

# Measuring within-winter movement rates of Tufted Duck *Aythya fuligula* and Common Pochard *A. ferina* based on ring re-encounter data

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## Abstract

Within-winter movements of birds are of interest for the identification of sub-populations and for the assessment of the risk of bird-transmitted diseases. The probability of a Tufted Duck *Aythya fuligula* or a Common Pochard *A. ferina* wintering in the Alpine region leaving this area during winter was estimated from capture and ring re-encounter data. A multi-state model was used to estimate this movement probability for each two-week period. Bias and precision of parameter estimates of the multi-state model were assessed using simulated data. These simulations indicated that there was a low level of bias in the estimated movement probabilities, but that precision levels were also low. The probability of Tufted Duck and Common Pochard moving >200 km from the ringing site within a two-week period after ringing was estimated at around 90% for both species. Although the precision of this estimate was low, by presenting the first quantitative measures of individual diving duck movements between the Alpine region and the rest of the Europe, the study contributes to an understanding of the within-winter dispersal of ducks across Europe.

**Key words:** bias, movement rates, multi-state model, precision, ring re-encounter data.

In contrast to seasonal migration patterns, within-winter movements have been studied less frequently. Previous studies have investigated the association between winter movements and cold weather conditions (Rustamov 1994; Ogilvie 1981; Ridgill & Fox 1990). However, in diving ducks within-

winter movements can occur independently of harsh weather conditions and over long distances (Keller *et al.* 2009; Sauter *et al.* unpubl. data). These movements can have important effects on population structure and on the extent to which individuals of different breeding populations mix during

winter (migratory connectivity; Webster *et al.* 2002). The occurrence of avian influenza has increased interest in patterns of movement, because birds are potential vectors of this virus (Atkinson *et al.* 2007). Up to now only indirect or relative measures of movement rates have been determined (*e.g.* Ridgill & Fox 1990; Kestenholz 1995; Keller *et al.* 2009). In this study, a model was constructed which estimated absolute movement rates of Tufted Duck *Aythya fuligula* and Common Pochard *A. ferina* (hereafter called Pochard) from the Swiss lakes north of the Alps (*i.e.* Lake Geneva to Lake Constance) to the rest of the European wintering area, using capture and ring re-encounter data. A multi-state model (Arnason 1972; Burnham 1993; Schwarz 1993) was adapted so that it could be used to estimate within-winter movement rates. This estimation was particularly challenging because the probability of re-encountering a metal-ringed diving duck within the same winter season is extremely low and re-encounter data are especially scarce. This made it very likely that the constructed models would be overparameterised, that some parameters would not be identifiable, and that the parameters would also be biased or show low precision (Schwarz 1993; Schaub 2009). We therefore used simulated data to test our model and tried in several ways (see Methods) to improve parameter estimates.

## Methods

### Species and study area

The two main study species were the Tufted Duck and the Pochard. Both species winter in central, western and southern Europe. In

Switzerland, January counts average 160,000 for Tufted Duck and 80,000 for Pochard (Keller & Burckhardt 2007). Both species are known to undertake more extensive within-winter movements than other duck species (Keller *et al.* 2009; Sauter *et al.* unpubl. data). Birds wintering in Switzerland regularly move to southern France or to the estuaries on the western coast of Europe within the same winter (Hofer *et al.* 2005, 2006). Movement rates therefore were expected to be relatively high for both species.

It has been shown that parameter estimates in multi-state models become more precise when inter-specific differences in movement rates are high (Thorup & Conn 2009; Korner-Nievergelt *et al.* in press; see also Schaub 2009 for a description of a similar mechanism). The Goosander *Mergus merganser* therefore was included as a reference species. This species only exceptionally moves south of Switzerland during winter (Scott & Rose 1996), and there were no within-winter ring re-encounters from outside the northern Alpine region in the data.

### Treatment of the data

Data from ducks ringed at Lake Sempach, central Switzerland (47°09'N, 8°07'E) during winters 1955–2007 and re-encountered during the same winter season were used in developing the model. The ducks were caught in a baited bow net, were individually marked with a metal ring attached to their tarsus, and were released immediately after ringing. Details of the catching method and ringing procedure are described by Hofer *et al.* (2005, 2006).

Our primary interest was in the movements during the December–February period, *i.e.* between the main autumn and spring migration periods. However, because parameters for the first and last time periods of a multi-state model often are not estimable, the study period was extended at both ends and included November and March. The data set consisted of re-encounters for 625 Tufted Ducks, 531 Pochards and 162 Goosanders (Table 1). Of these, 75%, 74% and 94% (for Tufted Duck, Pochard and Goosander, respectively) of the re-encounters were re-captures at the ringing site. A further 11%, 16% and 2% of re-encounters were reported by hunters. The remaining re-encounters were accidentally found ducks and, in one case, a re-sighting where the ring number was read in the field. The data were grouped into three different types of re-encounters (events) for analysis: recaptured or re-sighted alive  $\leq 200$  km from Lake Sempach (*raA*), recovered dead  $\leq 200$  km from Lake Sempach (*rdA*) and recovered dead  $> 200$  km from Lake Sempach (*rdB*). The area  $\leq 200$  km of Lake Sempach (area *A*) contains most of the water surface area for all four of the large Swiss pre-alpine lakes (Lake Geneva, Lake Neuchatel, Lake Lucerne and Lake Constance). The area  $> 200$  km from Lake Sempach was termed area *B*.

### Model development

A multi-state model described by Schwarz (1993), and further developed by Pradel (2005) in order to allow for undetectable states, was used to analyse the re-encounter data. In such models, the ducks are assumed to change between states at distinct time

points during the study period. Further, it is assumed that different observations, called “events”, can occur during distinct time periods conditional on the state of the ducks. In the current study, each duck could be in one of five different states, depending on its location and whether the bird was alive or dead (Table 2). Four different events were possible depending on the state of the bird: 1) not seen (*ns*), 2) recaptured or re-sighted within *A* (*raA*), 3) recovered within *A* (*rdA*), and 4) recovered within *B* (*rdB*, Table 2). There were no live recaptures or re-sightings in area *B*, so this potential event was not included in the model. The model assumes that the transition of ducks from one state to another occurs at the start of each time interval and that there is no backward movement within one winter. Time intervals were defined as two-week periods from December to February and as one-month periods in November and March.

The model contained three sets of parameters. The first set described the initial state probabilities, *i.e.* the probability that a newly released bird is in a given state. In our data, all birds were released in state *aA* (alive within area *A*), so that the initial state probabilities constituted a vector  $\mathbf{I} = [1,0,0,0,0]$ . The second set of parameters described the transitions between states and is called the transition matrix. Because the states contained information on both locality and survival, the transition matrix was described as a product of two matrices. The first matrix *M* contained the movement probabilities and the second matrix *Sf* contained survival and recovery probabilities, as proposed by Gauthier & Lebreton (2008).

$$M = \begin{matrix} & aA & fdA & aB & fdB & d \\ \begin{matrix} aA \\ fdA \\ aB \\ fdB \\ d \end{matrix} & \begin{bmatrix} 1-\psi & 0 & \psi & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}, \text{ and } Sf = \begin{matrix} & aA & rdA & aB & rdB & d \\ \begin{matrix} aA \\ fdA \\ aB \\ fdB \\ d \end{matrix} & \begin{bmatrix} S_A & f_A & 0 & 0 & 1-S_A-f_A \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & S_B & f_B & 1-S_B-f_B \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

The product of the M and Sf matrices gave the 5 × 5 transition matrix. In the first matrix M the parameter ψ was the

probability that a bird being alive in A moves to B. Because we assumed that there is no backward movement, birds alive in B

**Table 1.** The number of Tufted Duck, Pochard and Goosanders released and the number of re-encounters for each species and event. *raA* = re-captured or re-sighted ≤ 200 km from Lake Sempach, *rdA* = recovered ≤ 200 km from Lake Sempach, *rB* = recovered > 200 km from Lake Sempach.

Species	<i>n</i> released	<i>raA</i>	<i>rdA</i>	<i>rB</i>
Tufted Duck	20,058	473	114	38
Pochard	12,609	394	69	68
Goosander	1,628	152	9	1

**Table 2.** Description of the five state categories (unobserved) and the four event categories (observed) underlying the multi-state model used in this study.

State	Event
<i>aA</i> = bird alive ≤ 200 km of the place of ringing	<i>ns</i> = not seen
<i>fdA</i> = bird freshly dead ( <i>i.e.</i> it can be recovered by a finder) ≤ 200 km from the ringing site	<i>raA</i> = recaptured or re-sighted alive ≤ 200 km of the ringing site
<i>aB</i> = bird alive > 200 km from the ringing site	<i>rdA</i> = recovered dead ≤ 200 km of the ringing site
<i>fdB</i> = bird freshly dead > 200 km from the ringing site	<i>rdB</i> = recovered dead > 200 km of the ringing site
<i>d</i> = bird dead ( <i>i.e.</i> can no longer be recovered)	

had a probability of 1 of remaining there. The survival and recovery step  $Sf$  contained the probability that a bird survives ( $S$ ), the probability that it dies and is recovered ( $f$ ) and the probability that it dies and is not recovered ( $1-S-f$ ). The transition matrix  $Sf$  led to the temporary states:  $aA$  (alive within  $A$ ),  $rdA$  (recovered in  $A$ ),  $aB$  (alive within  $B$ ),  $rdB$  (recovered in  $B$ ) and  $d$  (dead).

The third set of parameters, the event matrix  $E$ , described the probability of a recapture or re-sighting event,  $\beta$ , for each of the five temporary states:

$$E = \begin{matrix} & ns & raA & rdA & rdB \\ \begin{matrix} aA \\ rdA \\ aB \\ rdB \\ d \end{matrix} & \begin{bmatrix} 1-\beta & \beta & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{bmatrix} \end{matrix}$$

Thus  $\beta$  was the probability of a duck being recaptured or re-sighted in  $A$ , given that it was alive at this location. The first column of  $E$  contained the probabilities that a bird was not seen during a given time interval, depending on its temporary state. This was  $1-\beta$  for ducks alive in  $A$ , 1 for ducks alive in  $B$  and 1 for those that were dead and no longer detectable (state  $d$ ). Because recovery probabilities  $f_A$  and  $f_B$  were specified in the transition matrix  $Sf$  to be the transition between the states  $aA$  and  $rdA$ , and between  $aB$  and  $rdB$ , the event probability for  $rdA$  and  $rdB$ , given the temporary states  $rdA$  and  $rdB$ , respectively, was fixed to 1. It is unusual to specify recovery probability within the transition matrix instead of within the event matrix. However, this parameterisation makes it possible to combine in an elegant

way the information of dead recoveries and live recaptures within the same model (Gauthier & Lebreton 2008).

For each cohort (*i.e.* for birds released at the same time), the probabilities ( $\hat{Y}$ ) of the four events ( $ns$ ,  $raA$ ,  $rdA$  and  $rdB$ ) for each time period were obtained by matrix multiplication:  $\hat{Y} = I \times M \times Sf \times \beta$ . Here  $\hat{Y}$  constituted the parameters (cell probabilities) of a multinomial model that was fitted to the data using maximum likelihood methods (Arnason 1972; Schwarz 1993).

An initial model, using Bayesian methods (software WinBUGS; Spiegelhalter *et al.* 2007), was fitted only to recovery data for Tufted Duck and Pochard. In this model, the  $S-r$  parameterisation was used instead of the  $S-f$  (with  $f = (1-S) * r$ ) parameterisation (see Gauthier & Lebreton 2008), with separate survival and movement probabilities estimated for each time period and species, whereas the recovery probabilities of one species was constrained as being proportional to the recovery probabilities for the other species. Parameter estimates were found to be biased, however, and had low precision (Körner-Nievergelt 2008). Several approaches were tried to improve precision (*e.g.* estimating survival based on long-term data, giving informative prior distributions, and fixing survival to realistic values), but without success.

In the second stage of model development, more information was used in estimating movement probabilities, namely: 1) the number of time intervals was increased by including data from November and March, 2) including a reference species (Goosander), and 3) using recapture and re-

sighting data in addition to the recovery data. The movement probability of the reference species was fixed at zero. As a consequence, re-encounter probabilities within 200 km of Lake Sempach could be estimated more precisely for Goosander. Additionally, if constraining the Tufted Duck and Pochard re-encounter probabilities to be proportionate to the re-encounter probability for Goosander, the precision of estimated re-encounter probabilities for the first two species might also increase. The model parameters were also constrained to be constant over different clusters of time intervals. Goodness of fit tests (U-CARE; Choquet *et al.* 2005) showed that transients might be present in all three groups: Tufted Duck  $\chi^2_6 = 221$ , Pochard  $\chi^2_5 = 95$  and Goosander  $\chi^2_5 = 78$ ;  $P < 0.001$  for all species. The time since release therefore was added to the model in order to account for transients' effects (Pradel 1993; Pradel *et al.* 1997). In this second stage, 17 models with differing parameter constraints were compared and the best model was selected on the basis of changes in the Akaike Information Criteria (QAICc; Appendix 1). E-SURGE (Choquet 2007) was used for the model selection process, because it is relatively easy to change parameter constraints in this software. However, model selection was difficult presumably because the likelihood function might not have contained one clear maximum, possibly because of overparameterisation or overdispersion. Only one model provided a reasonable fit to the data, the difference in QAICc in comparison with the second best model being 9.1 (Appendix 1). The two-week survival estimates were realistic

(*i.e.* were higher than annual survival probabilities taken from Rodway 2007 and Křementz *et al.* 1997) only in this best model. Model averaging therefore was not undertaken and the best model was used as the starting point for the final stage of the model selection process.

In the final stage, the best model from stage two was re-parameterised into the  $S$ - $f$  parameterisation described by Gauthier & Lebreton (2008) and fitted to the same data. With this parameterisation, only four biologically meaningful models were fitted, changing one parameter at a time. This model selection strategy is not in line with the theory of correct hypothesis testing (which would say that only *a priori* models should be tested; Anderson *et al.* 2000). However, this strategy was adopted because the scope of the study was to find a method for measuring movement probabilities, rather than to test hypotheses. In all models calculated during the final stage, estimated movement probabilities were relatively consistent between the different models, whereas estimated survival, recapture and recovery probabilities differed considerably.

### Simulations to assess bias and precision

In order to assess the bias of parameter estimates in the best model, five different data sets, each including data for all three species, were simulated based on the same underlying parameter values. Realistic (but arbitrary) underlying parameter values were chosen (Table 3). Two-week survival probability was assumed to be  $S = 0.97$  for all species (constant over time). Recapture probability was set to  $\beta = 0.05$  and recovery probabilities were set to 0.0015 (product

**Table 3.** True movement probabilities ( $\psi$ ) underlying the data simulation, used to assess bias and precision of parameter estimates. Movement probability is the probability that a bird being alive in area  $A$  moves to area  $B$  within a two-week period. The values were chosen arbitrarily with an arbitrary scatter around a realistic mean taken from earlier analyses (Korner-Nievergelt 2008; Keller *et al.* 2009).

Species	Nov	Dec1	Dec2	Jan1	Jan2	Feb1	Feb2	March
Tufted Duck	0.4	0.3	0.4	0.5	0.5	0.4	0.7	–
Pochard	0.5	0.4	0.5	0.6	0.6	0.5	0.8	–
Goosander	0	0	0	0	0	0	0	–

of mortality \* finding and reporting probability:  $(1-0.97)*0.05$  in  $A$  and to 0.0006  $((1-0.97)*0.02)$  in  $B$ . The sample sizes for the simulated data sets were the same as the sample sizes recorded for the real re-encounter data, *i.e.* 20,058 virtual birds of species 1 (as for Tufted Duck), 12,609 birds of species 2 (as for Pochard) and 1,628 of the reference species. The five simulated data sets differed solely due to random variation inherent to the multinomial distribution. Data simulation was undertaken in R 2.7.2 (R Development Core Team 2007).

The model was fitted to the five data sets and the bias was estimated by subtracting the true underlying parameter value from the estimated one. The precision of the estimates was assessed by inspecting the scatter of the estimates from the five data sets.

## Results

### Applying the model to the real data

The QAICc values obtained for the multi-state models indicated that two models

fitted the data better than the others (Table 4), and that there was no difference in the quality of fit for these two models (*i.e.*, QAICc  $\leq 2$ ). The first model included an additional parameter, which expressed the probability of recapture or re-sighting in the first time interval following ringing in comparison with subsequent time intervals. However, the difference in estimated recapture probability between newly ringed and previously ringed ducks was negligible. Furthermore, the other parameter estimates were very similar in these two models. Estimates for the simpler model (the second model in Table 4) therefore are presented in the figures.

The estimated movement probabilities were similar for Tufted Duck and Pochard. Of those individuals captured for the first time during winter, around 90% left area  $A$  within the next two weeks (upper figure in Fig. 1). Of those individuals that stayed for at least two weeks within  $A$  only 20–40% left the area every following two-week period. There was an increase in

**Table 4.** Final multi-state models (stage 3) describing the constraints on bird movement ( $\psi$ ), survival ( $S$ ), recovery probability ( $f$ ), and re-capture/re-sighting probability ( $\beta$ ) in the Tufted Duck, Pochard and Goosander data, including the modified Akaike information criterion (QAICc).  $\Delta$ AIC is the difference in QAIC relative to the best model.  $nP$  = number of parameters. Parameter constraints are defined by factors they are dependent on. A “+” sign indicates an additive effect, whereas a “.” sign indicates a multiplicative effect. The factors are:  $t$  = time (8 two-week periods),  $a$  = time since ringing (2 levels: first and subsequent two-weeks periods after ringing),  $month$  = month (5 levels),  $period$  = time classes (4 levels: November, 1 Dec–15 Jan, 16 Jan–28 Feb, March),  $g$  = group (3 species), and  $loc$  = location (2 levels: area  $A$  and area  $B$ ).

$\psi$	$S$	$f$	$\beta$	$nP$	QAICc	$\Delta$ AIC
t.g+a	period.g.loc	period.g.loc	month+g+a	52	14,280.4	0
t.g+a	period.g.loc	period.g.loc	month+g	51	14,282.4	2
t.g+a	period.g.loc	month.g.loc	month+g	56	14,296.6	16.2
t.g.a	period.g.loc	period.g.loc	month+g	70	14,307.1	27.7

movement probabilities in January and February.

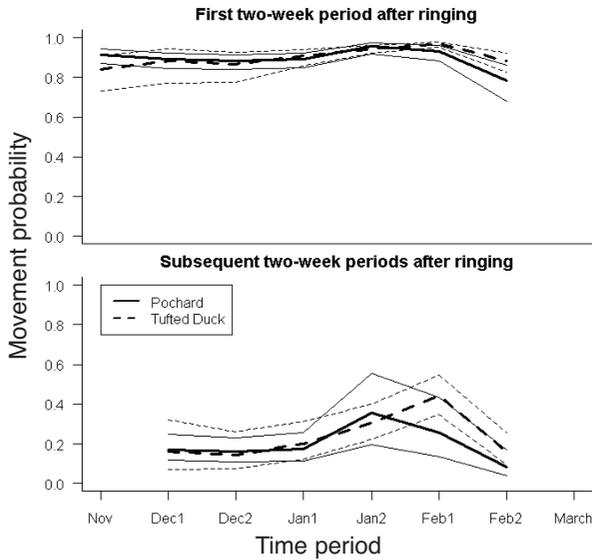
Estimated two-week survival probabilities were slightly lower > 200 km from Lake Sempach (Fig. 2). Survival decreased during winter for Pochard and Goosander, whereas a weak increase was observed for Tufted Duck. However, confidence intervals were large, perhaps because two-week survival probabilities may be close to 1 and therefore at the edge of the parameter space. This can make it difficult to estimate parameter values accurately. Estimated recapture or re-sighting probabilities increased over winter (Fig. 3). Pochard had the highest recapture or re-sighting probability and Goosander the lowest. Recovery probabilities were lower in area  $B$  than in area  $A$  (Fig. 4). In  $B$ , recovery

probabilities decreased over winter for both Pochard and Tufted Duck. In  $A$ , recovery probability increased for Tufted Duck, whereas it decreased for Pochard and Goosander.

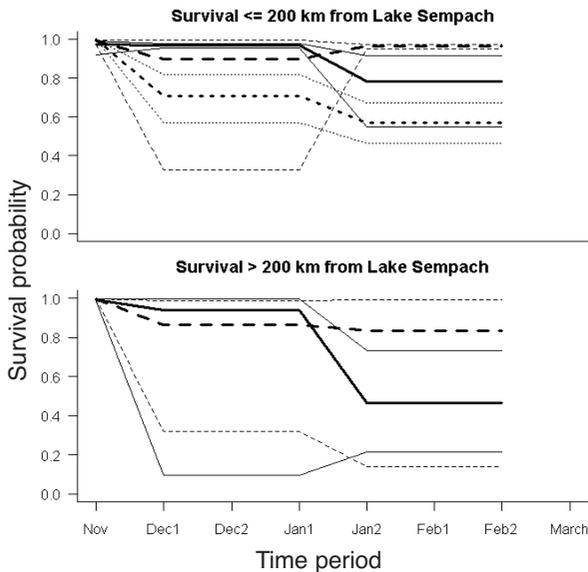
### Simulations to assess bias and precision

The precision of the estimates of movement probability was generally low and for every data set between two and four movement probabilities were not estimable (Fig. 5). There was a slight underestimation, especially for movement probabilities during the first two-week period after ringing (Fig. 5). However, confidence intervals included the true parameter value in most of the cases.

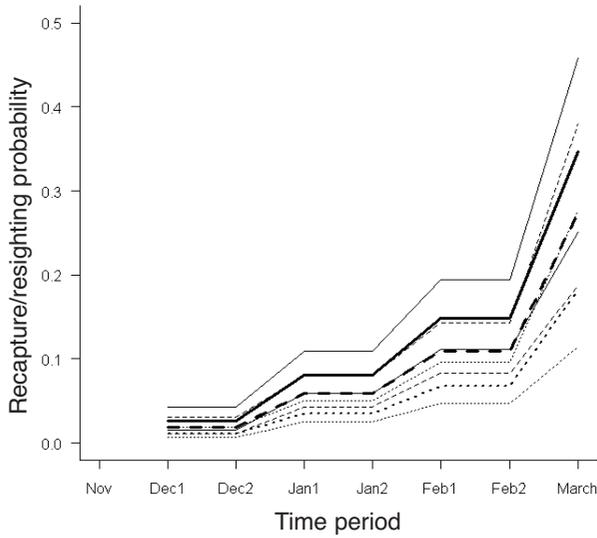
About half of the survival probabilities were not estimable (Fig. 6). Those survival estimates that were estimable mostly



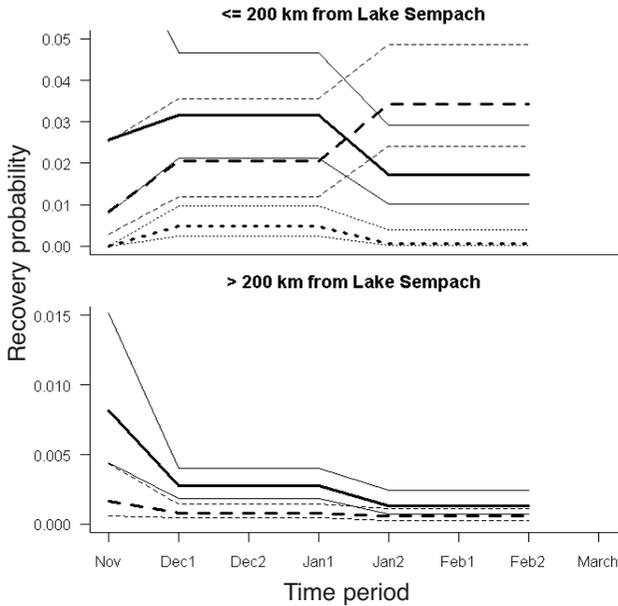
**Fig. 1.** Estimated two-week movement probabilities for Common Pochard (solid line) and Tufted Duck (broken line). Thin lines = 95% confidence intervals.



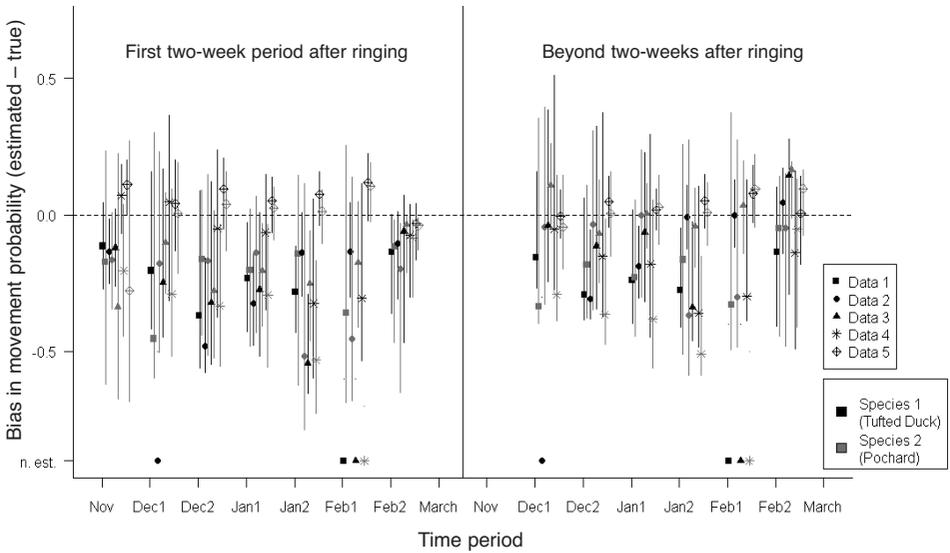
**Fig. 2.** Estimated two-week survival probabilities for Pochard (solid line), Tufted Duck (broken line) and Goosander (dotted line)  $\leq$  200 km from Lake Sempach (upper graph) and  $>$  200 km from Lake Sempach (lower graph). Survival for Goosander was not estimated for distances  $>$  200 km from Lake Sempach. Thin lines = 95% confidence intervals.



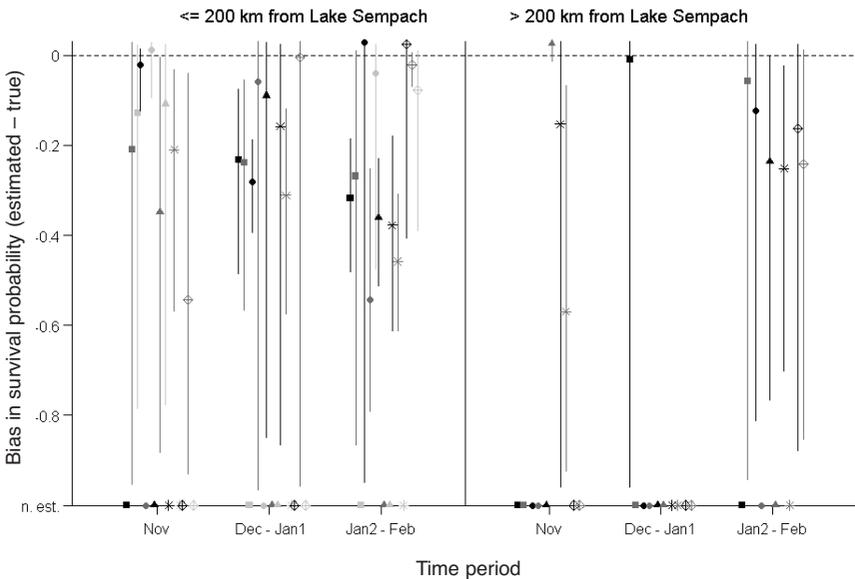
**Fig. 3.** Estimated recapture/re-sighting probabilities for Common Pochard (solid line), Tufted Duck (broken line) and Goosander (dotted line). Thin lines = 95% confidence intervals.



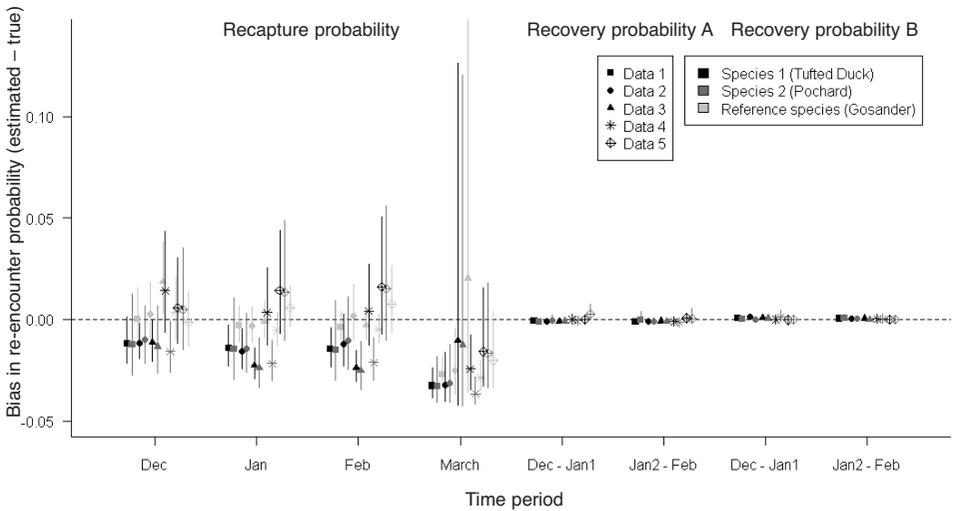
**Fig. 4.** Estimated recovery probabilities for Common Pochard (solid line), Tufted Duck (broken line) and Goosander (dotted line). Recovery probabilities for Goosander > 200 km from Lake Sempach were not estimated. Thin lines = 95% confidence intervals.



**Fig. 5.** Estimated bias in movement probability for each time period obtained from five simulated data sets. Vertical lines are 95% confidence intervals. n.est = non estimable.



**Fig. 6.** Estimated bias in survival probability obtained for five simulated data sets. For legend see Fig. 7. Dots on the lower border of the figure indicate non-estimable parameters.



**Fig. 7.** Estimated bias in recapture and recovery probabilities obtained for five simulated data sets. Vertical lines are 95% confidence intervals.

underestimated true survival probability (Fig. 6).

Recapture probabilities seemed to be underestimated in some data sets and overestimated in others (Fig. 7). Recovery probabilities seemed to be estimated precisely and without obvious bias.

## Discussion

The results of the simulation study, which assessed the bias and precision of parameter estimates, are important for the interpretation of parameters derived on fitting the model to the real data. The simulation study therefore is discussed before considering the real results.

### Bias and precision of parameter estimates

For the five simulated data sets, different parameters were not estimable, although the

five simulated data sets were based on the same underlying “true” parameter values and had the same sample sizes. The simulated data differed only through the random variation inherent in the multinomial distribution; ability to estimate movement probabilities and survival probabilities therefore depended on the random variation in the simulated data. This implies that, in our study or maybe generally, it is not possible to use simulations to assess precisely those parameters that can be identified in a specific example, because how the observed data differ from the expected values is not known. The plausibility of the estimates and their confidence intervals can give some information about the estimability of parameters in real datasets. For instance, in our real data example, estimated movement probabilities seemed appropriate, because the confidence

intervals were reasonable (*i.e.* they did not collapse to 0, nor did they include the whole parameter space (0,1); Fig. 1). In contrast, problems were evident in estimating survival probabilities; survival during November was not estimable and confidence intervals were very large for the other time periods (Fig. 2). Nevertheless, on fitting the model to the real data, there seemed to be fewer non-estimable survival parameters than when the model was fitted to the simulated data. This might be because we assumed constant survival over time for the simulated data, whereas in the real world survival might vary over time. Schaub (2009) showed that in multi-state models some parameters might be estimated with lower bias and higher precision if they show temporal variation. However, we performed many different simulations prior to this study, including a simulation of varying survival over time, some of which are presented in Korner-Nievergelt (2008). In Korner-Nievergelt (2008) and in the present study, survival estimates generally were negatively biased. Estimates of recapture and recovery probabilities were biased in some cases but seemed to be unbiased and precise in other cases. There was negligible bias in the movement probabilities, but precision was always low. Survival estimates therefore should not be interpreted in our study. Moreover, estimates of recapture and recovery probabilities, as well as movement probabilities, should be interpreted with great care.

This study suggests that the multi-state model can be an appropriate tool to measure movement rates of marked individuals. However, if these models are applied to ring

re-encounter data some difficulties can arise. These difficulties comprise non-estimability, low precision or even bias of some parameters. For some models, parameters might be non-identifiable because of intrinsic non-estimability, *i.e.* the model structure does not allow identification of some of the parameters. Such non-identifiability can be assessed numerically using computer algebra as described in Catchpole & Morgan (1997) and Catchpole *et al.* (2001). In the model presented here every parameter was intrinsically identifiable. Difficulties in estimating some of the parameters therefore might be attributable to characteristics of the data such as sparseness, low detection probabilities, only one release site, too many transient individuals and heterogeneity or other violations of the model assumptions. The precise cause of bias, low precision and non-estimability of parameters in the model were not identified, but possible reasons are discussed below.

Because one of the world's largest data sets of ringed ducks was used in this study, with > 20,000 Tufted Duck and > 12,000 Pochard ringed and released, it seemed unlikely that the data would be sparse. However, due to the low re-encounter probabilities of ringed birds for which no systematic searches were conducted, numbers of re-encounters were still low. It would be valuable to fit our model to a simulated data with very high sample sizes, *e.g.* 10,000 re-encounters per species. Unfortunately, limited computer capacity prevented such a simulation. Furthermore, the data contained no ducks ringed and released in area *B*, and there was little data

for assessing re-encounter probabilities in  $B$ . Indeed, there were no live re-capture or re-sighting records for this area. Among the recoveries in  $B$ , 76% and 78% of Tufted Duck and Pochard respectively were due to hunting. This percentage was lower in  $A$  (31% for Tufted Duck recoveries, 33% for Goosander and 41% for Pochard). Better estimates of recovery rates, and thus better estimates of movement rates, would be expected if the model is applied to data for ducks ringed and released at different sites across Europe.

The presented model assumed that parameters do not differ between individuals of the same species. This assumption is very likely to be violated. For example, survival probabilities in the studied species have been shown to be age-dependent (Blums *et al.* 1996). Age was determined for only two-thirds of the individuals analysed in this study, so age dependencies were not included, and the model might therefore have suffered from heterogeneity that has not been accounted for. This could lead to biased parameter estimates (Pledger *et al.* 2003).

### Estimated movement probabilities of Common Pochard and Tufted Duck

Estimated movement probabilities were generally high, but they were lower in December compared to January and February. This pattern corresponds to the pattern of stopover durations at Lake Sempach described for colour-marked individuals by Kestenholz (1995). He found that stopover duration at Lake Sempach was only about  $2 \pm 3.5$  days during November, January and February for both species. This

corresponds to a turnover rate of about 81% per two-week period. However, in December mean (minimal) stopover duration was  $17 \pm 12$  days ( $n = 5$ ) for Tufted Duck and  $14 \pm 10$  days ( $n = 2$ ) for Pochard; *i.e.*, a turnover rate of about 26% and 21% of birds present, respectively. The longer stopover durations in December compared to later in winter can be linked to the availability of whitefish (*Coregonus* sp.) eggs as a food resource during that time because of the spawning season. During the rest of the winter, food might have been very scarce on Lake Sempach for both species, because Zebra Mussels *Dreissena polymorpha*, which are the main food of Tufted Duck and also important for Pochard, colonised Lake Sempach only after the year 2000.

A duck leaving Lake Sempach could find good wintering places 80–130 km away (Lake Constance, Lake Neuchatel or Lake Geneva). The good concordance between stopover duration at Lake Sempach measured, based on studies of colour-marked ducks (Kestenholz 1995), and the probability of moving at least 200 km within a two-week period estimated in the current study, indicates that the ducks not only leave Lake Sempach but also might leave the Alpine area. This leads to the question of whether a representative sample of the duck population wintering in areas of the Alps was caught at Lake Sempach. For instance, the birds caught may have been predominantly from that part of the population that was passing through the region, whereas those individuals that intended to stay longer in the area did not land at Lake Sempach, but chose better wintering places. Further research is needed to answer this question.

Although precision of the estimated movement probabilities are low, the study contributes to an understanding of within-winter movements. This study presents the first quantitative measurement of exchange rates of individual diving ducks between the Alpine region and the rest of the European wintering area. These exchange rates seemed to be considerable.

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**Appendix 1.** Results from stage 2 of the model selection process (see Methods) describing constraints on the movement ( $\psi$ ), survival ( $S$ ), and re-capture/re-sighting ( $\beta$ ) parameters in multi-state models fitted to the Tufted Duck, Pochard and Goosander data, together with the modified Akaike Information Criteria (QAICc) generated on fitting the different models and a comment on whether survival estimates are realistic, based on published annual survival probabilities (Krementz *et al.* 1997).  $\Delta$ AIC is the difference in QAIC relative to the best model.  $nP$  = number of parameters. Parameter constraints are defined by factors they are dependent on. A “+” means an additive effect, whereas a “\*” means a multiplicative effect. The factors are: t = time (8 two-week periods), a = time since ringing (2 levels: first and subsequent two-weeks periods after ringing), month = month (5 levels), periods = time classes (4 levels: November, 1 Dec–15 Jan, 16 Jan–28 Feb, March), asymp = asymmetric time periods (4 levels: November, Dec–Jan, Feb, March), g = group (3 species), loc = location (2 levels: area A and area B).

$\psi$	$S$	$\beta$	$nP$	QAICc	$\Delta$ AIC	Comments (Plausibility of estimated $S$ )
t*g+a	periods*g	month*event+g	46	14,216.75	0	estimated $S$ plausible
t*g+a	loc*periods*g	month*event*g	75	14,225.84	9.1	estimated $S$ nearly plausible; realistic initial values given
t*g*a loc*	periods*g	month*event+g	69	14,226.95	10.2	estimated $S$ plausible
t*a*g	loc*t*a*g	month*event*g	119	14,250.57	33.8	$S$ not identifiable
t*a*g	loc*t*a*g	month*event+g	107	14,288.54	71.8	$S$ not identifiable
t*g+a	loc*periods+g+a	month*event+g	39	14,306.78	90.0	estimated $S$ not plausible
t*g+a*g	periods*g	month*event+g	40	14,307.30	90.6	estimated $S$ not plausible
t*g+a	loc+ periods+g+a	month*event+g	37	14,311.76	95.0	estimated $S \leq 200$ km not plausible, but $> 200$ km plausible

Appendix 1 (*continued*).

$\psi$	$S$	$\beta$	$nP$	QAICc	$\Delta AIC$	Comments (Plausibility of estimated $S$ )
t*g+a	loc*asympt+g+a	month*event+g	39	14,313.34	96.6	estimated $S \leq 200$ km not plausible, but $> 200$ km plausible
t*g*a	periods*g	month*event+g	51	14,313.43	96.7	estimated $S$ during first half of winter plausible but not during second half of winter
t*g+a	loc*periods*g	month*event+g	46	14,313.94	97.2	estimated $S$ not plausible
t*g+a	loc*periods+g	month*event+g	38	14,316.23	99.5	estimated $S$ not plausible
t*g+a	loc*t*g+a	month*event+g	79	14,317.11	100.4	$S$ not identifiable
t*g+a	loc*periods*g	month*event+g	46	14,317.14	100.4	estimated $S$ plausible; realistic initial values given
t*g+a	loc+periods*g	month*event+g	40	14,319.25	102.5	estimated $S$ not plausible
t*g+a	loc*season+g	month*event+g	36	14,325.96	109.2	estimated $S \leq 200$ km not plausible, but $> 200$ km plausible
t*g+a	loc+periods*g	month*event+g	40	14,329.58	112.8	estimated $S$ not plausible; realistic initial values given
t*g+a	season+g	month*event+g	34	14,329.76	113.0	estimated $S$ not plausible
t*g+a	periods+g	month*event+g	33	14,337.33	120.6	survival parameters fixed to 0.86 and 0.88
t*g+a	loc*periods+g	month*event	36	14,360.13	143.4	estimated $S \leq 200$ km not plausible, but $> 200$ km plausible
t*g+a	periods+g	month*event+g	33	14,381.90	165.2	survival parameters fixed to 0.96 and 0.98
t*g+a	periods+g	month*event+g	33	14,444.85	228.1	survival parameters fixed to 0.99