Behavioral and life history responses to extreme climatic conditions: Studies on a migratory songbird

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Abstract  Behavioral responses to environmental change are the mechanisms that allow for rapid phenotypic change preventing temporary or permanent damage and hence preventing reductions in fitness. Extreme climatic events are by definition rare, although they are predicted to increase in amplitude and frequency in the coming years. However, our current knowledge about behavioral responses to such extreme events is scarce. Here I analyze two examples of the effects of extreme weather events on behavior and life history: (1) A comparison of behavior and life history during extremely warm and extremely cold years relative to normal years; and (2) a comparison of behavior before and after the extremely early snowfall in fall 1974 when numerous birds died in the Alps during September-October. Behavioral and life history responses of barn swallows *Hirundo rustica* to extremely cold and extremely warm years were positively correlated, with particularly large effect sizes in cold years. Extreme mortality in barn swallows during fall migration 1974 in the Alps eliminated more than 40% of the breeding population across large areas in Central and Northern Europe, and this affected first arrival date, changes in timing and extent of reproduction and changes in degree of breeding sociality supposedly as a consequence of correlated responses to selection. Finally, I provide directions for research that will allow us to better understand behavior and life history changes in response to extreme climate change [Current Zoology 57 (3): 351–362, 2011].

Keywords  Barn swallow, Extreme climate, Hard selection, *Hirundo rustica*, Laying date, Second clutches, Sociality, Truncation selection

Behavior is the means by which animals through their actions directly respond to the environment. Because behavior allows animals directly to respond to novel environmental conditions, individuals that show an adequate behavioral response will have left more descendants than individuals over-reacting or not reacting to environmental change. Therefore, individuals that have survived rapid environmental changes constitute the proportion of the population that has responded appropriately (Price et al., 2003; Kinnison and Hairston, 2007; West-Eberhard, 2005). While this ought to be the case, it is difficult to pinpoint any single example showing that extreme environmental perturbations were overcome by display of any particular behavior.

Current climate change scenarios predict an increasing amplitude and frequency of extreme weather conditions, and current observations support this prediction (IPCC, 2007; Hurrell and Trenberth, 2010). However, if we consider observations based on reports by scientists that have themselves considerable experience with a particular biological model system, there are many unusual years (Weatherhead, 1986). This does not necessarily imply that biologists classify extreme events subjectively, but could just as well suggest that by using animals as bio-indicators a more sensitive and meaningful signal can be detected. However, because extreme weather events by definition are rare, the behavior that allows animals to survive such events has only rarely been described and even more rarely been analyzed with respect to their consequences for viability or fecundity. Thus, we know relatively little about behavior during extreme environmental events. Moreno and Møller (2011) reviewed the literature on the effects of extreme weather on reproductive failure, showing an average three-fold difference between normal and extreme years, while adult survival on average was reduced to one third of the normal level. Hence, there is scope for behavioral adjustment to such conditions having a significant impact on fitness components.

Most phenotypic traits show evidence of significant heritability (Roff, 1997; Lynch and Walsh, 1998). Given extensive evidence for heritability of phenotypes the

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relative scarcity of evidence for micro-evolutionary change is surprising (e.g., Hendry and Kinnison, 1999). For example, removal of small clutches from nests of the starling *Sturnus vulgaris* during a number of years eventually resulted in a micro-evolutionary response to artificial selection (Flux and Flux, 1982). A relatively uncommon approach is to rely on rare cases of extreme selection that should result in changes in phenotype following the selection episode, if the phenotypic traits had an additive genetic basis. If the change was a result of micro-evolution, we should expect the phenotypes in the generation after selection to differ from those before selection, but also that this shift in phenotypic distribution should be maintained for some time before oppositely directed selection eliminated the difference through convergence towards the pre-selection phenotype (assuming that the environment did not change). For example, Grant and Grant (2002) in their study of extreme selection due to El Niño in Galapagos finches *Geospiza fortis* and *G. scandens* showed a dramatic shift in phenotype due to selection, with the mean phenotype changing in the subsequent generation, followed by a return to the original phenotype as the selective regime changed. Likewise Brown and Brown (2000a) showed that mass mortality in the cliff swallow *Petrochelidon pyrrhonota* caused by an extreme cold spell in spring resulted in intense natural selection that changed the arrival schedule of this migratory bird in the subsequent year. This is indicative of a genetic basis for timing of migration. Migratory birds constitute an interesting model system for the study of the genetics of behavior because extensive laboratory experiments have shown evidence of timing, direction and amount of migratory behavior being under genetic control (Berthold and Querner, 1981; Berthold, 1999; Fiedler, 2005). Such genetic effects suggest that cases of intense natural selection on timing of migration should have consequences for the genetic composition of the population and hence for the distribution of phenotypes after selection compared to the situation before selection. Selection during extreme climatic events is likely to have important components of truncation selection that eliminates individuals relative to a threshold phenotype (Milkman, 1978; Crow and Kimura, 1979). The actual value of this phenotypic threshold will generally be more extreme during more extreme years, causing selection to be more efficient by reducing the number of selective deaths (Crow and Kimura, 1979).

A prime example of behavior during extreme weather is huddling behavior in several species of birds including swallows, martins and swifts. Huddling behavior is characterized by many conspecifics aggregating in a tiny space. This behavior is thus associated with loss of aggression and extreme reduction in individual distance. Huddling behavior has obvious survival benefits because it should reduce heat loss, as shown by data (Le Maho, 1977). During 40 years of fieldwork on barn swallows *Hirundo rustica* I have only once seen this behavior during an unusually cold period in spring 2002, showing that some kinds of behavior are rarely observed although their expression in unusual circumstances could still provide significant survival benefits. The literature on aerial insectivorous birds is full of references to this behavior during breeding, migration and winter (e.g., Fischer, 1869; Möller, 1994a; Brown and Brown, 1999, 2000a; Newton, 2007, 2008). A unique example was an early period of snowfall in Switzerland in September-October 1974 on the fall migration route of barn swallows and other migrants, resulting in more than one million barn swallows and house martins *Delichon urbica* settling in villages and towns (Glutz von Blotzheim and Bauer, 1985; Hannover, 1975; Ruge, 1974). Extreme huddling behavior allowed several hundred thousand individuals to be collected and transported across the Alps. If such behavior allows for short-term survival, this may suffice if the weather changes, as is often the case during snowfall created by passage of low pressure.

The objectives of this study were to investigate the behavior and life history of birds during extreme weather conditions. Although there is no generally accepted definition of ‘extreme’ weather, I compared the behavior of birds during the ‘most extreme’ and more ‘normal’ years. First, I compared breeding behavior and life history of barn swallows during the 10% most extreme years with all other years in a 40 years time series for the warmest and the coldest years, respectively. The basis for this analysis is that extreme climatic events differ qualitatively from normal events, and that this discontinuity is worthy of explicit study. Extreme climatic events only occur rarely, happening 5% or less of the time as judged from the expected distribution of the climate variable in question (e.g., http://www.emc.ncep.noaa.gov). Although this choice of 5% may seem somewhat arbitrary, this has not prevented climatologists from relating the frequency of such events to present global change and other factors. Here I used a 10% cut-off point to ensure that there were a reasonable number of events in the extreme category. Second, I compared the breeding behavior and life history of barn
swallows in 1974 with behavior in 1975 following the extreme mass mortality in the Alps in September-October 1974 described above. If mortality was non-random, I would expect behavior and life history in 1975 to differ from that in 1974. To this end I made two comparisons: First, 1974 vs. 1975, and, second, 1971–1974 vs. 1975–1978. The first comparison allows for a stringent test, while the second comparison allows for elimination of variation among years due to factors other than the mass mortality in fall 1974. More specifically, I predicted that (1) arrival date of the first individuals should be delayed and variance in arrival date reduced because early arriving males should have been selectively eliminated due to high frequency of second clutches and hence late departure, resulting in increased risk of mass mortality in the Alps, (2) laying date of the second clutch should be advanced because late laying individuals were selectively eliminated during mass mortality in the Alps, (3) the interval between clutches should be reduced because individuals with long intervals died disproportionately, (4) clutch size and annual fecundity should be reduced because individuals with smaller broods died less often during fall 1974, and, finally, that (5) social behavior should change as a correlated response to selection because colonial barn swallows reproduce later and more often have second clutches compared to solitarily breeding barn swallows, resulting in a reduction in the proportion of pairs breeding in large colonies.

1 Materials and Methods

1.1 Study sites

The data were collected at Kraghede (57°12'N, 10°00'E), Denmark, during May-September 1971–2010. The total study area covered ca. 15 km² between 1971 and 1976, but was progressively increased to ca. 30 km² between 1977 and 1986, 45 km² between 1987 and 1997 and 55 km² between 1998 and 2010 to compensate for population declines (Møller, 1994b). I collected all data personally, thereby preventing any heterogeneity in the data due to inter-observer variability.

Barn Swallows were captured at all farms within the study area. Mark-recapture estimates show that ca. 98% of all adults were captured during these events (Møller and Szép, 2002). Upon capture, each individual was measured and weighed using standard techniques since 1984 (Møller, 1994b). The analyses for the period 1984–2010 were based on 5237 captures of 3808 adult barn swallows.

1.2 Weather

I obtained information on mean temperature and precipitation for April–August 1971–2010 from Tylstrup that is located 7 km from the study area.

1.3 Arrival date

Arrival date was defined as the first capture date, recorded during bi-weekly capture sessions that began as the first males arrived. The precision of this estimate was assessed based on data from 1985–1990, when daily observations were made. Barn Swallows spend the night within their small breeding territory of a few square meters, and each male, if mated, sits next to his partner during the first couple of hours in the early morning and late in the evening (Møller, 1994b). During the six years adult barn swallows were watched daily for one hour from sunrise, and the identity of all color-banded individuals was recorded with binoculars.

The first observation of each individual in the season provided an estimate of the date of arrival. In addition, mist net captures as described above provided a second estimate of arrival date for each individual. The Pearson correlation coefficient between these two estimates of arrival date for each year separately ranged from 0.982 to 0.997, n = 10 to 46, P < 0.01, for males, and from 0.983 to 0.998, n = 5 to 44, P < 0.01, for females. A paired t-test revealed no significant differences between the two estimates for any year or sex (males: t < 1.23, P > 0.22; females: t < 0.28, P > 0.53). Thus my estimates based on first capture provide reliable estimates of arrival date for both males and females (see also Møller et al., 2003).

Protandry was defined as mean female arrival date minus mean male arrival date.

1.4 Reproduction

The nests of the adults were determined using color bands and individual patterns of color codes added to breast feathers of adults. I recorded laying date as the date of laying of the first egg, clutch size as the maximum number of eggs in the nest, and brood size as the number of fledglings. This was recorded for both first and second clutches, when a second clutch was found. Annual fecundity was the number of fledglings produced in first and second clutches combined (Møller, 1994b). The inter-clutch interval was the duration between the start of laying of the first clutch and the start of laying of the second clutch. The percentage of second broods was defined as the proportion of pairs initiating a second brood. Hatching success was brood size at hatching divided by clutch size, fledging success brood size at fledging divided by brood size at hatching and...
breeding success was brood size at fledging divided by clutch size.

Colony size was estimated as the total number of breeding pairs nesting in a farm. This definition makes sense because individuals only rarely visit neighboring farms as evidenced from fewer than 10 individuals out of more than 15,000 captures ever being recorded in another farm than the breeding farm.

The fraction of unmated males was defined at the proportion of males banded that never obtained a mate in a given breeding season.

1.5 Statistical analyses

I compared the coldest 10% of the last 40 years with the remaining 36 years and the warmest 10% of the last 40 years with the remaining 36 years, using an ANOVA design. Analyses using one, two or three extreme years, rather than four as in the present case, provided qualitatively similar results (results not shown). These analyses were based on more than 5,000 pairs, using the annual estimates or the annual means as observations.

I estimated effect sizes using Rosenthal’s (1991) conversion of F-statistics into Pearson’s product-moment correlations: $r = \sqrt{(F / (F + \text{denominator df})}$. Effect sizes were subsequently transformed using Fisher’s z-transformation before statistical analyses.

I used two different approaches to assess change in phenotype as a consequence of intense mortality in fall 1974: (1) comparison of phenotypes in 1974 and 1975; and (2) comparison of phenotype in 1971–1974 with that in 1975–1978. First, I compared estimates of arrival date, timing of reproduction, reproductive rates and breeding sociality during the breeding season 1974 before the selection event with estimates for the breeding population in 1975. Typically only 30% of adults survive annually, and because this percentage is likely to have been reduced by 40% to only 18%, as the observed reduction in population size between 1974 and 1975 was 40%. Among the breeding birds in 1975, 18% of the breeding pairs in 1974 (in total 18 individuals) must have survived, implying that 70% of all breeding birds in 1975 were yearling first time breeders that survived the selection episode. Second, I compared the phenotype in 1971–1974 with that in 1975–1978, assuming that a micro-evolutionary change between 1974 and 1975 would have been maintained for some time before being reversed by oppositely directed selection (assuming that the environment had not changed). I deliberately used two periods, each lasting four years to have a balanced design. Both periods were kept relatively short because any effects of micro-evolution would only be maintained for a short time, as the fitness advantages of early breeding, two clutches and a long inter-clutch interval would all tend to eliminate any difference between periods.

I square root arcsine-transformed the proportion of barn swallows with a second clutch and the proportion breeding in large colonies.

2 Results

2.1 Behavior during extreme and normal years

2.1.1 General effects on weather

The categorization of years into those with cold and warm summers was successful in the sense that mean temperature during April-August in cold years was 0.5°C lower than in normal years and 1.8°C higher in warm than in normal years (Table 1). Both cold and warm years tended to have more rainfall than normal years (Table 1), implying that the effects analyzed here may not only derive from temperature, but could be caused by other weather variables such as precipitation.

2.1.2 Effects of extreme weather on behavior and life history

The correlations between the variables listed in Table 1 were generally small with the exception of hatching, fledging and breeding success that were strongly positively correlated (Pearson $r > 0.5$), as were arrival dates for males and females, arrival dates with laying dates, clutch size and reproductive success, and the frequency of second broods with total reproductive success. These relationships should be considered when interpreting the subsequent results.

Several behavioral and life history variables differed significantly between years with extreme weather and years with normal weather (Table 1). In very warm years spring arrival date was advanced in both sexes, but disproportionately in males (Table 1). This led to a significant difference in proprandry, with males arriving disproportionately early compared to females in warm than in normal years (Table 1). In contrast, none of the tests for cold years showed a significant effect. Male body mass upon arrival was reduced significantly in the coldest years, while that was not the case in females (Table 1).

The effect of warm years on arrival also advanced laying date of the first clutch (Table 1), while there was no significant effect of cold years (Table 1). This effect on timing had disappeared by laying of the second clutch. Among reproductive variables only clutch size of the second clutch differed with respect to weather extremes, with clutch size being severely depressed in the warmest years (Table 1).
A larger fraction of barn swallows bred solitarily in the coldest years, and a larger fraction in large colonies with more than 15 pairs in the warmest years, when compared with normal years (Table 1).

Finally, the fraction of males that were unable to find a mate was significantly lower in the warmest years compared to normal years (Table 1).

Extreme events may be analyzed as a separate category or as a non-linear response. However, when I re-did all analyses by analyzing the linear and the quadratic components of temperature as predictor variables, none of the quadratic terms reached the level of significance (results not shown). Therefore, I can conclude that extreme events can be considered a qualitatively different category that cannot readily be analyzed in a continuous framework.

2.1.3 Effect sizes  
I estimated effect sizes for 23 characters with respect to very cold and very warm years. The unsigned effect size for the coldest years was 0.155 (SE = 0.023), n = 23, differing significantly from zero (t = 6.77, df = 22, P < 0.0001), while it was 0.058 (0.006), n = 23 for the warmest years, also differing significantly from zero (t = 9.52, df = 22, P < 0.0001). Effect size for the warmest years was significantly smaller than for the coldest years (paired t-test, t = 5.68, df = 22, P < 0.0001). The two series of effect sizes were strongly positively correlated (Pearson r = 0.96, t = 16.96, df = 21, P < 0.001).

2.2 Behavior and life history before and after an extreme weather event

2.2.1 Weather and response variables  
Barn swallows rely on flying insects as food, and they are therefore strongly affected by weather conditions. Therefore, I tested explicitly whether the response variables recorded before and after the extreme selection event in 1974 (Tables 2, 3) could be explained by weather conditions (mean temperature and rainfall during April-August), in a statistical models that also included log10-transformed population size as a predictor variable. Among the nine variables four were significantly related to temperature (first arrival date, male and female arrival date and first laying date: $F > 5.33$, $df = 1, 36$, $P < 0.027$) and two were related to rainfall (female arrival date, first laying date: $F > 4.64$, $df = 1, 36$, $P < 0.04$). Therefore, I included these predictor variables in the analyses in Table 3.

### Table 2  Phenotype of barn swallows during the breeding seasons 1974 and 1975

| Variable                      | Mean (SD) 1974 | Mean (SD) 1975 | F or $\chi^2$ | P       |
|-------------------------------|---------------|---------------|---------------|---------|
| Male arrival date             | 16.88 (1.30)  | 15.87 (1.05)  | 0.22          | 0.77    |
| Female arrival date           | 18.46 (1.27)  | 19.37 (1.53)  | −0.45         | 0.67    |
| Laying date first clutch      | 38.4 (1.8)    | 36.0 (0.9)    | 0.79          | 0.43    |
| Laying date second clutch     | 79.1 (5.3)    | 73.8 (5.2)    | 18.49         | < 0.001 |
| Inter-clutch interval         | 47.3 (5.7)    | 43.2 (5.8)    | 9.36          | < 0.01  |
| Clutch size first clutch      | 5.26 (0.42)   | 4.95 (0.41)   | 10.24         | < 0.001 |
| Second clutches (%)           | 70.0          | 53.6          | 2.23          | 0.14    |
| No. fledglings                | 6.56 (2.51)   | 5.34 (2.48)   | 4.45          | < 0.05  |
| Pairs in large colonies (%)   | 72.0          | 0.0           | 50.81         | < 0.0001|
| N individuals or pairs        | 50            | 30            |               |         |

### Table 3  Phenotype of barn swallows during the breeding seasons 1971–1974 and 1975–1978

| Variable                      | Mean (SE) 1971–1974 | Mean (SE) 1975–1978 | F or $\chi^2$ | P       |
|-------------------------------|---------------------|---------------------|---------------|---------|
| First arrival date            | −7.50 (1.04)        | −0.25 (0.95)        | 26.56         | 0.0021  |
| Male arrival date             | 15.75 (0.79)        | 16.51 (0.79)        | 0.48          | 0.52    |
| Female arrival date           | 18.86 (0.60)        | 18.83 (0.60)        | 0.00          | 0.97    |
| Laying date first clutch      | 35.8 (1.4)          | 38.0 (1.4)          | 1.30          | 0.30    |
| Laying date second clutch     | 75.4 (1.6)          | 78.1 (1.6)          | 1.47          | 0.27    |
| Inter-clutch interval         | 44.9 (1.1)          | 46.3 (1.1)          | 0.79          | 0.41    |
| Clutch size first clutch      | 4.80 (0.12)         | 4.74 (0.12)         | 0.13          | 0.73    |
| Second clutches (%)           | 74.7 (4.4)          | 51.6 (4.4)          | 10.47         | 0.018   |
| No. fledglings                | 6.90 (0.13)         | 5.47 (0.13)         | 57.85         | 0.0003  |
| Pairs in large colonies (%)   | 42.5 (15.7)         | 45.3 (15.7)         | 0.02          | 0.90    |
Weather in 1974 and 1975 was very similar with mean temperatures during April–August of 11.9 and 12.7°C and total rainfall during April–August of 174 mm and 199 mm.

2.2.2 Intensity of selection  The size of the breeding population in the study area declined by 40% from 1974 to 1975 (50 pairs vs. 30 pairs). An estimate of the relative magnitude of mortality during fall 1974 can be obtained by comparing the number of recoveries of banded birds (either dead or released after capture) with the numbers recorded during all other years 1971–1973 and 1975–2008. A total of 41 recoveries in 38 years if distributed evenly would provide 1.08 recoveries per year. However, a total of 37 were recorded in fall 1974 (Møller, 1978), which is 34 times greater than expected. This implies that mortality during fall 1974 was 34 times greater than normal.

2.2.3 Timing of migration  Mean male and female arrival dates in 1975 did not differ significantly from the values in 1974 (Table 2). The arrival date of the first individual was significantly later in 1975–1978 than in 1971–1974 (Fig. 1A; Table 3), and this effect was also significant after inclusion of temperature and rainfall as confounding variables ($F_{1,6} = 10.00, P = 0.034$). There was no significant difference between mean arrival dates in 1971–1974 and 1975–1978 (Table 3).

The variance in male arrival date in 1975 (33.19) was significantly smaller than the variance in 1974 (84.17; $F_{49,29} = 2.53, P = 0.004$). In contrast, that was not the case for variance for females (1974: 81.12, 1975: 69.96; $F_{49,29} = 1.16, P = 0.35$).

2.2.4 Timing and extent of reproduction

While mean laying date for the first clutch in 1974 did not differ significantly from the value in 1975, there was a highly significant difference for the second clutch that was much earlier in 1975 compared to 1974 (Fig. 1B; Table 2). This was due to a significant shortening of the interval between clutches by almost 10% (Table 2). These differences disappeared when comparing mean values for 1971–1974 and 1975–1978 (Fig. 1C; Table 3).

Mean size of the first clutch in 1974 was significantly larger than the mean value in 1975 (Table 2). This difference disappeared when comparing mean values for 1971–1974 with mean values for 1975–1978 (Table 3).

The proportion of barn swallows initiating a second clutch was lower in 1975 than in 1974, albeit not significantly so (Table 2). The mean value for the period 1971–1974 was significantly larger than for 1975–1978, with the difference being more than 30% (Fig. 1D; Table 3). This difference was also significant after inclusion of temperature and rainfall ($F_{1,6} = 29.33, P = 0.012$). The mean value in 1979 of 72.7% was similar to the value of 70% in 1974.

The total number of fledglings produced per year was significantly lower in 1975 than in 1974 (Table 2). This effect was independent of temperature and rainfall ($F_{1,6} = 25.28, P = 0.015$). This difference was maintained for several years as shown by the mean for 1971–1974 being 20% larger than the mean for 1975–1978 (Fig. 1E; Table 3). It was not until 1979 that the mean number of fledglings was larger than the values from 1971–1974.

When first clutches were large, there was a reduction in total number of fledglings ($F_{1,5} = 5.69, P = 0.048$, slope ($SE = -0.78$ (0.33), independent of the effect of mass mortality ($F_{1,5} = 107.27, P < 0.0001$).

2.2.5 Breeding sociality  While 72% of pairs bred in colonies with more than 15 pairs in 1974, none did so in 1975, which is a highly significant difference (Table 2). This was not due to a larger fraction of barn swallows breeding in large colonies in years with large population size (square-root arcsine-transformed proportion of pairs in colonies with more than 15 pairs in relation to $\log_{10}$ transformed population size: $F_{138} = 0.16, r^2 = 0.004, P = 0.69$). However, this difference disappeared over the years (Fig. 1F; Table 3).

3 Discussion

I adopted two different approaches for investigating the effects of extreme weather conditions on behavior and life history, comparing extreme and normal years, and comparing behavior and life history before and after a unique, but extreme weather event. In the first series of analyses, the effect of extreme weather similarly affected different kinds of behavior and life history during cold and warm years, as compared to normal years. Several kinds of behavior and life history were particularly affected by warm weather, with spring arrival and laying being advanced, clutch size reduced, degree of sociality increased and the frequency of unmated males reduced. While it might not be surprising that there are such effect, I am unaware of any other study reporting the responses for a diversity of traits to extreme weather conditions. In the second series of analyses, barn swallows experienced an extreme selection episode in the Alps in fall 1974, reducing breeding populations by 20%–50% across large parts of Germany and Denmark the following year. This selection event caused a dramatic shift in phenotype towards earlier first arrivals, a reduction in the variance in arrival date in males,
smaller first clutches, earlier second clutches and hence short intervals between first and second clutches, fewer second clutches and hence smaller seasonal reproductive success, and smaller colonies. These effects tended to disappear after a maximum of five years, as the phenotype reverted to that before the selection event.
The analyses and responses to extreme mass mortality in fall 1974 rest on the assumption that heritability and selection results in a response to selection as reflected by the breeders’ equation. Many of the traits analyzed here such as sociality, arrival date, morphology and nest size show significant heritability as reflected by parent-offspring resemblance in the order of 0.30 to 0.70 (Møller, 1994b, 2001, 2002, 2006 and unpublished), and these heritabilities have been confirmed in animal model analyses. If we analyze laying date for the second clutch (Table 2), the response (R) to selection in date between 1974 and 1975 is 5.3 days, which equals 0.53 standard deviation units. Heritability \( h^2 \) of laying date is 0.72. Because the intensity of selection \( S \) is \( R / h^2 \), we obtain \( S = 0.52 / 0.72 = 0.72 \). Given that only 18% of adults survived between 1974 and 1975, a selection coefficient of 0.72 is not impossible. We can make a similar analysis of clutch size for which \( R = 0.31, h^2 = 0.32 \) and \( S = 0.31 / 0.32 = 0.97 \). Again, this magnitude of intensity of selection is possible.

### 3.1 Behavior and life history in extreme and normal years

Behavior and life history differed between years with extreme weather and years with normal weather. Spring arrival date was advanced in warm springs, especially in males. Because males arrive earlier than females, males should suffer more from such effects than females as reflected by the higher degree of protandry in warmer years. Male body mass upon arrival was reduced in the coldest years as compared to normal years, while that was not the case in females. Again, this is as expected because males migrate and arrive earlier than females, and this should be more costly for males in particularly cold years. The effect of warm years on arrival had carry-over effects on laying date of the first clutch, while there was no similar effect of cold years. This effect on timing disappeared for laying date of the second clutch, suggesting that barn swallows with delayed laying of their first clutch had caught up by the time of their second clutch, suggesting that the delay was temporary rather than permanent. Interestingly, size of the first clutch was not significantly affected by extreme weather, while the size of the second clutch was. During very warm summers conditions for reproduction decline due to decreasing abundance of flying insects, and this seems to depress clutch size considerably.

Breeding sociality has an additive genetic basis (Brown and Brown, 2000b), and that is also the case in the barn swallow (Møller, 2002). A larger fraction of barn swallows bred solitarily in the coldest years, while a larger fraction bred in large colonies with more than 15 pairs in the warmest years, when compared with control years. This may suggest that sociality is a balanced polymorphism with solitary breeding being favored in cold years and large colonies in warm years. I could exclude the possibility that the fraction of birds breeding in large colonies was a simple consequence of population size because the two variables were not correlated.

Because the sexes differ in behavior, extreme weather events will differ in impact on the two sexes and ultimately result in biased sex ratios. Male-biased sex ratios can affect intensity of sexual competition, and an excess of unmated males causes an increase in the frequency of infanticide (Møller, 2004). Barn swallows typically have a slight excess of males (Møller, 1994b).

Here, I have shown that the fraction of unmated males was only 2.9% in the warmest years, but 8.2% in normal years. This should predict a decreasing trend in the frequency of infanticide, as already observed (Møller, 2004).

Effect sizes for the effects of extreme climatic events on behavior were considerably larger in cold than in warm years. This difference appeared despite the fact that the difference in temperature in very cold years was much smaller than on very warm years. These results suggest that cold weather has a disproportionately large effect on behavior. The two series of effect sizes were strongly positively correlated implying that the different kinds of characters responded in a similar way to very cold and very warm events.

### 3.2 Comparing behavior and life history before and after an extreme event

Comparison of phenotypes before and after extreme events allows for estimation of selection, but also for estimation of micro-evolutionary change, if changes in phenotype persist over time. The breeding sociality was a simple consequence of population size because the two variables were not correlated.
Mass mortality event occurred more than 1000 km south of the Danish breeding area, which implies that other changes in environmental conditions in the breeding or the migration areas are unlikely to have been the cause of selection. At least, weather conditions in the breeding area in 1974 and 1975 were benign and quite similar to conditions in 1971–1973 and 1976–1978. Annual adult survival rate of barn swallows from the study population is around 30% (Møller and Szép, 2002, although this survival rate is likely to have been reduced to only 18% during 1974–1975. Thus 70% of the population in 1975 consisted of yearlings, causing the comparison between the phenotype of breeding birds in 1974 with birds in 1975 to be largely statistically independent.

The second approach to investigate the consequences of mass mortality on phenotype was based on comparison of mean phenotypes in 1971–1974 with those in 1975–1978. This analysis was based on the assumption that changes in phenotype would last several years before being reversed by oppositely directed selection, as expected if the environment has not changed permanently. Indeed, only two phenotypic traits (proportion of pairs with a second clutch and mean number of fledglings per pair) maintained their low post-1975 levels until 1978, but even these were back to pre-1975 levels in 1979. These reversals to the phenotype present before the selection episode are as expected if the current phenotype is close to the optimum, and similar reversals to the phenotype prior to the selective event as opposed to permanent micro-evolutionary change have also been reported in other studies that investigated the effects of extreme weather-induced selection (Brown and Brown, 2000a; Grant and Grant, 2002).

Many phenotypic traits including life history characters show effects of density-dependence, because individuals reproduce later and at lower rates when population size is large (e.g., Roff, 1991). I did not enter population size in any of the statistical models because density-dependence is weak or absent for life history traits in the barn swallow (Møller, 1989). However, if there were any effects of density-dependence, this would make the observed relationships conservative.

Analyses of spring arrival, timing and extent of reproduction and degree of breeding sociality showed evidence of change in response to mass mortality during fall 1974 (Tables 2, 3). This provides indirect evidence suggesting that not only migratory behavior is affected by such mass mortality events, as already shown (Brown and Brown, 2000a; Gatter, 2000), but also phenotypic characters linked to migration, presumably through genetic correlations. Spring arrival of migratory birds in general (e.g., Lehikoinen and Sparks, 2010; Rubolini et al., 2007) and barn swallows in particular (Møller, 2008a) has advanced during recent decades in association with global warming. Hence, the null hypothesis for first arrival date during 1971–1978 would have been an advance rather than the delay that was actually observed during 1975–1978.

Mass mortality in the Alps in fall 1974 affected millions of barn swallows and house martins and had an enormous geographic scale as shown by decreasing breeding populations during summer 1975 (Bruderer and Muff, 1979; Meier and Mette, 1976; Møller, 1980; Ruge, 1974; Stokke et al., 2005). Similar events occurred in 1933 and several times during the 1800’s with barn swallows and house martins settling in villages and towns (Glutz von Blotzheim and Bauer, 1985). Breeding populations censused during 1974 and 1975 declined by 14%–51% across an area stretching more than 1100 km from Southern Germany to Northern Denmark. This implies that any local effects of this mass mortality event are unlikely to be swamped by gene flow from nearby, unaffected populations.

In conclusion, a severe mass mortality event in barn swallows that reduced population size by 20%–40% across a large geographical range in Europe had significant impact on the composition of breeding populations. Micro-evolutionary changes towards earlier arrival, smaller first clutches, earlier and fewer second clutches, and hence shorter intervals between clutches and smaller overall reproductive success, and smaller colonies were reversed after only a couple of years, with the frequency of second clutches and total production of fledglings per pair still being maintained at low levels in 1978 four years after the extreme mortality episode.

### 3.3 Prospects for future studies

I have analyzed long-term data on behavior, reproduction and survival for effects of extreme weather, using two different approaches. Such analyses rely on availability of data both before and after the extreme weather incident, and, thus, such analyses can only be made when data are collected continuously during a long-term research program. My analyses were restricted to a limited number of variables that may not necessarily constitute the best possible choice, mainly because the study was not designed for this purpose. However, we need to prepare for future extreme climatic events by building a battery of tests to be applied both before and after such events. Indeed, for the last five years I have collected information on such an ex-
tensive list of traits, waiting for the next extreme weather event to appear.

There is phenotypic variation in most traits, and that may also be the case for the ability to sustain and resist extreme weather conditions. One possibility is that this ability is a balanced polymorphism with one kind of individuals doing best under average conditions and another during extreme conditions. Therefore, we need to identify the phenotypes (and genotypes) most susceptible to extreme climatic events. This is only possible in situations where individuals can be identified from their unique numbered bands, and where individuals are followed throughout their lives. Møller (2008b) showed that long-tailed male barn swallows responded more strongly to climate change than short-tailed males, suggesting that condition-dependent secondary sexual characters may provide reliable information about ability to adapt to environmental change.

The analysis of the impact of the extreme snowfall event in fall 1974 clearly showed that the effect of mortality on the distribution of phenotypes after selection was maintained for several years, with the frequency of second clutches not returning to the pre-selection level until five years later in 1979. Given that annual adult survival rate in this barn swallow population is only around 30% (Møller and Szép, 2002), with an estimated adult survival rate of only 18% during 1974–1975, most individuals breeding in 1975 were yearlings. Therefore, the time to return to the phenotype before the extreme snowfall in 1974 reflects selection towards the pre-selection situation and heritability of the traits concerned. Thus, it is important in case of extreme weather events to monitor phenotypes for several years following the event, as done here and in previous studies (Brown and Brown, 2000a; Grant and Grant, 2002; Gatter, 2000).

Furthermore, if there is a genetic basis for behavior associated with extreme weather events, as suggested by the indirect evidence provided here, we need to take blood samples to allow for identification of genes involved in behavioral responses and for investigating the genetic architecture of such characters.

Finally, if extreme events happen more frequently in the future, selection may not be able to turn back the clock to pre-event phenotypes. A permanent evolutionary shift in phenotype could then be in the workings.

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