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Sources of variation in survival and breeding site fidelity in three species of European ducks

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Summary

1. We used long-term capture–recapture–recovery data and a modelling approach developed by Burnham (1993) to test a *priori* predictions about sources of variation in annual survival rates and fidelity within a population of individually marked females in three species of European ducks from a breeding ground study site in Latvia.
2. True annual survival was higher for diving ducks (tufted duck 0·72, common pochard 0·65) and lower for northern shoveler (0·52). Survival of female diving ducks was positively correlated with mean winter temperatures at Western European wintering areas, the relationship being much stronger for pochard.
3. We present the first unbiased estimates of breeding fidelity and permanent emigration in European ducks. Estimated fidelity rates were high (0·88–1·0) and emigration rates low (0–0·12) for all three species, and we found strong evidence for age-specific differences in fidelity of pochards. Unusual long-distance (up to 2500 km) breeding dispersal movements that we found in female tufted ducks have not been documented in any other European waterfowl and are most probably a result of saturated nesting habitats.
4. Fidelity was a function of patch reproductive success in the previous year for all three species providing support for the idea that patch success is an important cue influencing fidelity.
5. Fidelity probability increased to 1·0 for shovelers during the last 12 years of study following provision of critical improvements in nesting habitats and suggested that habitat conditions and reproductive success determined site fidelity and settling patterns for shoveler and probably also influenced fidelity of the two other species. In predictable habitats, fidelity is a parameter that reflects the integration of fitness components and is thus a good quantity for assessing the effectiveness of habitat management actions.

Key-words: Burnham model, nesting habitat saturation, reproductive success, permanent emigration, true survival.

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Introduction

Survival and fidelity to breeding grounds are important determinants of both individual fitness and population dynamics for migratory species. Within *Anatidae*, annual survival rates have been estimated for a number of species, although the majority of reliable estimates have come from North American studies. In particular, sources of variation in survival rates of Palearctic ducks have not been investigated widely using reliable inference methods. Parameters associated with fidelity have not been estimated well for many species of waterfowl or indeed any migratory birds. Some general patterns of variation in fidelity (e.g. sex-specific variation; see Mayr 1942; Greenwood 1980; Greenwood & Harvey 1982; Rohwer & Anderson 1988; Anderson, Rhymer & Rohwer 1992) are discussed widely and assumed to be known but have received little investigation using reliable inference methods (see Johnson, Nichols & Schwartz 1992; Nichols 1996). In fact a recent investigation of sex-specificity in fidelity of mallard ducks, *Anas platyrhynchos* L., to breeding grounds using

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recently developed inference methods found evidence of much greater fidelity of adult males, and a much smaller difference between fidelity of the sexes, than thought previously (Doherty *et al*. 2002).

Here we report results of analyses of data from a long-term study of ducks at Engure Marsh, an internationally important waterfowl nesting site in Latvia. We focus on the three important nesting species in the area, northern shoveler (*Anas clypeata* L., hereafter shoveler), common pochard (*Aythya ferina* [L.], hereafter pochard) and tufted duck (*Aythya fuligula* [L.]). Previous analyses have used capture–recapture data from this study to investigate age-specific variation in 'local' or 'apparent' survival rates which reflect the product of true survival and the probability of returning to the breeding area (fidelity) (Blums *et al*. 1996; Nichols, Hines & Blums 1997). Blums *et al*. (1996) used band recovery and capture–recapture data separately with an *ad hoc* approach to draw separate inferences about true survival of nesting females and the general magnitude of rates of fidelity for the two *Aythya* species, concluding that fidelity was very high. In this paper we use recently developed models (Burnham 1993) and associated computer software (White & Burnham 1999) to investigate sources of variation in both annual survival rates and fidelity, with emphasis on the latter parameter.

HYPOTHESES AND PREDICTIONS

Survival rates

Despite the commonsense idea that low temperatures should decrease survival probabilities through such mechanisms as increased metabolic needs for heat production and reduced availability of food resources on frozen water areas, there is surprisingly little strong evidence of such effects in waterfowl. Many of our beliefs about effects of winter weather on waterfowl come from reports of birds found dead during severe winters (e.g. Boyd 1964; Suter & van Eerden 1992). We are aware of no evidence that low winter temperatures translate into low annual survival rates. Perhaps the flexible selection of wintering grounds depending on weather and habitat conditions (e.g. Nichols, Reinecke & Hines 1983; Ridgill & Fox 1990) serves to mediate the influence of wintering ground conditions on waterfowl survival.

The Latvian long-term data set for migratory waterfowl wintering in areas of potentially harsh winter weather provided an opportunity to formally test for effects of winter temperature on true annual survival rates. Because Latvian shovelers winter over a very large area in two continents (Mednis 1990), we made no predictions about wintering ground conditions and survival in this species. However, pochards and tufted ducks winter mainly in Central Europe and along the Atlantic coast (Blums & Baumanis 1990) where conditions are sometimes quite harsh. Our prediction was that there would be a positive association between annual survival and winter temperature on the wintering grounds for pochards and tufted ducks.

Fidelity

For purposes of this study, fidelity (denoted as F_t) is the probability that a bird associated with the Engure Marsh study area in year t does not emigrate permanently to a different breeding area in year $t + 1$. Thus, F_t is the complement of the probability of permanent emigration. Note that studies of fidelity frequently include the concepts of permanent emigration *and* temporary emigration in the definition of fidelity. For example, Johnson & Grier (1988) provided evidence that ducks of some species overfly previously used breeding areas during years when those areas exhibited poor wetland conditions, but then returned during subsequent years when wetland conditions were favourable. Such temporary emigration is not included in our investigation of fidelity.

Prediction 1. The first general prediction was that yearling females experiencing their first spring season following hatch (denoted as SY, see Methods) and older females in at least their second spring season following hatch (denoted as ASY) would show similar rates of fidelity the following year. The basis for the prediction in tufted ducks was the similar local survival estimates (the complement of these include both death and permanent emigration) for the two age classes obtained by Blums *et al*. (1996). Local survival rates were lower for SY than for ASY birds for both pochards and shovelers, leaving open the possibility that the difference involved permanent emigration. Because of the direction of the difference between local age-specific survival estimates and because of the commonsense idea that increased experience with an area should lead to increased fidelity, we predicted that if we did find evidence of a difference in fidelity, it would indicate greater fidelity of older birds.

Prediction 2. The second general prediction was that fidelity should be a function of reproductive success in the previous year. Many empirical studies of waterfowl and other species provide some evidence that nest success influences return rates, statistics reflecting the product of survival probability, probability of returning to the breeding area (fidelity) and probability of recapture or resighting (see reviews in Gauthreaux 1982; Greenwood & Harvey 1982; Anderson *et al*. 1992; Johnson *et al*. 1992). Mihelsons, Mednis & Blums (1986) provided evidence that return rates of shovelers and tufted ducks to Engure Marsh were higher for females that were successful the previous year than for those that were not. Such conditional fidelity behaviour is expected to be more prevalent at stable nesting habitats where nest success in one year is a reasonable predictor of probability of success in the

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next year (Nichols 1996). Because of constant predator control and other management activities aimed at maintaining the carrying capacity of breeding habitats, Engure Marsh can be considered as a fairly stable wetland, especially for diving ducks. We thus predicted that fidelity, F_t (probability of permanently emigrating in year $t + 1$), should be a function of reproductive success in year t, where reproductive success is indexed by either nest success or duckling production at nesting areas.

Prediction 3. This prediction is based on habitat management that occurred during the study. The sampled areas of Engure Marsh included four natural islands: A (16 ha), B (0·8 ha), C (2·5 ha), and D (0·6 ha) with a total surface area at low water of approximately 20 ha, from 1960 to 1982. The islands were separated from each other by 0·8–1·4 km wide areas of open water, and large portions of islands were flooded frequently. Islands C and D were especially low and were occasionally not available for nesting. In addition, island C gradually overgrew with dense stands of reed and lost its importance as a shoveler breeding habitat by 1977. To increase the carrying capacity of island breeding habitats, many artificial elevated islands were constructed on the flooded sections of islands A and D during 1981–83. Beginning in 1984, 82 islands (total area 14·3 ha) were available for nesting within the previous island territory. We believe that fragmentation of islands improved nesting conditions and provided stable and predictable nesting habitats, especially for shovelers, as this species nested only on islands. We thus predicted that fidelity for shoveler should be higher during the last 12 years (1983–94) of the study period than during the first 23 years (1960–82) of the study.

Prediction 4. We believe that relatively high water levels in early spring were associated with better access to nesting sites and good feeding conditions that were critical for female shovelers during the prelaying and laying period. If the 'decision' about whether to settle or emigrate is made based on water conditions at Engure Marsh at the beginning of the breeding season, then we would expect water conditions to be associated with fidelity in the same year. However, in relatively stable wetlands such as Engure Marsh, it is also possible that wetland conditions in one breeding season are reasonable predictors of wetland conditions the next breeding season. We predicted that for shoveler there would be a positive relationship between fidelity and wetland conditions the same year (relationship between F_{t-1} and X_t, where X_t denotes wetland conditions in year t), but we tested for a lagged relationship as well (relationship between F_t and X_t).

Exploratory trend analyses

Finally, we considered models incorporating temporal trends in fidelity. We had no reason to suspect the existence of trends and thus make no specific predictions. These models should be considered as exploratory analyses only.

Methods

STUDY AREA AND FIELD METHODS

The study was conducted from 1960 to 1994 on the 35-km^2 Engure Marsh (57°15′ N, 23°07′ E), Latvia, Eastern Europe. The Engure Marsh is an isolated, shallow, permanently flooded palustrine wetland that has gradually changed from an open marsh to a hemi-marsh dominated by tall, robust hydrophytes such as common reed (*Phragmites australis* [Cav.] Trin. ex Steud.) and cattail (*Typha* spp.). The Marsh supports the largest breeding population of ducks in the Baltic countries and has been included in the list of internationally important waterfowl habitats under the Ramsar Convention. About 2000 pairs of 13 duck species nested on the marsh during the study period, with roughly 60% consisting of pochards, tufted ducks and shovelers; of these, approximately 99% of shovelers, 42% of tufted ducks and 25% of pochards nested within permanent sampling areas.

Each year two to three complete searches for duck nests were conducted on permanent sampling sites within the marsh from mid-May to late June. All breeding habitats within permanent sampling areas were searched systematically to locate nests by walking parallel transects. Effectiveness of probable nest searches was very high and few females were missed, as evidenced by estimated very high capture probabilities which ranged from 0·70 to 0·81 (see Results). In addition to the natural and artificial islands, nest searches were expanded to three isolated areas of persistent emergent marshes beginning in 1972, totalling approximately 111 ha of reed-beds and cattail stands, excluding open water. Thus, permanent sampling areas included natural and artificial islands 1960–94, and emergent marshes 1972–94.

Human activities were prohibited on islands and areas of emergent marshes during the breeding season but most of the marsh was open to waterfowl hunting from early August to early November. Different management activities such as construction of artificial islands (see Prediction 3), vegetation and predator control, and attraction of gulls and terns were conducted on all sampling areas throughout the study to prevent the decline of carrying capacity of breeding habitats. The two nearest major wetlands suitable for duck nesting were located 30 and 50 km from Engure Marsh and jointly supported relatively small populations of shoveler (*c.* 20 pairs), pochard (200) and tufted duck (80) during the study period.

Females were captured on nests during the last week of incubation using drop-door nest traps (Blums *et al.* 1983) or dip nets. Unmarked females were banded with conventional leg bands and aged using two different methods. First, about 66 300 day-old ducklings were marked individually using plasticine-filled leg bands

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(Blums, Mednis & Nichols 1994; Blums *et al.* 1999); subsequent recaptures of these birds as breeding females allowed us to assign them exact ages. Secondly, unmarked, incubating females were aged as yearlings (SY) or adults (ASY) using wing feather characteristics (Blums *et al.* 1996).

The survival and fidelity analyses were based on recaptures of these known-age birds at Engure Marsh and on band recoveries of birds shot and found dead at locations throughout Europe and north-west Asia. A large fraction of the recoveries came from hunting on Engure Marsh following the breeding season. More detailed information on the study site, field methods, predator control, and breeding populations is provided elsewhere (Blums *et al.* 1996; Viksne 1997; Viksne 2000).

DATA-ANALYTICAL APPROACH

In order to estimate both survival and fidelity, we used the model developed by Burnham (1993; see also Szymczak & Rexstad 1991) and based on both recapture and recovery data of marked birds. The following parameters are used in the modelling:

S_t = true survival; probability that a bird alive at the time of sampling (May–June) in year t is alive at the time of sampling in year $t + 1$;

F_t = fidelity probability; probability that a bird associated with Engure Marsh at the time of sampling in year t is still associated with (has not permanently emigrated from) Engure Marsh at the time of sampling in year $t + 1$, given that it is alive at that time;

p_t = capture probability; probability that a bird associated with Engure Marsh in the sampling period in year t is caught at that time;

r_t = reporting rate; probability that a marked bird that dies during the year interval between sampling occasions t and $t + 1$ is found and reported to the Latvian Bird Ringing Center.

Note that the above definitions of fidelity and capture probability admit the possibility of temporary emigration (Kendall, Nichols & Hines 1997) in which a bird might not breed in a particular year (hence not available for capture at Engure Marsh), yet still not be classified as a permanent emigrant from the marsh.

The basic idea underlying the model of Burnham (1993) is simple. Local survival rates estimated from capture–recapture data alone estimate the product of survival and fidelity to the study area (denoted product as S_tF_t). However, survival rates estimated from widespread band recoveries estimate true survival (S_t), as it is usually not possible for birds to permanently emigrate from all areas at which there is some chance of being recovered. An *ad hoc* approach for estimating F_t is simply to divide the local survival rate estimated from capture–recapture data by the true survival estimate based on band recovery data for the same birds (see Anderson & Sterling 1974; Hepp, Hoppe & Kennamer 1987; Blums *et al.* 1996). Burnham's (1993) approach includes both types of data (recoveries and recaptures) in the same likelihood, permitting direct estimation of both survival and fidelity.

We considered a number of different models in the *a priori* model set for each species and use notation similar to that suggested by Lebreton *et al.* (1992) to designate these models. For all four types of parameters, we designate a model including time-specific variation in a parameter using a 't' subscript, age with an 'a' subscript, and absence of variation over time and/or age with a '$(.)$'subscript. In addition, we developed notation for models with survival and/or fidelity modelled as a function of covariates.

Survival was modelled as a linear-logistic function of winter temperatures on Western European wintering grounds, and models containing this relationship were designated with the subscript '*wtemp*'. We used mean winter temperatures (December–February) in Denmark because mean winter anomalies (deviations from long-term mean temperature) in Denmark and Central Europe were strongly correlated (Frederiksen & Bregnballe 2000). Central Europe and the Atlantic coast (from France to Denmark) are important Latvian diving duck wintering grounds where median positions of winter recoveries for both species were located (Blums & Baumanis 1990), further supporting the use of Danish temperature data.

Based on our *a priori* hypotheses and predictions, as well as on common approaches for reducing numbers of parameters, we investigated several specific patterns of temporal variation in fidelity (see Tables 2 and 3). In addition, *a priori* hypotheses and predictions led us to develop models that included linear-logistic relationships between fidelity F_t and covariates associated with water conditions and reproduction (see Tables 2 and 3).

Model selection, and thus inferences about sources of variation in survival and fidelity, were based on Akaike's information criterion (AIC) (Akaike 1973; Burnham & Anderson 1998). We first assessed fit of the most general model in each data set using the bootstrap approach implemented in program MARK (White & Burnham 1999). Three hundred data sets were simulated based on the parameter estimates from the actual data, and the resulting deviances were compared with the deviance obtained using the actual data. In cases where there was some evidence of lack of fit, variance inflation factors, $\hat{c}$, were computed in MARK as the ratio of the deviance from the actual data to the mean deviance from the bootstrap replicates. These $\hat{c}$ values were used to compute quasilikelihood AIC values adjusted for sample size, QAICc (Burnham & Anderson 1998). Model-based standard error estimates were multiplied by $\sqrt{\hat{c}}$ in order to estimate standard errors adjusted for lack of fit (e.g. see Lebreton *et al.* 1992). Akaike weights (Burnham & Anderson 1998) were computed as reflections of relative evidence supporting each model. Although these weights sum to one for all the models in the model set, our tabled results do not include all models we considered; hence the weights will not sum to one for each table.

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Table 1. Number of newly marked releases, subsequent recaptures and dead recoveries of nesting female ducks from permanent study areas on Engure Marsh, Latvia

Species	Period	New releases	Live recaptures	Dead[a] recaptures	Dead[b] recoveries
Northern shoveler	1960–94	536	370	10	96
Common pochard	1976–92	1718	1551	56	175
Tufted duck	1976–92	809	1205	22	91

[a]Marked females that were killed on nests by different predators.
[b]Band recovery information was obtained from the Latvian Bird Ringing Center.

Results

BANDING, RECAPTURE AND RECOVERY DATA

We used samples of 3063 new releases, 3126 live recaptures and 362 dead recoveries of nesting female ducks to estimate true survival and breeding site fidelity at the Engure Marsh study site during two different time periods (Table 1).

MODEL FIT AND VARIANCE INFLATION FACTORS

The general model considered for the northern shoveler was model ($S_t\, p_t\, r_t\, F_t$), as recovery data were limited for this species and inadequate for fitting a full model with *SY* and *ASY* birds as separate ages. The deviance under this model was large relative to the bootstrap distribution indicating evidence of lack of model fit. We estimated the variance inflation factor as $\hat{c} = 1{\cdot}44$.

The general model for the pochard was model ($S_{a*t}\, p_{a*t}\, r_{a*t}\, F_{a*t}$) allowing full age by time interactions for each set of model parameters. The deviance under this model was large relative to the distribution of bootstrap deviances yielding a variance inflation of $\hat{c} = 1{\cdot}15$.

The full data set for tufted ducks contained a number of birds that were not aged and thus could not be used for fitting age-specific models. Thus, we first fit the general model ($S_{a*t}\, p_{a*t}\, r_{a*t}\, F_{a*t}$) to the reduced data set of aged birds. Using this reduced data set of aged birds, comparison of QAICc values for models ($S_{a*t}\, p_{a*t}\, r_{a*t}\, F_{a*t}$) and ($S_t\, p_t\, r_t\, F_t$), as well as for time-constant models with and without age, provided no evidence that any of the parameters exhibited age-specific variation. Thus, we decided to use the full data set including unaged incubating females and fitted general model ($S_t\, p_t\, r_t\, F_t$). The deviance of this model was somewhat large when compared to the distribution of bootstrap deviances, and the resulting variance inflation factor was computed as $\hat{c} = 1{\cdot}11$.

NORTHERN SHOVELER

The most parsimonious model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{c2}$; Table 2) had only five structural parameters: constant survival, capture and reporting probabilities but fidelity probabilities that were modelled as constant within each of the two time periods (before [1960–82] and after [1983–94] reconstruction of nesting islands) but different between the two periods. Surviving adult females of all ages returned to the previous breeding sites on islands of Engure Marsh with an estimated fidelity probability of 0·88 ($\widehat{SE} = 0{\cdot}05$) during the first period. However, during the second period, fidelity was estimated as 1·0. Note that this estimate on the boundary of the parameter space precludes estimation of SE and leads to a reduction in the number of estimable parameters (see Table 2). The most parsimonious model produced these time-constant parameter estimates: true annual survival ($\hat{S} = 0{\cdot}52$, $\widehat{SE}[\hat{S}] = 0{\cdot}02$), capture probability ($\hat{p} = 0{\cdot}81$, $\widehat{SE}[\hat{p}] = 0{\cdot}03$), and reporting probability ($\hat{r} = 0{\cdot}19$, $\widehat{SE}[\hat{r}] = 0{\cdot}02$).

We considered several other biologically reasonable models for fidelity that were supported (small

Table 2. Model selection results for northern shoveler

Model[a]	ΔQAICc[b]	Model weight[c]	Np[d]
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{c2}$	0·0	0·14	4
$S_{(c2)}\, p_{(.)}\, r_{(.)}\, F_{c2}$	0·41	0·11	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat2}$	0·67	0·10	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat1}$	1·98	0·08	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*succ}$	1·76	0·06	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*linear}$	1·95	0·05	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*prod}$	2·01	0·05	5
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat1*wat2}$	2·60	0·04	6
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat2*succ}$	2·67	0·04	6
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*succ}$	2·99	0·03	6
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	4.85	0.01	4
$S_t\, p_t\, r_t\, F_t$	208·96	0·0	137

[a]Model subscripts/covariates:
(.) = absence of variation over time and/or age; *c2* = parameter that is modelled as one constant during 1960–82 (prior island construction), and as a different constant during 1983–94 (following island construction); *tc* = time dependence in fidelity 1960–82, but constant 1983–94; *t* = time-dependence all period; *wat1* = water level metrics at nesting sites during early spring in year *t* + 1; *wat2* = water level metrics in year *t*; *succ* = mean annual nest success in year *t*; *linear* = linear trend (logit scale) in fidelity over time 1960–82; *prod* = total production of day-old ducklings at permanent study areas in year *t*.
[b]The difference between the QAICc value for the model with the lowest QAICc value and the model in question.
[c]Akaike model weights reflect relative weight of evidence in favour of the model in question given the model set and data.
[d]Number of parameters.

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Table 3. Model selection results for common pochard

Model[a]	ΔQAICc[b]	Model weight[c]	Np[d]
$S_{wtemp}\, p_t\, r_{(.)}\, F_a$	0·0	0·31	20
$S_{wtemp}\, p_t\, r_{(.)}\, F_{a*succ}$	1·42	0·15	22
$S_{wtemp}\, p_t\, r_{(.)}\, F_{a+t,\, prod}$	1·52	0·14	21
$S_{wtemp}\, p_t\, r_{(.)}\, F_{a*linear}$	1·79	0·13	23
$S_{a+t,\, wtemp}\, p_t\, r_{(.)}\, F_a$	1·94	0·12	21
$S_{a*t}\, p_{a*t}\, r_{a*t}\, F_{a*t}$	134·68	0·0	128

[a]Model subscripts/covariates: t = time-dependence, a = age dependence (*SY* and *ASY* females), *wtemp* = mean winter temperature in Western European wintering grounds, *linear* = linear trend (logit scale) over time.

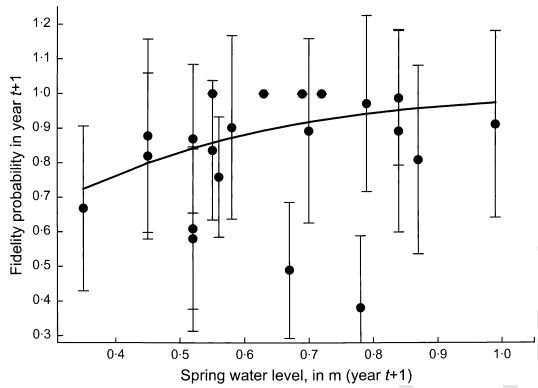

Fig. 1. Fidelity probability (± SE) of breeding female northern shovelers as a function of spring water level at Engure Marsh nesting sites during the premanagement period 1960–82. Point estimates shown are from the model with full time variation ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc}$), whereas the curve is based on estimates from the covariate model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat1}$). Note that reliable estimation of SE is not possible for fidelity estimates on the boundary of the parameter space.

ΔQAICc) by the data (Table 2). The model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat1}$), with spring water level in year t + 1 as a time-specific group covariate for fidelity during 1960–82, was supported by the data (ΔQAICc = 0·98) and suggested a weak positive relationship (slope parameter, $\hat{\beta}$ = 4·14, $\widehat{SE}[\hat{\beta}]$ = 4·59; approximate 95%CI = −4·83–13·17) between spring water level and the proportion of surviving females returning that same spring (Fig. 1). We obtained very similar results ($\hat{\beta}$ = 4·14, $\widehat{SE}[\hat{\beta}]$ = 3·7; 95%CI = −3·12–11·4; ΔQAICc = 0·67) when spring water level in year t (rather than in year t + 1) was included as a group covariate in the model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{tc*wat2}$). There was some support (ΔQAICc = 1·76) for our prediction that fidelity rates should be positively correlated with prior nest success; however, this model provided an imprecise estimate of the slope ($\hat{\beta}$ = 3·06, $\widehat{SE}[\hat{\beta}]$ = 7·0) with quite a large 95% confidence interval (95%CI = −10·64–16·77). In addition to alternative models for fidelity, we note that model ($S_{c2}\, p_{(.)}\, r_{(.)}\, F_{c2}$) also received support ΔQAICc = 0·41. Under this model, the survival probability estimate was smaller than before the construction of nesting islands ($\hat{S}$ = 0·49; $\widehat{SE}[\hat{S}]$ = 0·03) than during the years following construction ($\hat{S}$ = 0·55; $\widehat{SE}[\hat{S}]$ = 0·03).

COMMON POCHARD

The most parsimonious model for pochards ($S_{wtemp}\, p_t\, r_{(.)}\, F_a$) had 20 parameters, including a relationship between annual survival and the winter temperature covariate, time-dependence for capture probabilities and age-specific variation for fidelity probability (Table 3). There was a substantial difference between ΔQAICc values for the model ($S_{wtemp}\, p_t\, r_{(.)}\, F_a$) with age-specific variation in fidelity (ΔQAICc = 0·00) and the reduced model ($S_{wtemp}\, p_t\, r_{(.)}\, F_{(.)}$; ΔQAICc = 12·38), providing strong support for the model with age-specific variation. Thus our prediction about similar fidelity rates for *SY* and *ASY* females was not supported. The estimated fidelity probability for *SY* females ($\hat{F}$ = 0·88, $\widehat{SE}[\hat{F}]$ = 0·03) was lower than that for *ASY* birds ($\hat{F}$ = 1·00, SE not estimable).

In the most parsimonious model true annual survival probability varied over time. We used the random effects approach (Burnham *et al.* 1987) implemented in program MARK (Cooch & White 2001) on model ($S_t\, p_t\, r_t\, F_{a*t}$) to estimate the mean ($\bar{S}$ = 0·66, $\widehat{SE}[\bar{S}]$ = 0·02) and the true temporal variance (process variance = $\sigma^2[S_t]$) of pochard survival ($\hat{\sigma}[S_t]$ = 0·03, 95%CI = 0·0–0·09). Survival was positively related ($\hat{\beta}$ = 0·11, $\widehat{SE}[\hat{\beta}]$ = 0·02; 95%CI = 0·06–0·15) to mean winter temperatures in Western Europe (Fig. 2). Temporal variation in capture probability was also treated as a random effect, yielding an estimate of the mean, $\bar{p}$ = 0·73, $\widehat{SE}(\bar{p})$ = 0·02, and the true temporal variance ($\hat{\sigma}[p_t]$ = 0·06, 95%CI = 0·03–0·11). The constant reporting probability estimate ($\hat{r}$ = 0·12, $\widehat{SE}[\hat{r}]$ = 0·01) was lower than respective estimates for shoveler and tufted duck.

Model ($S_{wtemp}\, p_t\, r_{(.)}\, F_{a*succ}$) with mean annual nest success as a covariate for modelling fidelity was supported by the data also (ΔQAICc = 1·42) and suggested a positive relationship ($\hat{\beta}$ = 3·11, $\widehat{SE}[\hat{\beta}]$ = 2·98; 95%CI = −2·72–8·95) between nest success in year t and fidelity in year t + 1 (F_t) for *SY* females (Fig. 3). The fidelity estimate for *ASY* females was 1·0, so it did not make sense to ask questions about covariate relationships for this age group.

TUFTED DUCK

As noted above, we first conducted exploratory analyses with two age groups (*SY* and *ASY*) and then used QAICc for model selection to determine whether two age groups were needed in modelling any of the parameters. The model with the lowest QAICc did not include any age-specific parameters. This result allowed us to (i) use only one age group (*SY* + *ASY* females) in all further analyses and (ii) include in the data set all captured nesting females of unknown age. We generally prefer the approach of using QAICc in conjunction with a single data set and a single *a priori* model set, but our two-step approach seemed

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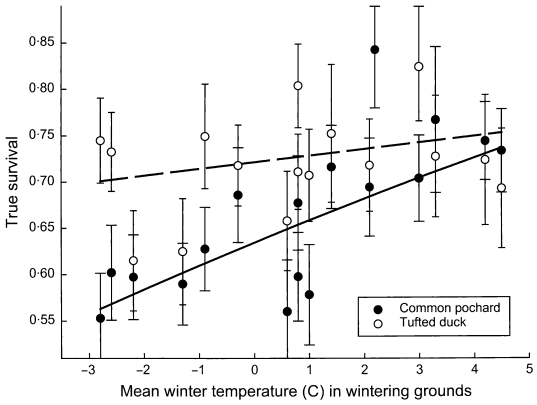

Fig. 2. True survival (± SE) of female common pochards and tufted ducks estimated as a function of mean winter (December–February) temperatures in Western European wintering grounds. For pochard, the point estimates shown are from the model with full time variation ($S_t\, p_t\, r_{(.)}\, F_a$), and the curve (solid line) is based on estimates from the covariate model ($S_{wtemp}\, p_t\, r_{(.)}\, F_a$). For tufted duck, the point estimates shown are from the model with full time variation ($S_t\, p_{(.)}\, r_{(.)}\, F_{prod}$), and the curve (dashed line) is based on the covariate model ($S_{wtemp}\, p_{(.)}\, r_{(.)}\, F_{prod}$).

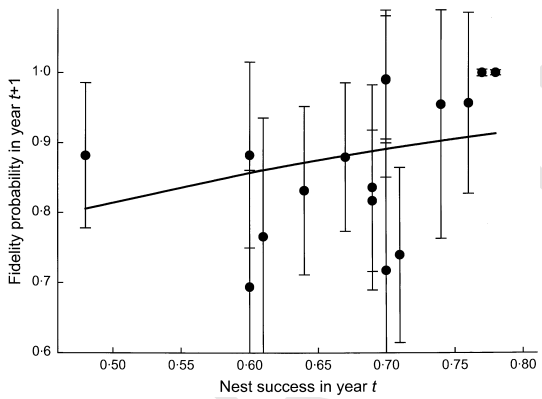

Fig. 3. Fidelity probability (± SE) of yearling female common pochards as a function of apparent nest success at permanent study areas in Engure Marsh. Point estimates shown are from the model with full time variation ($S_{wtemp}\, p_t\, r_{(.)}\, F_{a*t}$), whereas the curve is based on estimates from the covariate model ($S_{wtemp}\, p_t\, r_{(.)}\, F_{a*succ}$).

reasonable in this case, especially given the ability to increase the data set with birds of unknown age.

Subsequent analysis with one pooled age group revealed that the most parsimonious model was one with no temporal variation in any of the model parameters (Table 4). This reduced model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$) generated these parameter estimates: true survival ($\hat{S} = 0{\cdot}72$, $\widehat{SE}[\hat{S}] = 0{\cdot}02$) capture probability ($\hat{p} = 0{\cdot}80$, $\widehat{SE}[\hat{p}] = 0{\cdot}01$), reporting rate ($\hat{r} = 0{\cdot}13$, $\widehat{SE}[\hat{r}] = 0{\cdot}01$), and fidelity probability ($\hat{F} = 0{\cdot}97$, $\widehat{SE}[\hat{F}] = 0{\cdot}02$). Other biologically reasonable candidate models included model ($S_{wtemp}\, p_{(.)}\, r_{(.)}\, F_{prod}$) with temporal variation in survival associated with winter temperature and temporal variation in fidelity associated with duckling production (ΔQAICc = 0·72). This model provided

Table 4. Model selection reults for tufted dock

Model[a]	ΔQAICc[b]	Model weight[c]	Np[d]
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	0·0	0·27	4
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{prod}$	0·12	0·26	5
$S_{wtemp}\, p_{(.)}\, r_{(.)}\, F_{prod}$	0·72	0·19	6
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{linear}$	1·18	0·15	5
$S_{wtemp}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	1·70	0·12	5
$S_t\, p_{(.)}\, r_{(.)}\, F_{(.)}$	6·71	0·01	20
$S_{(.)}\, p_{(.)}\, r_{(.)}\, F_t$	15·07	0·0	19
$S_t\, p_t\, r_t\, F_t$	57·78	0·0	64

See notations in Tables 2 and 3.

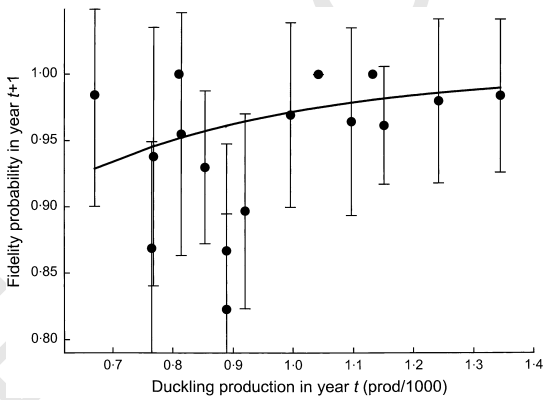

Fig. 4. Fidelity probability (± SE) of breeding female tufted ducks as a function of total duckling production at permanent study areas in Engure Marsh. Point estimates shown are from the model with full time variation ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_t$), whereas the curve is based on estimates from the covariate model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{prod}$).

good evidence that fidelity rates increased ($\hat{\beta} = 3{\cdot}72$, $\widehat{SE}[\hat{\beta}] = 2{\cdot}41$; 95%CI = −1·0–8·45) after years of good duckling production (Fig. 4). In addition, survival estimates under this model were modelled as a function of mean winter temperatures at wintering grounds ($\hat{\beta} = 0{\cdot}04$, $\widehat{SE}[\hat{\beta}] = 0{\cdot}03$; 95%CI = −0·02–0·10), suggesting that survival was higher during mild winters (Fig. 2). Nevertheless, this relationship between winter temperature and survival was weaker than that for pochard. Finally, the model ($S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{linear}$) incorporated a linear trend in fidelity and provided some evidence that fidelity rates declined over time at the Engure Marsh study site ($\hat{\beta} = -0{\cdot}09$, $\widehat{SE}[\hat{\beta}] = 0{\cdot}1$; 95%CI = −0·29–0·11; ΔQAICc = 1·18).

Discussion

The survival estimates for the three species were generally consistent with *a priori* expectations based on the literature of waterfowl population dynamics. For example, members of *Aythya* tend to have higher survival rates than members of *Anas* (e.g. see Johnson *et al.* 1992; Krementz, Barker & Nichols 1997), and the

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survival estimates were consistent with this pattern and with the general magnitudes of estimates expected from these two groups. Estimated recapture probabilities were extremely high for such a large-scale study. Temporary emigration (e.g. absence from the breeding area one year followed by a return in a subsequent year) was not addressed in this study, but is confounded typically with capture probability (Kendall *et al*. 1997). Temporary emigration probability cannot be larger than the complement of capture probability, $1 - p$, and was thus necessarily small in this study.

Fidelity and permanent emigration are virtually impossible to estimate using methods other than Burnham's (1993) model, so there are few estimates with which ours can be compared. The high estimates of fidelity are consistent with our expectations for these three species based on *ad hoc* methods for drawing inferences about fidelity (Blums *et al*. 1996). More generally, high fidelity to breeding areas has characterized the few species about which reasonable inferences have been drawn (Hepp *et al*. 1987; Lindberg *et al*. 2001; Doherty *et al*. 2002).

SURVIVAL AND WINTER TEMPERATURES

There was good evidence for an effect of temperatures on Western European wintering grounds on pochard survival, with predicted survival rates varying substantially over a moderate range of mean winter temperatures. The evidence of such a relationship was weaker for tufted ducks. The difference we found between the two species is not surprising because pochards, being inferior divers, are believed to be more vulnerable to food shortages occurring during harsh winter conditions on European wintering grounds and consequently may suffer higher mortality (Suter & van Eerden 1992). Evidence of a positive relationship between annual survival rates and winter temperatures has been provided for two other waterbird species wintering in Western Europe, common gulls (*Larus canus* L.; Rattiste & Lilleleht 1995) and cormorants (*Phalacrocorax carbo sinensis* [Blumenbach]; Frederiksen & Bregnballe 2000).

Despite general thinking that bad weather on wintering grounds should translate into lower annual survival, there has been very little evidence from previous work of such a relationship for waterfowl (e.g. see Fredga & Dow 1984). Perhaps one reason for this involves the integrative nature of annual survival rate. Annual survival can be viewed as the product of survival probabilities corresponding to shorter periods (e.g. as the product of 12 monthly survival probabilities). Thus, any 'signal' associated with the effects of an environmental variable on survival at one time of the year must be very strong to be detected in the presence of the noise associated with survival during the other times of the year, and their corresponding environmental influences (Nichols 1991). The evidence of an effect of wintering ground temperatures on pochard survival is stronger than any we have seen previously for any waterfowl species.

FIDELITY: AGE-SPECIFICITY

We predicted either no age-specificity of fidelity or, if age-specific differences were found, we predicted lower fidelity for *SY* females. Number of recoveries for both age classes were not adequate to investigate age-specificity in any parameters for shovelers. For the two species of *Aythya*, we found strong evidence of age-specific differences in fidelity for pochards, but very little evidence of age differences for tufted ducks. Fidelity estimates were 0·88 for *SY* pochards and 1·0 for *ASY* pochards. For tufted ducks of both ages, the fidelity estimate was 0·97.

The magnitudes of fidelity estimates are strongly influenced by the study design and the study area (Doherty *et al*. 2002), and we thus present a brief discussion of the nature of permanent emigration in this study. Because < 50% of pochards and tufted ducks from the marsh population nested within permanent sampling areas it cannot be ruled out that a small percentage of female diving ducks (defined as permanent emigrants for this study design) simply moved to other areas of the Engure Marsh and escaped capture. Our permanent sampling plots were partially isolated areas, separated from the rest of the marsh by large areas of open water or monotypical stands of reedbeds. The latter were never used by nesting shovelers and tufted ducks; however, some female pochards occasionally nested at these monotypical reedbeds. Overall, movements outside permanent study plots within the marsh were rare for both diving ducks, especially tufted duck.

Furthermore, we examined all band recovery information of females captured on nests and looked for direct evidence of long-distance breeding dispersal movements (emigration) out of Engure Marsh. Surprisingly enough, eight female tufted ducks were killed by hunters in non-migrational directions (European portions of Russia and north-west Asia) during the following breeding seasons (May–July) or shortly after (August–October). These recoveries were 800–2500 km away from previous nesting sites at Engure Marsh, clearly suggesting that these females did emigrate. None of these tufted ducks was marked at hatch, so it is unlikely that they were hatched at Engure Marsh and were probably temporary immigrants from areas located far away from Engure Marsh. In addition, these eight females nested at Engure only 1–2 breeding seasons, providing additional support for the idea that they were temporary immigrants. These data suggest that our fidelity estimate (0·97) for tufted ducks should reflect fidelity to the entire Engure Marsh and the very low estimate of permanent emigration (0·03) should reflect the true emigration rate out of the Engure Marsh to other distant nesting areas located up to 2500 km away. Long-distance breeding dispersal movement (emigration) of female tufted ducks to

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north-west Asia is a unique phenomenon and to our knowledge has not been documented in any other species of European waterfowl.

For pochards, there was no evidence of long-distance (> 600 km) emigration, however, we did record six band recoveries out of Engure Marsh in non-migrational directions (range 200–600 km), indicating that some females emigrated after attempting to breed at Engure. All these females were unbanded when first captured and were most probably young birds (two were aged as yearlings, one as 2-year-old, three of unknown age), and none nested more than once at Engure. These results suggest that the emigration rate (0·12) estimated for *SY* females probably reflects local movements out of permanent study plots within the marsh (mean breeding dispersal distances were 315 m [$\widehat{SE}$ = 36; n = 438] and 263 m [$\widehat{SE}$ = 17; n = 1447] for *SY* and *ASY* females, respectively) and some limited emigration (< 600 km) out of the marsh in nonmigrational directions. We suspect that some *SY* females may have emigrated out of Engure Marsh and settled along the Atlantic Flyway between Western European wintering areas and the Engure Marsh. These recoveries indicating emigration in the direction of normal fall migration cannot be separated from the rest of the recoveries occurring along migratory routes.

The new modelling approach and the additional data allowed us to reconsider our earlier tentative conclusion (Blums *et al*. 1996) that much of the difference between survival estimates of *SY* vs. *ASY* females for pochards reflected mortality rather than emigration. Our previous survival estimates (Blums *et al*. 1996) were based on capture–recapture data and thus reflected 'local' or 'apparent' survival. The models we used did not provide separate estimates of survival and permanent emigration. The combined models we used in this study, unlike capture–recapture models, provided no evidence of age-specificity, suggesting that the previously reported difference in pochard apparent survival could be at least partially attributed to different fidelity (estimates of 0·88 and 1·0) for females of the two age classes. Thus, incorporation of capture–recapture and band recovery information in a single model allowed us to improve precision and estimate true survival and fidelity/emigration at the same time.

We suggest that most confirmed emigrants of both diving duck species from our study system were birds of foreign origin that had temporarily immigrated to Engure and then moved away after 1–2 nesting attempts. We believe that the origin of these birds was more important than nest success as a determinant of emigration probability, because most (*c*. 80%) of these emigrants hatched broods successfully at their last nesting attempt on Engure Marsh.

FIDELITY: REPRODUCTIVE SUCCESS

There is an ample evidence that nest success may influence the probability of returning to the breeding area next year for birds in general (Gauthreaux 1982; Greenwood & Harvey 1982) and ducks in particular (Mihelsons *et al*. 1986; Lokemoen, Duebbert & Sharp 1990; Majewski & Beszterda 1990; Anderson *et al*. 1992; Johnson *et al*. 1992). Discussions of this relationship, and the study designs used to investigate it, are not always clear about whether the reproductive success that is the relevant cue to movement 'decisions' is measured at the level of the individual or the patch. The success or failure of an individual bird is a simple Bernoulli trial, and failure in a good location will generally not be a rare event. Reproductive success of many birds in a patch provides stronger evidence about the 'quality' of the area for nesting and brood-rearing and should be used as a cue, if it can be readily assessed (e.g. Danchin & Wagner 1997).

In terms of study design, it might be difficult to demonstrate an association between fidelity and success at the individual level if patch success is a more important cue than the success of individual birds (Switzer 1997; Doligez *et al*. 1999). For example, preliminary analyses (P. Blums, unpublished data) failed to lend support to the idea that breeding dispersal distances of successful breeders are shorter than those of unsuccessful breeders. However, in the present study, when we modelled fidelity as a function of apparent nest success of birds nesting at permanent plots (presumed patch success), we found a positive relationship between nest success in year t and fidelity in year $t + 1$ (F_t) for both pochards and shovelers. Thus, our prediction that fidelity rates should increase after years of higher nesting success was partially supported. However, for both species (especially shoveler), our slope estimates for the relationship were imprecise and confidence intervals large, perhaps because there was not much variation in success rates over time and overall nest success was high for all species. The relationship was stronger for pochard (with the lowest mean apparent nest success of 0·68) than for shoveler (apparent nest success 0·72). We found no evidence for this relationship for tufted duck, probably because the unweighted mean apparent nest success (0·81) was very high for this species. However, when we included the total number of day-old ducklings that hatched at permanent plots as a time-specific covariate in the model, we did find evidence of a positive relationship between duckling production and fidelity for the tufted duck. This relationship was positive also for pochard and shoveler; however, nesting success was a better predictor for these two species (see above). In contrast, the relationship between duckling production and subsequent offspring recruitment was negative in all three species (Blums, Clark & Mednis 2002).

FIDELITY: MANAGEMENT ACTIVITIES

Shovelers nested almost exclusively on the islands within permanent sampling areas, thus the entire local breeding population was monitored each year. Nesting

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female shovelers returned to the islands of Engure Marsh with constant probability of 0·88 during the 23-year period prior to construction of artificial islands and provision of critical improvements in nesting habitats (see Hypotheses and Predictions). During this period nesting habitats for shoveler were limited, as potential habitat on small islands (especially islands C and D) was frequently unavailable. Emigration rate of female shovelers was quite high (0·12) during this premanagement period.

Construction of artificial islands resulted in an increase in the amount of stable and predictable nesting habitat, and fidelity rate estimates jumped to the maximum of $\hat{F} = 1{\cdot}0$. Nesting habitat improvements, high nest success (0·79) and complete fidelity (1·0) resulted in a dramatic increase in the breeding population during the second half of the postmanagement period (annual averages were 52 nests during 1989–94, vs. 32 nests during 1960–88). Territorial behaviour is believed to limit population size of shovelers (Poston 1974; Vickery & Nudds 1984), and the nesting population was indeed quite stable for the initial 29 years of the study. We believe that fragmentation of islands not only improved the quality of nesting sites but also provided more open water interspersions required for isolation of each pair during the nesting period. As a result, carrying capacity of shoveler breeding habitats at Engure Marsh increased, and population size responded. Although shoveler home ranges can overlap to different degrees (Poston 1974), concentrated nesting has never been reported for this species (Cramp & Simmons 1977; DuBowy 1996). In this regard our density records of 39 nests/ha on an isolated cluster of five islands (total area 0·4 ha) in 1991 is probably the highest ever reported for shoveler. The density was even higher (100 nests/ha) if only one island (0·04 ha) of this cluster was considered. The two closest active nests were located only 1 m apart. These findings suggest that stable, high quality habitat conditions during the prebreeding and breeding periods (enlarged areas of shallow water optimal for feeding and courtship, constant predator control and attraction of gulls, establishment of grassy nesting cover and removal of trees and bushes, fragmentation of natural islands and destruction of robust emergents among and around the nesting islands) were critical cues that determined site fidelity and settling patterns in shoveler.

The population-dynamic consequences of habitat management are frequently difficult to assess, and we suggest that fidelity is a very useful parameter for this purpose. For avian species, local habitat can be related readily to at least one component of reproduction, nest success (e.g. Cowardin, Gilmer & Shaiffer 1985; Greenwood *et al.* 1995). Avian movements among habitats create difficulties when trying to estimate habitat-specific survival probabilities or to assess effects of habitat management on survival (Conroy 1993; Conroy *et al.* 1996). Fidelity is a parameter that should reflect the integration of fitness components. As long as habitat quality is predictable, in the sense that fitness realized in an area in one year should be a good predictor of fitness the next year, fidelity should provide an excellent measure of quality. Population-dynamic consequences of habitat management are notoriously difficult to assess (Johnson, Williams & Schmidt 1996), and we suggest that fidelity is a good parameter for such an assessment. Specifically, we view the increase in shoveler fidelity to Engure Marsh following intensive management activities as evidence of the effectiveness of these management actions. We believe the breeding shoveler population was near saturation during the premanagement period when emigration rate was high (0·12) yet stable and there was no evidence of trend or other temporal variation in fidelity.

FIDELITY: WATER LEVELS

During the years before intensive island management, we found some evidence that fidelity rates of shovelers tended to increase when spring water levels were high (both in year t and year $t + 1$), probably as a result of improved habitat quality (better access to nesting sites, improved pair isolation and foraging conditions) created by spring flooding during the prelaying and laying period. Good feeding conditions are especially critical for shovelers because females spend up to 3 weeks on the nesting sites storing nutrient reserves before the onset of egg laying (Afton 1979). Because shovelers are highly specialized foragers (Nudds & Bowlby 1984), females need specific habitat conditions and relatively more time than other dabbling ducks to supply nutrients for clutch completion. Study results thus provide evidence of an interaction between marsh management and water levels as determinants of fidelity and suggest that management activities increased the quality and predictability of nesting habitat to the extent that high fidelity existed regardless of water levels in the postmanagement period. We do not have any band recovery information on long-distance breeding dispersal movements of female shovelers, so we believe emigrants settled within a 200-km radius of Engure Marsh.

METHODOLOGY

In this study we made use of two types of data that will commonly be available for intensive capture–recapture studies of hunted species, live recaptures and dead recoveries. When used with models such as that of Burnham (1993), these data permit estimation of true annual survival rates and rates of fidelity, defined here as the complement of permanent emigration. Reasonable methods for estimating survival rates from capture–recapture and band-recovery data have been available for three decades (e.g. Jolly 1965; Seber 1965; Seber 1970), and survival rates have been estimated and studied for numerous waterfowl species (e.g. see Johnson *et al.* 1992; Krementz *et al.* 1997).

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Fidelity, on the other hand, has been investigated primarily via *ad hoc* methods that have not yielded strong inferences (Johnson *et al.* 1992). The ability to estimate and model this parameter is an important addition to the ecologist's methodological toolbox, as fidelity is the subject of numerous ecological and evolutionary hypotheses (e.g. Greenwood 1980; Greenwood & Harvey 1982; Anderson *et al.* 1992). The approach of Burnham (1993) is easily implemented in program MARK (White & Burnham 1999). Because waterfowl species are often hunted (primary source of recoveries), they are well suited for investigations of fidelity using this approach, and we recommend additional analyses of the type presented here (also see Doherty *et al.* 2002).

We note that some definitions of fidelity include both permanent and temporary emigration in its complement, whereas the approach of Burnham (1993) permits inference about permanent emigration only. Kendall *et al.* (1997) provided a means of estimating probabilities of temporary emigration using capture–recapture data collected according to the robust design of Pollock (1982). Recently, Lindberg *et al.* (2001) developed a model that combined the approaches of Burnham (1993) and Kendall *et al.* (1997) and thus permitted estimation of both temporary and permanent emigration. We believe that this model has the potential to be very useful and that researchers interested in fidelity should strongly consider the use of multiple sampling periods per breeding season in order to exploit this modelling approach.

In conclusion, statistical methods now exist to estimate fidelity properly and to investigate sources of variation in this parameter. The biological question(s) of interest will be the primary determinant of both logistical study design and statistical estimation methodology.

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