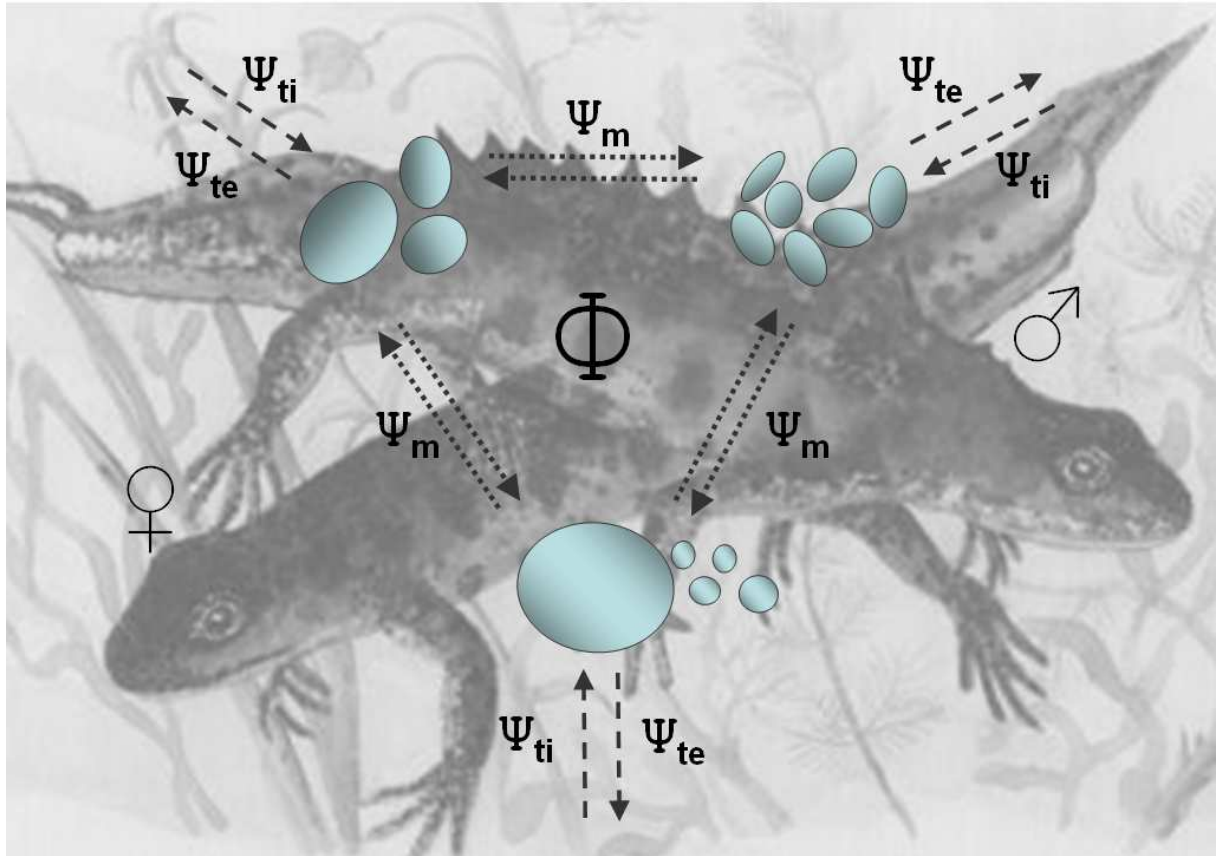


Population Dynamics of a Subdivided Population of the Crested Newt (*Triturus cristatus*)



A Thesis for the Degree of **Master of Science** in Biology/Ecology

submitted by

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ABSTRACT

Amphibians have evolved in dynamic landscapes where pond density was high and ponds often occurred in clusters. Moreover, populations were not isolated but formed a continuum from subdivided populations to metapopulations. Nowadays, amphibian populations are often isolated and forced to use single ponds as breeding sites. Subdivided populations that inhabit clusters of ponds are considered more primary and are thus valuable for studies of population dynamics.

Using multistate and Jolly-Seber capture-mark-recapture modeling techniques, I quantified the dynamics of a subdivided population of the crested newt, *Triturus cristatus*, that inhabits clusters of ponds for breeding. I estimated survival and recapture rates, migration between subpopulations, temporary emigration and immigration probabilities, and breeding and non-breeding population sizes. Annual survival was constant over time but lower for females (0.69) than for males (0.91). Pond fidelity of adults was high for two subpopulations, whereas every year both males (22-31%) and females (10-14%) of the third subpopulation changed to ponds of the other subpopulations for breeding. High rates of temporary emigration (0.39-0.57), i.e. changes from breeding in one year to non-breeding in the next, indicated that breeding is costly, probably due to high mortality and energetic costs of reproduction. Over four years the number of breeding animals of two subpopulations increased whereas in one subpopulation it decreased. Depending on the method used, the number of non-breeding adults was about the same as, or clearly exceeded the number of breeding crested newts. Furthermore, pond residence models based on a one-year data set showed that less than 60% of any year's breeding population is in the ponds at one time. The observed patterns of pond residence led to an analysis evaluating the optimal sampling effort for monitoring purposes.

This study provides evidence that probabilities to skip breeding opportunities can be high for crested newts. The estimated high temporary emigration and low immigration probabilities indicate that more than half of the breeding adults bred only once in their life.

ZUSAMMENFASSUNG

Amphibien sind in einer dynamischen Umwelt evoluiert, wo es viele Weiher gab und diese oft gehäuft vorkamen. Zudem waren Populationen nicht isoliert sondern bildeten ein Kontinuum von unterteilten Populationen zu Metapopulationen. Heutzutage sind Populationen von Amphibien oft isoliert und gezwungen, einzelne Weiher als Laichgewässer zu gebrauchen. Unterteilte Populationen, welche Weiheranhäufungen zur Laichablage benutzen, werden als ursprünglich betrachtet und sind deshalb wertvoll für populationsdynamische Untersuchungen.

Mittels Multistate und Jolly-Seber Fang-Wiederfang Modellierungsmethoden habe ich die Dynamik einer unterteilten Kammmolchpopulation, *Triturus cristatus*, quantifiziert, welche zur Laichablage eine Weiheranhäufung benützt. Ich habe Überlebens- und Wiederfangraten, Wanderraten zwischen den Subpopulationen, temporäre Emigrations- und Immigrationsraten (jährliche Wechsel von laichenden zu nicht-laichenden Kammmolchen, und *vice versa*), sowie Laich- und Nicht-Laichpopulationsgrößen geschätzt. Jährliches Überleben war konstant über die Zeit, jedoch tiefer bei Weibchen (0.69) als bei Männchen (0.91). Die Rückkehrbereitschaft zum Weiher war hoch für zwei Subpopulationen, wohingegen jedes Jahr viele Männchen (22-31%) und Weibchen (10-14%) von der dritten Subpopulation zu Weihern der anderen Subpopulationen wechselten. Hohe temporäre Emigrationsraten (0.39-0.57) deuten darauf hin, dass das Laichgeschäft mit hohen Kosten verbunden ist, wahrscheinlich aufgrund höherer Mortalität und energetischen Kosten der Reproduktion. Die Anzahl laichender Tiere in zwei Subpopulationen ist über vier Jahre gewachsen, die einer dritten Subpopulation jedoch gesunken. Die Anzahl nicht-laichender Adulten war etwa gleich gross bzw. grösser als die der laichenden Kammmolchen, je nachdem welche Methode für die Schätzung verwendet wurde. Des Weiteren zeigten Modelle, welche die Weiherbesetzung über ein Jahr beschreiben, dass weniger als 60% der laichenden Adulten sich zur selben Zeit in den Weihern aufhielten. Das beobachtete Muster der Weiherbesetzung führte zu einer Analyse, welche den optimalen Fangaufwand für Monitoringprojekte evaluiert.

Diese Studie liefert die Erkenntnis, dass die Wahrscheinlichkeiten adulter Kammmolche, Laichgelegenheiten auszulassen, gross sein können. Die hohen temporären Emigrations- und tiefen Immigrationsraten deuten darauf hin, dass mehr als die Hälfte der adulten Tiere nur einmal im Leben reproduziert.

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1 INTRODUCTION

Amphibians are declining worldwide and this process has been happening for several decades (Houlahan et al. 2000). Explanations for the global decline of amphibian species are manifold and cause-effect relationships not always unambiguously proven (Beebee and Griffiths 2005). Several possible causes have been reported such as habitat destruction, alteration, and fragmentation, alien species introductions and invasions, UV-B irradiation, chemical pollution, diseases, climate change, or various combinations thereof (Blaustein and Kiesecker 2002, Beebee and Griffiths 2005). However, elucidating factors that cause population declines is only one major area in the process of amphibian conservation research. Biologists should also aim to increase the ability to detect declines (Storfer 2003). The ability to detect declines may be enhanced if one knows how different demographic rates affect population fluctuations. A decline of a species is inevitably related with a change at the population level, i.e. changes in population dynamics and demography. To get insights into population dynamics, demographic parameters need to be estimated. The basic population model (Williams et al. 2002) includes all processes that influence changes in population size (N) over time (t), i.e., recruitment (B), immigration (I), mortality (D), and emigration (E).

$$N(t+1) = N(t) + B(t) + I(t) - D(t) - E(t)$$

An issue particularly relevant to studies of population dynamics of amphibians is whether local populations that utilize clusters of ponds function as a single population or as a metapopulation consisting of several discrete populations (Petranka et al. 2004, Jehle et al. 2005, Petranka and Holbrook 2006). In the former case migration between ponds is so high that apparent subgroups behave as a single breeding unit. In metapopulations, movement between ponds is restricted due to site philopatry, barriers to dispersal, or long distances between ponds (Petranka et al. 2004). Therefore, studying migration of the individuals of a population between different ponds within clusters of ponds is important to understand population dynamics. Other parameters such as survival and recruitment of distinct (sub)populations provide further insights into metapopulation dynamics. Differences in these parameters between subpopulations are of special interest because they indicate whether and to what degree subpopulations behave independently.

Amphibians have evolved in landscapes characterized by frequent disturbance events such as dynamic floodplains which provide a high diversity of waterbodies that can be used as breeding sites (Kuhn and Laufer 2001, Tockner et al. 2006). Nowadays, in the highly

fragmented landscape of Middle Europe, amphibians often inhabit single ponds, which are isolated from other ponds. Pond isolation is viewed as a critical determinant of pond use and population viability for many amphibian species (Marsh and Trenham 2001). Mann et al. (1991) showed that the major factor determining the presence of six amphibian species is ‘fragmentation of the habitat’, i.e. whether a site consists of a single or of multiple ponds. Thus, many amphibian species are more likely to occur in subdivided habitats.

Population dynamics and demography are commonly analyzed using capture-mark-recapture (CMR) modeling methods (Lebreton et al. 1992). Multistate models allow the estimation of survival and recapture probabilities, and also migration probabilities between distinct locations or populations. Moreover, multistate models can estimate breeding probabilities, i.e. probabilities that marked animals are present at the sampling site and do not skip breeding (Fujiwara and Caswell 2002, Kendall and Nichols 2002). Skipping breeding opportunities is known for amphibians (Bull and Shine 1979, Schmidt et al. 2002, Muths et al. 2006, Church et al. *in press*).

Studies on population dynamics of amphibians are generally accomplished by sampling animals at their breeding sites. In this way, one analyses the dynamics of the breeding population rather than the dynamics of the whole population. Studies that focus entirely on the breeding population do not cover all animals if there are animals that skip breeding opportunities. For modeling the breeding population (N_B = breeding population size), the basic population model (Williams et al. 2002) needs to be extended by adding temporary immigration (TI) and temporary emigration (TE), i.e. number of animals that change from the non-breeding to the breeding population, and *vice versa*, respectively:

$$N_B(t+1) = N_B(t) + B(t) + I(t) - D(t) - E(t) + TI(t) - TE(t).$$

This study aims to model population dynamics of a population of the crested newt (*Triturus cristatus*) in northern Switzerland from which CMR data have been collected over five consecutive years. The investigated population is of high value as the study site consists of many ponds that form three clusters. Therefore, it is likely that the population is subdivided into three subpopulations.

I will estimate all components of the breeding population model. Due to methodical limitations recruitment rates can not be estimated when breeding probabilities are included (Kendall and Nichols 2002). Further, I will estimate non-breeding population sizes and make recommendations how to best monitor populations of crested newts.

The crested newt (*Triturus cristatus*) is a long-lived and pond-breeding amphibian species (Thiesmeier and Kupfer 2000) and is threatened throughout Europe (Stopher et al. 1994). Up to the present, only a few studies exist on population dynamics of the crested newt. Most of them are focusing on a single population inhabiting a single pond (Hedlund 1990, Arntzen and Teunis 1993, Cooke 1995, Baker 1999). However, populations of *T. cristatus* are known to better survive when living in waterbody complexes as breeding habitat (Halley et al. 1996). Thus, the risk of extinction of populations inhabiting pond clusters is lower than the extinction risk of single pond populations. Further, due to decreased dispersal rates, isolated populations have higher extinction risks than subdivided populations (Griffiths and Williams 2000). Thus, subdivided populations of *T. cristatus* living in pond clusters are useful for studying population dynamics as such data may lead to results that might be of high value for better understanding the biology of the species. So far, there are no studies quantifying population dynamics of the crested newt using CMR modeling approaches to estimate survival and other population parameters of interest.

The specific questions that I will address are:

- (1) Does survival vary between subpopulations, sexes, over years and/or between seasons (summer and winter)?
 - (2) Does breeding probability vary between subpopulations, sexes and/or over years?
 - (3) Does migration vary between subpopulations and/or between sexes?
 - (4) Are breeding and non-breeding subpopulations increasing or decreasing? What is the minimum monitoring effort to accurately estimate population size?
-

2 MATERIALS AND METHODS

2.1 Study Species

My study focused on the crested newt (*Triturus cristatus*; Amphibia, Urodela), which is a long-lived and pond-breeding amphibian species; the breeding season lasts from the end of February until the middle of October depending on environmental factors (Thiesmeier and Kupfer, 2000). The crested newt is widespread over Europe. It is distributed from Central-France up to Great Britain in the west, to southern parts of Norway and Sweden in the north, to the Ural Mountains and Western-Siberia in the East, and to Central-France, Northern-Switzerland and Romania in the south (Arntzen and Wallis 1999). However, crested newts are a threatened species throughout Europe and are recognized as Threatened or Endangered (categorized by IUCN-criteria) in no less than 11 countries (Stopher et al. 1994). The causes of decline centre on a loss of lowland ponds and terrestrial habitats, pollution, fish stocking, and the general lowering of ground water tables in urban, industrial and intensive agricultural areas (Corbett 1994).

2.2 Study System

The study site was the man-made nature reserve Herzogenmatt which belongs to the commune Binningen (canton BL) in the north-western part of Switzerland (47°32' N, 7°33' E, 328 m a.s.l.). Ponds at the study site that are inhabited by crested newts are arranged in three clusters (Ash, Beech, and Chestnut) (Fig. 2.1). Within a pond-cluster distances between adjacent ponds are short (1-10 m). Clusters may represent populations or subpopulations. However, for reasons of lacking terminology, I will call groups of animals that inhabit the same cluster 'populations'.

The Chestnut complex includes four very small ponds (2-6 m²) and one very large pond (120 m²). The Ash complex is a cluster of eight ponds, which are all about the same size (6-10 m²), whereas in the Beech complex there are three larger ponds of approximately equal size (10-20 m²). Ponds of each complex are situated so close together that they are treated as a single location in this study. The three complexes are arranged in a triangle with Chestnut and Beech being much closer (20 m) to each other than both are to Ash (90 m). Ash lies 30 m higher in altitude than Beech and Beech is about 10 m higher than Chestnut. All ponds are permanent and vegetated within and around. The Chestnut ponds are provided with water from a little stream that is probably the reason why only these ponds are occupied by fish (T. Schwizer, *personal observation*).

Crested newts have been observed at the Herzogenmatt even before the nature reserve has been established in 1980 when only one pond was providing a habitat for newts. However, since then the populations are thought to have markedly increased (Prof. H. Durrer, *personal communication*).

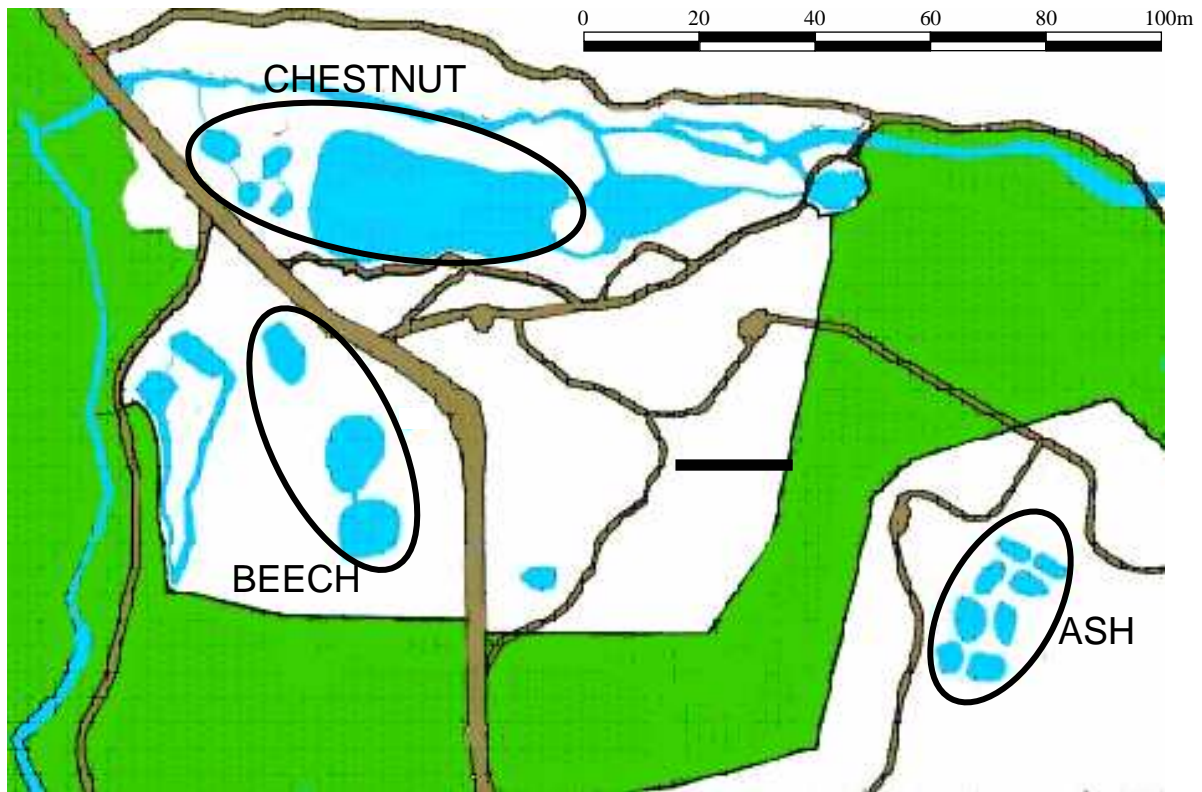


Fig. 2.1. Study site Herzogenmatt. Each of the three populations is associated with either pond complex Ash, Beech, or Chestnut. Ponds and streams are in blue. Green areas indicate shrubs or trees. White areas indicate low ground vegetation. Paths within the nature reserve are colored brown.

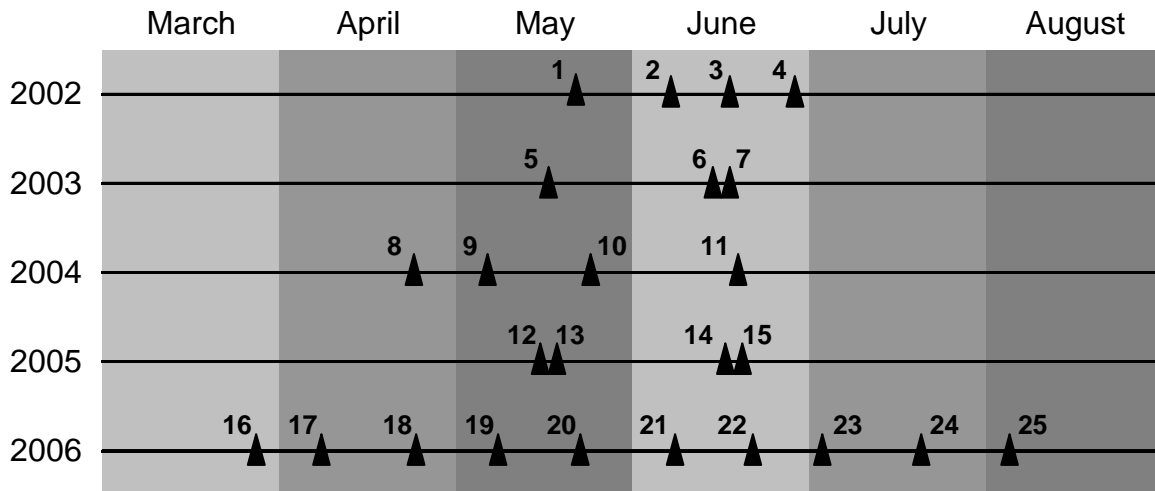
2.3 Capturing Methods

The crested newts were captured over five consecutive years, from 2002 until 2006. In 2002, 2004 and 2005, four capture occasions were accomplished, whereas in 2003 and 2006 three and ten capture occasions were conducted, respectively.

In 2002, the first sampling was in mid-May and roughly two weeks was chosen as the period between two consecutive capture occasions (Fig. 2.2). Since recapture rate was very low in 2002, an other capture scheme was chosen for 2003 and 2005, with a second sampling one to two days after the preceding one. Unfortunately, data have been lost from the second sampling in 2003. In 2004, we started already in mid-April, and again a two to three weeks interval between two sampling sessions was taken. In 2006 I wanted to cover the whole

breeding season, and thus started already by the end of March, capturing approximately every two weeks and accomplishing the last samples at the beginning of August.

Fig 2.2. Sampling scheme over five consecutive years. In total 25 sampling occasions were conducted.



The newts were captured from dusk to midnight by torching the shallow part of the ponds and using dip-nets. As dip-netting was not possible for the largest pond in the Chestnut complex, minnow-traps were set at night and checked for newts in the morning of the following day. After taking photographs, we released newts into the same ponds where we caught them. Males are easily distinguished from females by a black cloaca and by a black underside of the tail and the presence of a bright white stripe at the side of the tail (Thiesmeier and Kupfer 2000).

2.4 Reconstructing Individual Capture Histories

Crested newts are distinguishable individually by the belly pattern (Hagström 1973), which is typically an irregular array of black spots on a yellow or orange background (Fig. 2.3). These unique patterns change little after an animal reaches maturity (Arntzen and Teunis 1993). The capture history of each individual in the study was reconstructed from photographs in three steps: First I compared the images from individuals captured within a year and the same pond complex. Next I compared images between pond complexes to search for individuals that visited more than one pond complex within a breeding season. Finally, recaptures across years were found by comparing all images from every year against images from every other year. This time-consuming part of the study generated each individual's complete capture history.



Fig. 2.3. A photograph showing the belly pattern of an individual from the study site. Since all specimens of *T. cristatus* are distinguishable individually by the belly pattern, individual capture histories can be reconstructed by comparing the photographs from different capture occasions. (Photo by P. Ramseier).

2.5 Capture-Mark-Recapture Analysis

2.5.1 Goodness of Fit Testing

I tested goodness-of-fit (GOF) using program U-CARE 2.2 (Choquet et al. 2005). Single-state (Pollock et al. 1985) as well as multistate GOF tests (Pradel et al. 2003) were made for both males and females separately, using the data set where within year samples were pooled.

The single-state GOF is testing the assumptions of the Cormack-Jolly-Seber (CJS) model, which estimates survival and recapture probabilities under an open population framework (Pollock et al. 1985). Assumptions do not permit survival to differ between newly marked and previously marked individuals, or recapture probability to differ between animals encountered at the previous occasion and those not encountered. Subtest 2.CT is part of the single-state

GOF test (implemented in U-CARE) and was originally developed to detect immediate trap-response behavior (Pradel 1993). Schaub et al. (2004) found that this subtest is useful for detecting Markovian temporary emigration. In Markovian temporary emigration, the probability of an animal being absent from the sampling site is depending on whether or not an individual was absent during the preceding occasion (whereas in the case of 'random' temporary emigration all individuals have the same probability of being absent at a given occasion). Trap-response behavior and Markovian temporary emigration, both give similar results in this GOF test.

The multistate GOF (Pradel et al. 2003) is testing the assumptions of the Jolly-Move (JMV) model (Brownie et al. 1993) for multistate data. Multistate models allow for transitions between states, survival probabilities and recapture probabilities. In the JMV model, transitions vary by state of departure, state of arrival and time interval, survival probabilities vary by state of departure and time interval, and encounter probabilities vary by previous state, current state and date (Choquet et al. 2005). The multistate GOF tests whether the assumptions of the JMV model are met in the data.

2.5.2 Model Selection

Program MARK (Version 4.2) (White and Burnham 1999) was used for model computations. I used the small sample correction of Akaike's Information Criterion (AIC_c) (Akaike 1973, Hurvich and Tsai 1989) which is recommended unless sample size is large relative to the number of estimated parameters (Burnham and Anderson 2002). I used Akaike weights (ω_i) for determining which model best describes the data (Burnham and Anderson 2002). To account for model selection uncertainty, model averaging (Burnham and Anderson 2002) was used to calculate point estimates and standard errors of all parameters of interest.

AIC_c accounts for both model likelihood and number of parameters used in the modeling in that way that higher model likelihood and fewer parameters result in a lower AIC_c . Thus, the best model always has the lowest AIC_c . Akaike weights are derived from AIC_c differences (ΔAIC_c) and indicate the relative support of a model, given the data and the set of candidate models.

To account for model selection uncertainty (Burnham and Anderson 2002) parameters of interest were estimated by model-averaging, i.e. according to the weight of the particular model in the ranking. I selected those models that together carried 95% of the weights.

My data were sometimes too sparse and parameters were therefore not estimable, particularly in models where I allowed for a high number of parameters. In the model ranking I sometimes found that such high parameterized models were higher ranked than models with fewer

parameters that were estimable. I ignored and deleted models where more than half of the parameters of interest (in the particular modeling part) were inestimable.

2.5.3 Annual Survival, Temporary Emigration, Temporary Immigration, and Migration

I used multi-state (MS) capture-mark-recapture models (Brownie et al. 1993, Schwarz et al. 1993) for modeling annual survival, between-site migration over years (i.e. migration between pond complexes), temporary emigration, and temporary immigration as proposed by Fujiwara and Caswell (2002), and Kendall and Nichols (2002). Only data from adult individuals were used. Data from the same year were pooled to one annual occasion resulting in a five sample data set. I defined four states: three for each pond complex and one for the temporary emigrant state (i.e. for those animals that skip a breeding season) where animals are unobservable (recapture probability = 0). I separated two groups, males and females.

The MS model is composed of three parameters: recapture probability, survival probability, and transition probabilities between different states. I separated these three parameter types into five model components: recapture probability, survival probability, temporary emigration probability, temporary immigration probability, and probability of between-site migration. I defined a unique set of candidate models for each model component and used the step-down approach (Lebreton et al. 1992) to evaluate each of these component parameters. First, I determined the top model of recapture probability by comparing the various models in the candidate set while keeping the dimensionality of the other four model components high and constant. After determining the top model of recapture probability, I used that model to compare each of the candidate models for survival rate. Here, again, I kept the dimensionality of the transition probabilities (components 3-5) high and constant. These results were then used in my evaluation of the temporary emigration candidate model set, where I was keeping the dimensionality of temporary immigration and between-site migration (components 4 and 5) high and constant. Then, I used the top model of temporary emigration rate to compare each of the candidate models of temporary immigration while keeping the dimensionality of between-site migration (component 5) high and constant. Third, I evaluated the top model of between-site migration rate. After determining the overall best model, I evaluated whether the kind of temporary emigration was Markovian or random.

The step-down approach was useful to elucidate the model that best described the data. To account for model selection uncertainty, I compared the top model with various alternative models. I produced these alternative models by selecting all model component structures with

AIC differences lower than 3 to the top model in the component ranking and combining them in all possible combinations. These models were evaluated against each other in the 'overall model ranking', where the top model was included as well.

(1) Modeling Recapture Probabilities

Recapture probability (p) is a measure of the probability that a newt, which was caught previously, is caught again.

I expected that capture success (i.e. how many individuals we caught in a particular year compared to an other) positively influences p . Further, I expected that p in Chestnut is much lower than in Ash and Beech since minnow-trapping is far less successful than is dip-netting. In order to optimize the estimation of recapture probabilities, I created some special models in the candidate set. As it was obvious from the capture table (Tab. 3.1), in Ash and Beech capture success was highest in 2005 and 2006. In Chestnut maximal capturing number were reached in 2006. Further, capture numbers as well as capture methods were similar for Ash and Beech, but very much different for Chestnut. Using these observations and the expectation that sex has no influence on p , I created a set of candidate models. (Notations in sensu Lebreton et al. (2002): t = time (i.e. year), g = population, A/B/C = Ash/Beech/Chestnut, * = interaction).

- (1) $p(g*t)$
- (2) $p(t)$
- (3) $p(AB*t-C*t)$
- (4) $p(AB*3t-C*2t)$

Model (1) is the general model allowing for differences of p in every year (t) and all populations (g) with interaction. In comparison to model (2) I could test whether populations differ or not. Model (3) is setting the populations Ash and Beech (AB) equal but not Chestnut (C), and is again fully time-dependent. In model (4) temporal constraints for Ash and Beech were made in such a way that 2003 is equal to 2004 but different from 2005 and 2006 (i.e. three different estimates denoted as $3t$). For Chestnut, estimates of p from 2003 to 2005 were forced to be equal but different to those from 2006 (i.e. two time parameters ($2t$)).

(2) Modeling Survival Probabilities

Survival rate (Φ) is a measure of the probability that a newt survives and is present in the sampling area. Allowing animals to emigrate into a unobservable state, the latter condition is no more required.

Using the MS-approach with an unobservable state, survival rates are only estimable for breeders, but not for non-breeders (Kendall et al. 1997).

I wanted to test whether survival rates of breeders differ among sexes (sx) and among populations (g). Further, I was interested whether survival rates vary over time, either alone (t) or in an interactive (*) or an additive (+) manner. I set up the following candidate models:

- | | | | |
|-----|----------------|------|-------------------------|
| (1) | $\Phi(g*sx*t)$ | (7) | $\Phi(t)$ |
| (2) | $\Phi(g*t)$ | (8) | $\Phi(g*sx)$ |
| (3) | $\Phi(sx*t)$ | (9) | $\Phi(g)$ |
| (4) | $\Phi(g*sx+t)$ | (10) | $\Phi(sx)$ |
| (5) | $\Phi(g+t)$ | (11) | $\Phi(\text{constant})$ |
| (6) | $\Phi(sx+t)$ | | |

(3) Modeling Transition Probabilities

Transition probability (Ψ) is a measure of the probability that an animal changes its state from one occasion to the next, given that it survives. In my case, there are three distinct parts of the modeling: (a) temporary emigration (Ψ_{te}), (b) temporary immigration (Ψ_{ti}), and (c) between-site migration (Ψ_m).

a) Temporary Emigration

As in the modeling of survival rates, I was interested whether temporary emigration rates differ among sexes (sx) and populations (g), and whether they vary over time, either alone (t) or in an interactive (*) and additive (+) way. Hence, I evaluated the following 11 candidate models:

- | | | | |
|-----|---------------------|------|------------------------------|
| (1) | $\Psi_{te}(g*sx*t)$ | (7) | $\Psi_{te}(t)$ |
| (2) | $\Psi_{te}(g*t)$ | (8) | $\Psi_{te}(g*sx)$ |
| (3) | $\Psi_{te}(sx*t)$ | (9) | $\Psi_{te}(g)$ |
| (4) | $\Psi_{te}(g*sx+t)$ | (10) | $\Psi_{te}(sx)$ |
| (5) | $\Psi_{te}(g+t)$ | (11) | $\Psi_{te}(\text{constant})$ |
| (6) | $\Psi_{te}(sx+t)$ | | |

b) Temporary Immigration

I expected the information in the data to be too small to estimate temporary immigration using a high number of parameters, because animals must first emigrate before they can immigrate. Thus, I kept it simple right from the start of the modeling, only looking for a difference between males and females (sx), and therefore coming up with two models:

$$(1) \quad \Psi_{ti}(sx) \qquad (2) \quad \Psi_{ti}(\text{constant})$$

c) Between-Site Migration

Since I found only a small number (n=23) of animals migrating between pond-complexes in the data, I did not expect to detect temporal variation in the parameter estimates for between-site migration. Thus, I was looking for differences in sex (sx) and population (g), resulting in a set of four candidate models:

$$(1) \quad \Psi_m(g*sx) \qquad (3) \quad \Psi_m(sx) \\ (2) \quad \Psi_m(g) \qquad (4) \quad \Psi_m(\text{constant})$$

(4) Markovian or Random Temporary Emigration

To test (and confirm GOF test results) whether temporary emigration is Markovian or random I took the top model and mutated only the transition modeling part concerning temporary emigration and immigration.

The random model suggests that the probability of being a breeder is not dependent on whether the animal was a breeder or a non-breeder before, i.e. that the probability of changing from the non-breeder (nb) to the breeder state (b) is equal to the probability of remaining in the breeding state [$\Psi(nb \rightarrow b) = \Psi(b \rightarrow b)$]. The Markovian model suggests that temporary emigration is state-dependent, i.e. the probability of being a breeder is dependent on whether an animal was a breeder or a non-breeder in the preceding year. In this model, $\Psi(nb \rightarrow b)$ and $\Psi(b \rightarrow b)$ are allowed to be estimated separately.

2.5.4 Seasonal Survival

Again, I used multistate capture-mark-recapture models with an unobservable state (Kendall et al. 1997) for modeling survival rates over seasons. Only data from adult individuals were used. In this modeling approach I pooled those capture occasions which are very close to each other in time (i.e. 6 and 7, 12 and 13, 14 and 15 (Fig. 2.2)), which resulted in 22 occasions. I defined two states, an observable state for breeders and an unobservable state for non-

breeders. Animals were separated into six groups (3 populations x 2 sexes). In order to clearly assign migrating animals to one of the six groups I splitted capture histories by 'removing' and 'releasing' these animals as follows. Removals from the initial state can be done by replacing '1' by a '-1' at the last encounter before the migration event. Releases into the state after transition can be done by placing a '1' to the same occasion as the removal.

In this modeling approach I focused on the estimation of survival rates. The idea was to keep the modeling quite simple. The constraining of recapture probabilities (p) was not varied but rather set up in a way that many parameters were allowed to be estimated. The step-down approach guided the modeling. First, I evaluated the best model of transition probability (Ψ). Then the top model of survival probability (Φ) was selected.

Population recapture rates in the breeding state were constrained according to the results of the first analysis (see 3.2.2) where recapture rates of Ash and Beech are best explained when set equal, whereas those of Chestnut are different to the other two populations. Further, sex differences were not allowed. I did not constrain recapture probability in terms of time, i.e. I allowed 21 different estimates, one for each occasion. Thus, the only model for p was $p(AB*t-C*t)$. Recapture rates in the non-breeding state were set zero.

(1) Modeling Transition Probabilities

The 'decisions' of the animals of changing the breeding state or remaining in either the breeder or the non-breeder state are 'made' at the beginning of the breeding season. Thus, only the first transition rate (Ψ) of every year needs to be estimated (M. Schaub, *personal communication*). The rest is fixed to zero. Since I suspected that this assumption may negatively bias survival rates, I allowed for one more exit per year from the breeding state in an other approach as a comparison. However, estimates for survival rates were approximately the same, rejecting my bias suspicion (data not shown). In all models I allowed for four different Ψ to be estimated (i.e. temporal variation over years) because of the results in the first analysis (see 3.2.2). In the modeling process transition probabilities were always varied for both transition processes simultaneously.

The candidate model set contained four models. I was interested whether population (g) and/or sex (sx) are responsible for the variation in the data.

- | | | | |
|-----|--------------|-----|-------------------------|
| (1) | $\Psi(g*sx)$ | (3) | $\Psi(sx)$ |
| (2) | $\Psi(g)$ | (4) | $\Psi(\text{constant})$ |

(2) Modeling Survival Probabilities

The aim of this modeling approach was (a) to get estimates for seasonal survival rates (Φ) over two different seasons and (b) to detect whether there are differences between sexes, populations, and states. In all models I discriminated 'summer survival rate' and 'winter survival rate'. Summer survival was assigned to the period between the first and the last sampling of each year, whereas winter survival was assigned to the period between the last sampling of any year and the first sampling of the following year. In the candidate model set, I set up models to test whether there are differences in summer (st) and/or winter survival (wt) between breeders and non-breeders. Further, I tested whether differences in population (g) and sex (sx) were supported by the data. In order to account for the fact that summer and winter periods are not equal for all years I did not allow variation over time.

| | | | |
|-----|--------------------|------|-------------------------|
| (1) | $\Phi(g*sx*st+wt)$ | (9) | $\Phi(g*sx*wt)$ |
| (2) | $\Phi(g*st+wt)$ | (10) | $\Phi(g*wt)$ |
| (3) | $\Phi(sx*st+wt)$ | (11) | $\Phi(sx*wt)$ |
| (4) | $\Phi(st+wt)$ | (12) | $\Phi(wt)$ |
| (5) | $\Phi(g*sx*st)$ | (13) | $\Phi(g*sx)$ |
| (6) | $\Phi(g*st)$ | (14) | $\Phi(g)$ |
| (7) | $\Phi(sx*st)$ | (15) | $\Phi(sx)$ |
| (8) | $\Phi(st)$ | (16) | $\Phi(\text{constant})$ |

2.5.5 Population Sizes**Calculating Breeding Population Sizes**

I calculated annual population sizes and corresponding standard errors for all three breeding populations using an 'ad hoc' approach (Wood et al. 1998). In this approach, annual breeding population sizes ($N_{i,b}$) were calculated with numbers of captured animals and recapture probabilities from the annual survival analysis.

$$N_{i,b} = n_i/p_i$$

with

n_i : Total number of animals caught in year i,

p_i : I used the model-averaged recapture probability estimate.

The standard error (SE) of $N_{i,b}$ was approximated by using the formula (Wood et al. 1998)

$$SE(N_{b,i}) = n_i [SE(p_i)] / p_i^2$$

With the ad hoc approach I could not calculate the population size for the first year, because the recapture probability did not exist per se.

Calculating Non-Breeding Population Size

a) The Gimenez Method

The proportion of breeding animals can be calculated from average temporary emigration and immigration rates (O. Gimenez, *personal communication*)

$$N_b / (N_b + N_{nb}) = \Psi_{ti} / (\Psi_{te} + \Psi_{ti})$$

with

| | |
|---------------|------------------------------------|
| N_b : | Number of breeding animals |
| N_{nb} : | Number of non-breeding animals |
| Ψ_{ti} : | Average temporary immigration rate |
| Ψ_{te} : | Average temporary emigration rate |

b) The Schwizer Method

As an alternative method I made my own derivation of a formula for calculating non-breeding population sizes. I was motivated by unrealistic estimates of the proportion of breeding animals using the Gimenez method (as discussed in 4.5). In addition to Gimenez method, I included survival rates into the calculation. Notations are as follows.

| | |
|-----------------|---|
| $N_{b,i}$: | Number of breeders in year i (=breeding population size), |
| E_i : | Number of first-time non-breeders in year i, |
| I_i : | Number of breeders in year i that were non-breeders in year i-1, |
| $N_{nb,i}$: | Total number of non-breeders in year i (=non-breeding population size), |
| Φ_i : | Probability to survive between year i-1 and i (=survival rate), |
| $\Psi_{ti,i}$: | Probability to breed again in year i when being a non-breeder in year i-1 (=temporary immigration rate), |

$\Psi_{te,i}$: Probability to skip breeding in year i when breeding in year $i-1$ (=temporary emigration rate).

The number of first-time non-breeders in year i is dependent on the number of breeders in year $i-1$, the survival rate, between year $i-1$ and i , and temporary emigration rate between year $i-1$ and i .

$$E_i = N_{b,i-1} \Phi_i \Psi_{te,i}$$

The number of breeders in year i that were non-breeders in year $i-1$ is dependent on the total number of non-breeders in year $i-1$, survival rate between year $i-1$ and i , and temporary immigration rate between year $i-1$ and i .

$$I_i = N_{nb,i-1} \Phi_i \Psi_{ti,i}$$

Then,

$$N_{nb,i} = N_{nb,i-1} \Phi_i - I_i + E_i$$

$$N_{nb,i} = N_{nb,i-1} \Phi_i - N_{nb,i-1} \Phi_i \Psi_{ti,i} + N_{b,i-1} \Phi_i \Psi_{te,i}$$

$$N_{nb,i} = N_{nb,i-1} \Phi_i (1 - \Psi_{ti,i}) + N_{b,i-1} \Phi_i \Psi_{te,i} \quad (1)$$

Using (1) I calculated the total number of non-breeders for every year assuming equal survival of breeders and non-breeders.

Estimating Breeding Population Sizes

As an alternative method for the estimation of breeding population sizes, I analyzed my data using POPAN which is based on the general Jolly-Seber (JS) model (Schwarz and Arnason 1996). In contrast to the CJS-model, the JS-model accounts for immigration and emigration to and from the sampling area. In this way POPAN is able to estimate probabilities of entry (i.e. immigration) and probabilities of exit (i.e. emigration and mortality). From the estimated parameters, POPAN calculates many other parameters such as 'net number' and 'gross number' of breeding animals. The differentiation between the number of those individuals that were exposed to sampling ('net number') and the number of all individuals that have actually

been at the ponds ('gross number') allows for the estimation of (a) the net and gross number of animals that entered the study site between two occasions, (b) the number of animals present at each sampling occasion, and (c) the gross population size (as opposed to the net population size that is estimated).

For this modeling approach, I only used capture data of the adult animals from year 2006 since data from the other years were too sparse. I pooled data from the last two catching occasions, because the number of inestimable parameters was too high in the analysis with unpooled occasions.

I set up a candidate model set and used the step-down approach to evaluate each of the estimated parameters by first evaluating the best model for capture rate (p), second for apparent survival rate (Φ), and third for probability of entrance ($pent$).

As for recapture rates in my former analyses of these data, I assumed that p is time-dependent and equal for Ash and Beech but different from Chestnut. Three competing models were set up: $p(g^*t)$, $p(AB^*t-C^*t)$, $p(t)$. I expected Φ to vary over time and assumed variation across populations. Thus, the two competing models were $S(g^*t)$ and $S(t)$. I strongly expected that $pent$ is time-dependent. With the two competing models $pent(g^*t)$ and $pent(t)$ I could test whether there are differences between populations. I wanted to separate estimates for all three populations, thus having only one model for population size $N(g)$.

2.5.6 Optimal Sampling Effort

For monitoring purposes, one might want to know how much effort has to be expended for accurately estimating the abundance of a particular population. Using my data set (adults and juveniles) from 2006, I wanted to answer 2 questions.

1. How many occasions are necessary to get a accurate estimate of the population size?
2. How long is the optimal period for capturing to get an accurate estimate of the population size?

I analyzed the data from 2006 with the last and penultimate (24 and 25, respectively) capture occasions pooled using POPAN (Schwarz and Arnason 1996). I did not distinguish between the three populations but treated them as a single population.

To use the whole potential of the data, I estimated breeding population size using all nine occasions in 2006 which span over 17 weeks. Further, I produced several sets of capture histories by selecting some of the nine occasions in a systematic way. I always preferred

occasions 17-23 because during these occasions sampling success was much higher than before (16) and thereafter (24+25). Further, I tried to have balanced sets of capture histories in terms of how close two consecutive occasions were to each other and also in terms of first and last sampling dates. I ran all models using the JS-method POPAN implemented in MARK. I always used a four-model candidate set with time-dependence and time-invariance for both Φ and p , not varying pent . (Appendix 7.2).

- | | | | | | | | | | |
|-----|-----------|----------------------|------------------|-----|-----|-------------------------|----------------------|------------------|-----|
| (1) | $\Phi(t)$ | $p(t)$ | $\text{pent}(t)$ | N | (3) | $\Phi(\text{constant})$ | $p(t)$ | $\text{pent}(t)$ | N |
| (2) | $\Phi(t)$ | $p(\text{constant})$ | $\text{pent}(t)$ | N | (4) | $\Phi(\text{constant})$ | $p(\text{constant})$ | $\text{pent}(t)$ | N |

Model-averaging of each model set produced the estimates of interest.

To answer the question how the number of sampling occasions influences the estimate and its accuracy, I produced several data sets with 3 to 6 occasions (see Appendix 7.2). In order to exclude a potential effect of the period in which sampling has been done (second question), I only produced data sets where the last sampling occasion was 12 weeks after the first. I made six replicates of each number of sampling occasions.

To test whether the time period between the first and the last sampling occasion has an effect on the estimate and its accuracy, I produced several data sets with four occasions over the periods of 6, 8, 10, 12, and 14 weeks, with four replicates of each.

Using a quadratic curve fit, I plotted the number of occasions and the period between the first and the last sampling against population size estimate and coefficient of variance (as a measure of accuracy), respectively.

3 RESULTS

3.1 Capture Data

My CR data included a total of 1,509 captures (701 different adult and 107 different juvenile individuals). Among the adults, 635 females (363 individuals), and 738 males (338 individuals) were captured (Tab. 3.1).

During the comparison of photographs, I realized that juveniles are difficult to recognize in later years. Thus, I decided to include the juveniles only in the analysis of optimal sampling where I used only data from 2006. Belly patterns are known not to be fixed and to vary especially before reaching maturity (Arntzen and Teunis 1993). Existing black dots can grow in size and new dots can emerge. However, changes are gradual and patterns are enough diverse among specimens that I am confident to have correctly identified all adults over the years and all juveniles within 2006.

Table 3.1. Number of captures (C) and number of individuals (I) for all three populations over five consecutive years.

| POND SITE | SEX | 2002 | | 2003 | | 2004 | | 2005 | | 2006 | | TOTAL | |
|--------------|-----------|------|----|------|----|------|----|------|-----|------|-----|-------|-----|
| | | C | I | C | I | C | I | C | I | C | I | C | I |
| Ash | Males | 12 | 10 | 34 | 27 | 63 | 49 | 87 | 57 | 159 | 78 | 355 | 149 |
| | Females | 16 | 14 | 53 | 40 | 48 | 43 | 72 | 49 | 127 | 76 | 316 | 158 |
| | Juveniles | 18 | 15 | 22 | 19 | 13 | 9 | 14 | 13 | 23 | 19 | 90 | 75 |
| Beech | Males | 18 | 12 | 27 | 19 | 33 | 26 | 56 | 41 | 152 | 74 | 286 | 123 |
| | Females | 13 | 11 | 20 | 17 | 24 | 20 | 57 | 47 | 97 | 56 | 211 | 122 |
| | Juveniles | 1 | 1 | 4 | 4 | 2 | 2 | 2 | 2 | 27 | 15 | 36 | 24 |
| Chestnut | Males | 19 | 17 | 6 | 6 | 10 | 10 | 15 | 15 | 47 | 38 | 97 | 78 |
| | Females | 11 | 11 | 6 | 6 | 8 | 8 | 22 | 22 | 61 | 49 | 108 | 89 |
| | Juveniles | 4 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 4 | 10 | 8 |
| TOTAL | Males | 49 | 39 | 67 | 52 | 106 | 85 | 158 | 113 | 358 | 190 | 738 | 338 |
| | Females | 40 | 36 | 79 | 63 | 80 | 71 | 151 | 118 | 285 | 181 | 635 | 363 |
| | Juveniles | 23 | 20 | 26 | 23 | 15 | 11 | 17 | 15 | 55 | 38 | 136 | 107 |

3.2 Capture-Mark-Recapture Analysis

3.2.1 Goodness-of-Fit Testing

In single-state goodness-of-fit (GOF) tests I found that subtest 2.Ct is highly significant for males ($\chi^2=26.05$, $df=2$, $p<0.001$) and females ($\chi^2=26.27$, $df=2$, $p<0.001$), thus indicating Markovian temporary emigration. All the other subtests were not significant and therefore assumptions are not violated.

Multistate GOF test results showed no significance in potential violations of the JollyMove assumptions (Appendix 7.1).

3.2.2 Annual Survival, Temporary Emigration, Temporary Immigration, and Between-Site Migration

Model Selection

(1) Recapture probability

The top model was $p(AB*3t-C*2t)$ with an Akaike weight of 0.97 confirming my expectations that capture success may predict recapture rate (Tab. 3.2). In this model recapture probabilities were equal for Ash (A) and Beech (B), and different from Chestnut (C). Temporal constraints for Ash and Beech were made in such a way that 2003 is equal to 2004 but different from 2005 as well as 2006. For Chestnut, estimates of p from 2003 to 2005 were forced to be equal but different from those for 2006.

Table 3.2. Ranking of the four models in the candidate set for recapture probability (p). The ranking is based on lowest AIC_c values. ΔAIC_c is the AIC_c difference to the top model, ω_i is the Akaike weight, K is the number of estimable parameters, and Dev is the deviance of a model. All models were built with $\Phi(g*sx*t) \Psi_{te}(g*sx*t) \Psi_{ti}(sx) \Psi_m(g*sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|-----------------|----------------|------------|-----|--------|
| $p(AB*3t-C*2t)$ | 0.00 | 0.97 | 55 | 132.65 |
| $p(t)$ | 7.33 | 0.02 | 35 | 187.15 |
| $p(AB-C*t)$ | 9.22 | 0.01 | 56 | 139.41 |
| $p(g*t)$ | 14.71 | 0.00 | 58 | 139.97 |

(2) Survival probability

I excluded all models containing time-dependence because most of the survival parameters were not estimable. In contrast, in the models where survival was constant over time,

parameters were estimable. Among those models, the sex-specific model best explained the variation in the data ($\omega_i=0.73$) (Tab. 3.3). The model with constant survival probability structure was three times worse supported ($\omega_i=0.25$) than the top model.

Table 3.3. Ranking of all time-invariant models for survival probability (Φ). All models were built with $p(AB*3t-C*2t) \Psi_{te}(g*sx*t) \Psi_{ti}(sx) \Psi_m(g*sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|-------------------------|----------------|------------|----|--------|
| $\Phi(sx)$ | 0.00 | 0.73 | 16 | 185.70 |
| $\Phi(\text{constant})$ | 2.12 | 0.25 | 15 | 186.70 |
| $\Phi(g*sx)$ | 7.90 | 0.01 | 21 | 183.94 |
| $\Phi(g)$ | 11.06 | 0.00 | 20 | 182.95 |

(3) Transition probabilities

a) Probability of temporary emigration. – The top model was the fully time-dependent model without differences in sex and population ($\omega_i=0.42$) (Tab. 3.4). The model allowing for additive variation in sex and time was nearly as strong as the top model ($\omega_i=0.29$). Also, the population- and time-specific model had some support from the data ($\omega_i=0.16$). There is little support for an integrated interaction between sex and time in the fourth-ranked model ($\omega_i=0.11$).

Table 3.4. Ranking of the 11 models in the candidate set for temporary emigration rate (Ψ_{te}). All models were built with $p(AB*3t-C*2t) \Phi(sx) \Psi_{ti}(sx) \Psi_m(g*sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|------------------------------|----------------|------------|----|--------|
| $\Psi_{te}(t)$ | 0.00 | 0.42 | 14 | 158.47 |
| $\Psi_{te}(sx+t)$ | 0.76 | 0.29 | 14 | 159.23 |
| $\Psi_{te}(g+t)$ | 1.88 | 0.16 | 15 | 158.24 |
| $\Psi_{te}(sx*t)$ | 2.63 | 0.11 | 16 | 156.88 |
| $\Psi_{te}(g*sx+t)$ | 7.23 | 0.01 | 18 | 157.22 |
| $\Psi_{te}(g*t)$ | 10.02 | 0.00 | 19 | 157.87 |
| $\Psi_{te}(\text{constant})$ | 24.55 | 0.00 | 11 | 189.30 |
| $\Psi_{te}(g*sx*t)$ | 25.96 | 0.00 | 29 | 151.99 |
| $\Psi_{te}(sx)$ | 26.01 | 0.00 | 12 | 188.67 |
| $\Psi_{te}(g)$ | 28.61 | 0.00 | 13 | 189.18 |
| $\Psi_{te}(g*sx)$ | 31.46 | 0.00 | 16 | 185.70 |

b) Probability of temporary immigration. – Of the two models compared, the sex-specific model had a weight of 0.59, and therefore, it was slightly better than the model with constant temporary immigration probability ($\omega_i=0.41$) (Tab. 3.5).

Table 3.5. Ranking of the two models in the candidate set for temporary immigration rate (Ψ_{ti}). Both models were built with $p(AB*3t-C*2t) \Phi(sx) \Psi_{te}(t) \Psi_m(g*sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|------------------------------|----------------|------------|----|--------|
| $\Psi_{ti}(sx)$ | 0.00 | 0.59 | 14 | 158.47 |
| $\Psi_{ti}(\text{constant})$ | 0.76 | 0.41 | 13 | 159.23 |

c) Probability of between-site migration. – The most parsimonious model had a sex- and group-specific structure ($\omega_i=0.78$) (Tab. 3.6). The second-ranked model ($\omega_i=0.22$) endorses that there are substantial differences of migration behaviour between populations.

Table 3.6. Ranking of the four models in the candidate set for between-site migration (Ψ_m). All models were built with $p(AB*3t-C*2t) \Phi(sx) \Psi_{te}(t) \Psi_{ti}(sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|---------------------------|----------------|------------|----|--------|
| $\Psi_m(g*sx)$ | 0.00 | 0.78 | 19 | 215.24 |
| $\Psi_m(g)$ | 2.37 | 0.22 | 17 | 222.04 |
| $\Psi_m(sx)$ | 11.51 | 0.00 | 13 | 237.33 |
| $\Psi_m(\text{constant})$ | 11.95 | 0.00 | 12 | 239.87 |

Overall model selection

There was a significant amount of uncertainty in model selection as seven models were needed to carry more than 95% of the weight of evidence. Survival and recapture modeling structure were the same in all models, i.e. survival varied with sex, but not with populations and time. Recapture probability was the same for populations Ash and Beech (with three time-specific parameters) but different from population Chestnut (with two time-specific parameters). The seven top models differed only with respect to temporary emigration, temporary immigration and between-site migration probability. The model with time-specific temporary emigration, sex-specific temporary immigration and sex- and population-specific between-site migration probabilities garnered the majority of the weight ($\omega_i=0.40$) (Tab. 3.7). In comparison to the top model, the second-ranked model ($\omega_i=0.20$) differed only in temporary emigration

which was time- and sex-specific (additive). The third-ranked model ($\omega_i=0.14$) differed only with respect to temporary immigration which was constant, and the fourth-ranked model ($\omega_i=0.12$) differed only in between-site migration, which was no more sex- but only population-specific. The other models were combinations of these differences, carrying 0.04-0.05 of the total weight.

Table 3.7. Overall model ranking. Shown are only the top seven models carrying together 99% of the weights.

| Model | ΔAIC_c | ω_i | K | Dev |
|--|----------------|------------|----|--------|
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t) \Psi_{ii}(sx) \Psi_m(g*sx)$ | 0.00 | 0.40 | 19 | 211.03 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t+sx) \Psi_{ii}(sx) \Psi_m(g*sx)$ | 1.42 | 0.20 | 20 | 210.30 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t) \Psi_{ii}(\text{constant}) \Psi_m(g*sx)$ | 2.08 | 0.14 | 18 | 215.24 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t) \Psi_{ii}(sx) \Psi_m(g)$ | 2.37 | 0.12 | 17 | 217.66 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t+sx) \Psi_{ii}(\text{constant}) \Psi_m(g*sx)$ | 4.21 | 0.05 | 19 | 215.24 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t+sx) \Psi_{ii}(sx) \Psi_m(g)$ | 4.56 | 0.04 | 18 | 217.72 |
| $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t) \Psi_{ii}(\text{constant}) \Psi_m(g)$ | 4.62 | 0.04 | 16 | 222.04 |

Random or Markovian Temporary Emigration. – The model for Markovian temporary emigration was ranked higher than the one which described random temporary emigration (Tab. 3.8). The high AIC difference of 13.93 indicates a strong support for a Markovian manner of temporary emigration.

Table 3.8. Comparison of the Markovian and the random model used to describe temporary emigration. Both models were built on $\Phi(sx) p(AB3t-C2t) \Psi_{te}(t) \Psi_{ii}(sx) \Psi_m(g*sx)$.

| Model | ΔAIC_c | ω_i | K | Dev |
|-----------|----------------|------------|----|--------|
| Markovian | 0.00 | 1.00 | 12 | 183.10 |
| Random | 13.93 | 0.00 | 13 | 194.94 |

Parameter Estimation

Only the seven models shown in Tab. 3.7 were used for computing the model-averaged estimates for parameters of interest (Akaike weights were first recalculated).

(1) Recapture probability

For Ash and Beech estimated recapture rates were 0.55 ($SE_{uncond.}=0.100$) in 2003 and 2004, and 0.73 ($SE_{uncond.}=0.073$) in 2005 (Fig. 3.1). The parameter for 2006 was inestimable, probably because it was close to 1. For Chestnut, the recapture rate for 2003-2005 was

estimated very low (0.07) and with a relatively high variance ($SE_{uncond.}=0.039$). For the year 2006, the estimated Chestnut recapture rate was 0.74 ($SE_{uncond.}=0.189$).

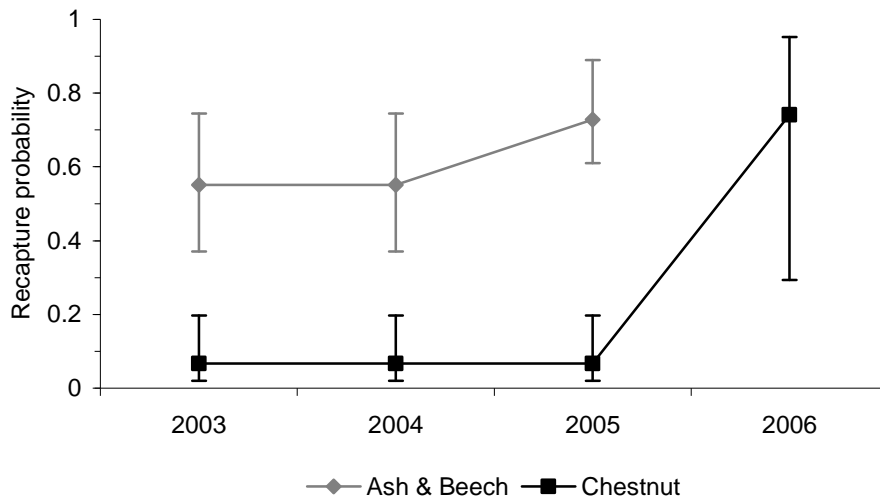


Figure 3.1. Annual recapture probabilities with corresponding 95% confidence intervals. Note the estimate for Ash and Beech was not estimable in 2006.

(2) Survival probability

Estimated annual survival probabilities were 0.91 ($SE_{uncond.}=0.083$) for males and 0.69 ($SE_{uncond.}=0.060$) for females (Fig 3.2).

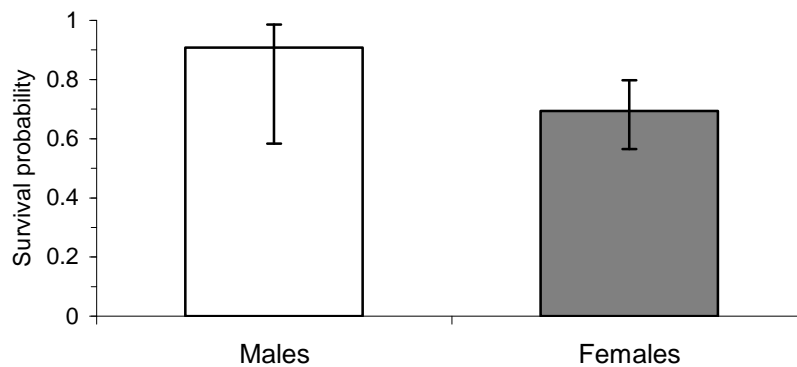


Figure 3.2. Annual survival probabilities with corresponding 95% confidence intervals of males and females.

(3) Transition probabilities

a) *Probability of temporary emigration.* – Estimates of annual temporary emigration rates were separately averaged for sexes and time intervals, i.e. for periods between two

consecutive breeding seasons. The parameters which reflect the temporary emigration rate between 2004 and 2005 could not be generated for both sexes because it was inestimable. Over all years, temporary emigration probabilities were higher for males than for females. Estimates of the males ranged between 0.40 ($SE_{uncond.}=0.170$) in the first period, 0.52 ($SE_{uncond.}=0.096$) in the second period, and 0.57 ($SE_{uncond.}=0.068$) in the last time-interval (Fig 3.3). Estimates of the females were 0.39 ($SE_{uncond.}=0.170$) in the first period, 0.50 ($SE_{uncond.}=0.112$) in the second period, and 0.55 ($SE_{uncond.}=0.072$) in the last time interval.

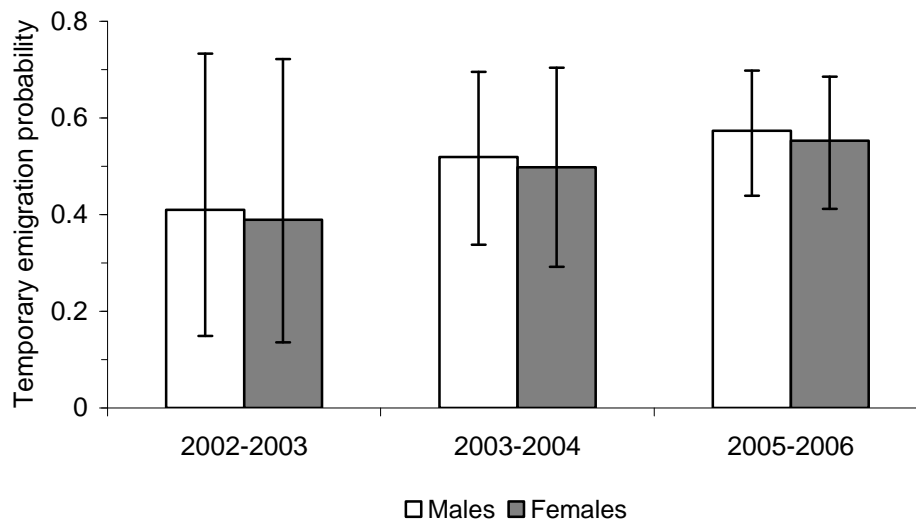


Figure 3.3. Annual temporary emigration rates of three years for males and females with corresponding 95% confidence intervals. The parameters for 2004-2005 were inestimable.

b) Probability of temporary immigration. – Annual rates for temporary immigration were lower for males (0.03, $SE_{uncond.}=0.032$) than for females (0.12, $SE_{uncond.}=0.061$) (Fig. 3.4).

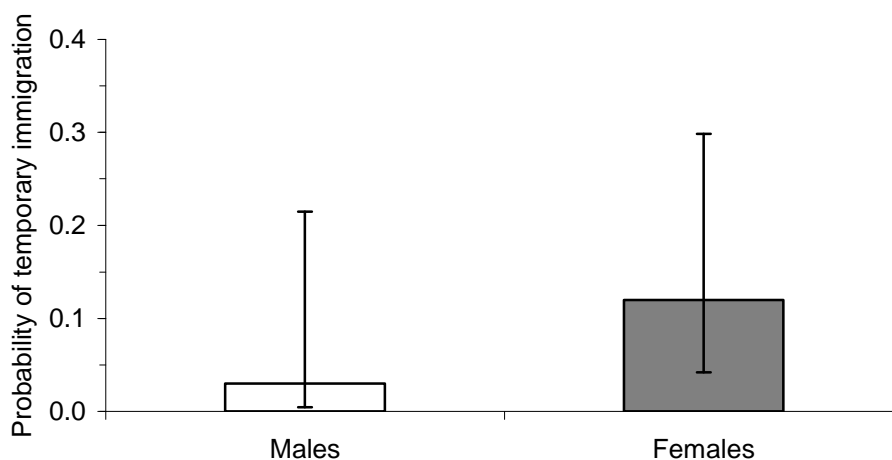


Figure 3.4. Temporary immigration rates of males and females with corresponding 95% confidence intervals.

c) *Probability of between-site migration.* – Migration probabilities per year ranged from 0.000 to 0.132 (Fig. 3.5). Highest migration rates for males (0.132, $SE_{uncond.}=0.059$) as well as for females (0.058, $SE_{uncond.}=0.051$) were estimated for animals migrating from Chestnut to Beech. Lowest rates (0.000, $SE_{uncond.}=0.000$) were found for male and female movements from Ash to Chestnut. Migration rates between pairs of populations were particularly unbalanced between Beech and Chestnut.

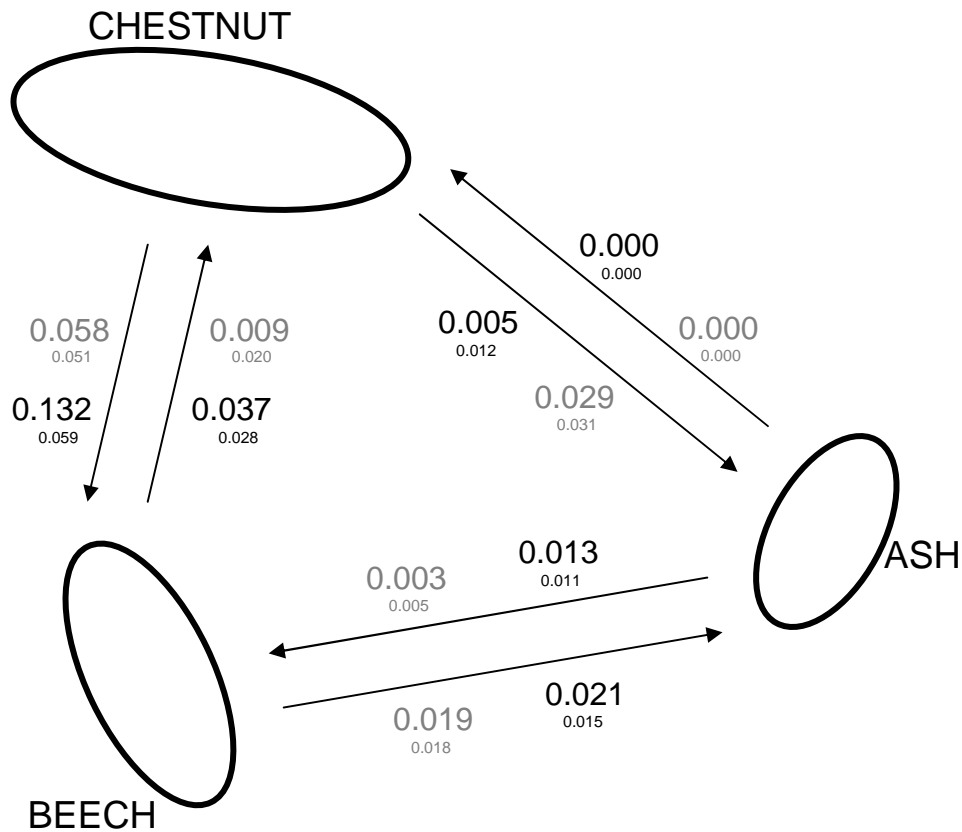


Figure 3.5. Migration rates of males (black) and females (grey) between the investigated complexes Ash, Beech, and Chestnut. Corresponding $SE_{uncond.}$ are given below the estimate.

3.2.3 Seasonal Survival

Model Selection

(1) Transition probability

The model without sex- and population-specific structure had overwhelming support ($\omega_i=1.00$) in the data compared to the three other models (Tab. 3.9).

Table 3.9. Ranking of the four models in the candidate set for transition probability Ψ between breeder- and non-breeder state. All models were built with $p(AB^*t-C^*t) \Phi(g^*sx)$. Note that for all models one transition parameter per year was estimated.

| Model | ΔAIC_c | ω_i | K | Dev |
|-------------------------|----------------|------------|----|---------|
| $\Psi(\text{constant})$ | 0.00 | 1.00 | 61 | 1821.44 |
| $\Psi(sx)$ | 13.34 | 0.00 | 68 | 1819.19 |
| $\Psi(g)$ | 20.23 | 0.00 | 75 | 1810.32 |
| $\Psi(g^*sx)$ | 61.91 | 0.00 | 93 | 1808.58 |

(2) Survival probability

Seasonal weekly survival probabilities were best explained when population- but not sex-differences were allowed and when summer but not winter survival was different between breeders and non-breeders ($\omega_i=0.44$) (Tab. 3.10). In the second-ranked model ($\omega_i=0.22$) populations were no more differing in survival, in comparison to the top model. Moreover, in the third-ranked model summer survival of breeders and non-breeders was no more different ($\omega_i=0.21$). There was also some support for the model where only population but not states differed in survival ($\omega_i=0.09$).

Table 3.10. Ranking of the 16 models in the candidate set for survival probability Φ . All models were built with $p(AB^*t-C^*t) \Psi(\cdot)$. Notations: 'st' = summer time, 'wt' = winter time.

| Model | ΔAIC_c | ω_i | K | Dev |
|----------------------|----------------|------------|----|---------|
| $\Phi(g^*st)$ | 0.00 | 0.44 | 56 | 1822.29 |
| $\Phi(st)$ | 1.39 | 0.22 | 50 | 1836.77 |
| $\Phi(constant)$ | 1.47 | 0.21 | 49 | 1839.03 |
| $\Phi(g)$ | 3.14 | 0.09 | 53 | 1831.99 |
| $\Phi(sx)$ | 5.60 | 0.03 | 51 | 1838.81 |
| $\Phi(sx^*st)$ | 7.41 | 0.01 | 53 | 1836.27 |
| $\Phi(g^*st+wt)$ | 9.27 | 0.00 | 57 | 1829.36 |
| $\Phi(g^*sx)$ | 13.01 | 0.00 | 59 | 1828.69 |
| $\Phi(g^*sx^*st)$ | 15.47 | 0.00 | 65 | 1817.86 |
| $\Phi(g^*sx^*wt)$ | 24.05 | 0.00 | 64 | 1828.67 |
| $\Phi(g^*sx^*st+wt)$ | 26.33 | 0.00 | 69 | 1819.78 |
| $\Phi(sx^*wt)$ | 50.33 | 0.00 | 52 | 1881.37 |
| $\Phi(g^*wt)$ | 56.09 | 0.00 | 55 | 1880.57 |
| $\Phi(st+wt)$ | 57.97 | 0.00 | 46 | 1902.01 |
| $\Phi(wt)$ | 57.97 | 0.00 | 46 | 1902.01 |
| $\Phi(sx^*st+wt)$ | 62.10 | 0.00 | 48 | 1901.83 |

Overall model selection

In the overall model ranking, all models with considerable weight (>5%) differed only in survival probability structure. Transition probability structure did neither vary with sex nor population, whereas recapture probability was best explained when fully time-dependent and when equal for Ash and Beech but not for Chestnut. The most parsimonious model was ($\Phi(g^*st) p(AB^*t-C^*t) \Psi(constant)$) carrying 44% of the weight of evidence in the candidate model set, where survival probabilities varied with population and between the two states (breeders and non-breeders) during the breeding time (Tab. 3.11). Further, there was some support ($\omega_i=0.22$) for the model where summer survival differed between the two states but survival was equal for populations. Almost the same support ($\omega_i=0.21$) got the model with no differences between either populations or states. In the fourth-ranked model ($\omega_i=0.09$) only populations but not states were differing in survival.

Table 3.11. Overall model ranking. Shown are only the four top models carrying together 96% of the weights.

| Model | ΔAIC_c | ω_i | K | Dev |
|--|----------------|------------|----|---------|
| $\Phi(g^*st) \rho(AB^*t-C^*t) \Psi(\text{constant})$ | 0.00 | 0.44 | 56 | 1822.29 |
| $\Phi(st) \rho(AB^*t-C^*t) \Psi(\text{constant})$ | 1.39 | 0.22 | 50 | 1836.77 |
| $\Phi(.) \rho(AB^*t-C^*t) \Psi(\text{constant})$ | 1.47 | 0.21 | 49 | 1839.03 |
| $\Phi(g) \rho(AB^*t-C^*t) \Psi(\text{constant})$ | 3.14 | 0.09 | 53 | 1831.99 |

Parameter Estimation

The main interest in this part of the study was on survival parameters that I estimated using multi-model inference based on the four top models (Tab. 3.11).

Summer survival probabilities (one for each state), and one winter survival probability were estimated for each population. Weekly summer survival rates for breeders were 0.919 ($SE_{\text{uncond.}}=0.0184$), 0.930 ($SE_{\text{uncond.}}=0.0111$), and 0.955 ($SE_{\text{uncond.}}=0.0227$) for population Ash, Beech, and Chestnut, respectively. Weekly summer survival rates for non-breeders were estimated as 0.971 ($SE_{\text{uncond.}}=0.0375$), 0.954 ($SE_{\text{uncond.}}=0.0265$), and 0.957 ($SE_{\text{uncond.}}=0.0398$) for population Ash, Beech, and Chestnut, respectively. Estimated mean weekly survival rates over wintertime were 0.9994 ($SE_{\text{uncond.}}=0.0016$), 0.9998 ($SE_{\text{uncond.}}=0.0009$), and 0.9976 ($SE_{\text{uncond.}}=0.0031$) for population Ash, Beech, and Chestnut, respectively (Fig 3.6).

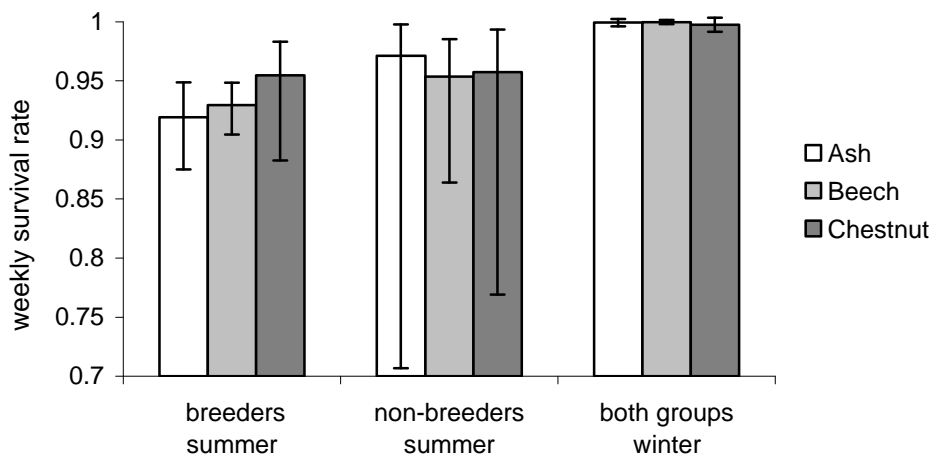


Figure 3.6. Weekly survival rates (with corresponding 95% confidence intervals) of breeders and non-breeders over the summer (breeding time) and survival rates of both groups over the winter (non-breeding time) were best explained by differences among populations. Note that the scale on the y-axis is from 0.7 to 1.0 in order to visualize the small differences between the populations.

3.2.4 Population Sizes

Breeding Populations over Four Years

The breeding population Ash increased in number of animals in the first time interval from 122 (SE=22.1) to 167 (SE=30.3), decreased over the second time interval from 167 (SE=30.3) to 146 (SE=14.5) and again increased in the third interval from 146 (SE=14.5) to 176¹ (Fig. 3.7). Population Beech was constantly growing in the number of breeding animals through all intervals, overall from 65 (SE=11.9) to 145¹. The number of breeders in Chestnut seems to have enormously increased from 180 (SE=106.3) to 556 (SE=327.6) over the first three years, but massively decreased the number in 2006 (117, SE=29.9) to a level below that of 2003 (Fig. 3.7). However, breeding population sizes calculated for Chestnut have huge 95% confidence intervals. In contrast, the respective values for Ash and Beech, recapture rate estimates for Chestnut were low ($p=0.07$) and errors relatively large (SE=0.039), resulting in a 95% confidence interval ranging from 0.02-0.20. Thus, the ad hoc estimation of population sizes for Chestnut is rather questionable and estimates are hardly meaningful. As a consequence, I did not include the Chestnut estimates into analysis of non-breeding populations.

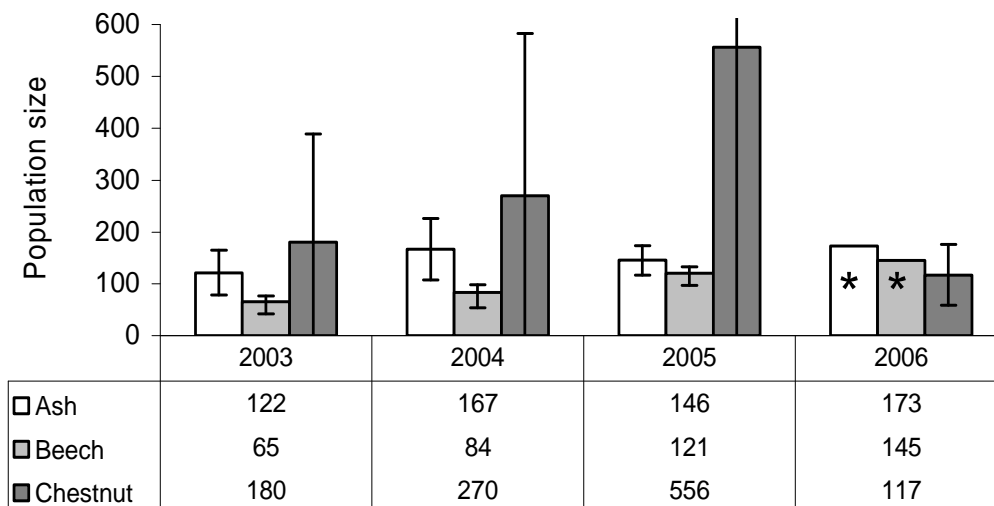


Fig. 3.7. Breeding population sizes of the three populations over four years. For 2006 population sizes of Ash and Beech (denoted with asterisks) were calculated based on the assumption that recapture rate was 1.00. Note that the 95% confidence interval of the Chestnut population size in 2005 is nearly reaching 1200.

¹ For 2006 there is no standard error because the estimate was computed assuming a recapture rate of 100%.

A known problem in maximum likelihood computations is the estimability of parameters when being close to the border (i.e. 0 or 1) (Burnham and Anderson 2002). Due to high sampling effort, I expect that the recapture rate of Ash and Beech in the year 2006 was indeed 100% or close to 100%, thus suggesting this to be the reason for the unsuccessful estimation of this parameter. Assuming that recapture rate was 1.00, all breeding animals would have been caught. According to the calculations of the ad hoc approach, the numbers of captured individuals would be equal to the total breeding population size.

Non-Breeding Populations over Three Years

a) Proportions of breeding animals based on Gimenez' method

Proportions of breeding animals for males and females were 0.08 (SE=0.07) and 0.19 (SE=0.09), respectively. Compared to the number of breeding animals, the number of non-breeding animals (juveniles excluded) was calculated 11.6 and 4.2 times higher for males and females, respectively. As I did not estimate numbers of breeding males and females separately, I calculated non-breeding population sizes using the average proportion of breeding animals from both sexes. Breeding and non-breeding population sizes for Ash and Beech are shown in Fig. 3.8 and Fig. 3.9.

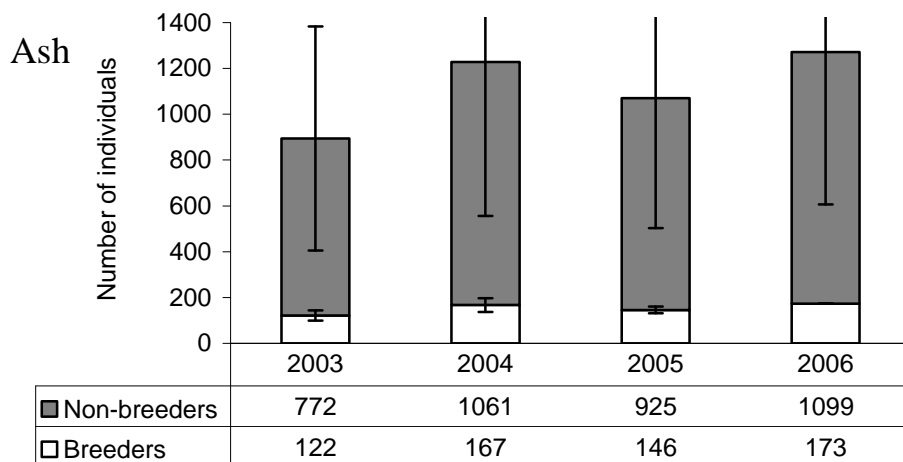


Fig. 3.8. Breeding and non-breeding population sizes of population Ash over 4 years with corresponding standard errors (SE) derived from breeding proportions based on the method proposed by Gimenez. Note that all positive and negative SE were equal. Positive SE are not shown entirely for non-breeding population sizes from 2004-2006.

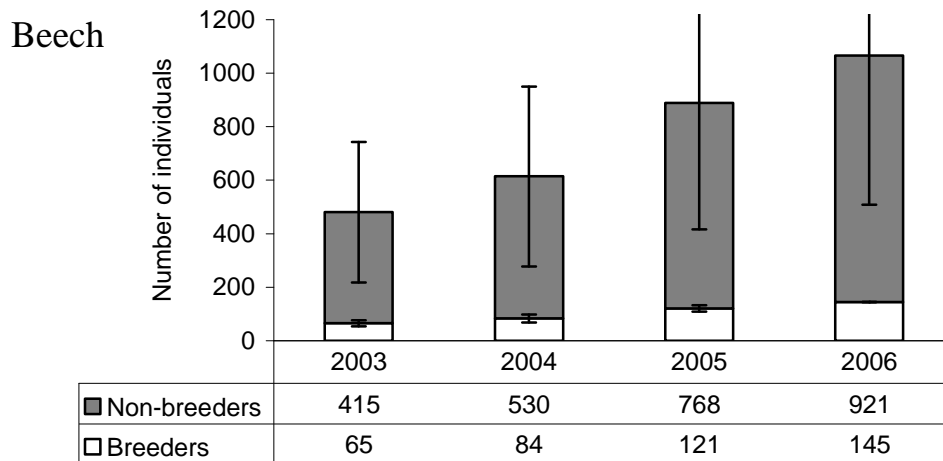


Fig. 3.9. Breeding and non-breeding population sizes of population Beech over 4 years with corresponding standard errors (SE) derived from breeding proportions based on the method proposed by Gimenez. Note that all positive and negative SE were equal. Positive SE are not shown entirely for non-breeding population sizes from 2005-2006.

b) Calculating non-breeding population sizes based on Schwizer's Method

From 2004-2006, breeding and non-breeding populations for both populations Ash and Beech had roughly the same size over all years. Non-breeding population sizes of both populations were increasing over all years from 144-180, and 85-135, respectively (Fig. 3.10; Fig 3.11). I calculated non-breeding population sizes for Ash and Beech in an iterative way, thus standard error propagation would lead to meaningless results. For reasons of simplification, I used average survival (assuming a sex-ratio of 1:1), and also average temporary emigration and temporary immigration rates over all years. I calculated population sizes of non-breeders based on the assumption that from 1996 – 2002 breeding population sizes were constant and low; I set population size to 100 animals for Ash and to 50 animals for Beech. This was necessary because meaningful estimates by using iterations can only be generated when including breeding population sizes of several years. For 2003-2005 I used the estimated breeding population sizes (Fig. 3.7).

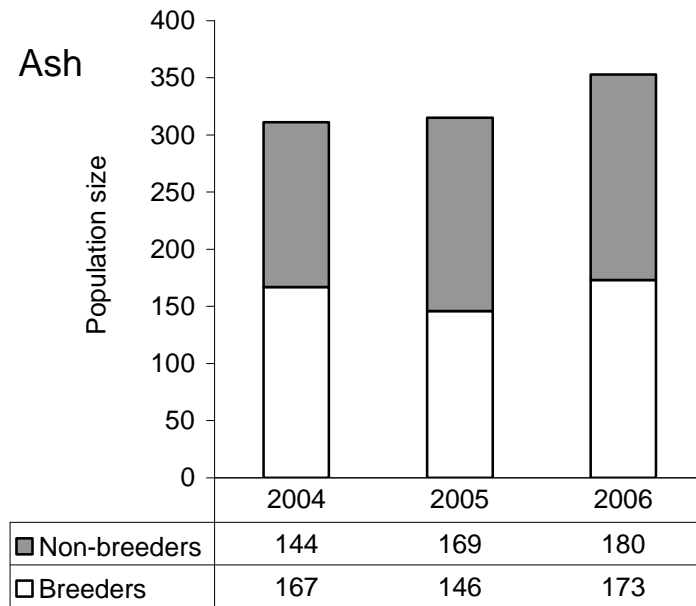


Fig. 3.10. Breeding and non-breeding population sizes of population Ash based on Schwizer's method. Note that these calculations did not include standard error propagation since they were done in an iterative way.

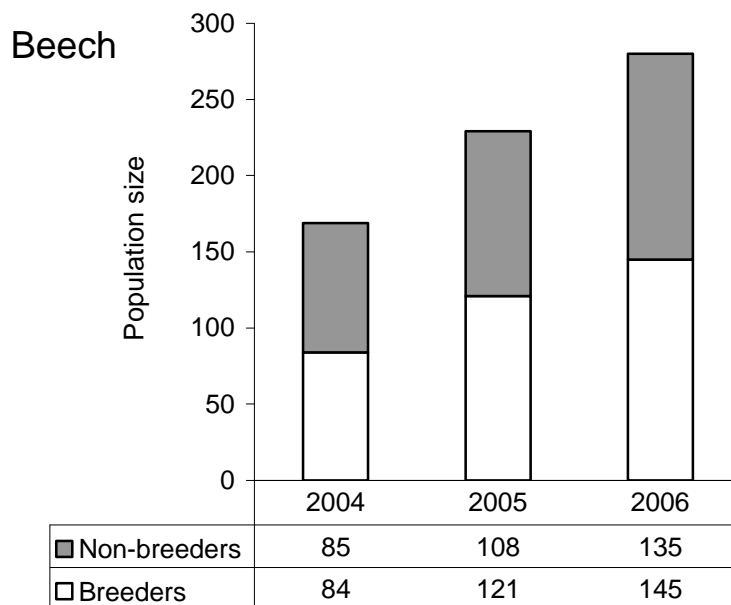


Fig. 3.11. Breeding and non-breeding population sizes of population Beech based on Schwizer's method. Note that these calculations did not include standard error propagation since they were done in an iterative way.

c) A comparison between Gimenez' and Schwizer's method

I calculated breeding proportions with variable temporary emigration and immigration rates using the calculation proposed by Gimenez. I used only temporary emigration and immigration rates within the 95%-confidence intervals of the estimates, that were 0.05-0.75 and 0.05-0.25 for emigration and immigration probabilities, respectively (Fig. 3.2; Fig. 3.3). Non-breeding population sizes were calculated with breeding populations of 100 individuals. Proportions of breeding animals were 0.06-0.86, i.e. non-breeding population sizes ranged between 17-1500 individuals (Appendix 7.3, Tab. A4).

Using again constant annual breeding population size (100 individuals) and constant annual survival rate (0.8), I calculated non-breeding population sizes over 25 years with variable temporary emigration and immigration rates based on Schwizer's method. I used only temporary emigration and immigration rates within the 95% confidence intervals of the estimates, that were 0.05-0.75 and 0.05-0.25 for emigration and immigration probabilities, respectively (Fig. 3.2; Fig. 3.3). In all calculations non-breeding population sizes per year were stabilized after 25 years. Non-breeding population sizes ranged between 9-250 individuals, i.e. proportions of breeding animals between 0.29-0.91 (Appendix 7.3, Tab. A5).

Gimenez' method produced higher estimates than my method for each combination of temporary emigration and immigration probabilities. Fig. 3.12 illustrates ratios between estimates of both methods for each point estimate. The higher temporary immigration probabilities were, the lower was the ratio between the point estimates of the two methods, i.e. the smaller was the relative difference between the estimates. The degree of temporary emigration had no influence on the ratio.

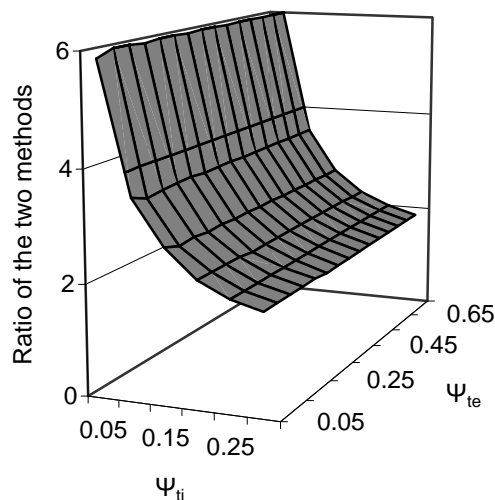


Fig. 3.12. Estimate ratios of non-breeding population size generated by two methods (Gimenez' and Schwizer's) in relation to temporary emigration and immigration rates.

Breeding Population Size of One Year Using POPAN

Model Selection

(1) Capture Probability

The top model ($p(AB^*t-C^*t)$) in the capture probability was time-dependent and assumed that populations Ash and Beech had the same capture probabilities but differed from Chestnut ($\omega_i=0.70$) (Tab. 3.12). Model $p(g^*t)$ had less than half of the support than the best model ($\omega_i=0.30$). The time-specific model $p(t)$ had no support in the data ($\omega_i=0.00$).

Table 3.12. Model ranking of the three models in the candidate set for capture probability. All models were built with $\Phi(g^*t)$ $\text{pent}(g^*t)$ $N(g)$. Note that variances are missing because POPAN does not calculate them.

| Model | ΔAIC_c | ω_i | K |
|-----------------|----------------|------------|----|
| $p(AB^*t-C^*t)$ | 0.00 | 0.70 | 54 |
| $p(g^*t)$ | 1.70 | 0.30 | 49 |
| $p(t)$ | 27.75 | 0.00 | 69 |

(2) Apparent Survival Probability

The survival rate turned out to be best explained when allowing for time- but not for population-specific survival probabilities ($\omega_i=1.00$) (Tab. 3.13).

Table 3.13. Ranking of the two models in the candidate set for capture probability. Both models were built with $p(AB^*t-C^*t)$ $\text{pent}(g^*t)$ $N(g)$.

| Model | ΔAIC_c | ω_i | K |
|--------------|----------------|------------|----|
| $\Phi(t)$ | 0.00 | 1.00 | 41 |
| $\Phi(g^*t)$ | 19.10 | 0.00 | 54 |

(3) Probability of Entrance

The structure of the top model for probability of entrance contained only time but not population ($\omega_i=0.88$) (Tab. 3.14). In comparison, the time- and population-specific model had only little support in the data ($\omega_i=0.12$).

Table 3.14. Ranking of the two models in the candidate set for probability of entrance. Both models were built with $p(AB^*t-C^*t) \Phi(t) N(g)$.

| Model | ΔAIC_c | ω_i | K |
|-----------|----------------|------------|----|
| pent(t) | 0.00 | 0.88 | 32 |
| pent(g*t) | 3.95 | 0.12 | 41 |

In the overall model ranking, only two models had support in the data. Model (S(t) p(g*t) pent(t) N(g)) was the top model ($\omega_i=0.88$) (Tab. 3.15). It was more than seven times stronger than the second-ranked model (S(t) p(g*t) pent(g*t) N(g)) ($\omega_i=0.12$) that differed only in the modeling of probability of entrance.

Table 3.15. Overall model ranking.

| Model | ΔAIC_c | ω_i | K |
|--------------------------------------|----------------|------------|----|
| S(t) p(AB* $t-C^*t$) pent(t) N(g) | 0.00 | 0.88 | 32 |
| S(t) p(AB* $t-C^*t$) pent(g*t) N(g) | 3.95 | 0.12 | 41 |

Estimated and Calculated Parameters

Breeding population sizes for 2006 were calculated for each population separately. Since the second-ranked model could not successfully generate all of the three population estimates I excluded it for parameter estimation.

Breeding population Chestnut was the largest population consisting of 271 adults (SE=53). In Ash, 230 breeding individuals (SE=14) were present, whereas for population Beech (196, SE=12) the lowest number of breeding adult crested newts was estimated (196, SE=12) (Fig. 3.13).

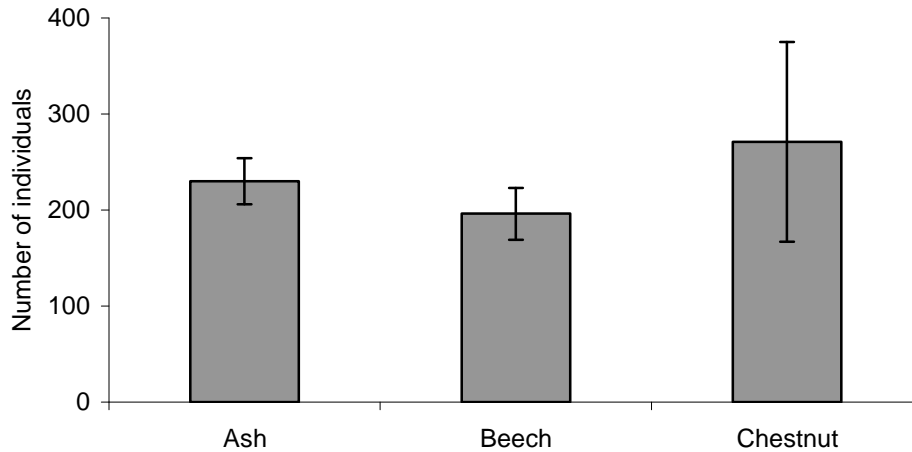


Figure 3.13. Breeding population sizes of the Ash, Beech, and Chestnut with corresponding 95%-confidence intervals.

Further, breeding population sizes for each sampling occasion could be calculated. Figure 3.14 shows the number of animals present at the ponds of population Ash over the breeding season and the cumulative breeding population sizes. From mid-April until the end of June 91 (39%) to 133 (58%) individuals of the total breeding population ($N_B=230$) were inhabiting ponds at the time of the sampling sessions. Since parameters for apparent survival rates and probabilities of entrance were the same for all populations, curves of abundance over time from Beech and Chestnut showed the same pattern as Ash.

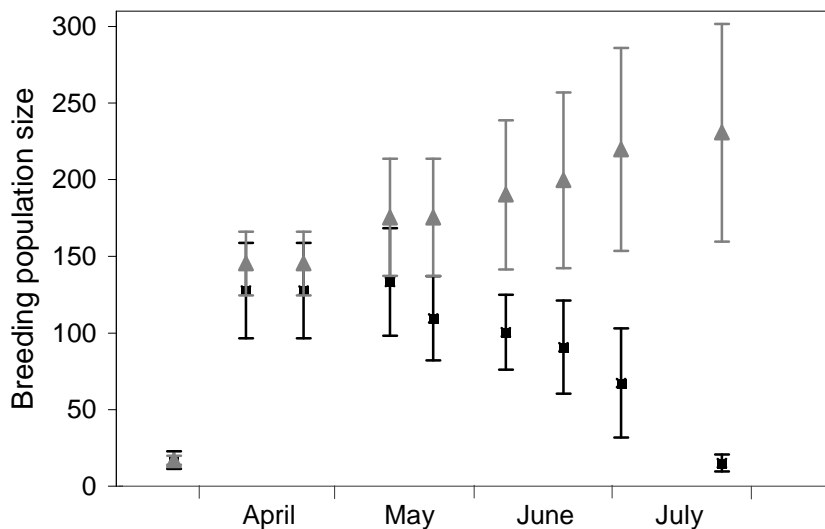


Figure 3.14. Black squares are calculated breeding population sizes per capture occasion at Ash with corresponding 95% confidence intervals. Grey triangles represent cumulative breeding population size of population Ash with 95% confidence intervals.

3.2.5 Optimal Sampling Effort

Using all nine capture occasions over the whole sampling period of 17 weeks in 2006, the estimated number of breeding animals was 704 (SE=43). This estimate mean can be seen as a reference, since it was performed using the whole information in the data.

Number of Capture Occasions

The number of capture occasions had a positive influence on the gross population estimate mean (Fig 3.15). However, the effect flattened with higher number of occasions. The number of occasions had a negative influence on the coefficient of variance of the estimate (Fig 3.16). Again, with higher number of occasions, the influence was decreasing. The optimum of sampling sessions over a sampling period of 12 weeks was 6, for both the height and the precision of the population size estimate.

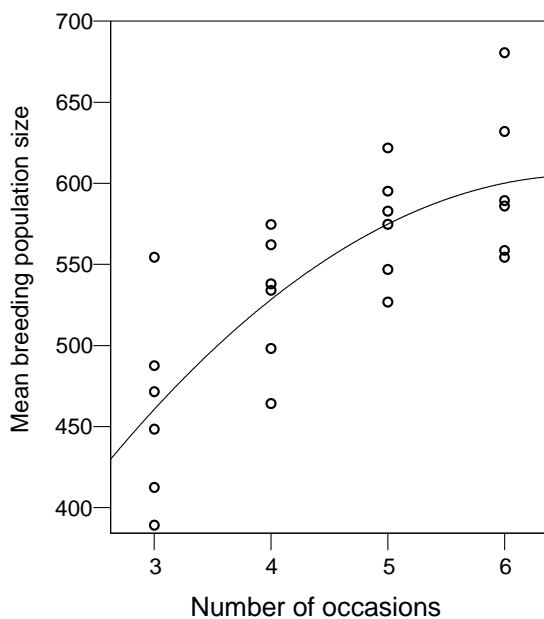


Figure 3.15. Mean estimates of breeding population size plotted against the number of sampling occasions.

$y = 130.2 + 142.0x - 10.6x^2$, with y : mean breeding population size, and x : number of sampling occasions.

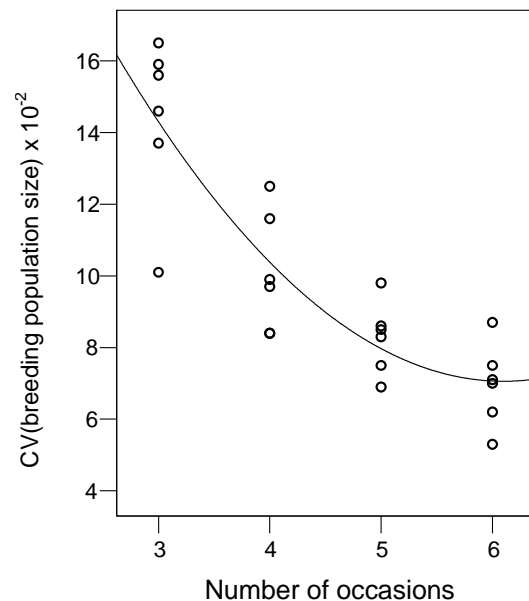


Fig. 3.16. Coefficient of variation (CV) of breeding population size plotted against the number of sampling occasions.

$y = 0.353 - 0.093x + 0.008x^2$, with y : CV of breeding population size estimates, and x : number of sampling occasions.

Period between First and Last Occasion

The period from the first to the last capture occasion had a positive influence on the estimate mean (Fig 3.17). However, the influence is decreasing with longer period. Also, the period from the first to the last capture occasion had a positive influence on the estimate's coefficient of variance (Fig 3.18). The optimum sampling period was 14 weeks when the number of samplings was four.

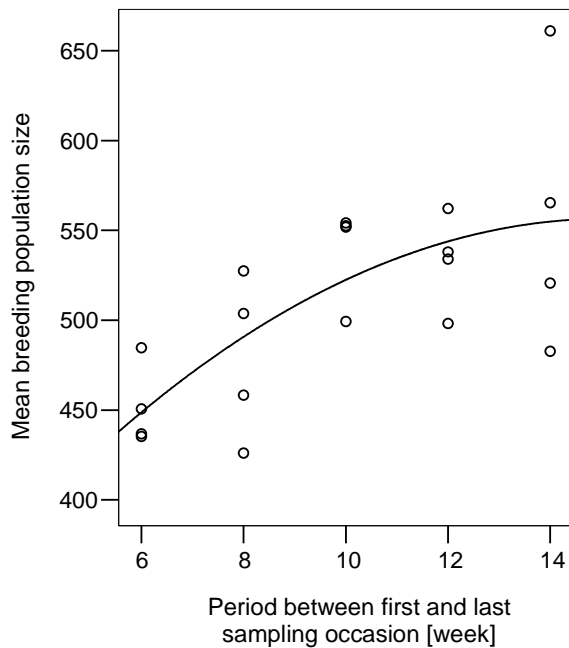


Figure 3.17. Mean estimates of breeding population size plotted against the period between first and last sampling occasions in weeks.

$y = 260.8 + 39.1x - 1.3x^2$, with y : mean breeding population size, and x : period between first and last sampling occasion in weeks.

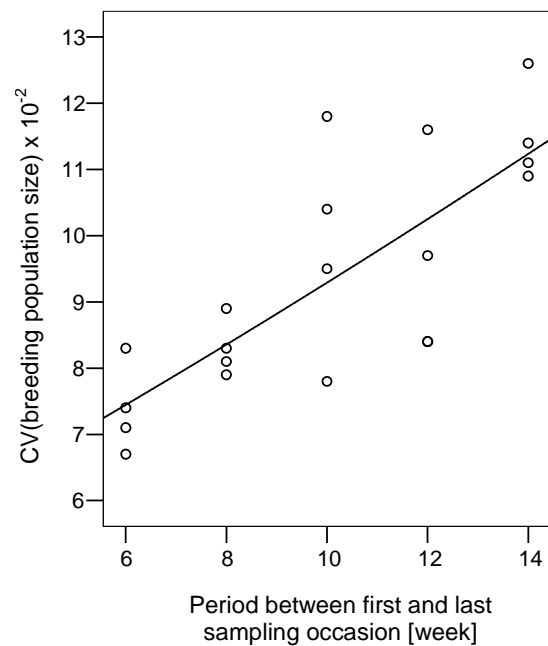


Figure 3.18. Coefficient of variation (CV) of breeding population size plotted against the period between first and last sampling occasions in weeks.

$y = 4.865 + 0.411x + 0.003x^2$, with y : CV of breeding population size estimates, and x : period between first and last sampling occasion in weeks.

4 DISCUSSION

Multistate CMR models showed that annual survival of breeding crested newts was higher for males than females. Further, survival over the breeding time was estimated to be lower for breeders than for non-breeders but equal for both categories over the non-breeding time. Temporary emigration was Markovian and estimated emigration probabilities were high and variable over years, whereas temporary immigration probabilities were relatively low. Consequently, non-breeding populations had about equal or higher sizes than breeding populations, depending on the method used for estimating their size. Breeding probabilities were higher for females than for males. Breeding site fidelity was generally high but population Chestnut showed relatively high between-site migration. Breeding populations generally increased over the study period. The temporal pattern of pond residence, analyzed for one year, showed that at most 60% of the breeders were present at one time. Evaluations of Jolly-Seber models using various combinations of sampling occasions showed that sampling for monitoring breeding populations should be done at least 6 times over 14 weeks.

4.1 Survival

Annual survival probabilities of breeding crested newts were 0.91 (SE=0.083) for males and 0.69 (SE=0.060) for females (Fig. 3.2). This is at the upper range of most published data [e.g. 0.33-0.57 (Arntzen and Teunis 1993), 0.50 (Glandt 1982), 0.65 (Hedlund 1990), 0.23-0.61 (Sewell et al. 2005)]. Only Baker (1999) (0.31-1.00) and Hagström (1979) (0.70-0.80) reported survival rates over several years in the range of my estimates. Glandt (1982), Hedlund (1990), Arntzen and Teunis (1993), and Baker (1999) estimated survival probabilities using 'sampling efficiency' that they calculated from numbers of animals captured and population size estimates. Nowadays, however, these calculations are seen as obsolete nowadays because there are now better ways to deal with capture probabilities (Lebreton et al. 1992). Only Sewell et al. (2005) applied present-day CMR methods to estimate survival probabilities. In contrast to my study, Sewell et al. (2005) did not include breeding probabilities, thus potentially leading to negatively biased survival estimates (Kendall and Nichols 2002, Schaub et al. 2004).

The difference in annual survival probabilities between males and females is considerable. Only few studies separately analyzed survival rates of male and female crested newts. My findings are consistent with those of Baker (1999), who found that males survived generally

better than females. Higher reproductive energy expenditure of females might explain the difference in survival between the sexes. This idea is consistent with Muellner's (1991) finding that male crested newts gained mass during the aquatic seasons, whereas females just maintained their mass. Stoefer (1997) showed that in one year both males and females of a population gained mass over the aquatic season, but males gained more than females. However, over the intermediate non-breeding season and during the breeding season of the second year both sexes lost mass, but mass loss was always higher for females than for males (Stoefer 1997).

Weekly survival rate during the non-breeding period (i.e., fall, winter) was equal for breeders and non-breeders, whereas over the breeding time survival was lower for breeders than for non-breeders (Fig. 3.6). A study on the pond-breeding tiger salamander (*Ambystoma tigrinum*) found the same pattern between breeding and non-breeding animals over the breeding and the non-breeding season (Church et al. *in press*). My results suggest that breeding newts in the ponds are at higher mortality risk than non-breeding individuals. Therefore, reproduction may be costly in terms of survival over the breeding period (discussed below).

4.2 Temporary Emigration and Breeding Probabilities

The goodness-of-fit test indicated that temporary emigration was Markovian in nature. The Markovian temporary emigration models showed that, depending on the year, 39% (SE=17.0%) to 55% (SE=7.2%) of breeding females and 40% (SE=17.0%) to 57% (SE=6.8%) of breeding males skipped breeding in the following year (Fig. 3.3). Moreover, once breeding animals had been absent from the breeding site, only low proportions of males (3%, SE=3.2%) and females (12%, SE=6.2%) returned to the ponds (temporary immigration rates, Fig. 3.4). The higher temporary emigration rates and lower temporary immigration rates of the males indicate that breeding probabilities of males are lower than of females.

High rates of emigration after breeding suggest that breeding is costly for crested newts. This is consistent with the increased mortality of breeding animals over the breeding season compared to non-breeding animals (Fig. 3.6). However, during the non-breeding period probabilities to survive were the same for breeders and non-breeders (Fig. 3.6). This leads to the conclusion that the energy spent for reproduction did not limit post-breeding survival. It appears that crested newts desisted breeding in order to avoid the higher mortality risks in the aquatic habitat, in that way increasing individual fitness. On the other side, individual fitness

increases through reproduction too. This means that temporary emigration entails a cost resulting in a trade-off between survival and reproduction.

Temporary immigration probability estimates were very low compared to emigration probabilities; i.e. most of those animals that once stopped breeding never bred again. This is fairly astonishing since individual fitness does not increase anymore when once having stopped reproduction, assuming the costs of skipping breeding might be higher than the survival costs of breeding.

One explanation that animals live on but do not reproduce is that reproductive energy is so high that many crested newts can not afford to breed multiple times. Like reaching sexual maturity (Ryser 1996), saved energy might need to reach a certain energy threshold to make a breeding attempt. An animal that does not reach this threshold skips breeding and thereby increases its residual reproductive value, i.e. acquires more energy than it needs for maintenance and growth, thereby filling its energy reserves that can be used for future reproduction. My results suggest that only few non-breeding animals reach the assumed threshold.

This is the first study that quantified probabilities of temporary emigration and immigration of the crested newt using CMR methods. Compared to Hedlund (1990), I found higher probabilities of skipping breeding opportunities. The assumption of Hedlund (1990) that recapture probability was 100% may be wrong and therefore breeding probabilities were underestimated. Geographic variation among populations could also be the reason for the difference. As it has been shown for other amphibian species (Fretey et al. 2004, Muths et al. 2006, Church et al. *in press*), temporary emigration seems to be a trait of the life history of *T. cristatus*. Long-term CMR data from earlier studies on the population dynamics of the crested newt should be re-analyzed using multistate modeling methods in order to elucidate the degree of temporary emigration of other populations.

4.3 Migration and Pond Fidelity

Probabilities that crested newts chose different pond sites for breeding over the study period were generally low (Fig. 3.5). The low between-site migration rates suggest that breeding site fidelity is a more advantageous strategy. Individuals return to sites where they bred in the past. Fidelity of adult crested newts to their breeding sites is well-reported (Kupfer and Kneitz 2000, Oldham and Humphries 2000, Sinsch et al. 2003). Migrating juveniles, rather than

adults, may provide for genetic exchange between populations. Juvenile migration is known to be high (Kupfer and Kneitz 2000).

Of those animals that bred again in the following year the Chestnut population showed highest emigration probabilities (males 22 – 31%, females 10 – 14%, Fig. 3.5). Males from Ash and Beech were 10.5 and 2.3 times, respectively, less likely to change the breeding site than Chestnut males, whereas migration probabilities of the females of Ash and Beech were even 34.4 and 3.1 times, respectively, lower than those of the females from Chestnut. The tendency that more Chestnut adults change their breeding site could be explained by the presence of fish in the large pond of Chestnut. This pond is the only one at the study site a stream is flowing in and where fish (species unknown) were caught during fieldwork. Among amphibians, crested newts seem to be particularly sensitive to fish predation on larval stages (Swan and Oldham 1993) which is thought to have a substantial influence on population recruitment (Arntzen and Teunis 1993, Baker 1999). On the other side, the large Chestnut pond is providing a high habitat quality in terms of low mortality risk for breeding adults (Fig. 3.6). Furthermore, among other attributes, habitat suitability for the crested newt includes pond area as a measure for biological productivity (Oldham et al. 2000). Since it is thought that amphibians have evolved in dynamic environments (Kuhn and Laufer 2001), where ponds are temporary and therefore fish predation is minimal (Griffiths 1997), the large pond may be deceptive for breeding site selection, and thus might be acting as an ecological trap (Schlaepfer et al. 2002). Consequently, in the context of metapopulation dynamics, Chestnut could act as a 'sink' population and only persists through juvenile animals immigrating from 'source' populations (*sensu* Pulliam (1988)). A number of studies described metapopulation structure for the species (e.g. Griffiths and Williams 2000; Kupfer and Kneitz 2000). However, these explanations are just speculative. Quantifying metapopulation dynamics and revealing causes of variable migration among populations would require much more than the migration analysis of breeding animals between the three populations. Additional approaches needed include analyses of population demography of juveniles *and* adults, of population genetics, and correlations of both data sets with environmental variables. Even to decide whether the investigated populations function as a metapopulation or as a single breeding unit, these other analyses would be necessary.

4.4 Breeding Population Sizes

Over a period of four years, populations Ash and Beech increased in numbers of breeding animals, whereas Chestnut decreased. Population growth can originate from various demographic parameters, generally when recruitment rate outweighs adult mortality. Considering that temporary emigration probabilities for breeders (Fig. 3.3) were 5-7 times higher than the probability for a non-breeder to breed again (i.e. temporary immigration, Fig. 3.4) and that, over the years, the non-breeding populations had roughly the same size as the breeding populationsa (Fig. 3.10, 3.11), more animals left the breeding population than non-breeders re-entered it. Further, since survival was constant (Fig. 3.2), temporary emigration rates and breeding population sizes increased over time (Fig 3.3; Fig. 3.7), I expect the proportion of first-time breeders to have increased as well. Thus, the breeding population is likely to have grown due to high recruitment rates over the preceding years. However, numbers of captured juveniles over time do not indicate such a trend (Tab. 3.1).

There is a discrepancy between the breeding population size estimates for 2006 derived from the two different methods, the Jolly-Seber model POPAN and the 'ad hoc' approach using annual recapture rates (Fig. 3.7; Fig. 3.13), although confidence intervals overlap slightly. One reason might be that, unlike the ad hoc approach, POPAN is able to estimate the number of breeding animals that were not exposed to sampling (Schwarz and Arnason 1996). To explain the differences between the estimates, this would imply that about a fourth of all breeding animals in Ash and Beech, and even more than half of the animals in Chestnut, were in the pond only during the time between two consecutive sampling sessions. These animals have either bred for a shorter period than one sampling interval or they emigrated temporarily over one or several sampling sessions. Temporary emigrants within breeding seasons as well as short breeding activities have been reported in drift fence studies (e.g., Kupfer 1996; Sewell et al. 2005). However, the proportion of these animals is unlikely to be 50%, since the majority of breeding newts is expected to stay in the pond for several weeks (Kupfer 1996). Therefore, the large variation in the Chestnut estimates can hardly be explained by within-year temporary emigrants. It is more likely that the POPAN method is simply more powerful since the information in the data is conserved by using all annual sampling occasions separately, whereas all occasions are pooled in the ad hoc approach. Moreover, it is unlikely that I caught all individuals that were present during the sampling sessions. I assumed this for estimating breeding population sizes for Ash and Beech since the recapture parameters of the last sampling session could not be estimated. As a consequence, I probably underestimated the breeding population sizes of 2006.

4.5 Non-Breeding Population Sizes

Based on Gimenez' method I could show that the proportion of breeding adults was 8% for males and 19% for females. Assuming a sex-ratio of 1:1, only 13.5% of the total adult population participated in breeding in any year. Thus, mean non-breeding population size of Ash and Beech ranged from 772-1099 and 415-921, respectively (Fig. 3.8, Fig. 3.9). However, these estimates have huge standard errors since the precision of temporary emigration and immigration rate estimates was fairly low. Results from my alternative method to calculate non-breeding population sizes, results showed that about half of the total adult newt population was breeding in any year (Fig. 3.10, Fig. 3.11).

In contrast to Gimenez' method, my approach was based on some simplifications and assumptions. I did not include standard error propagation since calculations were done in an iterative way. Further, calculations were based on the assumption that breeding population sizes for Ash and Beech were 100 and 50 individuals, respectively, and temporary emigration and immigration rates were constant over 25 years. Nevertheless, I assess the results of my approach to be more realistic than those using Gimenez' method because I included a survival parameter into the calculation. The comparison of the two methods (Fig. 3.12) showed that the lower temporary immigration rate was chosen, the higher was the difference between the two methods. On the other side, probability of temporary emigration had no influence on the relative difference. Obviously, Gimenez' method is much simpler and more precise than the method I developed. However, by not accounting for survival probabilities Gimenez' method is systematically overestimating the proportion of breeding animals and thus non-breeding population size (because they do not die). Even though the method I proposed is only a weak estimation in terms of precision, the results still provide a more realistic impression of the adult proportion that does not attempt breeding although still living.

Although the mean estimates of the two methods diverge highly, both approaches show that the numbers of non-breeding animals of all populations are considerable.

4.6 Pond Residence

Population size estimates for each occasion showed that from mid-April until mid-June 39-58% of all animals breeding in 2006 were present at one time (Fig. 3.14). Explanations about the temporal pattern of pond occupation are manifold. Animals could have entered and exited the breeding habitat in a staggered fashion with an immigration peak in early April and a prolonged emigration peak beginning in mid-May. It is also possible, that one fraction of the

breeding population was in the ponds over the whole breeding period, whereas animals of an other fraction entered in a staggered fashion staying only for some days. Something between the two alternatives might be most likely because other studies report that entering animals were caught over a long period during spring and stayed variably for several weeks (Sewell et al. 2005).

Moreover, in a study on a population with a long aquatic period from early March to early November, the time spent in the aquatic habitat varied individually from 8 to 30 weeks (Kupfer 1996). Long-term data from Kupfer (1996) as well as from Blab and Blab (1981) showed that migration to and from the breeding ponds occurred over a time period of 3–11 weeks. In contrast to my findings, both studies reported that periods of immigration and emigration were not overlapping. This implies that during the period between the last immigrant and the first emigrant all animals were present.

Habitat changes and the relative time an animal spends in each habitat are dependent on ecological factors. The ratio of mortality and growth rate has been proposed to be critical for habitat selection and habitat changes (Werner 1986). Since growth rate is related to food abundance and food quality, an animal selects the good food habitat. According to Werner's (1986) model food abundance and quality in the aquatic habitat of the investigated crested newts must be higher than in the terrestrial habitat, since mortality is higher as well (Fig. 3.6). Both food and mortality might limit the residence time of a breeding crested newt in the pond. This idea is particularly relevant for crested newts since they are known to occupy the aquatic habitat even when they are not breeding. Sexually mature animals stay in the pond after reproduction; even juveniles are in the pond for feeding (Thiesmeier and Kupfer 2000). Moreover, the food and mortality limitations could be another cause for adults not to breed every year. Further studies are needed that investigate how growth rate and mortality interact and affect pond residence time.

4.7 Optimal Sampling Effort

My analyses showed that sampling should be done over a period of 14 weeks (when sampling four times) for accurately estimating the breeding population size with the JS-method POPAN (Fig 3.17, Fig. 3.18). However, precision of the estimate was lower (i.e. the coefficient of variance was higher) for longer sampling periods, probably because of lower recapture rates. This is not surprising assuming the temporal pattern of pond residence described above and given that over a period of about 9 weeks only about half of the breeding population is present

at one time (Fig. 3.14). Sampling during the peak season from mid-April to mid-June is likely to generate highest numbers of captures. Therefore, I suggest that the timing of the sampling is set in such a way that the peak season is included.

When sampling over 12 weeks, an effort of 6 sampling sessions appears to be adequate for a realistic and precise estimate (Fig 3.15 and Fig 3.16). Considering the pond residence pattern (Fig. 3.14), this is not surprising when assuming that the more sampling is done, the higher the detectability is, and thus the higher the number of individuals captured (affecting the estimate) and the recapture rate are (affecting precision of the estimate). I therefore suggest that at least 6 sampling sessions should be done for the monitoring of the three populations.

Using the data set of the entire breeding population, the breeding population estimate was even higher than the maximum of the regression curves. This indicates that the suggested sampling effort of 6 occasions over 14 weeks will probably still underestimate breeding population size, even though relatively slightly.

Conclusion

If an amphibian population is sampled at the breeding site, it is too simple to model the population dynamics by using the basic population model (Williams et al. 2002) including population size (N), recruitment (B), immigration (I), mortality (D), and emigration (E).

$$N(t+1) = N(t) + B(t) + I(t) - D(t) - E(t).$$

The extension of this equation by the parameters temporary emigration and immigration enables to model breeding populations and thereby separating breeding and non-breeding populations:

$$N_B(t+1) = N_B(t) + B(t) + I(t) - D(t) - E(t) + TI(t) - TE(t).$$

Using CMR multistate models breeding population sizes (N_B), mortality (D), immigration (I) and emigration (E), as well as temporary immigration (TI) and temporary emigration (TE) can be estimated. In order to model the population as a whole, the implementation of a model for the non-breeding population would be necessary. Therefore, sampling in the terrestrial habitat would be advantageous because survival probabilities and population sizes of the non-breeding population would be directly estimable. Furthermore, temporary emigration and immigration probabilities could be estimated with more precision. However, amphibian species like the crested newt are hard to catch on land. Thus with only pond sampling a simpler model can be made. The model's equation consists of only four parameters, i.e. non-

breeding population size (N_{NB}), mortality (D), temporary emigration (TE) and temporary immigration (TI):

$$N_{NB}(t+1) = N_{NB}(t) - D(t) + TE(t) - TI(t).$$

Immigration and emigration (analogous to the breeding population model) are not necessary to be included as these parameters can not be separated from those in the breeding population model when only breeding but not non-breeding animals are captured. The sum of both breeding and non-breeding population model are the expression of the whole population:

$$\begin{aligned} N(t+1) &= N_B(t+1) + N_{NB}(t+1) \\ &= N_B(t) + N_{NB}(t) + B(t) + I(t) - D_B(t) - D_{NB}(t) - E(t). \end{aligned}$$

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7 APPENDICES

7.1 GOF Test Results

Tab. A1. Single-state GOF test results for males and females.

| Subtest | Group | χ^2 | df | p |
|--------------|---------|----------|----|--------|
| TEST2.CT | Males | 26.055 | 2 | <0.001 |
| | Females | 26.268 | 2 | <0.001 |
| TEST2.CL | Males | 0.000 | 1 | 1.000 |
| | Females | 0.000 | 1 | 1.000 |
| TEST3.SM | Males | 2.460 | 2 | 0.408 |
| | Females | 1.792 | 2 | 0.292 |
| TEST3.SR | Males | 5.483 | 3 | 0.598 |
| | Females | 1.845 | 3 | 0.138 |
| Sum of tests | | 63.902 | 16 | <0.001 |

Tab. A2. Multistate GOF test results for males and females.

| Subtest | Group | χ^2 | df | p |
|--------------|---------|----------|----|-------|
| TEST WBWA | Males | 0.000 | 1 | 1.000 |
| | Females | 0.000 | 1 | 1.000 |
| TEST M.ITEC | Males | 2.256 | 2 | 0.265 |
| | Females | 1.068 | 1 | 0.277 |
| TEST M.LTEC | Males | 0.001 | 1 | 0.974 |
| | Females | 0.002 | 1 | 0.959 |
| TEST 3G.SR | Males | 3.378 | 8 | 0.908 |
| | Females | 10.826 | 7 | 0.146 |
| TEST 3G.Sm | Males | 7.685 | 9 | 0.566 |
| | Females | 1.642 | 7 | 0.977 |
| Sum of tests | | 26.858 | 38 | 0.928 |

7.2 Sampling Occasion Selection for Monitoring Problem

Tab. A3. Data sets produced for monitoring analysis and population size estimates derived using the modeling package POPAN.

| Sampling period [weeks] | Number of occasions | Occasions used | Population size estimate | Standard error | Coefficient of variation |
|-------------------------|---------------------|----------------|--------------------------|----------------|--------------------------|
| 6 | 4 | 2-3-4-5 | 437 | 36 | 0.08 |
| 6 | 4 | 3-4-5-6 | 485 | 36 | 0.07 |
| 6 | 4 | 4-5-6-7 | 435 | 31 | 0.07 |
| 6 | 4 | 5-6-7-8 | 451 | 30 | 0.07 |
| 8 | 4 | 2-3-4-6 | 458 | 36 | 0.08 |
| 8 | 4 | 3-4-5-7 | 527 | 47 | 0.09 |
| 8 | 4 | 4-5-6-8 | 504 | 41 | 0.08 |
| 8 | 4 | 5-6-7-9 | 426 | 35 | 0.08 |
| 10 | 4 | 1-3-4-6 | 552 | 58 | 0.10 |
| 10 | 4 | 2-4-5-7 | 499 | 47 | 0.09 |
| 10 | 4 | 3-5-6-8 | 552 | 43 | 0.08 |
| 10 | 4 | 4-5-8-9 | 554 | 66 | 0.12 |
| 12 | 4 | 1-3-5-7 | 538 | 52 | 0.10 |
| 12 | 4 | 2-4-6-8 | 498 | 42 | 0.08 |
| 12 | 4 | 3-5-7-9 | 562 | 65 | 0.12 |
| 12 | 4 | 2-3-7-8 | 534 | 45 | 0.08 |
| 14 | 4 | 1-2-7-8 | 565 | 61 | 0.11 |
| 14 | 4 | 1-4-5-8 | 661 | 83 | 0.13 |
| 14 | 4 | 2-3-8-9 | 521 | 58 | 0.11 |
| 14 | 4 | 2-5-6-9 | 483 | 55 | 0.11 |
| 14 | 6 | 1-2-4-5-6-7 | 554 | 39 | 0.07 |
| 14 | 6 | 2-3-5-6-7-8 | 559 | 30 | 0.05 |
| 14 | 6 | 3-4-6-7-8-9 | 632 | 48 | 0.08 |
| 14 | 6 | 1-2-3-4-6-7 | 586 | 41 | 0.07 |
| 14 | 6 | 2-3-4-5-7-8 | 589 | 37 | 0.06 |
| 14 | 6 | 3-4-5-6-8-9 | 681 | 59 | 0.09 |
| 14 | 5 | 1-3-4-6-7 | 583 | 49 | 0.08 |
| 14 | 5 | 2-4-5-7-8 | 575 | 43 | 0.07 |
| 14 | 5 | 3-5-6-8-9 | 622 | 52 | 0.08 |
| 14 | 5 | 1-2-4-5-7 | 547 | 47 | 0.09 |
| 14 | 5 | 2-3-4-6-8 | 527 | 36 | 0.07 |
| 14 | 5 | 3-4-6-7-9 | 595 | 58 | 0.10 |
| 14 | 4 | 1-2-7-8 | 464 | 46 | 0.10 |
| 14 | 4 | 3-4-8-9 | 575 | 72 | 0.12 |
| 14 | 3 | 1-4-7- | 788 | 181 | 0.23 |
| 14 | 3 | 2-5-8- | 448 | 62 | 0.14 |
| 14 | 3 | 3-6-9- | 389 | 61 | 0.16 |
| 14 | 3 | 1-5-7- | 472 | 69 | 0.15 |
| 14 | 3 | 2-6-8- | 412 | 42 | 0.10 |
| 14 | 3 | 3-4-9- | 554 | 164 | 0.30 |

7.3 Non-Breeding Population Size Calculations

Tab. A5. Point estimates of non-breeding population size for variable temporary emigration and immigration probabilities based on Gimenez' method.

| | | Temporary immigration probability | | | | | |
|----------------------------------|------|-----------------------------------|------|------|------|------|------|
| | | 0.05 | 0.10 | 0.15 | 0.20 | 0.25 | 0.30 |
| Temporary emigration probability | 0.05 | 100 | 50 | 33 | 25 | 20 | 17 |
| | 0.10 | 200 | 100 | 67 | 50 | 40 | 33 |
| | 0.15 | 300 | 150 | 100 | 75 | 60 | 50 |
| | 0.20 | 400 | 200 | 133 | 100 | 80 | 67 |
| | 0.25 | 500 | 250 | 167 | 125 | 100 | 83 |
| | 0.30 | 600 | 300 | 200 | 150 | 120 | 100 |
| | 0.35 | 700 | 350 | 233 | 175 | 140 | 117 |
| | 0.40 | 800 | 400 | 267 | 200 | 160 | 133 |
| | 0.45 | 900 | 450 | 300 | 225 | 180 | 150 |
| | 0.50 | 1000 | 500 | 333 | 250 | 200 | 167 |
| | 0.55 | 1100 | 550 | 367 | 275 | 220 | 183 |
| | 0.60 | 1200 | 600 | 400 | 300 | 240 | 200 |
| | 0.65 | 1300 | 650 | 433 | 325 | 260 | 217 |
| | 0.70 | 1400 | 700 | 467 | 350 | 280 | 233 |
| 0.75 | 1500 | 750 | 500 | 375 | 300 | 250 | |

Tab. A6. Point estimates of non-breeding population size for variable temporary emigration and immigration probabilities based on the method I proposed.

| | | Temporary immigration probability | | | | | |
|----------------------------------|------|-----------------------------------|------|------|------|------|------|
| | | 0.05 | 0.10 | 0.15 | 0.20 | 0.25 | 0.30 |
| Temporary emigration probability | 0.05 | 17 | 14 | 12 | 11 | 10 | 9 |
| | 0.10 | 33 | 29 | 25 | 22 | 20 | 18 |
| | 0.15 | 50 | 43 | 37 | 33 | 30 | 27 |
| | 0.20 | 67 | 57 | 50 | 44 | 40 | 36 |
| | 0.25 | 83 | 71 | 62 | 56 | 50 | 45 |
| | 0.30 | 100 | 86 | 75 | 67 | 60 | 55 |
| | 0.35 | 117 | 100 | 87 | 78 | 70 | 64 |
| | 0.40 | 133 | 114 | 100 | 89 | 80 | 73 |
| | 0.45 | 150 | 129 | 112 | 100 | 90 | 82 |
| | 0.50 | 167 | 143 | 125 | 111 | 100 | 91 |
| | 0.55 | 183 | 157 | 137 | 122 | 110 | 100 |
| | 0.60 | 200 | 171 | 150 | 133 | 120 | 109 |
| | 0.65 | 217 | 186 | 162 | 144 | 130 | 118 |
| | 0.70 | 233 | 200 | 175 | 156 | 140 | 127 |
| 0.75 | 250 | 214 | 187 | 167 | 150 | 136 | |

7.4 Electronic Appendix Contents

File '*MSc Thesis Thomas Schwizer.pdf*' is the print version of this report

Folder '*data*'

- '*raw data.xls*' containing the full data set
- '*raw data compact.xls*' containing the data set in which the necessary information for the analyses is packed

Folder '*analysis*'

- Folder '*annual survival and transitions*'
containing the input file and all output files (.dbf and .fpt)
from MARK
 - Folder '*breeding population size and pond occupancy*'
containing the input file and all output files (.dbf and .fpt)
from MARK
 - Folder '*seasonal survival*'
containing the input file and all output files (.dbf and .fpt)
from MARK
 - Folder '*monitoring analysis*'
containing the input files and all output files (.dbf and .fpt)
from MARK
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