much higher mortality during the first year of life than later (Sargeant and Raveling 1992, Johnson et al. 1992), and (2) natal philopatry in ducks is much weaker than breeding philopatry (reviewed by Rohwer and Anderson 1988, Anderson et al. 1992).

Survival probabilities of shoveler ducklings were higher than for both species of diving ducks. We believe shoveler ducklings have higher absolute survival during the first year of life and this may be true also for other dabbling ducks (see Bengtson 1972). An alternative explanation might be that some proportion of female diving ducks may have emigrated permanently for their breeding to other suitable areas within the marsh or out of the marsh, and that this emigration is responsible for the lower survival probability estimates for pochard and Tufted Duck ducklings. Although some evidence supports this notion (Blums et al. 1989, this study), we believe the relative importance of emigration in the complement of survival was minor for all three species. Circumstantial inferences about emigration can be drawn from the data on population composition reported by Mihelsons et al. (1986). They estimated that 91% of female shovelers breeding at Engure Marsh were of local origin and only 9% were immigrants. Most of the latter were young first breeding females hatched outside Engure Marsh. There is no evidence that emigration within the marsh may have affected survival estimates of shoveler ducklings because nearly the entire nesting population was captured each year during the study.

Survival probabilities of Tufted Duck ducklings were half that of pochard and may result either from higher post-hatch mortality, more permanent emigration out of sampling areas, or a combination of these. Indeed, Blums et al. (1989) demonstrated that the degree of long-distance natal dispersal ("gross natal dispersal," sensu Greenwood 1980) seems to be higher for Tufted Ducks than pochards. Blums et al. (1989) also reported that for all indirect recoveries of bands during April–November of ducklings banded in Latvia that were never detected returning to their native wetland, revealed significantly more recoveries for Tufted Duck than for pochard classified as long-distance natal dispersal movements (65 vs. 23%, $P < 0.001$). However, the sex of emigrating birds in most cases was unknown.

Yearly variation in survival probabilities of ducklings did not parallel that of adults for any of the three species, suggesting that different factors affect survival of ducklings versus older birds. Prefledged ducklings are more vulnerable to different mortality agents, and the brood-rearing period is especially important to the dynamics of waterfowl populations (Sedinger 1992, Johnson et al. 1992).

Most mortality occurs during the first two weeks after hatching, when ducklings are still small and thermoregulatory ability is incompletely developed (reviewed by Sargeant and Raveling 1992). We believe much of the variation in survival probabilities of ducklings during their first year of life can be linked to the 5–10 day period immediately after hatch as reported by other investigators (Bengtson 1972, Hill and Ellis 1984, Savard et al. 1991, Wayland and McNicol 1994, Sayler and Willms, in press).

Mihelsons et al. (1986) suggested that not only recaptures of females which return to breed on the native marsh but also band recoveries of fledged young of either sex, banded at hatch and never recorded returning to the birth place, can provide useful information on survival. It is possible that the use of all band recovery information will permit additional inferences about duckling survival rates and the time period (soon after hatching) when ducklings are most vulnerable to different mortality agents, most importantly to adverse weather.

PHILOPATRY

Similarity between survival rate estimates obtained using band recovery and capture-recapture models demonstrates that female Tufted Ducks and pochards at Engure Marsh are extremely philopatric and nearly all surviving birds return to breeding sites used previously. Hepp et al. (1987) used this method to test philopatry in Wood Ducks but they compared survival rates of two different populations that may have exhibited different survival. The numbers of bandings and recoveries used for our band recovery analyses, however, were smaller than data sets commonly used by North American biologists. Our data provide some evidence that not all female Tufted Ducks are strongly philopatric: two females immigrated to Engure Marsh from breeding areas located as far as 170 and 290 km to the north-east (Estonia) and north (Finland), respectively. Both birds were marked and recaptured on the nests and, to our knowledge, are the only confirmed cases of effective breeding in ducks after long-distance breeding dispersal.

We did not test philopatry for shovelers because banding and recovery data were too limited for reasonable use with band recovery models. There is little evidence on permanent emigration out of Engure Marsh for breeding female shovelers (Mihelsons et al. 1986, Blums et al. 1989). Return rates to previous breeding sites have been relatively high both at Engure Marsh, Latvia (Blums and Mednis 1986) and Canada (Sowls 1955; Arnold and Clark, in prep.). This information provides evidence that female shovelers may be strongly philopatric.

Recent advances in development of models for combined analysis of band recovery and recapture data (Szymczak and Rexstad 1991, Burnham 1993) offer the potential for efficient use of all available band encounter information. The use of these new models can likely improve precision and permit separate estimates of survival and permanent emigration probabilities if recovery and recapture data are incorporated in a single model. Such models are efficient and provide a formal test for philopatry.

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