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Long-term decline in Common Swift *Apus apus* annual breeding success may be related to weather conditions

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We analyzed the effect of average monthly temperatures and precipitations (May–July) and of the North Atlantic Oscillation (NAO) on the breeding success of the Common Swift (*Apus apus*) in Třeboň (South Bohemia) from 1980–1997. Breeding success consistently declined during the observation period. We found that precipitations in May and temperatures in June were positively, and the previous year's May NAO was negatively associated with the percentage of nests that failed to produce any offspring. We found opposite associations between these climatic factors and the average production in nests that did produce offspring. Our results thus suggest that climate (change) may have negatively affected the output of the breeding population. Some of our associations between breeding performance and climate contradict previous observations. Hence, the association between climatic conditions and breeding success in Swift remains not fully explored, and additional long-term studies are needed to clarify the effects of abiotic factors on swift reproduction.

1. Introduction

The biology of synanthropic birds, especially swifts, has been intensively studied (e.g., Thomson *et al*. 1996). However, specific aspects of their biology are still poorly understood, primarily due to the difficulty of accessing the nest. Swifts, similar to other aerially feeding birds, are extremely sensitive to weather conditions (Martins & Wright 1993), as quantity and accessibility of their food is particularly dependent on climatic factors. Incubation can be prolonged during spells of poor weather (Cramp 1985). Although chicks are adapted for survival in harsh conditions (Cramp 1985), the length of the fledging period is strongly dependent on insect abundance, which in turn depends on weather (Hudec 1983).

Common Swifts may reduce the clutch size by ejecting 1–2 eggs from the nest in cold and rainy weather (Lack 1956) in order to increase the survival probability of the remaining eggs. Prolonged periods of incubation and breeding, or egg rejection during periods of harsh weather may – in theory – lead to larger offspring mortality and lower fecundity. Thus, climate is likely to be the main factor affecting swift reproduction (Cucco *et al*. 1992), with better breeding success in dry warm summers. However, most studies examining the influence of weather conditions on breeding success used only several years of data (Lack & Lack 1951, Martins & Wright 1993), which is making extrapolation difficult due to temporal variability in abiotic conditions. A notable exception is the 39-years study by Thomson *et al*. (1996). Therefore, additional long-term studies are necessary for us to understand the relationship between weather conditions and breeding success in swifts.

In the Czech Republic, the Alpine Swift, *Apus melba* (Hudec 1983) has a sporadic occurrence, and the Common Swift (*Apus apus*) is thus the only regularly occurring and breeding species in the order Apodiformes. In this paper, we use a seventeen-year data set on the Common Swift colony in Třeboň (South Bohemia) to analyze the effect of monthly weather conditions on annual breeding success, particularly on the number of offspring fledged. We discuss our results in respect to other studies.

2. Methods

2.1. Species studied

In the Czech Republic, the Common Swift lives mainly synantropically and is still considered a common bird. It is present from May through July when small insects are abundant prey items (Hudec 1983, Cramp 1985). Nests are placed in dark cavities, corners, on beams, cornices of buildings, in holes in walls, in rock slots and sporadically in tree cavities or in boxes for birds. Swifts usually breed in the same nest every year (Hudec 1983).

Their food consists almost exclusively of flying insects and airborne spiders of small to moderate size (Lack & Owen 1955, Cramp 1985). In Europe, over 500 prey species were recorded in swifts, mainly aphids, *Hymenoptera, Coleoptera* and *Diptera* (Glutz & Bauer 1980, Cramp 1985). Prey is caught in flight. Although swifts usually feed close to their nest, their foraging range may extend up to 7–8 km from the colony, dependent on weather (Cramp 1985).

Common Swifts breed once a year and the female lays 2–3 eggs (Lack & Lack 1951), with a second compensatory clutch, which is never laid in the same nest (Hudec 1983). Incubation takes about 20 days (Hudec 1983) and hatching success is approximately 58% (Lack & Lack 1951). The fledging period is variable, but averages about 6 weeks in poor weather (Hudec 1983, Cramp 1985).

Environmental changes evidently influence the behavior and population ecology of birds (Furness & Greenwood 1993). Factors like latitude (Wydham 1986), climate (Lack 1947), taxonomy and body size (Saether 1985) can influence length of the breeding season and clutch size.

2.2. Study area

Our data were collected in Třeboň (South Bohemia). This town is situated in a region with abundant woods and ponds, which may positively affect the availablity of prey items. Most of the data were collected from a single nesting colony of 30–40 pairs. The colony was situated on a building (10 m high), which is adjacent to a park and a suburb dominated by gardens. About 25 nests were accessible for inspection. This nesting site had existed before we started our observations, probably since 1965. The colony size gradually declined due to repair of the building and the colony was almost extirpated due to repair of the whole facade in 1998–1999. Of the original 40 pairs, only one pair nested here in 2000 and only two pairs with one successful breeding in 2001. Part of the data originates from three other nesting places with a small number of nesting pairs (up to five). These small colonies went extinct after the building's roof had been repaired. We observed the nests from 1980–1997, except in 1981.

2.3. Data collection

We measured breeding success as the number of large feathered young present in particular nests;

Table 1. Numbers of nests, in which 0, 1, 2, 3, or 4 offspring survived in individual years.

Year	Number of survivors				
	0	1	2	3	4
1980	0	2	8	11	1
1982	2	3	13	11	0
1983	1	2	14	10	0
1984	4	3	6	13	0
1985	3	3	8	10	0
1986	2	1	7	7	0
1987	4	4	9	5	0
1988	2	2	5	8	1
1989	0	3	4	12	0
1990	2	4	5	7	1
1991	2	4	11	4	0
1992	4	0	8	8	0
1993	2	0	8	7	0
1994	4	3	2	7	0
1995	6	1	3	6	0
1996	7	2	5	2	0
1997	5	4	0	6	0

we also monitored the percentage of nests where no offspring survived. Inspections took place every year in June and July.

Weather conditions were characterized by average monthly temperatures and rainfall during the breeding season: May, June and July. The weather data were collected at the weather station of the Institute of Botany, Academy of Sciences of the Czech Republic. This station is only 500 m away from the study sites. To link our paper to a large body of other climate related papers, we also used the North Atlantic Oscillation (NAO) data (Hurrell et al. 2003), which refer to swings in the atmospheric sea level pressure difference between the Arctic and the subtropical Atlantic. Over the middle and high latitudes of the Northern Hemisphere it is the most prominent and recurrent pattern of atmospheric variability.

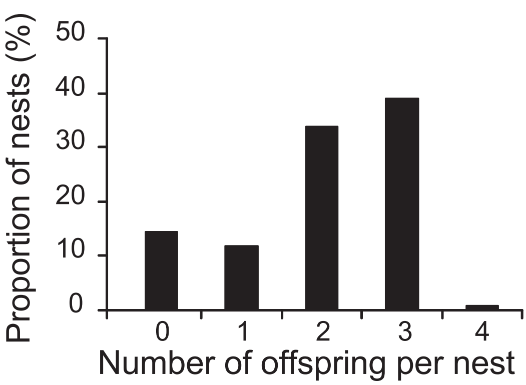

Fig. 1. Frequency distribution of the number of offspring in all nests (see also Table 1).

2.4. Statistical analyses

We used linear regression and correlation analysis to examine the relationship between weather conditions and breeding success. Bonferroni correction was applied where appropriate.

3. Results

3.1. Reproduction in the study population

A total of 344 nests were studied from 1980–1997 with 15–29 nests per year (Table 1). We found that usually two to three feathered young survived per breeding attempt, with four survivors being a rare exception (three out of 344 cases in our data). This finding is consistent with other studies (Hudec 1983, Cramp 1985, Thomson *et al*. 1996). Interestingly, these three cases of four fledglings were all observed in the same nest – most likely it was the same breeding pair. Most frequently, three offspring (134 cases) or two offspring (116 cases), bur rarely four offspring (3 cases) survived (Fig. 1). The percentage of nests where no offspring survived was increased during the study period (Fig. 2), and the average number of offspring per nest (excluding the failed nests) was negatively associated with the year of observation (Fig. 2). Although these two breeding characteristics were highly negatively correlated, it was clear that the breeding success consistently declined during the observation period.

3.2. Weather and reproduction

Precipitations in May and temperatures in June were significantly negatively associated with the breeding success, measured either as the percent-

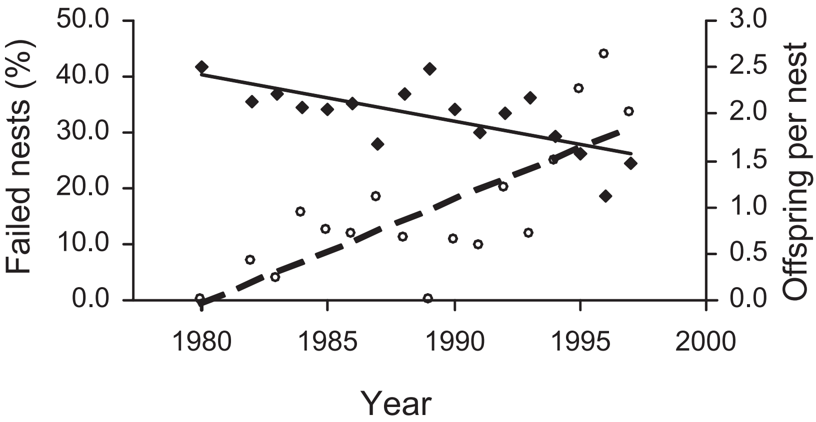

Fig. 2. Annual trends in the percentage of nests that failed, i.e. where no offspring survived (open dots and dotted line y = 1.9x – 3700, R^2 = 0.59) and in the average number of offspring per nest (filled diamonds and solid line y = –0.050x + 101, R^2 = 0.51).

age of nests, where at least some offspring survived, or as the average number of offspring per nest excluding unsuccessful nests (Table 2, Fig. 3). Associations with temperatures and precipitations in other months showed similar trends (positive association of the percentage of nests, where no offspring survived and negative association of the number of offspring per nest with temperatures and precipitations), but were not statistically significant (Table 2).

Table 2. Correlation coefficients of the relationships between climatic factors and characteristics of breeding success and between climatic factors and year. Significant values (P = 0.05) boldfaced.

	Temperature			Precipitations		
	May	June	July	May	June	July
Average number of offspring	–0.06	**–0.34**	–0.17	**–0.45**	–0.10	–0.01
% of unsuccessful breeding attempts	0.25	**0.37**	0.14	**0.48**	0.14	–0.07
Year	**0.36**	**0.40**	0.20	0.24	0.22	0.06

Table 3. Correlation coefficients of the relationships between NAO data for the year of observation (same year = only Jan.–July) and for the preceding year (preceding year) and characteristics of breeding success. Significant values (P = 0.05) boldfaced.

Breeding Success	Month											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Same year												
Total nests	–0.20	–0.19	–0.27	0.06	0.11	–0.33	0.29					
Av.offspr.	0.21	0.04	0.08	0.14	0.22	0.06	–0.13					
% unsucc.	–0.12	0.04	0.00	–0.21	–0.21	0.09	0.05					
Preceding year												
Total nests	0.11	0.06	–0.20	–0.23	0.09	–0.18	0.19	0.18	0.12	0.02	–0.01	0.19
Av.offspr.	–0.27	0.05	–0.34	0.11	**0.58**	–0.36	0.12	–0.14	0.04	–0.27	0.09	0.32
% unsucc.	0.22	–0.12	0.22	–0.10	**–0.48**	0.36	–0.13	0.18	–0.20	0.12	–0.11	–0.23

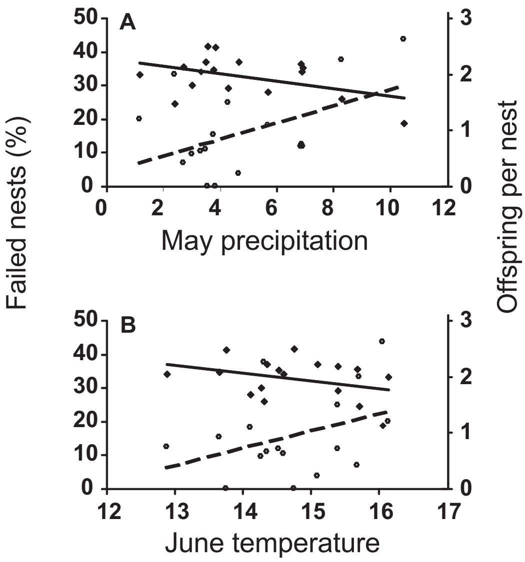

Fig. 3. Weather variables and the percentage of nests that failed (i.e. no offspring survived) indicated by open dots and dotted line, and of the average number of offspring per nest indicated with filled dots and solid line. Weather variables where in (A) May precipitation (nest failure = 5.2x – 61, R^2 = 0.14; offspring number = –0.14x + 3.96, R^2 = 0.12, and (B) June temperature nest failure = 2.50x + 4.0, R^2 = 0.23; offspring number = –0.07x + 2.3 R^2 = 0.20).

The R^2 values (captions of Figs. 2 and 3) demonstrated that the most important determinant of breeding success was year: breeding success declined over the years. Of the climatic factors, especially May precipitations and June temperature were important.

The only statistically significant correlations after Bonferroni correction were a positive correlation between the average number of offspring and NAO in the May month of the previous year, and a concordant negative correlation between the proportion of failed nests and NAO in May in the previous year (Table 3).

4. Discussion

Temperatures in June appear to be important for the breeding success of the Common swift, because June is a sensitive period, when hatching occurs and the adults start feeding the young. Martins and Wright (1993) hypothesize that swift breeding success is strongly influenced by brood reduction soon after hatching. Our results on a Czech Swift colony indicate that warmer June weather correlates with lowered reproductive output. However, Thomson *et al.* (1996) found a positive correlation, which became more pronounced in the last years of their study. These contrasting results make that a general conclusion on whether the association between the June temperatures and breeding success is positive or negative cannot be made. More long-term studies are needed to resolve this dilemma. Neither our observations, nor Thomson *et al.* (1996) provide any evidence that mean daily maximum temperatures in other months during the breeding season (May and July) would have a significant effect on annual reproductive success.

It was previously shown that chick mortality is negatively associated with ambient temperature and amount of sunshine and positively associated with rainfall and wind speed (Lack & Lack 1951, Hudec 1983, Cramp 1985, Martins & Wright 1993). This should – in theory – lower the breeding success (average number of offspring surviving until fledging) when climatic conditions are adverse. It is therefore interesting that several previous studies did not find any influence of rainfall on annual reproductive success (Cucco *et al.* 1992, Thomson *et al.* 1996). According to our data, precipitations in May were negatively correlated with breeding success. May is the period when swifts lay their eggs, and at this time they probably also reduce clutch size with extensive rainfall (Lack 1956, Hudec 1983).

The importance of climate in May is further supported by the correlations between breeding success and the NAO in the month May of the previous year. However, it remains unclear how the global climate (as indicated by the NAO index) in the preceding year may have affected the breeding success in the current year. One possible explanation may be that climate during the pre-breeding period affect the physical condition of swifts, which would affects breeding performance in the following year.

Contrary to Thomson *et al.* (1996), the breeding success in our colony declined during the observation period. In addition, both monthly temperatures and amount of rainfall have shown an increasing trend (Table 1). Thus cause and consequence remain unclear in our case: did increasing temperatures and amount of rainfall lead to reduced breeding success, or was the temporal decline of breeding success caused by something else, and just coincided with increasing temperatures and amount of rainfall? Because of the colony extinction, it has now become impossible to determine whether the temporal decline in breeding success of our population was a consequence of weather conditions leading to declining number of aerial insects, of human activities, of aging of the colony, or possibly of invasion of the parasitic fly *Crataerina pallida* into long existing nesting places.

The influence of climatic conditions on other swift species seems to be lower than that on the Common Swift: Lack and Arn (1947) found for the alpine swift that clutch sizes and numbers of fledged young were not related to the weather in May. In their 12-years study of Pallid Swift (*Apus pallidus*), Cucco *et al*. (1992) found that the clutch size was not related to rain or temperature. However, in contrast to the Common Swift, this species is able to postpone oviposition in case of bad weather. For example, Cucco *et al*. (1992) found that unfavorable weather conditions during May induced most females to postpone egg laying until June.

Our results indicate that weather conditions may influence the breeding success of the Common Swift, the most important factors being precipitations in May and temperatures in June. However, because other authors had presented contrasting results (Thomson *et al*. 1996), our findings highlight the necessity of performing more long-term studies. Although swifts are long-lived birds, the influence of weather conditions on their breeding success in particular years cannot be neglected. Because of the widespread population decline of this species, ornithologists should pay attention to its conservation.

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Sään vaikutus tervapääskyn pesimistulokseen

Tutkijat analysoivat touko–heinäkuun keskilämpötilojen ja sademäärien sekä NAO-indeksin vaikutusta tervapääskyn pesimistulokseen Třeboňissa, Etelä-Böömissä (Tsekin tasavalta) vuosina 1980–1997. Tutkimusjakson aikana tervapääskyjen pesimistulos heikkeni. Toukokuun sademäärä, ja kesäkuun lämpötila (yhteys positiivinen) sekä edellisvuoden toukokuun NAO-indeksi (yhteys negatiivinen) vaikuttivat pesien tuhoutumisalttiuteen (tuhoutuneiden pesien osuus). Tutkijoiden mukaan tulokset viittaavat siihen, että ilmasto (ja sen muutos) on heikentänyt tutkimuspopulaation lisääntymistulosta. Koska tulokset ovat osin ristiriitaisia aikaisempien havaintojen kanssa, kirjoittajat korostavat (uusien) pitkäaikaistutkimusten merkitystä selvitettäessä abioottisten tekijöiden, kuten ilmasto, vaikutusta tervapääskyn lisääntymiseen.

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