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Estimating natal dispersal movement rates of female European ducks with multistate modelling

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Summary

1. We used up to 34 years of capture–recapture data from about 22 100 new releases of day-old female ducklings and multistate modelling to test predictions about the influence of environmental, habitat and management factors on natal dispersal probability of three species of ducks within the Engure Marsh, Latvia.
2. The mean natal dispersal distances were very similar (*c*. 0·6–0·7 km) for all three species and were on average 2·7 times greater than breeding dispersal distances recorded within the same study system.
3. We were unable to confirm the kinship hypothesis and found no evidence that young first-nesting females nested closer to their relatives (either mother or sister) than to the natal nest.
4. Young female northern shovelers, like adults, moved from small islands to the large island when water level was high and vice versa when water level was low before the construction of elevated small islands. Movement probabilities between the two strata were much higher for young shovelers than adults, suggesting that young birds had not yet developed strong fidelity to the natal site. Movements of young female tufted ducks, unlike those of shovelers, were not dependent on water level fluctuations and reflected substantial flexibility in choice of first nesting sites.
5. Data for young birds supported our earlier conclusion that common pochard nesting habitats in black-headed gull colonies were saturated during the entire study period. Young females, like the two adult age groups, moved into and out of colonies with similar probability. Fidelity probability of female pochards to each stratum increased with age, being the lowest (0·62) for young (DK) females, intermediate (0·78) for yearlings (SY) and the highest (0·84) for adult (ASY) females.
6. Young female tufted ducks, like adults, showed higher probabilities of moving from islands to emergent marshes when water levels were higher both before and after habitat management. The relationship between the spring water levels and movement was much weaker for young females than for adults.
7. Young female diving ducks exhibited much stronger (compared to adults) asymmetric movement with respect to proximity to water, with higher movement probabilities to near-water locations than away from these locations.
8. Local survival of day-old ducklings during the first year of life was time-specific and very low (means for different strata/states 0·01–0·08) because of high rates of emigration and prefledging mortality.

Key-words: dispersal distances, local survival, multistate modelling, natal dispersal, site fidelity.

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Introduction

Dispersal and its complement, fidelity, are important components of avian life-history that affect the structure and dynamics of populations (Johnson & Gaines 1990; Dieckmann, O'Hara & Weisser 1999; Clobert *et al*. 2001). Dispersal probability is generally higher for young birds from natal sites than for breeding adults from nesting sites (Greenwood 1980; Greenwood & Harvey 1982; Lebreton *et al*. 2003), and under some conditions natal dispersal may therefore have more effect on the genetic structure and dynamics of avian populations than breeding dispersal. Despite the potential importance of natal dispersal for avian populations studies of this behaviour are uncommon, and the individual effects of natal dispersal and juvenile mortality on avian recruitment and population dynamics are frequently unresolved because these parameters are confounded under many sampling schemes (Lebreton *et al*. 1992). Separation of mortality and natal dispersal requires that young birds are associated with a natal site and that they are marked prior to fledging from that site with a tag or band that can be used to identify these individuals as adults. Young birds, particularly precocial young, may be difficult to associate with a natal site and the smaller size of young may prevent the use of markers that can be retained on adult birds. Additionally, marked individuals must be sampled at sites away from the natal area to examine how characteristics of the origination and destination sites affect natal dispersal. High rates of juvenile mortality and low probability of detecting dispersed individuals result frequently in small samples of dispersed young and prevent separate estimation of mortality and dispersal. Finally, appropriate analytical tools must be used to obtain unbiased estimates of survival, detection probability and dispersal (e.g. Brownie *et al*. 1993; Nichols 1996).

Our overall objective was to estimate separately natal movement probabilities between different strata and local survival of female ducklings during the first year of life for three over-water and ground-nesting duck species (northern shovelers, *Anas clypeata* L., hereafter shovelers; common pochards, *Aythya ferina* [L.], hereafter pochards; and tufted ducks, *A. fuligula* [L.]), and to investigate sources of variation in these rates based on a priori hypotheses. We used multistate modelling and addressed hypotheses about differences in movement probabilities associated with management, habitat strata that differ with respect to effects of changes in water level, presence of gull colonies and proximity to water. We also investigated kinship hypotheses that predict benefits associated with nesting near close relatives.

This paper provides an age-specific extension (with the duckling age group added) of a companion paper (Blums *et al*. 2003) on breeding dispersal movements of adult ducks from the same study site. Our modelling approach and examination of natal dispersal and fidelity required that we also include data about movements of these birds as adults. Because information about adult movement was addressed thoroughly in the previous paper, we focus here on the natal movements of young female ducks from hatching to first breeding.

HYPOTHESES AND PREDICTIONS

Prediction 1

Studies on birds have provided evidence that site fidelity is age-specific and that natal dispersal distances are typically greater than breeding dispersal distances (e.g. Greenwood & Harvey 1982; Paradis *et al*. 1998). We predicted that natal dispersal probabilities and distances will be greater than breeding dispersal probabilities and distances for all three duck species within the Engure Marsh study system.

Prediction 2

Some evidence suggests that yearlings may benefit from breeding in association with close relatives (e.g. Greenwood, Harvey & Perrins 1979; Anderson, Rhymer & Rohwer 1992). This kinship hypothesis predicts that a returning yearling tends to nest closer to its dispersing mother than to its natal nest. To test this prediction, we compared the natal dispersal distances of nonsib yearlings and the distances between the nests of these yearlings and their mothers in the same year.

Prediction 3

Another prediction of the kinship hypothesis is that returning yearling sisters originating from the same brood settle closer to one another than to their natal nest. We compared the natal dispersal distance of each sister with the distance between the nests of respective sisters at their first breeding. When multiple siblings from the same brood were captured during one breeding season, we only used the pair of siblings with the shortest and longest natal dispersal distance.

Prediction 4

This prediction is based on habitat management that occurred during the study and was tested using data from the two species that nested extensively on islands, shovelers and tufted ducks. Shoveler nesting was completely restricted to islands, whereas tufted ducks nested both on islands and in emergent marshes and were able to move to marshes when islands became unavailable. The sampled areas (Fig. 1) of Engure Marsh included a large island A (16 ha), and a cluster of three small islands [B (0·8 ha), C (2·5 ha), and D (0·6 ha)] with a total surface area of all four islands of approximately 20 ha at low water and 8 ha at high water, from 1960 to 1982. Large portions of islands

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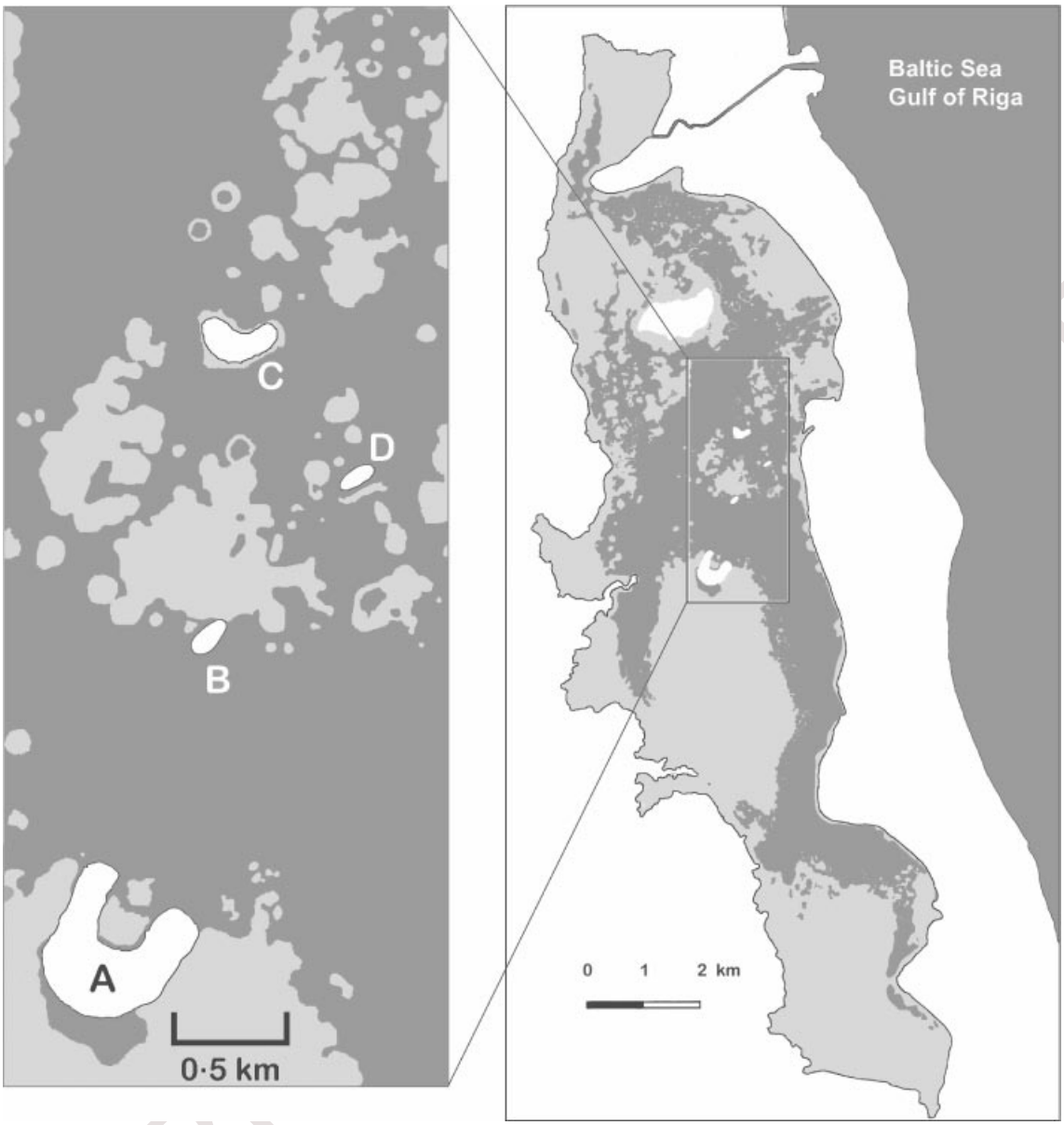

Fig. 1. Engure Marsh study site with permanent plots (inset) located at the central part of the marsh. Light-shaded areas are emergent marshes and dark-shaded areas are open water. White areas around the marsh are mainly woodlands. Grassy islands at permanent plots are indicated by letters A, B, C, D.

were flooded frequently in spring, and island C gradually overgrew with dense stands of reed and lost its importance as breeding habitat after 1978. To increase the amount of nesting habitat with stable breeding conditions, many artificial elevated islands were constructed on the flooded sections of islands A and D during 1981–83. Beginning in 1984, 81 islands (total area 11·8 ha) were available for nesting within the previous island territory, all located > 0·4 km from coastline. The artificial islands were never flooded. These management activities improved nesting conditions and provided stable and predictable nesting habitats, especially for shovelers, as this species nested only on islands.

Because young females are much less philopatric than adults (Rohwer & Anderson 1988; Anderson *et al*. 1992), we predicted that (i) natal dispersal probabilities would be higher for young females than for adults, regardless of habitat conditions, both during the premanagement and post-management periods; (ii) young female shovelers, like adults, would move at higher rates from the large island (stratum *L*) to small islands (stratum *S*) when water level was low and in the opposite direction when water level was high during the premanagement period; (iii) movement of young shovelers will be reduced and the relationship between natal dispersal movements (large islands vs. small islands) and water level will not hold following management, as conditions were more stable following island creation; and (iv) the relationship (ii) will not hold for tufted ducks because this species, unlike shoveler, can nest also in emergent marshes.

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Prediction 5

Several researchers (e.g. Liberg & Schantz 1985; Waser 1985) have proposed an intrasexual-competition hypothesis to explain age-related differences in dispersal. This hypothesis states that young birds are behaviourally subordinate to adults and either are excluded from breeding if the population is saturated or are forced to move to poor quality sites where their fitness will be reduced. We have provided evidence (Blums *et al*. 2003) that gull colonies are high-quality nesting sites. Pochards, like many other duck species, nest in association with black-headed gulls (*Larus ridibundus* L.) at Engure Marsh, and survival and nest success of adult pochards in gull colonies are higher than outside colonies. Because pochard nesting habitats in gull colonies were saturated and because adult movement was constant and of similar magnitude into and out of colonies (Blums *et al*. 2003), we predicted that young first-nesting females, being inferior breeders, will move out of colonies with higher probabilities than into the colonies. Under a hypothesis that ability to breed in quality habitat increases with age, we predicted that dispersal probabilities out of gull colonies should be highest for ducklings and lowest for adult (after first year) breeders.

We also predicted that local survival of ducklings, unlike that of adults, will be lower in colonies than outside colonies. This prediction was based on our observation that black-headed gulls may occasionally kill newly hatched ducklings soon after hatch, prior to the ducklings' departure of colonies for brood rearing habits. We used only data on pochards to test these predictions because most tufted ducks and shovelers nested in gull colonies or in association with waders.

Prediction 6

Our earlier work (Blums *et al*. 2003) provided evidence that adult female tufted ducks showed higher probabilities of moving from islands to emergent marshes when water levels were higher both before and after habitat management. Consideration of a possible relationship between movement and water level for young birds led to two competing predictions. On one hand, the expected greater fidelity of older birds led us to expect less movement in general from this group, relative to young birds. On the other hand, we hypothesized that high water levels improved nesting conditions in emergent marshes and predicted that this relationship will be much weaker for young first-nesting females because of lack of nesting experience and/or competing ability. We did not have a prediction about which of these considerations was more important.

Prediction 7

Adult female diving ducks exhibited asymmetric movement with respect to proximity to water (< 2 m vs. > 2 m from water line), with higher movement probabilities to near-water locations than away from these locations (Blums *et al*. 2003). We predicted that because young females are less philopatric, this asymmetry would be even more pronounced for young females when they moved from hatching to first breeding sites.

Methods

STUDY AREA AND FIELD METHODS

The study was conducted from 1961 to 1994 on the 35-km^2 Engure Marsh (57°15′ N, 23°07′ E), Latvia, Eastern Europe. Engure Marsh is an isolated, shallow, permanently flooded palustrine wetland that has gradually changed from an open marsh to a hemi-marsh. About 2000 pairs of 13 duck species nested on the marsh annually during the study period, with roughly 60% consisting of pochards, tufted ducks and shovelers. In addition, on average more than 16 000 pairs of colonial black-headed gulls nested annually at permanent study areas during 1972–94, with many gull colonies of variable sizes scattered widely over emergent marshes and islands.

Permanent study areas (Fig. 1) included islands and irregular clusters of persistent emergent marshes that were separated from each other, the rest of the marsh and coastline by larger areas of open water or monotypical stands of reed-beds. Females were captured on nests during the last week of incubation using drop-door nest traps (Blums *et al*. 1983) or dip nets. Unmarked incubating females were banded with conventional leg bands and aged (Blums *et al*. 1996). Newly hatched ducklings were captured by hand at nests and individually marked with plasticine-filled oval leg bands (Blums, Mednis & Nichols 1994). Movement analyses were based on subsequent recaptures of nesting females that were banded at hatch. Few ducklings were sexed, so the number of released female ducklings was based on a 50 : 50 sex ratio (Blums & Mednis 1996; Blums *et al*. 1996: 64). More detailed information on study sites, field methods, management practices and breeding populations of ducks and gulls is provided in a companion paper (Blums *et al*. 2003), and elsewhere (Blums *et al*. 1996; Viksne 1997; Viksne 2000).

Statistical methods

DISPERSAL DISTANCES

Prediction 1

Prediction 1 involved possible differences between natal and breeding dispersal distances. Breeding dispersal distances were obtained for adult (> 1-year-old) birds caught as breeders in two successive years. In order to obtain an adequate sample size for natal dispersal, we obtained dispersal distances for ages 0–1 (ducklings to yearlings) as well as 0–2 (ducklings to

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2-year-olds) for birds not seen as yearlings. We used a two-sample Kolmogorov–Smirnov test to test the similarity of distributions between observed dispersal distances for the 0–1 and 0–2 transitions.

Prediction 2

Our test of prediction 2 conditioned on birds that were captured both as ducklings (year t) and yearlings (year $t + 1$) and whose mothers were also captured in year $t + 1$. To exclude possible influence of returning sisters, we used only broods for which a single duckling returned as a yearling. We computed the distance between each yearling's nest and both (i) its natal nest and (ii) the nest of the mother in year $t + 1$. A paired t-test was then used to compare these two distances for recaptured yearlings.

Prediction 3

Our test of this prediction conditioned on broods from which at least two birds were captured as ducklings (year t) and then again as yearlings (year $t + 1$). In cases where > 2 brood-mates were recaptured, the females with the shortest and longest natal dispersal distances were selected. For each brood a pair of sisters was thus selected, yielding two natal dispersal distances (movement between t and $t + 1$) and a single distance between sister nests (in year $t + 1$). Paired t-tests were used to compare the between-sister distance with (i) the shorter, and (ii) the longer of the two natal dispersal distances.

MULTISTATE MODELLING

Predictions 4–7 involve movement probabilities and, secondarily, local survival probabilities. Proper inference about these parameters based on studies of marked animals should incorporate capture probability parameters (e.g. Williams, Nichols & Conroy 2002: 334–337). Thus, multistate capture–recapture models (e.g. Arnason 1973; Hestbeck, Nichols & Malecki 1991; Brownie *et al.* 1993) were used to estimate movement probabilities between strata, exactly as in our companion paper (Blums *et al.* 2003). The more general models also included location-specific survival and capture probabilities. Survival probability is the probability that an animal alive in the study system in year t survives and is present in one of the sampled strata in year $t + 1$. Capture probability is the probability that an animal alive and associated with a sampled stratum in year $t + 1$ is captured. Movement probability is the conditional probability that an animal alive in one stratum in year t is in one or the other of the two strata in year $t + 1$, given that the individual survives the annual sampling interval. The definition of a stratum depends on the question(s) addressed. Because of our focus on natal dispersal and age-specific variation in movement, our general models retain separate parameters by bird age (duckling vs. older birds).

The general models also included time-specific (year-specific) variation in parameters. When this general structure of time-specificity was retained in the models used for estimation, we used the random effects approach of Burnham & White (2002) implemented in program MARK (White & Burnham 1999) to estimate the mean parameter and its standard error, denoted as $(\hat{E}[\theta]), \hat{S}E(\hat{E}[\theta])$ where θ denotes the parameter of interest. This standard error includes components associated with both true temporal variation in the parameter and sampling variation associated with the estimation process. The random effects approach also permits estimation of the true temporal variance of the parameter (process variance $= \sigma^2 - \theta_t$), so we report $\hat{\sigma}(\theta_t)$ as well.

The model sets for the different analyses were tailored to the hypotheses of interest and the associated a priori predictions. For each set of questions, we developed and fitted a number of models and then used AIC_c (Hurvich & Tsai 1989; Burnham & Anderson 2002) as the criterion for discriminating among the models and selecting those that provided good, parsimonious descriptions of the variation in the data. Model selection results are presented in terms of ΔAIC_c values, where ΔAIC_c represents the difference between the AIC_c value for a particular model and the AIC_c value for the model with minimum AIC_c. Models with small ΔAIC_c (e.g. < 2) are well supported by the data, whereas models with large ΔAIC (e.g. > 10) are not well-supported. We also computed Akaike weights (Burnham & Anderson 2002) as metrics reflecting relative support for the different models in the model set. The weight w_i for model i can be interpreted loosely as the weight of evidence in favour of that model being most appropriate, given the data and given the model set. All computations associated with the multistate models (model fitting, parameter estimation, AIC computation) were carried out using program MARK (White & Burnham 1999; Cooch & White 2003).

Prediction 4

Data for shovelers and tufted ducks over the entire study period of 34 years (1961–94) were available to test the three parts of prediction 4. This prediction focused on three possible sources of variation in movements between the large and small islands: age, habitat management activities and water levels. We thus developed models with parameters for state L, nest location on the large island; and state S, nest location on one of the small islands. The most general model in the model set for shovelers and tufted ducks included separate survival (S), capture (p), and movement ($\varnothing$) parameters for each year (t), each age class (a, duckling and older) and each of the two location strata (s, large island and small islands) and is denoted as model (S_{a*s*t} p_{a*s*t} $\varnothing_{a*s*t}$). Notation for model parameters denotes time and age as subscripts and location state as a superscript, and * denotes an interaction between factors.

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For example, ψ^{SL}_{DKt} denotes the probability that a duckling (DK) nesting on the large island in year t, nests on one of the small islands in year $t + 1$, given that the bird is alive and in the study system in $t + 1$.

The first part of prediction 4 concerned age-specificity of movement, with the expectation of greater movement of young birds (ducklings to yearlings) than older birds. This prediction was tested by comparing AIC_c values for models that did and did not include age-specific movement parameters. Specifically, we predicted that $\psi^{LS}_{DKt} > \psi^{LS}_{ADt}$ and $\psi^{SL}_{DKt} > \psi^{SL}_{ADt}$.

The second part of prediction 4 involved the influence of year-to-year variation in water level during the premanagement period, 1960–82. Stratum- and age-specific movement probabilities for large and small islands were modelled as a linear-logistic function of annual water-level. For example, probabilities of moving from the natal stratum to the other stratum as a yearling were modelled as:

$$logit(\psi^{LS}_{DKt}) = \beta_1 + \beta_2 wat_{t+1}, \text{ and } logit(\psi^{SL}_{DKt}) = \beta_3 + \beta_4 wat_{t+1},$$

where wat_{t+1} is water level in year $t + 1$, and β_1, β_2, β_3, and β_4 are parameters to be estimated (movement model notation $\psi_{DKs*wat}$). The probability of moving from the large island to small islands was predicted to decrease with increasing water levels (predict $\beta_2 < 0$), while the probability of moving from small islands to the large island was predicted to increase with increasing water levels (predict $\beta_4 > 0$).

The third part of the prediction was a decrease in movement probabilities, and any influence of water levels on these probabilities, in the years following management, 1983–94. We thus developed several models incorporating different hypotheses about water level dependence before and after habitat management.

Prediction 5

Because this prediction focused on birds nesting both inside and outside gull colonies, only the data for pochards were applicable. We developed a set of models based on state c, nest location within gull colony; and state o, nest located outside gull colony. We fit these models to birds in the three age classes banded over the 17-year period, 1976–92. The most general model fit to pochard data was model (S_{a*s*t} p_{a*s*t} $\varnothing_{a*s*t}$), with separate model parameters for each age class (DK, SY, ASY), state (s, inside and outside gull colony), and year of the study. Previous work led us to expect the need for models including age- and time-specific variation in survival and time-specific variation in capture probability (Blums *et al*. 1996; Blums *et al*. 2002).

Constraints on movement and survival parameters were used to construct models of the different hypotheses of interest. In some models we constrained movement out of gull colonies, ψ^{co}, to be equal for the three age classes, whereas in others, movement was age-specific. We also constructed models with equal survival for birds inside and outside gull colonies ($S^c = S^o$) and with state-specific survival. The relative magnitudes of age- and state-specific estimates were then compared against predictions.

Prediction 6

We developed models expressing different hypotheses about sources of variation in tufted duck movement probabilities between emergent marsh and island nesting locations. Nest location data were available for the longer period (1972–92), and a set of models was developed for these data. The two states of interest were state i, nest located on island, and state m, nest located in emergent marsh. Previous analyses found no demographic differences between SY and ASY (e.g. Blums *et al*. 1996; Blums *et al*. 2002), so age-specific questions focused on differences between these breeding-aged birds and ducklings. The most general model fit to these data was thus (S_{a*s*t} p_{a*s*t} ψ_{a*s*t}). We predicted that movement between islands and marshes was influenced by water levels in the system, leading to movement models of the type developed for shovelers (see above). Specifically, movement to and from islands for birds in each age class was modelled as a linear-logistic function of water depth:

$$logit(\psi^{im}_t) = \beta_1 + \beta_2 wat_{t+1}, \text{ and}$$
$$logit(\psi^{mi}_t) = \beta_3 + \beta_4 wat_{t+1} \quad \text{(see prediction 4).}$$

We developed a series of such models in which state-specific movement probabilities were written as possibly different functions of water level depending on the time period with respect to management actions.

Prediction 7

This prediction concerned expected differences in age-specific probabilities of movement between areas nearer and farther from water for diving ducks. Data needed to assign nests to these states were collected only during the 8-year period 1985–92, and this fact motivated our development of a specific model set to assess this prediction for both species. States were defined as state n, nest location near (< 2 m) water, and state d, nest location distant (> 2 m) from water. The most general model in this set was model (S_{a*s*t} p_{a*s*t} ψ_{a*s*t}), with separate model parameters for each age class, state (near and distant from water), and year of the study. We considered models with three age classes (DK, SY, ASY) for pochards and only two age classes (DK, $SY + ASY$) for tufted ducks. Some additive models (Lebreton *et al*. 1992) were fitted, but the primary prediction was higher movement probabilities to locations near water than to locations distant from water ($\psi^{nd} < \psi^{dn}$). The difference in these movement probabilities $\psi^{nd} - \psi^{dn}$ was predicted to be larger for ducklings, as these birds exhibit less fidelity than older birds.

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Table 1. Models used to assess variation in natal movement probabilities of female northern shovelers (n = 2720/452)[e] between small islands and a large island at Engure Marsh, Latvia, 1961–94

Model[a]	ΔAIC_c[b]	Model weight[c]	Np[d]
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$	0·0	0·31	48
$S_{AD2s1,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$	0·83	0·20	49
$S_{AD1s2,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$	1·05	0·18	49
$S_{AD2t,\ DKs+t}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$	1·90	0·12	49
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat4}$	3·13	0·06	46
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat3,\ s+wat3}$	3·78	0·05	49
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat3}$	3·80	0·05	51
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs+wat3}$	6·24	0·01	48
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKwat5}$	25·12	0·0	45
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*t_pre}$	31·84	0·0	86
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{s*wat5}$	38·50	0·0	43
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{AD/DKs*wat2}$	45·96	0·0	42
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	283·49	0·0	330
$S_{s+t}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$	491·10	0·0	47
$S_s\ p_s\ \varnothing_s$	649·17	0·0	6

[a]Model subscripts/covariates:
t = year; a = age (two age groups: *AD* [*SY* + *ASY*] and *DK* [ducklings]); s = stratum (small [*S*] islands vs. large [*L*] island); *2t* = survival different for premanagement (1961–82) and post-management (1983–94) periods but constant within each period and equal for the two strata; *1s2* = survival constant with no stratum-specifity (1961–82), constant and stratum-specific (1983–94); *2s1* = survival constant and stratum-specific (1961–82), constant with no stratum-specifity (1983–94); *wat* = models with movement (t to t + 1) modelled as a function of water level measured at nesting sites during early spring in year t + 1; *s∗wat2* = different water dependence in movement in both directions (*SL* & *LS*, 1961–82), single movement parameter for both directions (1983–94); *s∗wat3* = different water dependence in movement in each period and direction; *s + wat3* = different water dependence in movement in each direction, but for each direction movement was parallel for the two periods; *s∗wat3*, *s + wat3* = different water dependence in movement from *L* to *S* in each period, different but parallel water dependence in movement from *S* to *L* for the two periods; *s∗wat4* = different water dependence in movement in each direction for the entire period; *s∗wat5* = different water dependence in movement in the two directions (1961–82), different but constant movement in both directions (1983–94); *wat5* = similar water dependence in movement in both directions (1961–82), single movement parameter for both directions (1983–94); *DKs∗t_pre* = no water covariate, different time-dependent movement in both directions (1961–82), different but constant movement in both directions (1983–94).
[b]The difference between the AIC_c value for the model with the lowest AIC_c value and the model in question.
[c]Akaike model weights reflect the amount of evidence in favour of the model in question given the model set and data. The full model set does not appear in the table.
[d]Number of parameters.
[e]Number of day-old duckling new releases/recaptures.

Results

BANDING AND RECAPTURE DATA

We used samples of 22 114 new releases of day-old female ducklings and 2185 subsequent recaptures of these birds as nesting females to estimate local survival and movement probabilities for young shovelers, pochards and tufted ducks between different strata at the Engure Marsh study site during different time periods (Tables 1–3). A subset of these data was also used to draw comparative inferences about natal dispersal distances as described above. In addition to females banded as ducklings we used also new releases and subsequent recaptures of adult females (see Blums *et al*. 2003 for sample sizes).

NATAL DISPERSAL DISTANCES

We recorded 1464 natal dispersal movements of females within the Engure Marsh. Most (1318; 90%) of these females were 1 year old (movement from 0 to 1) or 2 years old (0–2) when first recaptured. There was no difference (Kolmogorov–Smirnov two-sample test, P > 0·65) in distributions of natal dispersal distances between these two age categories for any of the three species.

The distribution of observed natal dispersal distances (range 0–10 626 m) was highly leptokurtic, with > 50% of movements being < 322 m and < 10% being > 1872 m. The average natal dispersal distances (± SE) were very similar for all three species: 667 ± 48 m (range 3–4259 m, n = 264) for shoveler; 629 ± 39 m (range 0–10 626 m, n = 580) for pochard; 651 ± 36 m (range 0–5348 m, n = 474) for tufted duck. The average breeding dispersal distances (± SE) were much smaller for all three species (Blums *et al*. 2003): 247 ± 28 m (range 0–3114 m, n = 324) for shoveler; 239 ± 16 m (range 0–9202 m, n = 1691) for pochard; 228 ± 11 m (range 0–4143 m, n = 1870) for tufted duck; so our prediction of longer dispersal distances for young birds was supported. The maximum dispersal distances that we could observe with our sampling design were 4326 m for shovelers, 12 471 m for pochards and 12 273 m for tufted ducks. Very few first-time breeding females [2 (0·3%) pochards, and 3 (0·6%) tufted ducks] used the

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Table 2. Models used to assess variation in natal movement probabilities of female common pochards between strata at Engure Marsh, Latvia

Model[a]	ΔAIC_c[b]	Model weight[c]	Np[d]
Movement between gull colonies and outside, 1976–92 (n = 9248/744)[e]			
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{a}$	0·0	0·45	87
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{ADa2s,\ DKs}$	1·54	0·21	89
$S_{ADa*s,\ DKs+t}\ p_{a*s*t}\ \varnothing_{a}$	1·90	0·17	88
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{a*s}$	3·56	0·07	90
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{ADa3s,\ DKs}$	3·65	0·07	89
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{ADa,\ DKs}$	5·61	0·03	88
$S_{(a*s)+t}\ p_{a*s*t}\ \varnothing_{a}$	13·25	0·0	88
$S_{AD(.),\ DKt}\ p_{a*s*t}\ \varnothing_{ADa2s,\ DKs}$	31·13	0·0	87
$S_{ADa*s,\ DKt}\ p_{a*s*t}\ \varnothing_{s}$	56·16	0·0	86
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	116·52	0·0	256
$S_{s+t}\ p_{a*s*t}\ \varnothing_{ADa2s,\ DKs}$	1837·0	0·0	86
Movement between < 2 m and > 2 m zones, 1985–92 (n = 4868/389)[e]			
$S_{ADa+t,\ DKt}\ p_{a*s*t}\ \varnothing_{ADs*t,\ DKs}$	0·0	0·57	59
$S_{ADa+t,\ DKs+t}\ p_{a*s*t}\ \varnothing_{ADs*t,\ DKs}$	1·14	0·32	60
$S_{ADa+t,\ DKt}\ p_{a*s*t}\ \varnothing_{ADs*t,\ DK(.)}$	4·46	0·06	58
$S_{ADa+t,\ DKt}\ p_{a*s*t}\ \varnothing_{s*t}$	8·85	0·01	57
$S_{ADa+t,\ DKt}\ p_{a*s*t}\ \varnothing_{a*s}$	9·80	0·0	49
$S_{ADa+t,\ DKt}\ p_{s}\ \varnothing_{ADs*t,\ DKs}$	22·89	0·0	33
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	46·70	0·0	112

[a]Model subscripts: a = age (three age groups: DK, SY, and ASY; DK = ducklings, AD = SY and ASY females); s = strata (gull colonies vs. outside areas, or < 2 m vs. > 2 m zone); $ADa2s$ = single movement parameter in both directions for SY females, movement different but constant in both directions for ASY birds; $ADa3s$ = single movement parameter in both directions for ASY females, movement different but constant in both directions for SY birds. For other notation see Table 1.

same nest bowl where they were hatched or moved < 2·1 m from the natal nest.

NATAL DISPERSAL BEHAVIOUR IN THE PRESENCE OF KIN

The presence of the mother breeding at the same area did not appear to influence nest site selection by the daughter. Dispersing non-sib yearling females did not nest closer to their mothers than to their natal nests (shoveler: $t_{46} = -0{\cdot}99$, $P = 0{\cdot}33$; pochard: $t_{138} = -1{\cdot}63$, $P = 0{\cdot}11$; tufted duck: $t_{121} = -1{\cdot}38$, $P = 0{\cdot}17$). Negative t-values indicate that young females of all three species tended to nest closer (51–111 m, $n = 308$) to their natal nests rather than to their mothers. The test results were very similar ($P > 0{\cdot}11$) if only cases when mothers have dispersed > 200 m from previous nests were considered. Thus, our prediction was not supported.

Another kinship hypothesis prediction that yearling sisters settle closer to one another than to their natal nest was also not supported. If the shortest dispersal distance only of each sister pair was considered, young females nested closer to their natal nests for diving ducks (pochard: $t_{44} = -4{\cdot}75$, $P < 0{\cdot}0001$; tufted duck: $t_{46} = -3{\cdot}52$, $P = 0{\cdot}001$) but not for shoveler ($t_{29} = -1{\cdot}12$, $P = 0{\cdot}27$). If only the longest dispersal distance was considered there was no clear evidence for diving ducks (pochard: $t_{44} = 1{\cdot}43$, $P = 0{\cdot}16$; tufted duck: $t_{46} = 1{\cdot}84$, $P = 0{\cdot}07$), but young sister shovelers ($t_{29} = 2{\cdot}48$, $P = 0{\cdot}02$) tended to nest closer to each other than to the natal nest. Thus, the paired comparisons tests were inconclusive (negative for the shortest and positive for the longest natal dispersal distances of each sister pair) and provided little support for the kinship hypothesis with the possible exception of shovelers. The test results were very similar for all species if we excluded sister pairs that dispersed < 200 m.

MOVEMENTS OF YOUNG NORTHERN SHOVELERS

We modelled natal dispersal movements of females between a large island A and a cluster of three small islands (B, C, D; see Fig. 1) during two different time periods, prior to and following the construction of artificial islands. The most parsimonious model (Table 1) had time-specific duckling survival that was not stratum-specific and movement probabilities that varied by water level and stratum during premanagement years but by only stratum (not time or water level) in post-management years. The large ΔAIC_c for a similar model without age-specificity of movement parameters (Table 1) provided strong evidence of age-specific differences in rates of movement, with young females showing larger movement probabilities than older birds (see below and Blums *et al.* 2003).

For the premanagement period, annual movement (t to $t + 1$) from hatching to first breeding was modelled as a function of spring water level in year $t + 1$. Models not containing water level as a time-specific covariate for ducklings during the premanagement period had $\Delta AIC_c > 30$ and weights approaching 0. Like adults,

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Table 3. Models used to assess variation in natal movement probabilities of female tufted ducks between strata at Engure Marsh, Latvia

Model[a]	ΔAIC_c[b]	Model weight[c]	Np[d]
Movement between small islands and a large island (1961–94; n = 6673/546[e])			
$S_{AD2s1,\ DKs+t}\ p_{s*t}\ \varnothing_{ADs*wat2,\ DKs1}$	0·0	0·46	111
$S_{AD2s1,\ DKs+t}\ p_{s*t}\ \varnothing_{ADs*wat5,\ DKs1}$	1·09	0·26	112
$S_{AD2s1,\ DKs+t}\ p_{s*t}\ \varnothing_{ADs*wat2,\ DK2t}$	2·60	0·12	110
$S_{AD2s1,\ DKs+t}\ p_{s*t}\ \varnothing_{ADs*wat2,\ DKs*wat2}$	4·17	0·06	113
$S_{AD2s1,\ DKs+t}\ p_{s*t}\ \varnothing_{ADs*wat2,\ DKs*wat5}$	4·57	0·05	114
$S_{AD2s1,\ DKt}\ p_{s*t}\ \varnothing_{ADs*wat2,\ DKs1}$	17·68	0·0	110
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	241·88	0·0	330
Movement between islands and emergent marshes (1972–92; n = 7948/735[e])			
$S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat8}$	0·0	0·31	33
$S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat8}$	1·07	0·18	33
$S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat9}$	1·80	0·12	34
$S_{AD3s2,\ DKs+t}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat8}$	1·94	0·12	34
$S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs4}$	2·30	0·10	32
$S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DK(.)}$	8·57	0·0	29
$S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs2}$	9·44	0·0	30
$S_{AD3s2,\ DK4st}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat8}$	66·10	0·0	17
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	143·69	0·0	200
Movement between < 2 m and > 2 m zones (1985–92; n = 2529/147[e])			
$S_{AD(.),\ DKt}\ p_{a*s}\ \varnothing_{a*s}$	0·00	0·62	14
$S_{AD(.),\ DKs+t}\ p_{a*s}\ \varnothing_{a*s}$	1·22	0·34	15
$S_{a*t}\ p_{a*s}\ \varnothing_{a*s}$	6·89	0·02	20
$S_{AD(.),\ DKt}\ p_{a*s}\ \varnothing_{a}$	8·04	0·01	12
$S_{a}\ p_{a*s}\ \varnothing_{a*s}$	10·42	0·0	8
$S_{a*s*t}\ p_{a*s*t}\ \varnothing_{a*s*t}$	50·31	0·0	70

[a]Model subscripts/covariates: a = age (see Table 1); s = stratum (islands vs. marshes, or < 2 m vs. > 2 m zone); *DKs1* = different but constant movement from large island to small islands during premanagement (1972–82) and post-management periods (1983–92), single constant from small islands to large island during all periods; *DKs2* = different but constant movement in both directions during all periods; *DKs4* = different but constant movement in each direction and period; *DK2t* = different but constant movement in each period and equal in both directions (no state); *DK4st* = different but constant survival for each stratum and period; *3s2* = constant survival (single parameter) for marshes (1972–92) and islands (1972–82), different but constant for islands (1983–92); *s + wat7* = different (but parallel) water dependence in movement from islands to marshes during each period, single constant from marshes to islands during the entire period; *s + wat8* = different (but parallel) water dependence in movement from islands to marshes during each period, different but constant movement from marshes to islands during each period; *s + wat9* = different (but parallel in both periods) water dependence in movement in 2 directions. See other notation in Tables 1 and 2.

young females moved with higher probabilities from the large island to a cluster of three small islands (ψ_t^{LS}) in years when spring water level was lower ($\hat{\beta} = -8{\cdot}14$, $\hat{SE}[\hat{\beta}] = 2{\cdot}92$; 95%CI = –13·87 to –2·42; Fig. 2). Movement was stronger in the opposite direction (ψ_t^{SL}) when spring water level was higher ($\hat{\beta} = 5{\cdot}58$, $\hat{SE}[\hat{\beta}] = 2{\cdot}47$; 95%CI = 0·74–10·42; Fig. 2). Confidence intervals (95%) for the $\hat{\beta}$ were either entirely negative or positive, providing strong support for the relationship between local breeding dispersal movements and water level. The magnitudes of the $\hat{\beta}$ s provide some evidence that the relationships were even stronger for young females than adults (Blums *et al.* 2003). Our results thus supported the existence of the predicted relationship between spring water conditions and movement during the premanagement period.

For the post-management period, the natal dispersal movements were best modelled as stratum-specific but constant over time. The estimated movement probability from the large island to small islands was much smaller ($\hat{\psi} = 0{\cdot}12$, $\hat{SE}[\hat{\psi}] = 0{\cdot}04$) than the probability of moving in the opposite direction ($\hat{\psi} = 0{\cdot}39$,

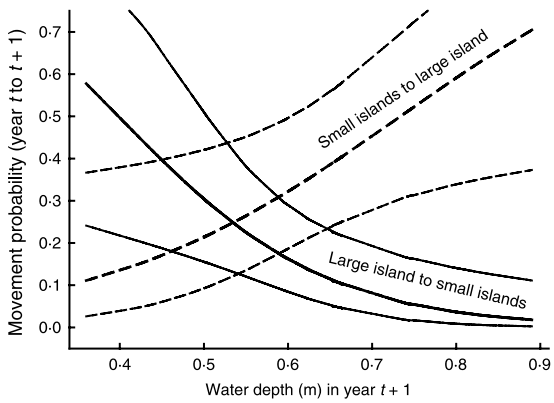

Fig. 2. Natal movement probabilities of female northern shovelers between the large island (A) and a cluster of small islands (B, C, D) as a function of spring water level at Engure Marsh, Latvia, during the premanagement period, 1961–82. The curves (mean and 95% CI) are based on estimates from the most parsimonious covariate model ($S_{AD2t,\ DKt}\ p_s\ \varnothing_{ADs*wat2,\ DKs*wat5}$). Dashed lines denote movement from small islands to large island, and solid lines denote movement from large island to small islands. Water level metrics are on the dates when 10% of females initiated nesting.

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$\hat{SE}[\hat{\psi}] = 0{\cdot}07$) suggesting possible habitat quality differences between the two strata. Different models (e.g. *s*wat4*) imposing the same time-specific relationship between movement probabilities and water level for the entire study period had $\Delta AIC_c > 3{\cdot}1$. The *wat3* models, with movement modelled as different functions of water levels in the pre- and post-management periods, received some support (Table 1). Unlike the situation with adult birds (Blums *et al*. 2003) and contrary to our prediction, estimated rates of movement following management remained relatively large for young birds.

We used the random effects approach (see Statistical methods) to estimate the mean local survival probability and its standard error for ducklings ($\hat{E}[S] = 0{\cdot}08$, $\hat{SE}(\hat{E}[S]) = 0{\cdot}009$), as well as the true temporal variance of survival ($\hat{\sigma}[S_t] = 0{\cdot}036$, 95%CI = 0·021–0·058). The estimated temporal variance was substantial relative to the magnitude of the mean survival estimate, indicating large year-to-year variation in duckling survival. A competing model with state-specific local duckling survival received some support (ΔAIC_c = 1·90), providing weak evidence of higher local survival of ducklings on the large island.

MOVEMENTS OF YOUNG COMMON POCHARDS

Movement between gull colonies and areas without gull colonies within marsh habitats

We used the most parsimonious model (Table 2) with time-specific, but not stratum-specific, local survival for ducklings to estimate movement probabilities between gull colonies and locations outside gull colonies (modelled as two states) within the marsh habitat. Females of each age group moved into and out of gull colonies with similar probabilities that decreased with age: ducklings, $\hat{\psi} = 0{\cdot}38$, $\hat{SE}[\hat{\psi}] = 0{\cdot}03$, 95%CI = 0·32–0·44; SY, $\hat{\psi} = 0{\cdot}22$, $\hat{SE}[\hat{\psi}] = 0{\cdot}02$, 95%CI = 0·18–0·27; ASY, $\hat{\psi} = 0{\cdot}16$, $\hat{SE}[\hat{\psi}] = 0{\cdot}01$, 95%CI = 0·13–0·18. Thus, fidelity probability ($\hat{F} = 1 - \hat{\psi}$) to respective strata increased with age: ducklings = 0·62, $SY = 0{\cdot}78$, and $ASY = 0{\cdot}84$. Our prediction that young females would move out of colonies with higher probability than into colonies received some support ($\Delta AIC_c = 1{\cdot}54$) but the difference (0·05) between the two movement estimates was small. Models with stratum-specific movement and no age-specificity received virtually no support ($\Delta AIC_c > 56{\cdot}0$). The lowest proportion (mean ± SE) of yearlings (0·18 ± 3·1; $n = 17$ years) among the breeders and the highest breeding density of pochards (up to 68 nests/ha) and all duck species (up to 103 nests/ha), were recorded at selected areas of largest gull colonies in emergent marshes (Fig. 3).

The mean local survival probability for ducklings was low ($\hat{E}[S] = 0{\cdot}06$, $\hat{SE}(\hat{E}[S]) = 0{\cdot}007$) and similar for both strata. The standard error reflecting true temporal variation of duckling survival was estimated as $\hat{\sigma}[S_t] = 0{\cdot}025$, 95%CI = 0·015–0·045. As was the case for shovelers, the relative temporal variation in duckling survival was large.

Movement between < 2 m and > 2 m zones

The most parsimonious model (Table 2) indicated that natal movement probabilities between < 2 m and > 2 m zones were stratum-specific and also differed between ducklings and older birds. Young females moved in the direction closer to water with much higher probability ($\hat{\psi}^{dn} = 0{\cdot}62$, $\hat{SE}[\hat{\psi}^{dn}] = 0{\cdot}06$) than away from water ($\hat{\psi}^{nd} = 0{\cdot}32$, $\hat{SE}[\hat{\psi}^{nd}] = 0{\cdot}06$). The model with no stratum-specific variation in movement for young birds was not well supported ($\Delta AIC_c = 4{\cdot}46$; Table 2)

MOVEMENTS OF YOUNG TUFTED DUCKS

Movement between islands and emergent marshes

The most parsimonious model (Table 3) had time-specific duckling survival, that was not stratum-specific. Time-dependent movement from islands to emergent marshes was modelled as a function of water level in the spring of year $t + 1$ and parallel during the premanagement (1972–82) and post-management (1983–92) periods (Fig. 4). There was a parallel increase ($\hat{\beta} = 3{\cdot}94$, $\hat{SE}[\hat{\beta}] = 1{\cdot}96$; 95%CI = 0·10–7·77) in movement probability from islands to emergent marshes with increases in water level during both time periods (premanagement: 0·15–0·53, and post-management: 0·04–0·22). The best supported model with no water covariates ($\Delta AIC_c = 2{\cdot}30$, Table 3) estimated movement probability that was constant but much higher during the premanagement period (e.g. $\hat{\psi}^{mi} = 0{\cdot}33$, $\hat{SE}[\hat{\psi}^{mi}] = 0{\cdot}05$, 95%CI = 0·24–0·45) than during the post-management period (e.g. $\hat{\psi}^{mi} = 0{\cdot}10$, $\hat{SE}[\hat{\psi}^{mi}] = 0{\cdot}06$, 95%CI = 0·03–0·27). Movement probability from islands to marshes for a specific water level under the low-AICc model was much higher during the premanagement years than following management. In contrast, movement probability from marshes to islands was best modelled as different constants during each period (premanagement: $\hat{\psi}^{mi} = 0{\cdot}14$, $\hat{SE}[\hat{\psi}^{mi}] = 0{\cdot}04$, 95%CI = 0·07–0·24; post-management: $\hat{\psi}^{mi} = 0{\cdot}29$, $\hat{SE}[\hat{\psi}^{mi}] = 0{\cdot}06$, 95%CI = 0·19–0·42). The mean local survival for ducklings was very low and similar in emergent marshes and islands ($\hat{E}[S] = 0{\cdot}032$, $\hat{SE}(\hat{E}[S]) = 0{\cdot}005$, $\hat{\sigma}[S_t] = 0{\cdot}021$, 95%CI = 0·014–0·034).

Movement between a cluster of small islands and a large island

The most parsimonious model (Table 3) estimated different but constant movement probabilities for ducklings from the large island to small islands during the premanagement ($\hat{\psi}^{LS} = 0{\cdot}24$, $\hat{SE}[\hat{\psi}] = 0{\cdot}04$) and post-management ($\hat{\psi}^{LS} = 0{\cdot}04$, $\hat{SE}[\hat{\psi}] = 0{\cdot}04$) periods. The movement probability ($\hat{\psi}^{SL} = 0{\cdot}12$, $\hat{SE}[\hat{\psi}] = 0{\cdot}04$) from small islands to large island was modelled as a single

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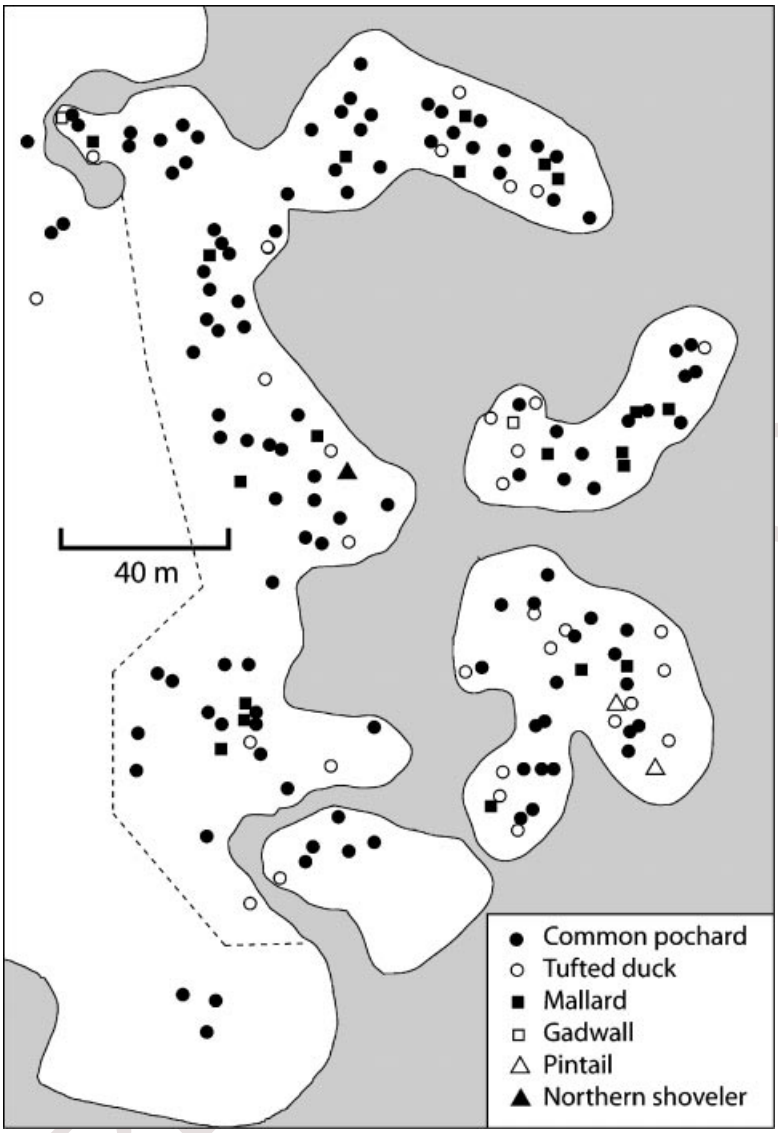

Fig. 3. Concentrated nesting of six duck species within a dense colony of black-headed gulls in emergent marshes, Engure Marsh, 1977. Common pochards and tufted ducks were dominant species at this high quality nesting habitat. White areas are emergent marshes and dark-shaded areas are open water. Symbols denote duck nests; dashed line denotes the border of gull colony.

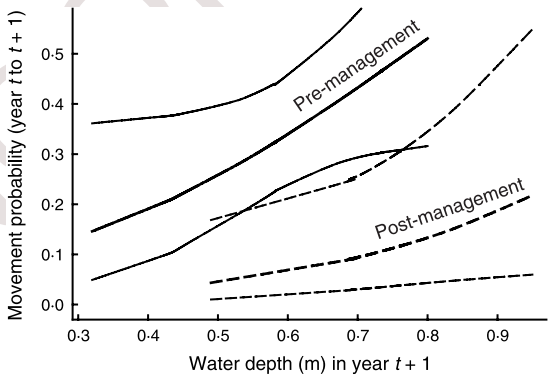

Fig. 4. Natal movement probabilities of female tufted ducks from islands to emergent marshes as a function of spring water level during premanagement (solid lines) and post-management (dashed lines) periods. The curves (mean and 95% CI) are based on estimates from the most parsimonious covariate model ($S_{AD3s2,\ DKt}\ p_s\ \varnothing_{ADs+wat7,\ DKs+wat8}$). Water level metrics are on the dates when 10% of females initiated nesting.

constant during the entire study period. Models containing water level as a time-specific covariate for different time periods were not well supported ($\Delta AIC_c > 4{\cdot}1$).

Unlike for shoveler, the pattern of temporal variation in survival was parallel for large and small islands. The mean local survival probability for ducklings was very low both on large island ($\hat{E}[S] = 0{\cdot}037$, $\hat{S}E(\hat{E}[S]) = 0{\cdot}006$, $\hat{\sigma}[S_t] = 0{\cdot}027$, 95%CI = 0·017–0·042) and small islands ($\hat{E}[S] = 0{\cdot}013$, $\hat{S}E(\hat{E}[S]) = 0{\cdot}003$, $\hat{\sigma}[S_t] = 0{\cdot}01$, 95%CI = 0·004–0·019).

Movement between < 2 m and > 2 m zones

Movement probabilities were best modelled as age- and stratum-specific but constant over time (Table 3). As for pochards, young female tufted ducks breeding for the first time moved in the direction closer to water with much higher probability ($\hat{\psi}^{dn} = 0{\cdot}60$, $\hat{S}E[\hat{\psi}^{dn}] =$

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0·09) than away from water ($\hat{\psi}^{nd} = 0{\cdot}17$, $\hat{SE}[\hat{\psi}^{nd}] = 0{\cdot}07$). Models with other than $\varnothing_{a*s}$ notation were not well-supported ($\Delta AIC_c > 8{\cdot}0$).

Discussion

The 'true' rates of natal fidelity and dispersal are largely unknown, not only for waterfowl but for most bird species. To our knowledge only a couple of studies have used modern statistical methods (i.e. joint recapture/recovery models) to estimate fidelity and permanent emigration of young female ducks to natal sites. Arnold *et al*. (2002) estimated that 26% of young female redheads [*Aythya americana* (Eyton)] that survived in any given year emigrated permanently from the study area in Manitoba, Canada, yielding 74% natal fidelity rate for this redhead population. Doherty *et al*. (2002) estimated that emigration rates of hatch-year female mallards (*Anas platyrhynchos* L.) were 0·60 and 0·01 from large study areas in Alberta and Saskatchewan, Canada. The respective fidelity probability (0·99) of young mallards in the Saskatchewan area seems very high and can probably be attributable to the large size of the reference area in Saskatchewan (89 sites bounded by latitudes 49°40′/53°30′ N and 102°00′/109°40′ W).

The studies of Arnold *et al*. (2002) and Doherty *et al*. (2002) investigated permanent emigration, but these studies investigated only sources of variation associated with the site of origin because the destination sites were not sampled. The present study is the first to address between-season movement of young ducks for the situation in which both the origination and destination sites are sampled.

NATAL DISPERSAL DISTANCES

The mean natal dispersal distances were very similar (*c*. 0·6–0·7 km) for all three species and were on average 2·7 times greater than breeding dispersal distances recorded within the same study system; thus our prediction was supported. This finding is consistent with the general pattern observed in other bird taxa (Greenwood & Harvey 1982; Paradis *et al*. 1998) that natal dispersal distances are greater than breeding dispersal distances. Because there is very limited published information available on natal dispersal distances for overwater- and ground-nesting waterfowl (Lokemoen, Duebbert & Sharp 1990), and because observed distances will be functions of the sampled area, the distribution of potential breeding sites within the sampled area (Blums *et al*. 2003) and sample sizes, we believe that between-study comparisons are not useful.

NATAL DISPERSAL BEHAVIOUR IN THE PRESENCE OF KIN

We found no evidence that young females selected nest sites closer to their relatives (either sister or mother) than to the natal nest. Thus, we were unable to support the hypothesis that yearlings may benefit from breeding in association with close relatives (Greenwood 1980; Anderson *et al*. 1992). Our findings are consistent with those of Ruusila, Pöysä & Runko (2001), who reported that daughters' nest site selection in cavity-nesting common goldeneyes was not associated with the presence of their mothers. This Finnish study did not have enough data to explore associations between sisters. Semel & Sherman (2001) recently showed that female wood ducks (*Aix sponsa* [L.]) recognized and actively avoided parasitizing close relatives (mothers and daughters) in Illinois, USA. The authors rejected the kin selection hypothesis and concluded that there is no evidence of nepotism in wood ducks. To our knowledge this study has provided the first evidence of kin recognition among breeding ducks, although the authors did not explain *how* females recognized their relatives.

MOVEMENT BETWEEN SMALL ISLANDS AND A LARGE ISLAND (SHOVELER AND TUFTED DUCK)

Overall, the pattern of movement between the large island and small islands of young female shovelers was very similar to that of adult birds. Young females moved from small islands to the large island when water level was high and vice versa when water level was low during the premanagement period. However, the movement probabilities between the two strata for a specific water level were much higher for young birds than adults. Fidelity of adults to the entire Engure Marsh system was virtually complete (1·0; Blums *et al*. 2002) and movement probability between large and small islands approached zero (Blums *et al*. 2003) during the post-management period. Despite stable and predictable nesting habitats, movement probability of young females was also relatively high during the post-management period (0·12–0·39) when young females were 3·3 times more likely to move from small islands to the large island than vice versa. Because shovelers are territorial (Poston 1974), we believe this difference was mainly due to space limitations on small islands (1·2 ha) vs. the large island (6·3 ha).

For young tufted ducks the time-specific model with water level covariates was poorly supported, so we concluded that young female tufted ducks, unlike shovelers, were not greatly influenced by water level fluctuations but were flexible in choosing their first nesting sites before strong site fidelity was developed. Unlike shovelers, tufted ducks nested readily both on islands and overwater, so females could easily move to emergent marshes when nesting conditions deteriorated on islands.

For tufted duck, and especially shoveler, movement probabilities between the two strata were higher for young females than for adults, during both pre- and post-management periods, suggesting that young birds

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had not yet developed strong nest site fidelity to the natal site. Thus, all predictions for both species were supported except that young shovelers did not exhibit reduced movements during the post-management period.

MOVEMENTS BETWEEN GULL COLONIES AND HABITATS WITHOUT GULL COLONIES (POCHARD)

The results of our analyses support our earlier conclusion (Blums *et al*. 2003) that pochard nesting habitats in black-headed gull colonies were saturated during the study period. Evidently because of this saturation females of each age group moved into and out of gull colonies with similar probability. A dramatic expansion of black-headed gulls on Engure Marsh occurred during 1958–72 when the breeding population of gulls exploded from 600 to about 26 000 pairs (Viksne, Janaus & Stipniece 1996) and remained relatively stable during 1972–92. Similarly, the number of pochard nesting attempts was relatively stable (on average 163 nest attempts/year) in gull colonies at permanent study plots during 1972–92. However, the breeding population increased during the same period outside gull colonies. We believe the colony habitats became saturated before 1976 when this pochard movement study was initiated. The fidelity probability of female pochards to both strata increased with age, being the lowest (0·62) for young, intermediate (0·78) for *SY* and the highest (0·84) for *ASY* females. The increase in nest-site fidelity with age may be a common pattern in waterfowl as evidenced by some studies in geese (Cooke *et al*. 1983; Lindberg & Sedinger 1997).

We found also some support for the prediction that young females should move out of gull colonies to the first nesting sites with higher probabilities than into the colonies. Indeed, relatively fewer *SY* females than *ASY* females nested in gull colonies than outside, and colony-nesting females were of better quality (Blums *et al.* 2003) than those nesting outside colonies. These facts suggest that only a limited number of high quality yearlings could gain access to saturated nesting habitats in gull colonies, where breeding density of pochards and other duck species, and thus competition for available nest sites, was high (Fig. 3). Models with time-specific movement were poorly supported, suggesting relatively little variation in movement probabilities into and out of colonies for different age groups (including young females).

Our prediction that local survival of ducklings, unlike that of adults, would be lower in gull colonies than outside colonies was not supported. The mean local survival (0·06) was similar for both strata suggesting that occasional mortality of newly hatched ducklings in the crowded situations (Fig. 3) in dense colonies of black-headed gulls immediately following hatching either was negligible and did not affect first year survival rates, or else was balanced by decreased predation from other sources. This finding was not surprising, because different factors affect annual survival of ducklings vs. adult birds (Blums *et al*. 1996). Overall, the benefits (in terms of very high nest success and low female nesting mortality) gained from nesting in association with gulls far outweighed the negligible costs (some harassment and rare cases of newly hatched ducklings killed by black-headed gulls) not only for pochards but most probably for all other duck species that nested in black-headed gull colonies at Engure Marsh.

MOVEMENT BETWEEN ISLANDS AND EMERGENT MARSHES (TUFTED DUCK)

We have shown that adult female tufted ducks were equally likely to choose islands and emergent marshes for nesting if both habitats were available (Blums *et al*. 2003) and that there was little exchange of nesting females between the two habitats over time. We also provided evidence that water influenced availability, as adult females showed higher probabilities of moving from islands to emergent marshes when spring water levels in year $t + 1$ were higher.

As with adults, there was a strong interaction between natal dispersal movements and spring water levels. Young females showed higher probabilities of moving from islands to emergent marshes when water levels (in year $t + 1$) were higher, both before and after habitat management (Fig. 4). We believe high water levels improved nesting conditions in emergent marshes for tufted ducks (Blums *et al*. 2003), and females of all age groups tended to move from islands to marshes in years when water level was high. However, this relationship was much weaker for young than for adult females ($\hat{\beta} = 3{\cdot}9$ vs. $9{\cdot}6$) probably because young first-nesting females did not have prior nesting experience and thus could not assess marsh habitat advantages adequately at high water levels, or they were prevented from moving to better quality marsh habitats by superior adults. Thus our prediction 6 was fully supported.

On average, young females moved for their first breeding attempt from islands to marshes with much higher probability (0·33) during the premanagement period than during the post-management period (0·10). The movement probability from marshes to islands was smaller (0·14) during the premanagement period and larger (0·29) during the post-management period. We believe the young females moved away from natal islands with higher probabilities during the premanagement period when nesting conditions on islands were unpredictable because of spring flooding, but the movement was predominantly in the opposite direction (from marshes to islands) after provision of critical improvements in island nesting habitats (see prediction 3).

Movement probability for a specific water level was much lower during the 1983–92 period following the island management (Fig. 4). Evidently critical improvements in island habitats were beneficial not only for shovelers but also for tufted ducks because

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reduced flooding most probably increased fidelity and minimized dispersal movements of all island-nesting duck species.

MOVEMENT BETWEEN < 2 M AND > 2 M NESTING ZONES (DIVING DUCKS)

As predicted, young female diving ducks, like adults, moved in the direction closer to water from the > 2 m zone with much higher probability than away from water. Female diving ducks usually escape by diving when attacked by predators during the incubation period so all age groups should benefit when they nest as closely as possible to the water's edge. The difference in movement probability (in direction closer to water vs. away from water) was larger for young females than for adult age groups, suggesting that this difference may be the result of stronger adult site fidelity.

MOCAL SURVIVAL OF DAY-OLD DUCKLINGS

Local survival estimates for ducklings were time-specific and very low (means 0·01–0·08). In all but one analysis, the annual survival estimates (and long-term means) were equal for the two strata that were compared. These results suggest that duckling survival during the first year of life was typically not affected by the quality of particular hatching sites (for example, gull colonies and areas located outside colonies, etc.) but rather by year-to-year variation in habitat conditions at common brood rearing areas.

There are three main reasons for our relatively low duckling survival estimates. First, ducks exhibit much higher mortality during the first year of life than later (Johnson, Nichols & Schwartz 1992; Sargeant & Raveling 1992). Secondly, an unknown but relatively large proportion (up to 0·26 for redheads (Arnold *et al.* 2002) and 0·60 for mallards (Doherty *et al.* 2002)) of fledged females may have emigrated permanently. Thirdly, most estimates of juvenile survival are based on young birds marked just prior to or just after fledging (Johnson *et al.* 1992). Our estimates of annual survival for ducklings are based on individuals banded at hatch. These estimates of annual survival therefore include mortality that occurs before fledging. Because capture–recapture models have not been used to estimate annual survival rates of day-old ducklings by other researchers, comparable data are not available. We encourage other investigators to sex and band ducklings at hatch and use combined models (Burnham 1993) to investigate true fidelity and survival rates of day-old ducklings.

Conclusion

A common approach to dispersal research is to consider two types of movement, natal dispersal and breeding dispersal, with their frequently separate causes and consequences (e.g. Clobert *et al.* 2001). In previous papers, we used relatively new and little-used band recovery and capture–recapture models to investigate breeding dispersal of female ducks based on a long-term study of marked birds at Engure Marsh, Latvia (Blums *et al.* 2002; Blums *et al.* 2003). Because of the ability to mark newly hatched ducklings (Blums *et al.* 1994), we were able to extend the modelling of Blums *et al.* (2003) to investigate sources of variation in within-system natal dispersal for these same duck species. In particular, our use of the multistate modelling approach for locations within the Engure Marsh system permitted us to investigate hypotheses about causes of movement that incorporate characteristics of sites of both origination and destination (Nichols & Kendall 1995; Lindberg *et al.* 1998; Blums *et al.* 2003).

Our different analyses for all three species provide strong evidence that rates of dispersal from one breeding season to the next tend to be much higher for first-year birds than for older breeders. This result is consistent with the idea that previous breeding experience in a location confers some sort of fitness advantage to breeding females. Ducklings do not experience behaviours associated with breeding and nesting, so fidelity to the natal site is not as likely to be advantageous. Except for this predicted difference between magnitudes of young and adult movement, the general patterns of variation in movement (e.g. in response to water conditions, management activities, proximity to water, etc.) of young were very similar to those of adult females. We view this work as complementary to our previous work with breeding dispersal and believe that these analyses combine to provide a fairly good picture of the dispersal process in these three duck species.

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