

Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture–recapture models

Michael Schaub^{1,2*} and Johann von Hirschheydt¹

¹Swiss Ornithological Institute, CH-6204 Sempach, Switzerland; and ²Institute of Ecology and Evolution – Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

Summary

1. Theoretical models predict a negative effect of current reproduction on breeding dispersal, survival and future reproduction, and many studies confirm these predictions. Yet, results of most previous studies may be difficult to interpret because the fate of the affected individuals cannot always be observed. Detection is almost always imperfect and some individuals emigrate from the study area, resulting in biased estimates of both survival and dispersal.

2. Most studies bypass these problems with strong assumptions. We use a multistate capture–recapture model that does not require these assumptions. States are defined based on classes of reproductive success and on observed dispersal events within the study area. By accounting for imperfect detection within the study area, the model allows estimation of the effect of reproductive success on apparent survival, dispersal probabilities within the study area and the annual transition probabilities among classes of reproductive success. Based on an assumption about the estimate of real survival, the model allows the estimation of total dispersal that is not specific to a fixed study area.

3. We applied this model to capture–recapture data of 2262 adult barn swallows (*Hirundo rustica*) sampled from 1997–2004 in eight local populations in Switzerland.

4. We found that dispersal within the study area decreased with increasing reproductive success in both sexes, that reproductive success was not affected by preceding dispersal and that apparent survival of females but not of males increased with increasing reproductive success. Apparent survival of females with high reproductive success was identical to apparent survival of males suggesting that this estimate of apparent survival (0.48) was close to true survival. Total breeding dispersal was generally higher in females and it increased with decreasing reproductive success in both sexes. Current reproductive success depended on reproductive success in the preceding year suggesting that individual differences were of importance.

5. Our study highlights that reproductive success was an important factor affecting breeding dispersal and population turnover. While unsuccessful males mainly remained in the local populations, many unsuccessful females left them. Population turnover of adult swallows was mainly due to unsuccessful females.

Key-words: bias, capture-recapture, *Hirundo rustica*, spatial scale, true survival

Introduction

The dynamics of a local population are driven by variation in the number of surviving adults remaining in the local population, the number of local recruits establishing in the population, and the number of immigrants. The reproductive success of

breeders may affect population growth rates directly through recruitment into the local population, and indirectly if reproductive success affects breeding dispersal, survival, and subsequent reproduction (Dijkstra *et al.* 1990; Hoover 2003). Dispersal between breeding locations in consecutive years (breeding dispersal), survival, and future reproduction may all depend on current reproduction, because current reproduction may have costs that would affect other fitness-related

*Correspondence author. E-mail: michael.schaub@vogelwarte.ch

characters (Stearns 1992). Hence, reproductive success plays a central role in the dynamics of a local population, both directly and indirectly.

Theory predicts that current reproductive success has a strong impact on breeding dispersal: in a predictable environment, failed breeders may aim to increase their fitness by dispersing to a better habitat (Switzer 1993). Results from many empirical studies (insects: Alcock 1993, mammals: Apollonio, Scotti & Gosling 2003, birds: Shields 1984; Switzer 1997; Haas 1998; Doligez *et al.* 1999; Hoover 2003; Città & Lindberg 2007) have provided support of the predicted negative relationship between current reproductive success and breeding dispersal.

Life-history theory predicts a negative correlation between current reproductive effort and future survival or between current and future reproduction due to physiological or microevolutionary trade-offs (Stearns 1992). The empirical evidence is ambiguous in birds. In some studies the predicted negative relationships were confirmed (e.g. Dijkstra *et al.* 1990; Saino *et al.* 1999), but not in others (Gustafsson & Sutherland 1988; Hanssen *et al.* 2005). Variation in the environment or in individual quality may lead to variation in the acquisition of energy that can dominate the allocation variation (van Noordwijk & de Jong 1986). Therefore, it is possible to obtain opposite results even in single populations in different years.

Apart from a possible impact of current reproduction, breeding dispersal and survival are very likely to be affected by the sex and age of the individuals. In birds, breeding dispersal probability tends to be lower in males than in females and to decrease with age (Greenwood & Harvey 1982; Switzer 1993; Winkler *et al.* 2004). Survival rates of species without strong sexual dimorphism are often not sex specific, and if there are differences, the survival rates tend to be higher in males (Payevsky *et al.* 1997; Siriwardena, Baillie & Wilson 1998). Adult survival typically first increases with age and later decreases (Tavecchia *et al.* 2001), but subtle patterns are often difficult to detect (Cam & Monnat 2000).

Studying effects of current reproduction on breeding dispersal, survival or future reproduction needs longitudinal data on individuals. The difficulties are that some of the surviving individuals are not recorded, because they either settle outside the study area, or the researcher fails to detect them even if they did not leave the study area. If it is assumed that all survivors are recorded the following years, estimates of dispersal and survival are biased and conclusions flawed (Martin, Clobert & Anderson 1995). Dispersal is underestimated, because birds settling outside the study area (i.e. those individuals that have dispersed the longest distances) cannot be encountered and will often be assumed to have died (Winkler *et al.* 2004). Survival will also be underestimated due to a failure to record all survivors in the study population and due to emigration from the study area. Even if capture–recapture models are applied that account for imperfect detection, the estimated apparent survival rates underestimate true survival because of permanent emigration. Clearly, estimates of dispersal and apparent survival are dependent on the extent and shape of the study area (Cilimburg *et al.* 2002;

Marshall *et al.* 2004; Schaub *et al.* 2006). The larger the study area is, the higher is the chance that dispersing individuals remain in it, and thus apparent survival approaches true survival and within study area dispersal probability approaches total dispersal probability. This dependence on the specific spatial design of a study is particularly worrisome. Another concern is that the probability of encountering an individual depends on its reproductive success or other individual characteristics, in which case the sample will not be random. Despite these concerns, many studies have nonetheless assumed that all individuals that have survived are equally likely to be encountered in a subsequent year (e.g. Shields 1984; Gustafsson & Sutherland 1988; Saino *et al.* 1999; Hanssen *et al.* 2005).

Multistate capture–recapture models provide a solution to most of these problems (Nichols *et al.* 1994; Doligez *et al.* 2002; Brown *et al.* 2003; Cam *et al.* 2004; Kendall & Nichols 2004). These are probabilistic models that allow estimating state-specific apparent survival and recapture probabilities as well as transition probabilities among states. States can be defined as geographical locations to study dispersal or as classes of reproductive success to study the impact of current reproduction and combinations thereof. Multistate models have so far not been used for simultaneously studying the effect of current reproduction on dispersal, apparent survival, and future reproduction (but see Doligez *et al.* 2002).

We developed a multistate model in which the states reflect different classes of reproductive success and whether or not an individual has dispersed within the study area. This model allows testing of whether apparent survival, dispersal within the study area, and future reproduction are affected by current reproductive success, while at the same time accounting for imperfect detection within the study area. In addition, it is possible to test whether dispersal within the study area is associated with improved reproduction in the next year and, based on an assumption about true survival, to estimate total dispersal probabilities, i.e. dispersal probabilities that are not dependent on the size of the study area. We used this multistate model to study the effect of current reproductive success on breeding dispersal, apparent survival and future reproductive success in a small migratory passerine, the barn swallow *Hirundo rustica* L. We tested whether these relationships differed between sexes and age classes.

Material and methods

STUDY SPECIES

The barn swallow (hereafter 'swallow') is a small (~20 g), socially monogamous migratory passerine living in agricultural landscapes (Turner 2006). It feeds in flight up to 500 m from the nest, mainly on small aerial invertebrates (Turner 2006). Swallows prefer to breed in barns and stables that contain cattle (Ambrosini *et al.* 2002), where it is typical to raise two broods each containing four to six nestlings during a breeding season. Adults are usually faithful to their breeding sites (Shields 1984; Saino *et al.* 1999; Turner 2006). In a study based on dead recoveries of ringed individuals, survival probabilities of adults tend to be higher in males than in females, yet the difference was not significantly different from zero (Siriwardena *et al.* 1998).

Table 1. Characteristics of the eight study areas. Given are the study area names, coordinates, altitude, area size, the minimum and maximum possible dispersal distance within the study areas, the number of breeding locations, covered years, and total number of adults included

Study area	Coordinates	Altitude (m a.s.l.)	Study area size (km ²)	Distance among locations (m)		Number of locations	Years covered	Number of individuals
				Minimum	Maximum			
Baulmes	6°31'E, 46°47'N	600	1	44	612	10	1997–2003	143
Buus	7°51'E, 47°30'N	500	12	30	3245	24	1997–2003	421
Giez	6°36'E, 46°48'N	500	1	36	566	12	1997–2003	136
Pays d'Enhaut	7°08'E, 46°28'N	1100	20	41	12017	43	1999–2003	247
Riviera	9°01'E, 46°18'N	300	5	20	2843	25	1997–2003	244
Sarganserland	9°26'E, 47°02'N	500	12	22	5019	30	1997–2003	296
Vaulruz	6°59'E, 46°37'N	800	10	41	5110	43	1999–2003	300
Wauwilermoos	8°01'E, 47°10'N	500	18	32	7998	45	1999–2004	475

STUDY AREA AND DATA COLLECTION

We studied swallows that were at least 1 year old in eight areas across Switzerland, for a period of 5 to 7 years (Table 1). The number of potential breeding locations, which were mainly farms, varied between study areas from 10 to 45 and the distances among them ranged from 20 m to 12.1 km. All breeding locations were visited every week during the breeding season (April to September) to record number of eggs, hatchlings and nestlings in occupied swallow nests. All nestlings were ringed when 5 to 15 days old. Nestlings usually leave the nest at 20 days after hatching (Turner 2006). The number of nestlings alive on the last nest visit before fledging was taken as the number of fledglings of a brood. This number was adjusted if dead nestlings were detected in the nest after the brood had fledged. Adults were trapped and ringed when roosting with their chicks on or near the nest. This procedure ensured that each individual could be assigned as a functional parent of a given brood.

We calculated the total number of fledglings produced annually by each individual. Furthermore, we recorded whether an individual dispersed within the study area from 1 year to another. Dispersal within the study area was defined as the change of the breeding location between years. A breeding location was mostly a specific barn or stable at a farm, but sometimes also a non-agricultural building. Using this definition of dispersal ensured that all swallows classified as dispersed moved to a different building. The maximum possible dispersal distances within the study areas ranged from 0.56 to 12.1 km (Table 1). Individuals that changed nests between years within the same building were not considered as having dispersed. In the very rare cases where couples changed the breeding location within the same breeding season (0.8%, $n = 2447$ broods), we used the location of the first brood as the reference breeding location. Data from breeding locations that could not be accessed during the complete duration of the study were eliminated from the analysis.

CONCEPTUAL MODEL

Swallows that are present in the study area can have different fates regarding subsequent survival, dispersal, reproduction and recapture. To study the probabilities of these fates, we envision the following model. Conditional on first recording with a certain reproductive success, swallows may (i) return to the study area (apparent survival), they may (ii) disperse within the study area, given that they returned (dispersal within study area), they may (iii) change reproductive

success, given that they returned and whether or not they dispersed within the study area, and (iv) they may be recaptured, given their reproductive success of the current year. This model is presented as a fate diagram in Fig. 1. In the following, we describe how to prepare the data and how to fit this model within the multistate capture–recapture framework in order to estimate the unknown parameters.

DATA PREPARATION

For each individual, we constructed a multistate capture–recapture history, with the states referring to the reproductive success in a given year and within-study area dispersal. The states were defined as follows. First, we classified the annual reproductive success into three categories [n, no fledglings produced (no reproductive success); m, one to six fledglings produced (medium reproductive success); h, more than six fledglings produced (high reproductive success)]. The threshold of six nestlings was chosen because the maximum number of fledglings in one brood recorded in this study was six (mean \pm SD: 4.1 ± 1.1 fledglings, $n = 2387$ broods). Thus, individuals having produced more than six fledglings raised at least two successful broods, whereas one to six nestlings could have been produced in one or more broods. The category of no reproductive success was chosen to include the most extreme case of failure although the sample size of this class remained low. The main reason for complete brood failure was adverse weather, while nest predation occurred only rarely. To record dispersal within the study area, we secondly classified the current breeding location of the individuals relative to the location of the last observed breeding (classes 'same' and 'different'). Individuals that were captured for the first time were allocated to the state 'same'. However, because we defined dispersal as the change of breeding locations from 1 year to the next, the transition 'same' to 'different' is equivalent to the transition 'different' to 'same'. Therefore, individuals could also have been allocated to the state 'different' at first capture to get the same results, it would just require that the subsequent coding of states is adapted accordingly (see Appendix S1, Supporting information, Fig. 1). The pairs of dispersal states 'same' to 'different' and 'different' to 'same' indicate dispersal, whereas the pairs 'same' to 'same' and 'different' to 'different' indicate philopatry. The combination of three categories of reproductive success by two pairs of dispersal states resulted in six different states: No reproductive success without and with dispersal (states 1 and 2); medium reproductive success without and with dispersal (states 3

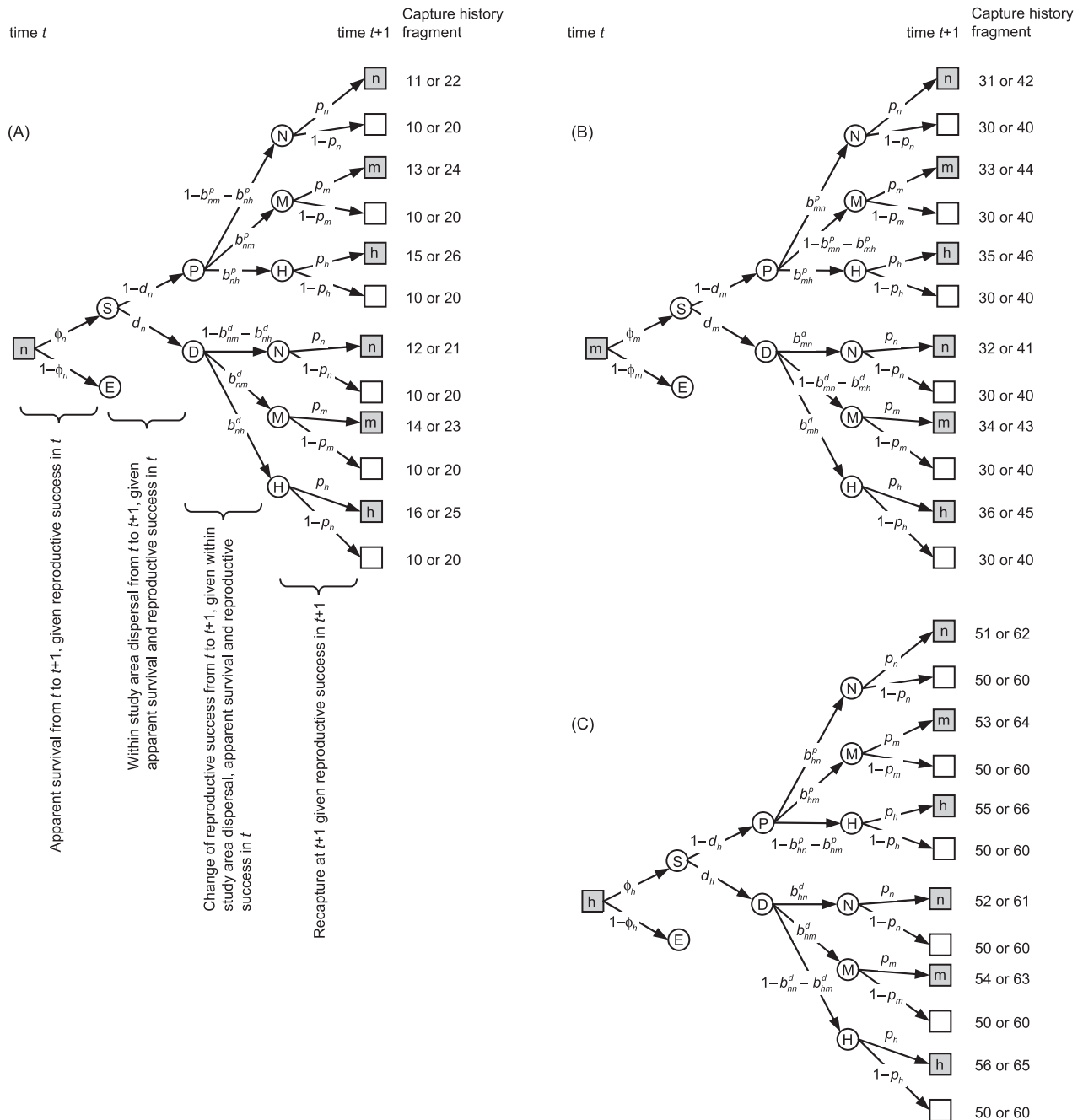


Fig. 1. Fate diagram of a marked swallow from time t to time $t + 1$ that had at time t no (A), medium (B) or high (C) reproductive success. The observed states are shown as squares with grey background, non-observed states are shown as squares with white background. Intermediate states are shown with circles: S, survived and returned to the study area; E, dead or emigrated permanently from the study area; P, philopatric, i.e. reproduces at the same location than during the preceding year; D, dispersed within the study area, i.e. reproduces at another location than during the preceding year; N, no reproductive success; M, medium reproductive success; H, high reproductive success. The possible transition among states are shown by arrows and parameterized (ϕ : apparent survival rate, d : within study area dispersal rate, b^p : change reproductive success given philopatry, b^d : change reproductive success given dispersal within study area, p : recapture rate). The resulting capture history fragments from each of these possible fates are shown and coded in the same way as the input data.

and 4); and high reproductive success without and with dispersal (states 5 and 6). For example, consider an individual with the capture history 106. This adult was caught in the first year, when it produced no fledglings; it was not recaptured in the second year, but was recaptured in the third year in a different location than at the previous encounter, where it produced more than six fledglings.

MULTISTATE CAPTURE–RECAPTURE MODEL

We used a multistate capture–recapture model (Williams, Nichols & Conroy 2002) to analyse the data. Notice that the capture history above contains uncertainty about the location and the reproductive success of the swallow in the second year. This uncertainty is

captured in a probabilistic model. The probability of obtaining this capture history for an individual picked at random is

$$P(106) = \phi_{n,1} \times \left[\begin{aligned} &(1 - d_{n,1})(1 - b_{nm,1}^p - b_{nh,1}^p)(1 - p_{n,1})\phi_{n,2}d_{n,2}b_{nh,2}^d p_{h,2} + \\ &(1 - d_{n,1})b_{nm,1}^p(1 - p_{m,1})\phi_{m,2}d_{m,2}b_{mh,2}^d p_{h,2} + \\ &(1 - d_{n,1})b_{nh,1}^p(1 - p_{h,1})\phi_{h,2}d_{h,2}(1 - b_{nh,2}^d - b_{mh,2}^d)p_{h,2} + \\ &d_{n,1}(1 - b_{nm,1}^d - b_{nh,1}^d)(1 - p_{n,1})\phi_{n,2}(1 - d_{n,2})b_{nh,2}^p p_{h,2} + \\ &d_{n,1}b_{nm,1}^d(1 - p_{m,1})\phi_{m,2}(1 - d_{m,2})b_{mh,2}^p p_{h,2} + \\ &d_{n,1}b_{nh,1}^d(1 - p_{h,1})\phi_{h,2}(1 - d_{h,2})(1 - b_{nh,2}^p - b_{mh,2}^p)p_{h,2} \end{aligned} \right] \quad \text{eqn 1}$$

The first three terms of the sum describe the possibility that the swallow was at the same location at occasion two than at occasion one with either no, medium or high reproductive success, respectively. The last three terms of the sum describe the possibility that the swallow was at a different location at occasion two than at occasion one again with either no, medium or high reproductive success, respectively. The parameters in the model are $d_{x,t}$ which is the probability that an individual with reproductive success x [$x = (n, m, h)$ for reproductive success (0, 1–6, > 6), respectively] in year t breeds at a different location in year $t + 1$, given that the individual has survived and has not emigrated from the study area (within study area dispersal probability); $b_{xy,t}^d$ is the probability that an individual with reproductive success x in year t has reproductive success y in year $t + 1$, given that the individual dispersed within the study area between year t and year $t + 1$, has survived and has not emigrated from the study area (probability to change among classes of reproductive success given dispersal); $b_{xy,t}^p$ is the probability that an individual with reproductive success x in year t has reproductive success y in year $t + 1$, given that the individual has not dispersed within the study area between year t and year $t + 1$, has survived and has not emigrated from the study area (probability to change among classes of reproductive success given philopatry); $p_{x,t}$ is the probability that a marked individual with reproductive success x is captured, given that it is alive and present in the study area at time t (recapture probability); $\phi_{x,t}$ is the probability that an individual with reproductive success x in year t survived and did not emigrate from the study area between years t and $t + 1$ (apparent survival probability). Appendix S2, Supporting information provides a matrix formulation of the model. Based on the frequency of each observed capture history, the likelihood can be written as a product of multinomials, and the maximum likelihood estimates of parameters and their standard error obtained numerically (Williams *et al.* 2002).

ESTIMATING TOTAL DISPERSAL

Our multistate model estimates dispersal within the study area, hence only individuals that remained within it are included and this estimate sets a minimum for total dispersal. Following Burnham (1993), the emigration probability from the study area of individuals with reproductive success x (E_x) could be estimated from the apparent survival rates (ϕ_x) and true survival (S_x), as

$$E_x = 1 - \frac{\phi_x}{S_x} \quad \text{eqn 2}$$

An estimate of total dispersal probability (D_x), i.e. dispersal probability independent of the study area, is then the sum of emigration from the study area and the dispersal within the study area:

$$D_x = E_x + (1 - E_x)d_x \quad \text{eqn 3}$$

GENERAL APPROACH TO MODEL SELECTION

We performed a goodness-of-fit test (GOF, Pradel, Wintrebert & Gimenez 2003) of a global multistate model in which survival, transition and recapture parameters differed among states, sex, study areas and time, using program U-CARE (Choquet *et al.* 2001). The GOF was not significant ($\chi_{372}^2 = 160.91$, $P = 1.00$), indicating that the model fits the data adequately.

We used program E-SURGE (Choquet *et al.* 2009) for modelling and parameter estimation. Appendix S2 describes how to fit the model with E-SURGE. We formulated a priori a number of different models each representing a different combination of one hypothesis for each of the four basic parameter types (recapture, apparent survival, dispersal within the study area, change of reproductive success). Model selection was based on the Akaike's information criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i ; Burnham & Anderson 2002). First, we tested different hypotheses referring to variation in recapture probability (p) and change of reproductive success (b^d , b^p) while keeping the most complex structure of apparent survival and dispersal. In a second step, we modelled apparent survival (ϕ) and dispersal within study area (d) using the smallest set of models for recapture and change of reproductive success for which the w_i sum to 0.9 (90% confidence set of models). Next, we tested the impact of relative age on all parameter types except for recapture. Here we used the 90% confidence set of models from the second modelling step, and added age structures. Finally, we tested whether apparent survival, within-study area dispersal and changes of class of reproductive success differed among study areas. We then calculated model averaged parameter estimates and based our inferences on them.

HYPOTHESES

Recapture probability

Since the capture effort differed among study areas, we only considered models with different recapture probabilities for each study area. Moreover, because females are easier to catch at the nests than males, we a priori also assumed that recapture probabilities differed between sexes. Individuals that produce many fledglings in several broods stay longer in the study area than unsuccessful individuals and may therefore have a higher recapture probability. We considered models in which the recapture probabilities of the three reproductive success states differed (additive: $p_{\text{sex} \times \text{site} \times \text{success}}$, with interaction: $p_{\text{sex} \times \text{site} \times \text{success}}$) or were the same ($p_{\text{sex} \times \text{site}}$).

Change of reproductive success

The reproductive success in year $t + 1$ may be independent of the reproductive success in year t (random transition), or it may depend on it (Markovian transitions). The latter is to be expected if there are strong individual differences in the reproductive performance or if breeding success changes with age. In contrast, random changes among classes of reproductive success can be expected if reproductive success is mainly determined by environmental effects. The model presented in the Appendix S2 refers to Markovian transitions. To fit random transitions requires the constraints $b_{nm,t}^p = b_{nm,t}^p = b_{nm,t}^p$, $b_{nm,t}^p = b_{nm,t}^p = b_{nm,t}^p$, $b_{nh,t}^p = b_{nh,t}^p = b_{nh,t}^p$, $b_{nh,t}^p = b_{nh,t}^p = b_{nh,t}^p$, $b_{nh,t}^d = b_{nh,t}^d = b_{nh,t}^d$, $b_{nh,t}^d = b_{nh,t}^d = b_{nh,t}^d$, $b_{nh,t}^d = b_{nh,t}^d = b_{nh,t}^d$, $b_{nh,t}^d = b_{nh,t}^d = b_{nh,t}^d$. Furthermore, the probability to change classes of reproductive success may depend on previous dispersal within the study areas (i.e. $b_{xy,t}^p \neq b_{xy,t}^d$) or it may be independent of

previous dispersal (i.e. $b_{xy,t}^p = b_{xy,t}^d$). In the former case, dispersal has consequences for next reproduction, in the latter case not. The probability to change classes of reproductive success may in addition differ between sexes. The combination of these factors (random or Markovian transitions, dependence on dispersal, sex) led to the formulation of 12 different candidate models (see Appendix S3, Tables S1–S4, Supporting information for a full list of models).

Dispersal

Dispersal within the study area (d) might be affected by the reproductive success in the previous year and may differ between sexes. There may be interactions between the two, e.g. if dispersal probability depends on reproductive success in females only. We considered six different models representing these hypotheses (no sex difference, no impact of reproductive success: d ; sex difference, no impact of reproductive success: d_{sex} ; no sex difference, impact of reproductive success: d_{success} ; impact of reproductive success in males only: $d_{\text{m, success}}$; impact of reproductive success in females only: $d_{\text{m, f, success}}$; impact of reproductive success in both sexes differentially: $d_{\text{sex*success}}$).

Apparent survival

Apparent survival (ϕ) might depend on the reproductive success, if the probability to leave the study area permanently (emigration) or to survive depends on reproductive success. This may differ between the sexes, and thus we used the same six structures to model apparent survival as we used for modelling dispersal within the study areas.

Age effects

Adult swallows cannot be aged (Jenni & Winkler 1994) and therefore we studied effects of age since initial marking (relative age) rather than true age. The structure of the best model identified so far was tested for relative age effects on d , b^p , b^d or ϕ . As swallows are short-lived (Møller & Szep 2002), we only used two age classes. The first one spans the year following first encounter as adult (first encounters), and the other includes all later years (later encounters). Relative age effects might be present in none, in only one, in two or in all parameter types, thus, we considered eight further models.

Study area effects

The global model included study area effects on all parameters, but we fitted only models where the recapture rate was study area specific. In order to test, whether d , b^p , b^d or ϕ differed between study areas, we applied further tests by comparing models with and without study area effects, respectively, on apparent survival, within-study area dispersal and changes of class of reproduction. Apparent survival could also increase with increasing extension of the study areas. We therefore fitted models in which ϕ was a linear function of the square root of the size of the study areas.

Results

We ringed 2262 adult swallows (944 males, 1318 females), of which 699 individuals were recaptured at least once (326 males, 373 females). We registered 3282 (1451 males, 1831 females) captures, of which 140 (60 males, 80 females) had no, 1258 (538 males, 720 females) had medium and 1884 (853 males, 1031 females) had high reproductive success. We recorded 1020 recapture events (507 males, 513 females), of which 157 (59 males, 98 females) occurred at a different location than the previous capture and 863 at the same location (448 males, 415 females).

MODEL SELECTION

The full results of the three model selection steps are provided in Tables S5–S7, Supporting information. Table 2 shows the result of the final step, thus presents the overall best models. The 90% confidence set contained eight models, reflecting some uncertainty regarding model selection. Still, some patterns emerging for the parameters of interest were unambiguous (Table 2). Apparent survival rate clearly depended on the reproductive success in females, while in males there was substantial uncertainty. The top ranked model contained such an effect, but the next best three models did not. Likewise, there was some uncertainty about an age effect on apparent survival, yet both top ranked models were in support for an age effect. Subsequent dispersal within the study area was

Table 2. Results of the final modelling step for apparent survival (ϕ), within study area breeding dispersal (d), probability of changing reproductive success among classes from one year to another (b^p , b^d) and recapture probability (p). The previous modelling steps and a complete list of all fitted models are provided in Tables S5–S7

Models for ϕ and d	Models for b^p and b^d	Model for p	Deviance	Np	ΔAICc	w_i
$\phi_{\text{sex*success*age}}$, $d_{\text{sex*success*age}}$	$(b_M^p = b_M^d)_{\text{*age}}$	$p_{\text{sex*site+success}}$	6172.41	55	0.0000	0.3316
$\phi_{\text{(m; f; success)*age}}$, $d_{\text{sex*success*age}}$	$(b_M^p = b_M^d)_{\text{*age}}$	$p_{\text{sex*site+success}}$	6182.75	50	0.0090	0.3301
$\phi_{\text{m; f; success}}$, $d_{\text{sex*success*age}}$	$b_M^p = b_M^d$	$p_{\text{sex*site+success}}$	6206.12	40	2.8125	0.0813
$\phi_{\text{m; f; success}}$, $d_{\text{sex*success*age}}$	$(b_M^p = b_M^d)_{\text{*age}}$	$p_{\text{sex*site+success}}$	6194.14	46	3.1571	0.0684
$\phi_{\text{sex*success*age}}$, $d_{\text{sex*success}}$	$(b_M^p = b_M^d)_{\text{*age}}$	$p_{\text{sex*site+success}}$	6191.24	48	4.3755	0.0372
$\phi_{\text{(m; f; success)*age}}$, $d_{\text{sex*success*age}}$	$b_M^p = b_M^d$	$p_{\text{sex*site+success}}$	6200.07	44	4.9739	0.0276
$\phi_{\text{sex*success}}$, $d_{\text{sex*success*age}}$	$b_M^p = b_M^d$	$p_{\text{sex*site+success}}$	6205.14	42	5.9357	0.0170
$\phi_{\text{m; f; success}}$, $d_{\text{sex*success}}$	$b_M^p = b_M^d$	$p_{\text{sex*site+success}}$	6221.57	34	5.9835	0.0166

Np, number of estimated parameters; ΔAICc , difference in small sample size adjusted Akaike's information criterion between the current and the best model; w_i , Akaike weight. The best eight models with $\sum w_i \geq 0.90$ are presented. Definitions of subscripts for model notation: M, Markovian transitions; sex, gender; site, study area; success, current reproductive success; age, relative age effect; *interaction of effects; +, additive effects.

clearly affected by reproductive success and differed by sex and relative age. There was strong evidence that the probability to change classes of reproductive success was independent on previous dispersal, that it was Markovian and the same in both sexes. Little uncertainty occurred regarding effects of relative age. Finally, the recapture probability had an additive effect of the reproductive success on sex and study area differences.

In order to test whether the parameters of interest differed among sites, we compared the most parsimonious model (Table 2) with models that had interactive site effects. The comparison revealed that site effects were not important for all parameters of interest (apparent survival: $\Delta\text{AICc} = 86.85$; within study area dispersal: $\Delta\text{AICc} = 68.39$; changes of class of reproductive success: $\Delta\text{AICc} = 85.46$). However, a model in which apparent survival changed linearly with the extension of the study area was nearly identical ($\Delta\text{AICc} = 0.04$) to the most parsimonious model. Apparent survival increased slightly with increasing extension of the study areas [slope on logit scale: 0.014 (SD: 0.041)].

PARAMETER ESTIMATES

Based on the 90% set of confidence model (Table 2), we calculated model averaged parameter estimates. Apparent survival probabilities of males of both age classes and with medium or high reproductive success were similar (Fig. 2). The confidence intervals of apparent survival of males without reproductive success were wide reflecting considerable uncertainty. Apparent survival of females increased with reproductive success. When reproductive success was high, apparent survival of both males and females were about 0.48, and not statistically different (z -test, first encounters: $z = -0.29$, $P = 0.39$; later encounters: $z = -0.98$, $P = 0.16$). Moreover, first encountered females with medium reproductive success tended to have higher apparent survival rates than later encountered females ($z = 1.62$, $P = 0.052$).

The probability of dispersal within study areas was higher in first than in later encountered individuals and decreased with increasing reproductive success in males and first encountered females (Fig. 3). It slightly increased with reproductive success in later encountered females. Individuals of both sexes that experienced high reproductive success had low subsequent dispersal probabilities.

Under the assumptions that swallows with a high reproductive success do not emigrate from the study sites and that survival is independent of reproductive success, their apparent survival (0.48) equals true survival, allowing to calculate total dispersal probability (eqn 3). Subsequent total dispersal probability decreased steeply in both sexes with reproductive success, and was higher in females than in males when reproductive success was medium or high (Fig. 3). In females, there was no obvious age effect as evidenced by the large overlaps of the confidence intervals, but first encountered males without reproductive success had higher subsequent dispersal probabilities than later encountered males.

Overall, the probabilities of achieving none or medium reproductive success were similar and clearly lower than

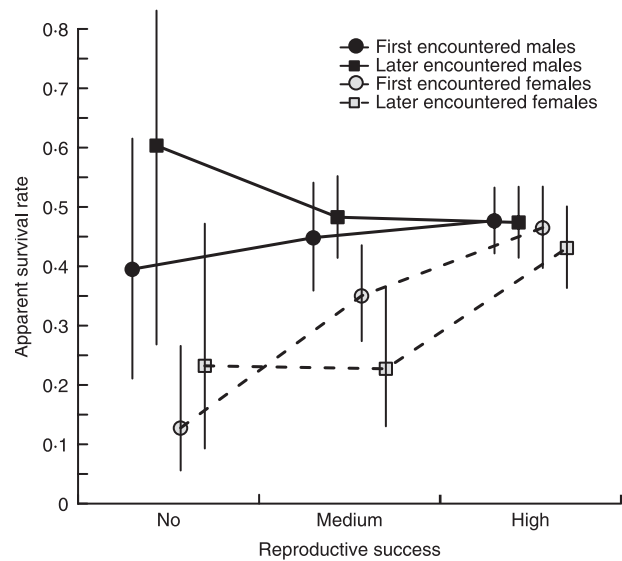


Fig. 2. Model averaged annual apparent survival rates of adult swallows in relation to their reproductive success in year t . Given are the estimates for both sexes and for two relative age classes: first encountered, adult swallows in their first year after marking; later encountered, adult swallows in later years. The vertical lines show the 95% unconditional confidence intervals.

achieving high reproductive success (Fig. 4). They depended on the reproductive success in the previous year and on the relative age of the birds, but not on previous dispersal within the study area and on sex (Table 2). The probability of having high reproductive success was enhanced when the reproductive success was already high in the preceding year compared to when there was none. The probability of having no reproductive success tended to be lower when reproductive success in the previous year was high compared to when there was none. Both indicate differences in quality among individuals. Although relative age effects were supported by model selection, it is difficult to see clear patterns. The probability to have no reproductive success in year $t + 1$ was higher in first than in later encountered individuals that had medium or high reproductive success in year t , whereas the probability to have high reproductive success in year $t + 1$ was higher in later than in first encountered individuals that had medium or high reproductive success in year t . This may point towards an increase of reproductive performance with age.

Discussion

A multistate capture–recapture model accounting for imperfect detection showed that the reproductive success of swallows had a strong impact on their subsequent breeding dispersal and reproductive success the following year, as well as on female apparent survival. The negative relationship between current reproduction and subsequent dispersal followed the predictions derived from theoretical models (Switzer 1993). The probability to change the class of reproductive success depended on the reproductive success in the previous year but

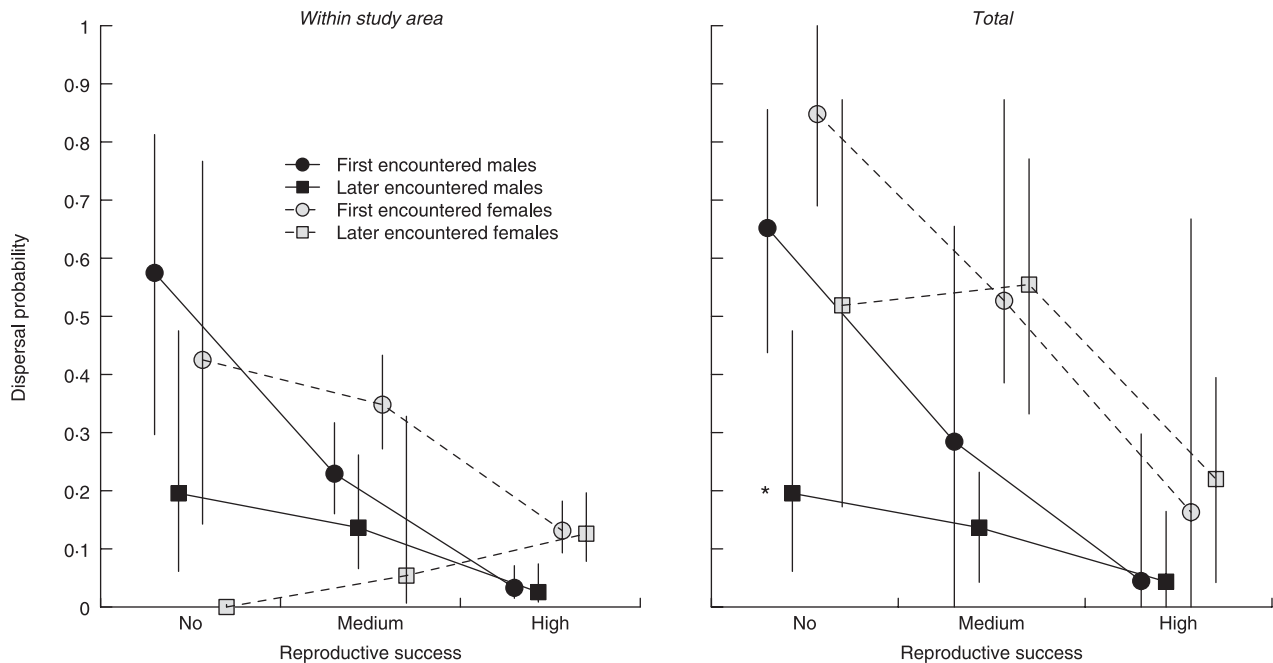


Fig. 3. Model averaged breeding dispersal probability within the study area as well as total breeding dispersal probability of swallows in relation to reproductive success in the previous year. Given are the estimates for both sexes and for two relative age classes: first encountered, adult swallows in their first year after marking; later encountered, adult swallows in later years. The vertical lines show the 95% unconditional confidence intervals. *For later encountered males without reproductive success true dispersal was assumed to be identical to dispersal within study area, because the apparent survival was > 0.48 suggesting no emigration from the study areas.

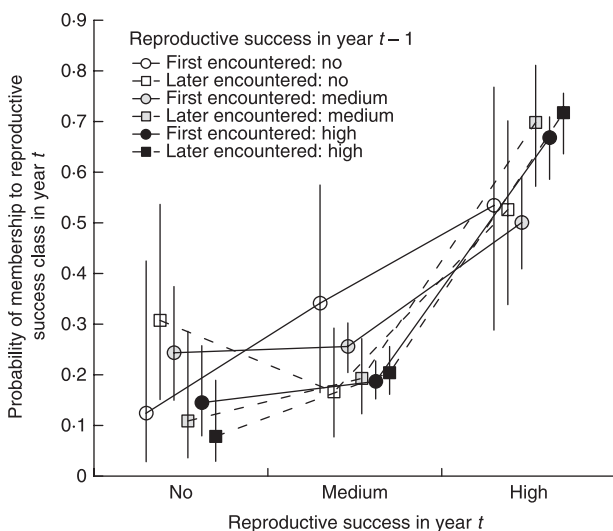


Fig. 4. Model averaged probability to be in one of the three reproductive success classes given the reproductive success in the previous year and conditional on survival within the study areas of adult swallows. The different symbols and lines refer to two relative age classes and to three classes of reproductive success in year $t - 1$. The vertical line shows the 95% unconditional confidence intervals.

not on previous dispersal. This suggests that individual differences in reproductive performance were of importance and that dispersal had no consequence in terms of subsequent reproduction. Apparent survival of females increased with reproductive success suggesting that low reproductive success caused emigration from the study areas.

The separate study of survival and dispersal based on capture–recapture data is difficult, because true survival and emigration are confounded (Williams *et al.* 2002; Cilimburg *et al.* 2002). Using capture–recapture data, we here estimated in addition dispersal within study area, thus we added a finer spatial scale, which allowed getting more information about dispersal. Although it remains impossible to know whether variation of apparent survival mainly reflects variation in true survival or variation in emigration, more confident inferences were obtained, because part of the dispersal behaviour is known.

An important advantage of using our multistate capture–recapture model is that imperfect detection within the study area is accounted for. For example, the recapture probability of swallows with no reproductive success was consistently lower than in swallows with high reproductive success [e.g. recapture probability of females from Pays d’Enhaut: no reproductive success: 0.12 (SE: 0.09), high reproductive success: 0.99 (SE: 0.01)]. The fact that most of our main results agree with studies that have not included detection probabilities should not be taken as evidence that not accounting for imperfect detection causes generally no important bias. However, if detection probabilities are high, the bias is probably low.

Our approach requires a definition of a dispersal event. While we defined the change of the breeding location as a dispersal event, one could envision also to define only movements larger than a certain distance as dispersal events. The former focuses more on the behavioural decision an individual has conducted (breed at another location), the latter may focus more on the different environment (e.g. foraging habitat). In any case, the

estimated probabilities of within-study area dispersal change with the definition of the dispersal event. Therefore, we recommend to thoroughly think about a clear definition of dispersal that needs to be linked with the research goal.

To estimate the parameters of interest using the multistate model requires a large sample size. For this reason, we have combined the data from different study sites. Our omnibus tests for site effects provide no evidence for differences among sites. Although the power of these tests is likely relatively low, we are confident that large differences were not present and that our main conclusions were not the result of site-specific differences, but were due to general patterns present in all study sites.

This study design may permit good approximations of true survival rates from capture–recapture data. If we had not considered reproductive success, estimated apparent survival would be lower than ~ 0.48 and clearly different between sexes [Cormack–Jolly–Seber model $\phi_{\text{sex}}, p_{\text{sex} \times \text{site}}$, males: 0.44 (SE: 0.02), females: 0.34 (SE: 0.01)]. Based on the finding that successful breeders usually do not disperse in many bird species (Shields 1984; Haas 1998; Doligez *et al.* 1999; Hoover 2003), we suggest that apparent survival rates of successful breeders provide close estimates of true survival. It is critical to consider that reproduction and survival skills may be positively correlated within individuals (Cam *et al.* 2002), and thus survival of high quality individuals might be estimated and not the population mean.

Adult swallows are known to be highly faithful to their breeding locations (Shields 1984; Saino *et al.* 1999; Turner 2006). These conclusions are mostly based on calculating the proportion of individuals known to be philopatric to their breeding location as well as on observed dispersal distances. Applied to our data, most returning individuals appear to be philopatric to the same breeding location (males: 88.4%, $n = 507$; females: 80.9%, $n = 513$), most observed dispersal occurred over less than 1 km (males: 91.5%, $n = 59$; females: 88.8%, $n = 98$) and mean observed dispersal distances were short (males: 34 m, $n = 507$; females: 89 m, $n = 513$) supporting the view that adult swallows are philopatric. The results from our multistate model, which takes imperfect capture and previous reproductive success into account, confirm that those swallows are highly philopatric, which successfully raised fledglings in the preceding year (Fig. 3a). However, our analysis also shows that unsuccessful breeders can experience considerable dispersal. With conventional analysis dispersal of unsuccessful breeders is not detected, because, (i) their proportion is relatively low, (ii) their recapture probability is much less than that of successful breeders rendering them to be underrepresented in the sample, and (iii) because the reproductive success is often not considered. This highlights that our model can provide additional insights into dispersal behaviour, which is difficult to detect otherwise.

EFFECTS OF REPRODUCTION ON SURVIVAL

If variation in apparent survival of barn swallows largely reflected variation in true survival, we would have expected no

or only a slight sex-specific difference (Payevsky *et al.* 1997; Siriwardena *et al.* 1998), which was not confirmed by our data. Females had on average lower apparent survival probabilities than males, and we conclude that a larger fraction of females than of males emigrated from the study area. This conclusion is supported by the observed longer dispersal distances in female barn swallows (Shields 1984). Dispersal within study area declined with increasing reproductive success in both sexes, suggesting that apparent survival of individuals with high reproductive success was closer to true survival than apparent survival of individuals with lower reproductive success. Taken together, there is evidence that true survival of barn swallows was close to apparent survival of males with high reproductive success (~ 0.48).

It has been shown in other studies that the parental investment involved in rearing offspring may affect adult survival negatively. For instance, double-brooded female house martins (*Delichon urbicum* L.) survived less well than single-brooded ones (Bryant 1979). In swallows, Saino *et al.* (1999) reported reduced survival in adults rising experimentally enlarged broods. In our study, model averaged estimates of apparent survival of later encountered males, which are supposed to be close to true survival, were slightly declining with increasing reproductive success. However, because of individual variation in the ability to acquire resources (van Noordwijk & de Jong 1986), this result from our observational study shall not be taken as strong evidence for the existence of costs of reproduction in terms of survival. In future studies, brood size manipulation experiments should be combined with methods that allow to correct for imperfect detection probabilities to get more conclusive results.

EFFECTS OF REPRODUCTION ON DISPERSAL

We estimated dispersal at two spatial scales, within study area dispersal and total dispersal, but total dispersal is the biologically more interesting parameter. The estimate of total dispersal relies on the assumption that true survival was 0.48 and independent of the reproductive success, for which we have given some supporting arguments. Yet, due to individual differences in quality, low-quality individuals are likely to have both low reproductive success and low survival. In this case, the estimated total dispersal (Fig. 3b) is an overestimation of dispersal in particular for individuals with low reproductive success. In line with many other studies (Shields 1984; Haas 1998; Doligez *et al.* 1999; Hoover 2003; Città & Lindberg 2007), we found that unsuccessful swallows preferably dispersed to another breeding location the next year.

Dispersal is an advantageous behavioural response allowing individuals to improve reproductive success, if environmental conditions are temporally autocorrelated and hence predictable (Switzer 1993). The reproductive success of swallows is largely determined by the abundance of air-borne insects (Bryant & Turner 1982), and food supply may be predictable insofar as the abundance of flying insects is positively affected by the presence of cattle and habitat elements such as hedges, orchards or water bodies with a favourable supply

(Møller 2001; Grübler, Morand & Naef-Daenzer 2008). However, the change of class of reproductive success was independent on previous dispersal within the study area, thus dispersal turned out not to be advantageous for improving reproductive success. This can safely be concluded for males whose dispersal largely occurred within the study area, but less so for females, as a larger fraction of them emigrated from the study area where the reproductive success could not be assessed. This result agrees with some studies (Newton & Marquiss 1982; Pasinelli *et al.* 2007), but not with others, which reported increased fitness after dispersal (Pärt & Gustafsson 1989; Forero *et al.* 1999). It is difficult to imagine how dispersal could have evolved if there would be no fitness benefits. There are two possible reasons which can explain the apparent lack of this relationship. First, we used relatively coarse categories of reproductive success with which it is difficult to detect subtle effects. It is possible that costs of dispersal in swallows are low and the improvement of reproduction only needs to be small for dispersal becoming adaptive. Second, owing to our definition of dispersal, the foraging habitat has often not changed significantly after dispersal, and thus the reproductive success is unlikely to improve.

EFFECTS OF CURRENT ON FUTURE REPRODUCTION

Current reproductive success depended on previous reproductive success and on relative age, but not on preceding dispersal within the study area and there were no sex differences. Although the transition probabilities between classes of reproductive success were Markovian (Table 2), it is difficult to see obvious patterns (Fig. 4). The reproductive success of individuals tended to remain in the same state in consecutive years, suggesting individual differences in breeding performance. Individual differences in reproductive performance have been demonstrated to be linked to morphological traits in swallows (Møller 1993). Similarly, although model selection supported an impact of relative age on reproductive performance, it is difficult to see clear patterns, because the effects were not strong and consistent and the confidence intervals wide. Based on theory, reproductive performance should increase first and decline later with age (Forslund & Pärt 1995). A slight increase with age could be evidenced by higher probabilities to have high reproductive success in later encountered individuals. This pattern was not present in individuals that had no reproductive success in the previous year. The necessary restriction to two relative age classes may have masked the detection of a clearer pattern.

Our study highlighted that the reproductive success was an important factor impacting breeding dispersal and thus population turnover. While unsuccessful males only dispersed over short distances and mainly remained in the local population, many unsuccessful females left the local population. Population turnover of adult swallows was thus mainly due to unsuccessfully breeding females, and, given individual differences in reproductive skills, due to low-quality individuals.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Definition of the states

Appendix S2. Description of how the multistate capture-recapture model is fitted

Appendix S3. Meaning of the model fragments that were used to analyse the capture–recapture data, and modelling results

Table S1. Notation and meaning of the six structures used for modelling apparent survival (ϕ)

Table S2. Notation and meaning of the six structures used for modelling dispersal within study areas (d)

Table S3. Notation and meaning of the 12 structures used for modelling change of reproductive success (b^p , b^d)

Table S4. Notation and meaning of the three structures used for modelling recapture (p)

Table S5. Results of the first modelling step for recapture (p) and the probability to change among classes of reproductive success from 1 year to another (b^p , b^d)

Table S6. Results of the second modelling step for apparent survival (ϕ) and within study area breeding dispersal probabilities from one year to another (d)

Table S7. Results of the final modelling step for assessing effects of relative age (since initial capture) on apparent survival (ϕ), within study area breeding dispersal (d), and probability of changing reproductive success among classes from one year to another (b^d , b^p)

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