WEATHER IN THE BREEDING AREA AND DURING MIGRATION AFFECTS THE DEMOGRAPHY OF A SMALL LONG-DISTANCE PASSERINE MIGRANT

BÅRD G. STOKKE,[1,2,4] ANDERS PAPE MØLLER,[2] BERNT-ERIK SÆTHER,[1]
GOETZ RHEINWALD,[3] AND HANS GUTSCHER

[1]Department of Biology, Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway;
[2]Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Université Pierre et Marie Curie, 7 quai St. Bernard,
Case 237, F-75252 Paris Cedex 05, France; and
[3]Schönblick 10, 53562 St. Katharinen, Germany

ABSTRACT.—Migratory birds are subject to the effects of various weather systems during the year. Fluctuations in population size may depend on survivorship of juveniles and adults at various stages of the annual cycle. Severe weather conditions can lower survival, especially in migrating passerines that feed on insects. We investigated the effects of climate and density dependence on survival in a population of Common House-Martins (Delichon urbicum), including variables of weather experienced both in their breeding areas and during autumn migration. Unfavorable weather conditions during autumn migration had a severe negative effect on adult apparent survival, irrespective of sex; whereas temperature in the breeding area and population size explained a significant proportion of variance in juvenile survival. Thus, weather conditions experienced in different areas can regulate various age classes in different ways, which suggests that climate change can have a significant but complex influence on demography in passerine populations. Received 11 December 2003, accepted 15 November 2004.

Key words: breeding, capture–recapture, Common House-Martin, Delichon urbicum, demography, migration, survival, weather.

El Clima de las Áreas de Cría y de la Época de Migración Afectan la Demografía de un Ave Paserina Pequeña que Migra a Grandes Distancias

RESUMEN.—Las aves migratorias están sujetas a los efectos de varios sistemas climáticos durante el año. Las fluctuaciones en el tamaño poblacional pueden depender de la supervivencia de los juveniles y los adultos en varias etapas del ciclo anual. Las condiciones climáticas severas pueden disminuir la supervivencia, especialmente en aves paserinas migrantes que se alimentan de insectos. En este estudio investigamos los efectos del clima y de factores dependientes de la densidad sobre la supervivencia en una población de Delichon urbicum (Hirundinidae), incluyendo variables climáticas a las que las aves se enfrentan tanto en sus áreas de cría como durante la migración de otoño. Las condiciones desfavorables durante la migración de otoño tuvieron un fuerte efecto negativo sobre la supervivencia aparente de los adultos, independientemente del sexo. Por su parte, la temperatura en el área de cría y el tamaño poblacional explicaron una proporción significativa de la variaza en la supervivencia de los juveniles. Por tanto, las condiciones climáticas experimentadas en distintas áreas pueden regular las diferentes clases de edad de modos distintos, lo que sugiere que el cambio climático podría tener una influencia significativa pero compleja sobre la demografía de las poblaciones de aves paserinas.

---

[4]E-mail: bard.stokke@bio.ntnu.no

VARIATION IN CLIMATE can have profound effects on survival, both in sedentary (Sæther et al. 2000, Loison et al. 2002) and in migratory birds (Sillett et al. 2000, Jonzén et al. 2002). Large-scale climatic change may particularly influence population dynamics in migrating birds that breed in temperate areas and winter in the subtropics or tropics (Sæther et al. 2004). To understand the effects of climate on population dynamics, it is important to analyze how variation in climate can affect demography (Sillett et al. 2000).

Survival is one of the most important components of lifetime reproductive success (Clutton-Brock 1988). Appropriate estimates of survival are essential for studying factors shaping the probability of survival. Capture–mark–recapture models (Lebreton et al. 1992) have been widely used to test for the influence of age, sex, climate, and individual covariates on the survival of animals (e.g. Catchpole et al. 2000, Loison et al. 2002). To enable identification of biological processes responsible for variation in survival rates, random-effects models have been developed to decompose the total variance from point estimates into a sampling variance and a process variance (Burnham et al. 1987, Burnham and White 2002, Franklin et al. 2002). That true process variance is important for revealing sources of temporal variation in survival (e.g. Gould and Nichols 1998).

Hirundines are small passerine birds that rely heavily on flying insects for food (Turner and Rose 1989). Abundance of such insects is strongly influenced by weather conditions (Turner and Rose 1989); climatic change may thus have particularly strong effects on demographic parameters in hirundines, including survival. Both strong winds and low temperatures have negative effects on foraging efficiency (Ormerod 1989). Especially important, in that respect, are weather conditions in feeding areas before and during the long autumn migration from the European breeding grounds to the winter destination in sub-Saharan Africa (Pilastro and Magnani 1997). However, unfavorable weather also affects foraging in hirundines during breeding (Bryant 1973, Jones 1987, Brown and Brown 1998), which can cause food shortage among nestlings (Bryant 1975, Christe et al. 2001). It is well known that scarcity of food during ontogeny can have profound effects on life history (Gebhardt-Henrich and Richner

1998). Although nestlings of Common House-Martins (*Delichon urbicum*; hereafter "house-martins") are capable of slowing down their rate of development, and enter torpor when weather conditions are temporarily bad (Bryant 1975, Prinzinger and Siedle 1988), weight loss resulting from bad weather still increases nestling mortality (Rheinwald 1971).

The house-martin is a socially monogamous and monomorphic hirundine. By using capture–mark–recapture models together with random-effects models, we analyzed the effects of various demographic parameters and weather on apparent survival rates in a German population of house-martins during a 10-year period (1967–1976). Annual counts showed that the population size dropped markedly between 1969 and 1970, and again between 1974 and 1975. The decline from 1969 to 1970 was associated with a period of unfavorable weather at the breeding site (Rheinwald 1970), which apparently had a negative effect on breeding success and thus on population size the following year. Furthermore, in 1974, house-martins were catastrophically affected by harsh weather before and during autumn migration. Several hundred thousand birds were found dead or dying in the Swiss Alps and in surrounding areas, victims of heavy snowfall and low temperatures in late September and October (Ruge 1974, 1975; Hannover 1975; Meier and Mette 1976; Glutz von Blotzheim and Bauer 1985). Some evidence suggests that population sizes were strongly reduced the following year (Meier and Mette 1976).

In general, we lack an understanding of whether variation in a demographic variable translates into effects on population dynamics because of compensatory interseasonal effects in demography or the effects of density-dependent variation. However, in the White-throated Dipper (*Cinclus cinclus*), climate-induced changes in population size mainly operate through variation in survival (Loison et al. 2002). In migratory species, such effects become even more difficult to document, because conditions during migration or in winter may strongly affect demography and thus influence population dynamics (Sæther et al. 2000, Sillett et al. 2000). Our objective was to assess, by means of capture–recapture analyses, how variation in local climate during the breeding season and during migration, including an extreme weather event and subsequent mass

die-off, affected temporal variation in survival. Furthermore, we considered how variation in a large-scale climatic phenomenon, the North Atlantic Oscillation (NAO; Visbeck et al. 2001), contributed to variation in survival.

METHODS

Our study is based on data collected in Riet (48°55'N, 8°50'E), Stuttgart, southwestern Germany, in 1961–1976 (for a detailed description of the study area, see Rheinwald and Gutscher 1969). Capture and banding of nestlings and adults were done in 1967–1976 (Rheinwald 1975). However, data regarding sex were unavailable for the first two years. Only nestlings that survived to fledging (hereafter "juveniles") were included in analyses. A total of 3,732 individuals was banded during that period, including 433 males, 470 females, 3,075 juveniles, and 657 adults. Only birds that were at least one year old when caught were sexed, so individuals caught as juveniles and not recaptured later were of unknown sex.

Size of the breeding population (in number of pairs) in any specific year was estimated by counting occupied nests in all colonies within the village, with population size varying between 103 and 234 pairs.

To examine the effects of climate on apparent survival, we obtained several indices of meteorological conditions. To get a good estimate of the weather during autumn migration, we obtained data on precipitation and temperature from the Disentis weather station in the Swiss Alps. We also collected the same data from three other Swiss weather stations (Interlaken, Zurich, and Davos), but the Disentis data were best suited for models based on corrected Akaike's Information Criterion (AIC_c) values. Models made with data from the other three stations were always poorer, but there was, in general, high correlation among data from all four stations, for both precipitation and temperature. For simplicity, we present only results obtained with data from Disentis. Mean precipitation (in millimeters) and temperature (°C) for 20 September through 15 October—the period when most house-martins migrate through the areas in question (see e.g. Hannover 1975, Ruge 1975, Meier and Mette 1976)—were used in analyses. We also obtained data on weather during the breeding season (15 May–15

September) from the weather station at Stuttgart-Echterdingen, Germany, located close to the breeding site. However, because climate may vary significantly over short intervals, we also partitioned the breeding season into two shorter periods, corresponding approximately to the timing of the first (15 May–14 July) and second broods (15 July–15 September) at the breeding site (Glutz von Blotzheim and Bauer 1985). We also counted the number of days during the breeding season when the temperature dropped below 10°C, which enabled us to obtain a more sensitive measure of changes in weather regimes at the breeding site. Finally, we included the NAO index in analyses as an additional, larger-scale index of climate variation (e.g. Ottersen et al. 2001, Visbeck et al. 2001, Jonzén et al. 2002). That index reflects the relative air-pressure difference between Iceland and the Azores and has been found to correlate with variation in local climate over large areas (Hurrell 1995). In addition, we investigated density-dependent effects on apparent survival rates of both adults and juveniles by including the size of the breeding population as a variable.

Analyses were performed using capture–mark–recapture models (Lebreton et al. 1992) implemented in the program MARK (White and Burnham 1999). Apparent survival (ϕ) was estimated from one breeding season to the next as the probability of returning to the site used in the previous year. True survival is expressed as S, and d is the probability of dispersal. Thus, apparent survival becomes $\phi = S(1 - d)$. Recapture probability (p) is the probability of capturing a previously marked bird during the breeding season. In general, the conditional probability of recapturing an individual depends on the conditional survival rates in the population and the capture rates at each occasion (Lebreton et al. 1992).

Analyses were performed on two separate data sets. The first data set included all individuals of known sex (i.e. individuals that were captured as adults; ≥1 year old). That allowed us to test for both sex differences and variation in adult apparent survival rates over time. Data were available for 1969–1976. The second data set was based on all individuals of known age—that is, individuals captured as juveniles (subscript c) or adults (subscript ad). We could thus test for effects of age and time on apparent survival—allowing us to examine

factors affecting juvenile apparent survival. For that analysis, we had access to data for 1967–1976. For the first data set, "sex" is the effect of sex and t is the effect of time; interaction effects are indicated with an asterisk (*) and additive effects with a plus sign (+). For the second data set, additive effects of time (i.e. parallel covariation over time) were grouped between parentheses—for example, (ϕ_c, ϕ_{ad})—following the procedure of Loison et al. (2002).

Again following the procedure of Loison et al. (2002), we analyzed the data in three stages. First, we assessed the fit of the general models used as starting points in analyses by performing goodness-of-fit (GOF) tests using the program RELEASE (Burnham et al. 1987) and a bootstrapping procedure; both those analyses were performed using MARK (White and Burnham 1999). For the first data set (adult birds), we assessed the fit of the Cormack-Jolly-Seber (CJS) model $\phi(sex*t)p(sex*t)$ using RELEASE, and then assessed the fit of the same model by employing the bootstrap procedure (500 simulations). For the second data set (age-model), we assessed the fit of the model $\phi_c(t)\phi_{ad}(t)p_c(t)p_{ad}(t)$ using both RELEASE and the bootstrap procedure. Following the procedure of Gaillard et al. (1997), Ringsby et al. (1999), and Loison et al. (2002), the Test 3.SR component of juveniles was not included, because we expected a lower survival of individuals in that group. Overdispersion can occur if events depend on each other, or if survival probabilities vary among individuals; to correct the estimates of the sampling variances and covariances, a variance inflation factor, C, can be estimated as $\hat{C} = \chi^2/df$ (Lebreton et al. 1992). Tests for overdispersion ($\hat{C}$) were performed using chi-square values of both the RELEASE and bootstrap procedures (Loison et al. 2002).

In the second stage, we tested for the effect of sex (first data set), age (second data set), and time on apparent survival and recapture probabilities. Random-effects models were used to obtain an estimate of the true process variance (σ^2). Using that procedure, we subtracted the sampling variance (σ_s^2) from the total variance (σ_{tot}^2) to obtain the real process variance of the temporal variation in apparent survival rates (Loison et al. 2002).

In the third stage, we assessed the effect of climate and population density on variation in apparent survival rates over time for adults and juveniles. A logit link was used between covariates and survival rates (Lebreton et al. 1992, Loison et al. 2002). By using random-effects models, we calculated the amount of process variance explained by the external covariates (for an explanation of the approach, see Loison et al. 2002).

Models were selected on the basis of AIC_c values, which avoids the problems of arbitrary or biased model choice (Burnham et al. 1995).

RESULTS

SURVIVAL RATES IN RELATION TO SEX AND AGE

In this section, we present results for model selection and the effect of sex and age on apparent survival and recapture in house-martins.

Goodness-of-fit testing and model selection.—For all birds of known sex, the goodness of fit of the CJS model tested with RELEASE (Test 2 + 3) was satisfactory (sexes pooled: $\chi^2 = 24.30$, df = 25, $P = 0.502$; males: $\chi^2 = 16.70$, df = 13, $P = 0.212$; females: $\chi^2 = 7.57$, df = 12, $P = 0.818$). Thus, the assumptions of the CJS model were not violated. The GOF test yielded $\hat{C} = 1.03$, which again is satisfactory and does not indicate significant overdispersion.

The bootstrap GOF test on the CJS model without sex effects produced the same results, yielding $\hat{C} = 1.17$. Probability of obtaining a value at least as high as the observed deviance under CJS was 0.40. This indicates a good fit of the data to the CJS model. However, to correct for the slight lack of fit of the model to the data, we proceeded by adjusting $\hat{C}$ from 1.0 to 1.17.

For all birds of known age, the goodness of fit of the CJS model $\phi_c(t)\phi_{ad}(t)p_c(t)p_{ad}(t)$ tested with RELEASE (Test 2 + 3) was satisfactory when the Test 3.SR component of the juveniles was removed ($\chi^2 = 30.20$, df = 27, $P = 0.310$; juveniles: $\chi^2 = 14.21$, df = 9, $P = 0.156$; adults: $\chi^2 = 15.99$, df = 18, $P = 0.593$). The GOF test yielded $\hat{C} = 1.59$, which again is satisfactory and does not indicate significant overdispersion.

The bootstrap GOF test for the CJS model $\phi_c(t)\phi_{ad}(t)p_c(t)p_{ad}(t)$ produced the same results, yielding $\hat{C} = 1.77$. The probability of obtaining a value at least as high as the observed deviance under CJS was 0.25. This indicates a good fit of the data to the CJS model. However, we proceeded by adjusting $\hat{C}$ from 1.0 to 1.77.

Sex, age, and time effects on survival and recapture.—For all birds of known sex, there was a considerable difference in AIC_c between models $\phi(sex+t)p(t)$ and $\phi(t)p(t)$ (Table 1). The former model was the best among all sets of models before we included covariates based on climate, which indicates a large additive effect of sex and time on apparent survival. Annual variation in adult survival rates of the two sexes was correlated (Fig. 1; $r_{sp} = 0.829$, $P = 0.042$, $n = 6$), indicating that similar factors influenced survival of the two sexes. However, the small difference in AIC_c between models $\phi(t)p(sex+t)$ and $\phi(t)p(t)$ implies that there are only minor sex differences in recapture probabilities (Table 1). The estimate of mean recapture probabilities over all years was 0.822 ± 0.062 (SE) and $0.884 \pm$ 0.057 for males and females, respectively, and 0.831 ± 0.056 for both sexes combined.

Because of the pronounced effect of sex, we obtained separate sex-specific estimates of the process variance in apparent survival. For males, the process variance in apparent survival rates was 0.038 ± 0.093, with a mean of 0.458 ± 0.044. Correspondingly, for females, the process variance was 0.039 ± 0.096, with a mean of 0.362 ± 0.045. In contrast, the sampling variance for males made up only 14.2% of the total variance, whereas the corresponding figure for females was 13.6%. The shrunken estimates for apparent survival (Fig. 1) are therefore very close to the maximum-likelihood estimates for apparent survival.

For all birds of known age, the best model before we included external covariates was the

TABLE 1. Capture–mark–recapture models for adult house-martins, ranked by AIC_c.

Model	AIC_c	ΔAIC_c	Number of estimated parameters	Model deviance
$\phi(sex+Dis.temp.)p(t)$	1,466.821	0.00	9	93.153
$\phi(sex+t)p(t)$	1,470.999	4.18	14	87.122
$\phi(sex+t)p(sex+t)$	1,472.629	5.81	15	86.700
$\phi(t)p(t)$	1,474.133	7.31	12	94.350
$\phi(sex+t)p(.)$	1,475.572	8.75	9	101.904
$\phi(t)p(sex+t)$	1,475.842	9.02	13	94.014
$\phi(sex+Dis.prec.)p(t)$	1,477.425	10.60	9	103.756
$\phi(sex)p(t)$	1,479.791	12.97	8	108.153
$\phi(sex+NAO)p(t)$	1,479.881	13.06	9	106.212
$\phi(sex+Stu.2temp.)p(t)$	1,480.112	13.29	9	106.443
$\phi(t)p(.)$	1,480.415	13.59	8	108.777
$\phi(sex+Stu.days)p(t)$	1,480.787	13.97	9	107.118
$\phi(sex+Stu.prec.)p(t)$	1,481.482	14.66	9	107.813
$\phi(sex+Stu.1temp.)p(t)$	1,481.636	14.82	9	107.968
$\phi(sex+Stu.1prec.)p(t)$	1,481.743	14.92	9	108.075
$\phi(sex+Stu.temp.)p(t)$	1,481.772	14.95	9	108.103
$\phi(sex+Stut.2prec.)p(t)$	1,481.783	14.96	9	108.115
$\phi(sex+n)p(t)$	1,481.821	15.00	9	108.153
$\phi(.)p(t)$	1,484.685	17.86	7	115.074
$\phi(sex*t)p(sex*t)$[a]	1,484.842	18.02	23	82.368
$\phi(sex)p(.)$	1,494.752	27.93	3	133.217
$\phi(.)p(.)$	1,499.733	32.91	2	140.209

[a]Goodness-of-fit test (GOF; evaluation of fit between model and data) using RELEASE (MARK), and GOF test using bootstrapping procedure (500 runs) (MARK).

Abbreviations: ΔAIC_c = difference in AIC value from the model with the lowest AIC, ϕ = apparent survival, p = recapture probability, t = time effect, sex = sex effect, * = interaction effect, + = additive effect, Dis. = data from Disentis weather station, Stu.1 = data from Stuttgart-Echterdingen weather station in the period 15 May–14 July, Stu.2 = data from Stuttgart-Echterdingen weather station in the period 15 July–15 September, Stu.days = number of days with temperature below 10°C (data from Stuttgart-Echterdingen weather station, 15 May–15 September), temp. = temperature (°C), prec. = precipitation (mm), NAO = North Atlantic Oscillation, n = population size (pairs). For other details on abbreviations and model simplifications, see text.
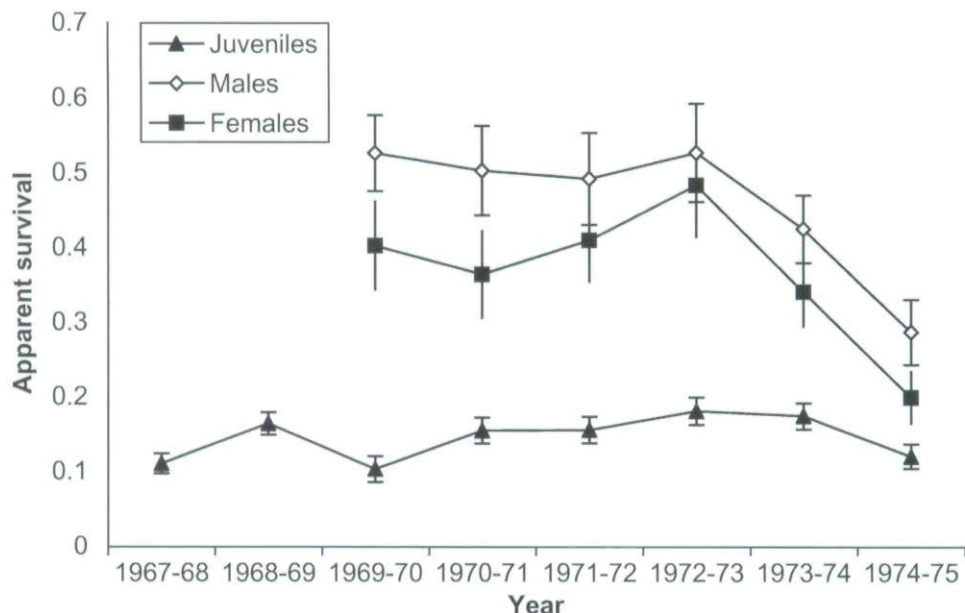
FIG. 1. Estimated mean survival rates (± SE) of adult male, adult female, and juvenile house-martins during the period 1967–1976, based on shrunken estimates obtained using random-effects models.

one that included age- and time-specific variability in survival (Table 2). Thus, there were differences between juveniles and adults in apparent survival, but not in recapture probabilities. Furthermore, there was temporal variation in both juvenile and adult survival. Mean recapture probability over time for birds marked as juveniles was 0.822 ± 0.041; whereas for birds marked as adults, it was 0.852 ± 0.033.

Process variance in juvenile apparent survival was 0.011 ± 0.030, with a mean of 0.145 ± 0.013. Sampling variance made up only 16% of the total variance in apparent survival; thus, the shrunken estimates for apparent survival (Fig. 1) are close to maximum-likelihood estimates for the juveniles.

INFLUENCE OF CLIMATE AND POPULATION DENSITY ON SURVIVAL

In this section, we focus on the external variables that explain temporal variability in apparent survival rates of adults and juveniles. Because of the effect of sex, we investigated temporal variance in apparent survival for males and females separately.

Adult survival.—Temporal variation in apparent survival rates among birds of known sex was best explained by temperature during autumn migration (measured at Disentis). Thus, the additive effects between sex and temperature during autumn migration had the most profound effect on temporal variation in apparent survival of adults in this population of house-martins (Table 1). In both females and males, temperature during autumn migration explained >90% of temporal variation in survival (Table 3). The slope of the relationship between temperature during autumn migration and adult apparent survival supports that finding (males: slope = 0.903 ± 0.045; females: slope = 0.770 ± 0.068). In addition, precipitation during autumn migration explained a very large proportion of the variation in adult apparent survival (males: slope = -0.650 ± 0.080; females: slope = -0.610 ± 0.082). Variation in NAO explained a significant proportion (18.1%) of the variation in male apparent survival, whereas no such effect was present in females (Table 3). No effect of population size was found on survival of adult house-martins, regardless of sex (Table 3).

Juvenile survival.—The external variable that best accounted for temporal variation in apparent survival rates among juveniles was number of days with temperatures below 10°C during the breeding season (Table 2). In fact,

TABLE 2. Capture–mark–recapture models for house-martins marked as juveniles and adults, ranked by AIC_c. Age structure of apparent survival and recapture probabilities are indicated by subscripts c for juveniles and ad for adults. For explanations of abbreviations and model simplifications, see Table 1 and text.

Model	AIC_c	ΔAIC_c	Number of estimated parameters	Model deviance
$\phi_c(\text{Stu.days})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,571.706	0.00	12	122.107
$\phi_c(t)\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,580.625	8.92	19	116.924
$\phi_c(\text{Stu.1temp.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,583.180	11.47	12	133.582
$\phi_c(\text{Stu.2temp.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,584.946	13.24	12	135.347
$\phi_c(n)\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,585.334	13.63	12	135.735
$\phi_c(\text{NAO})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.312	14.61	12	136.714
$\phi_c(\text{Stu.2prec.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.509	14.80	12	136.910
$\phi_c(\text{Stu.1prec.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.542	14.84	12	136.944
$\phi_c(\text{Dis.temp.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.565	14.86	12	136.740
$\phi_c(\text{Dis.prec.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.579	14.87	12	136.811
$\phi_c(\text{Stu.prec.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.594	14.89	12	136.995
$\phi_c(\text{Stu.temp.})\phi_{ad}(t)p_c(.)p_{ad}(.)$	2,586.594	14.89	12	136.995
$(\phi_c,\phi_{ad})(t)p_c(.)p_{ad}(.)$	2,587.108	15.40	11	139.521
$\phi_c(t)\phi_{ad}(t)p_c(t)p_{ad}(t)$ [a]	2,590.332	18.63	26	112.485
$\phi_c(t)\phi_{ad}(t)p(.)$	2,595.468	23.76	19	131.767
$\phi(t)p(.)$	2,757.248	185.54	10	311.670
$\phi(.)p(.)$	2,758.158	186.45	2	328.627
$\phi(.)p(t)$	2,759.356	187.65	9	315.788
$\phi(t)p(t)$	2,764.340	192.63	16	306.689

[a] Goodness-of-fit test (GOF; evaluation of fit between model and data) using RELEASE (MARK), and GOF test using bootstrapping procedure (500 runs) (MARK).

80.4% of the variation in apparent survival could be explained by that variable (Table 4). The slope between juvenile survival and the number of days with temperatures below 10°C during the breeding season also was highly significant (slope = –0.846 ± 0.017). In addition, population size explained a significant proportion (28.1%) of the variation in apparent survival rates among juveniles (Table 4). There was a strong negative relationship between juvenile apparent survival and population size (slope = –0.673 ± 0.024).

DISCUSSION

The temporal variation in apparent survival rates obtained here was closely associated with fluctuations in estimated number of breeding pairs in the population (Table 3 and Fig. 1). Furthermore, the *"Schwalbenkatastrophe"* in autumn 1974 led to higher-than-normal mortality in adults in our population (Fig. 1). Our results indicate that the effect of temperature was significantly larger than the effect of precipitation, but that both variables influenced survival of adults. Extreme weather conditions at the premigration and early-migration phase could be very detrimental to insectivores such as hirundines, and especially for the house-martins, which usually feed at higher altitudes than other species of the swallow family, such as the Barn Swallow (*Hirundo rustica*; Cramp 1988). Low temperatures and heavy precipitation may thus lead to a shortage of food (Williams 1951, 1961) in a period when Barn Swallows usually store energy before the migration to tropical Africa across the Alps and through France and Italy (Pilastro and Magnani 1997, Rubolini et al. 2002). However, house-martins do not deposit much fat before migration (Glutz von Blotzheim and Bauer 1985, Cramp 1988), and this species is therefore especially vulnerable to bad weather during migration because they lack energy reserves. Juvenile apparent survival was influenced far less by bad weather during autumn migration (Tables 2 and 4). A possible

TABLE 3. Temporal variation in adult apparent survival of house-martins, explained by covariates. For explanations of abbreviations and model simplifications, see Table 1 and text.

Model	Variance	Variance explained (%)
Males		
$\phi(t)$	0.03788	–
ϕ(NAO)	0.03102	18.1
$\phi(n)$	0.03828	0.0
ϕ(Dis.prec.)	0.02872	24.2
ϕ(Dis.temp.)	0.00010	99.7
ϕ(Stu.prec.)	0.04500	0.0
ϕ(Stu.1prec.)	0.04302	0.0
ϕ(Stu.2prec.)	0.04213	0.0
ϕ(Stu.temp.)	0.04040	0.0
ϕ(Stu.1temp.)	0.04200	0.0
ϕ(Stu.2temp.)	0.03572	5.7
ϕ(Stu.days)	0.03771	0.0
Females		
$\phi(t)$	0.03907	–
ϕ(NAO)	0.04206	0.0
$\phi(n)$	0.04054	0.0
ϕ(Dis.prec.)	0.02498	36.1
ϕ(Dis.temp.)	0.00230	94.1
ϕ(Stu.prec.)	0.03977	0.0
ϕ(Stu.1prec.)	0.04275	0.0
ϕ(Stu.2prec.)	0.04038	0.0
ϕ(Stu.temp.)	0.04127	0.0
ϕ(Stu.1temp.)	0.04219	0.0
ϕ(Stu.2temp.)	0.04031	0.0
ϕ(Stu.days)	0.03890	0.4

TABLE 4. Temporal variation in juvenile apparent survival of house-martins, explained by various covariates. For explanations of abbreviations and model simplifications, see Table 1 and text.

Model	Variance	Variance explained (%)
$\phi(t)$	0.01054	–
ϕ(NAO)	0.01487	0.0
$\phi(n)$	0.00758	28.1
ϕ(Dis.prec.)	0.01129	0.0
ϕ(Dis.temp.)	0.01092	0.0
ϕ(Stu.prec.)	0.01298	0.0
ϕ(Stu.1prec.)	0.01001	5.0
ϕ(Stu.2prec.)	0.01154	0.0
ϕ(Stu.temp.)	0.01465	0.0
ϕ(Stu.1temp.)	0.01021	3.1
ϕ(Stu.2temp.)	0.01321	0.0
ϕ(Stu.days)	0.00207	80.4

explanation is that natal dispersal is higher than breeding dispersal (von Gunten 1963, Szép 1995). Even though juveniles may be affected as seriously as adults by bad weather, the effect is not detected when studying only a single population. For house-martins in Riet, previous studies have found that juveniles tend to return to their birth site (Rheinwald and Gutscher 1969, Rheinwald 1975). Therefore, another explanation for the lower effect of bad weather during autumn migration on juvenile apparent survival could be that juveniles may start migration earlier than adults. Many juveniles may have been able to cross the Alps before the onset of bad weather, thereby experiencing lower mortality than adults.

The high correlation in temporal variation in apparent survival between males and females in the present study is further supported by the findings that both sexes are mostly affected by the same variables (Tables 1 and 3), which is in agreement with other studies on sexually monomorphic hirundines (Szép 1995, Brown and Brown 1996) but contrary to what has been found in a sexually dimorphic hirundine (Møller and Szép 2002). The lower annual survival rates in females may be attributable to sex differences in postnatal dispersal. Females are often less faithful to a breeding area than males, especially after breeding failure (von Gunten 1963). Alternatively, females may have lower survival rates than males because of larger reproductive investment.

There was a negative correlation between NAO index values and survival in adult male house-martins (Table 3). High NAO values correspond to wet summers and autumns in Northern Europe (Møller 2002), which could lead to poor foraging conditions and low insect abundance (Williams 1951, 1961). The effect of large-scale climatic conditions on survival has been detected in other studies (e.g. Sillett et al. 2000, Jones et al. 2002, Loison et al. 2002), and Møller (2002) found that variation in such climatic conditions affected the relative importance of first and second clutches in Barn Swallows. However, juvenile and female apparent survival were apparently less affected by NAO (Tables 3 and 4), which again may be a result of lower site-fidelity in those groups, so that potential effects of NAO are hidden by dispersal.

Weather at the breeding site appeared to have little effect on apparent survival of adults, but explained most of the variance in apparent survival of juveniles (Tables 3 and 4). Thus, when the temperature falls below 10°C, juveniles suffer high mortality, whereas adults apparently manage to survive such periods without heavy losses. Brown and Brown (2004) found that postfledging survival of juvenile Cliff Swallows (*Petrochelidon pyrrhonata*) was negatively influenced by bad weather in the breeding area; their explanation was that parents invested less in offspring in years with bad weather. A similar explanation may apply to house-martins. Bryant (1979) found that adult mortality occurred mainly outside the breeding season, and other studies have shown that bad weather during the breeding season is most likely to influence the rate of food delivery to nestlings (Löhrl 1971; Rheinwald 1971, 1979; Hund and Prinzinger 1979). However, adult house-martins also can suffer significant mortality because of bad weather at the breeding site (Rheinwald 1970), like other hirundines (Brown and Brown 1998); the lack of evidence for that effect in our study could well be masked by the much more severe effects of unfavorable weather during autumn migration.

Population size had a pronounced effect on juvenile apparent survival (Table 4). A large population size led to relatively fewer annual recoveries than a small population size. Thus, surplus individuals (i.e. juveniles) tended to disperse more or experience lower survival (or both) because of density-dependent effects. Density dependence in local recruitment seems to be a general phenomenon in small passerines (Sæther et al. 2002).

Dramatic reduction of the breeding population following extreme weather conditions (as in autumn 1974) has usually been followed by a rapid recovery (Glutz von Blotzheim and Bauer 1985). That was the case in our study population: the number of breeding pairs increased from 103 in 1975 to 165 in 1978 (B. G. Stokke et al. unpubl. data). Our results demonstrate that higher juvenile survival resulting from reduction in population size may be an important component of that increase—thus illustrating the interaction between density-dependent variation and stochastic effects in the demography of small passerines. Given that extreme weather is predicted to become more frequent

with climate change (Easterling et al. 1997), we can expect that future survival rates of species like house-martins will depend more on adverse weather conditions than is currently the case.

Literature Cited

Brown, C. R., and M. B. Brown. 1996. Coloniality in the Cliff Swallow. University of Chicago Press, Chicago.

Brown, C. R., and M. B. Brown. 1998. Intense natural selection on body size and wing and tail asymmetry in Cliff Swallows during severe weather. Evolution 52:1461–1475.

Brown, C. R., and M. B. Brown. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. Behavioral Ecology and Sociobiology 56:498–511.

Bryant, D. M. 1973. The factors influencing the selection of food by the House Martin *Delichon urbica* (L.). Journal of Animal Ecology 42:539–564.

Bryant, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117:180–216.

Bryant, D. M. 1979. Reproductive costs in the house martin (*Delichon urbica*). Journal of Animal Ecology 48:655–675.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph, no. 5.

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. Journal of Applied Statistics 29: 245–264.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy

in the analysis of capture–recapture data. Biometrics 51:888–898.

CATCHPOLE, E. A., B. J. T. MORGAN, T. N. COULSON, S. N. FREEMAN, AND S. D. ALBON. 2000. Factors influencing Soay sheep survival. Applied Statistics 49:453–472.

CHRISTE, P., F. DE LOPE, G. GONZÁLEZ, N. SAINO, AND A. P. MØLLER. 2001. The influence of environmental conditions on immune responses, morphology and recapture probability of nestling House Martins (*Delichon urbica*). Oecologia 126:333–338.

CLUTTON-BROCK, T. H., ED. 1988. Reproductive Success. University of Chicago Press, Chicago.

CRAMP, S., ED. 1988. Handbook of the Birds of Europe, the Middle East and North Africa, vol. V: Tyrant Flycatchers to Thrushes. Oxford University Press, Oxford.

EASTERLING, D. R., B. HORTON, P. D. JONES, T. C. PETERSON, T. R. KARL, D. E. PARKER, M. J. SALINGER, V. RAZUVAYEV, N. PLUMMER, P. JAMASON, AND C. K. FOLLAND. 1997. Maximum and minimum temperature trends for the globe. Science 277:364–367.

FRANKLIN, A. B., D. R. ANDERSON, AND K. P. BURNHAM. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. Journal of Applied Statistics 29:267–287.

GAILLARD, J.-M., J.-M. BOUTIN, D. DELORME, G. VAN LAERE, P. DUNCAN, AND J.-D. LEBRETON. 1997. Early survival in roe deer: Causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502–513.

GEBHARDT-HENRICH, S., AND H. RICHNER. 1998. Causes of growth variation and its consequences for fitness. Pages 324–339 *in* Avian Growth and Development (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.

GLUTZ VON BLOTZHEIM, U. N., AND K. M. BAUER, EDS. 1985. Handbuch der Vögel Mitteleuropas. Band 10/I. Passeriformes (1. Teil). AULA-Verlag, Wiesbaden.

GOULD, W. R., AND J. D. NICHOLS. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79:2531–2538.

HANNOVER, B. 1975. Schwalbenkatastrophe im Herbst 1974. Vogelkundliche Hefte Waldeck-Frankenberg/Fritzlar-Homberg 1:77–79.

HUND, K., AND R. PRINZINGER. 1979. Untersuchungen zur Ortstreue, Paartreue und Überlebensrate nestjunger Vögel bei der Mehlschwalbe *Delichon urbica* in Oberschwaben. Die Vogelwarte 30:107–117.

HURRELL, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. Science 269:676–679.

JONES, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): An experimental study using precision electronic balances. Journal of Animal Ecology 56:229–245.

JONES, I. L., F. M. HUNTER, AND G. J. ROBERTSON. 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. Oecologia 133:38–44.

JONZÉN, N., A. HEDENSTRÖM, C. HJORT, Å. LINDSTRÖM, P. LUNDBERG, AND A. ANDERSSON. 2002. Climate patterns and the stochastic dynamics of migratory birds. Oikos 97:329–336.

LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

LÖHRL, H. 1971. Die Auswirkungen einer Witterungskatastrophe auf den Brutbestand der Mehlschwalbe (*Delichon urbica*) in verschiedenen Orten in Südwestdeutschland. Die Vogelwelt 92:58–66.

LOISON, A., B.-E. SÆTHER, K. JERSTAD, AND O. W. RØSTAD. 2002. Disentangling the sources of variation in the survival of the European dipper. Journal of Applied Statistics 29:289–304.

MEIER, W., AND M. METTE. 1976. Die Auswirkungen der Zugkatastrophe im Herbst 1974 auf den Schwalbenbestand im unteren Edertal. Vogelkundliche Hefte Edertal 2:113–123.

MØLLER, A. P. 2002. North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. Journal of Animal Ecology 71:201–210.

MØLLER, A. P., AND T. SZÉP. 2002. Survival rate of adult Barn Swallows *Hirundo rustica* in relation to sexual selection and reproduction. Ecology 83:2220–2228.

ORMEROD, S. J. 1989. The influence of weather on the body mass of migrating swallows *Hirundo rustica* in South Wales. Ringing and Migration 10:65–74.

OTTERSEN, G., B. PLANQUE, A. BELGRANO, E. POST, P. C. REID, AND N. C. STENSETH. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14.

PILASTRO, A., AND A. MAGNANI. 1997. Weather conditions and fat accumulation dynamics in pre-migratory roosting Barn Swallows *Hirundo rustica*. Journal of Avian Biology 28: 338–344.

PRINZINGER, R., AND K. SIEDLE. 1988. Ontogeny of metabolism, thermoregulation and torpor in the House Martin *Delichon u. urbica* (L.) and its ecological significance. Oecologia 76: 307–312.

RHEINWALD, G. 1970. Die Einwirkung der Witterungskatastrophe Anfang Juni 1969 auf die Mehlschwalben (*Delichon urbica*) verschiedener Altersklassen in Riet. Die Vogelwelt 91:150–153.

RHEINWALD, G. 1971. Gewichtsentwicklung nestjunger Mehlschwalben (*Delichon urbica*) bei verschied. Witterungsbedingungen. Charadrius 7:114–120.

RHEINWALD, G. 1975. The pattern of settling distances in a population of House Martins *Delichon urbica*. Ardea 63:136–145.

RHEINWALD, G. 1979. Brutbiologie der Mehlschwalbe (*Delichon urbica*) im Bereich der Voreifel. Die Vogelwelt 100:85–107.

RHEINWALD, G., AND H. GUTSCHER. 1969. Dispersion und Ortstreue der Mehlschwalbe (*Delichon urbica*). Die Vogelwelt 90:121–140.

RINGSBY, T. H., B.-E. SÆTHER, R. ALTWEGG, AND E. J. SOLBERG. 1999. Temporal and spatial variation in survival rates of a House Sparrow, *Passer domesticus*, metapopulation. Oikos 85:419–425.

RUBOLINI, D., A. GARDIAZABAL PASTOR, A. PILASTRO, AND F. SPINA. 2002. Ecological barriers shaping fuel stores in Barn Swallows *Hirundo rustica* following the central and western Mediterranean flyways. Journal of Avian Biology 33:15–22.

RUGE, K. 1974. Europäische Schwalbenkatastrophe im Oktober 1974: Bitte 1975 auf die Brutbestände achten! Die Vogelwarte 27: 299–300.

RUGE, K. 1975. Die Schwalben-Katastrophe 1974 im süddeutschen Raum. Ornithologische Mitteilungen 27:9–12.

SÆTHER, B.-E., S. ENGEN, AND E. MATTHYSEN. 2002. Demographic characteristics and population dynamical patterns of solitary birds. Science 295:2070–2073.

SÆTHER, B.-E., W. J. SUTHERLAND, AND S. ENGEN. 2004. Climate influences on avian population dynamics. Advances in Ecological Research 35:185–209.

SÆTHER, B.-E., J. TUFTO, S. ENGEN, K. JERSTAD, O. W. RØSTAD, AND J. E. SKÅTAN. 2000. Population dynamical consequences of climate change for a small temperate songbird. Science 287:854–856.

SILLETT, T. S., R. T. HOLMES, AND T. W. SHERRY. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

SZÉP, T. 1995. Survival rates of Hungarian Sand Martins and their relationship with Sahel rainfall. Journal of Applied Statistics 22: 891–904.

TURNER, A., AND C. ROSE. 1989. A Handbook to the Swallows and Martins of the World. Croom Helm, London.

VISBECK, M. H., J. W. HURRELL, L. POLVANI, AND H. M. CULLEN. 2001. The North Atlantic Oscillation: Past, present, and future. Proceedings of the National Academy of Sciences USA 98:12876–12877.

VON GUNTEN, K. 1963. Untersuchungen an einer Dorfgemeinschaft von Mehlschwalben, *Delichon urbica*. Der Ornithologische Beobachter 60:1–11.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–S139.

WILLIAMS, C. B. 1951. Changes in insect populations in the field in relation to preceding weather conditions. Proceedings of the Royal Society of London, Series B 138: 130–156.

WILLIAMS, C. B. 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. Philosophical Transactions of the Royal Society of London, Series B 244:331–378.

Associate Editor: R. L. Holberton