

Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird

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Abstract. Recent climate change has affected spatial and temporal patterns of temperature and precipitation, but also wind speed. Wind affects the abundance and the distribution of flying insects and can therefore influence the abundance of food for insectivores including insectivorous birds. I tested for temporal trends in wind speed, assessed the effect of wind speed on the abundance of flying insects, and tested for effects of wind speed on reproduction and adult survival rate, using long-term data on the barn swallow *Hirundo rustica* from 1971–2011. Wind speed varied largely independently among the months April–August, with a decreasing trend during 1971–2011 for July only. The abundance of flying insects decreased strongly with increasing wind speed during summer. Decreasing wind speed during July coincided with the pre-laying period of the second brood of the barn swallow, and years with stronger wind in July had lower abundance of food before laying during 1997–2011 and lower breeding success. Adult barn swallows had lower body mass in years with windy summers, and adult annual survival rate to the next year decreased both when wind speed increased and when body mass was reduced. These findings suggest that wind plays an important role in the ecology of insectivorous birds as shown by relationships with reproductive success and survival.

Key words: barn swallow; body mass; breeding success; food availability; *Hirundo rustica*; insects; survival rate.

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INTRODUCTION

Recent climate change has many facets that have influenced the phenology, distribution and abundance of numerous organisms (IPCC 2007). Since initial studies in the 1980s (Berthold 1991), studies of climate change effects on living beings have increased rapidly in recent years (e.g., Parmesan and Yohe 2003, Root et al. 2003, Møller et al. 2010). The effects of climate change may act directly through effects on plants and animals (e.g., Schwartz et al. 2006), or indirectly through effects on timing, abundance and distribution of food (e.g., Thackeray et al. 2010). Many studies

have investigated changes in the phenology and peaks in food abundance and their effects on consumers (Both 2010, Dunn et al. 2011), and responses at higher trophic levels are generally weaker than at lower levels (e.g., Thackeray et al. 2010). Most studies to date have investigated effects of change in temperature on biological phenomena for the obvious reason that temperature-dependent effects are deemed important for most biological processes. Several studies have indicated that such climate change effects on individuals also have higher level consequences by influencing population sizes and population trends negatively (Both et al. 2006,

2010, Møller et al. 2008, Saino et al. 2011).

Few studies have investigated other components of climate change than changes in mean temperature (Møller et al. 2010). These studies include studies of the effects of precipitation (e.g., Møller 2011), wind (e.g., Weimerskirch et al. 2012) and storms (e.g., Michener et al. 1997, Laurance and Curran 2008). A few studies has also started to investigate the effects of extreme weather conditions rather than mean conditions on animals (e.g., Jiguet et al. 2003, Møller 2011, Moreno and Møller 2011, Dolenc et al. 2011).

Wind speed and direction and the frequency of storms have changed in recent years (e.g., Trenberth 2007, Hurrell and Trenberth 2010, Weimerskirch et al. 2012). Wind is an important meteorological parameter through its effects on the chill factor and hence homeothermy, locomotion and ease of locating and capturing prey. Wind can strongly affect the availability of food as shown for foraging sandwich terns *Sterna sandvicensis* that have difficulty to locate fish when the sea surface is perturbed (Dunn 1975). Likewise, insectivorous birds have difficulty to catch insects during windy conditions when sites with available food are reduced to leeward areas close to trees and bushes (Turner 1980). Strong winds can also increase the cost of flight, and depending on prevailing wind directions wind speed can affect the net energy gain for foraging adults, with consequences for reproductive success (Weimerskirch et al. 2012).

The objectives of this study were to test for (1) temporal trends in wind speed. Subsequently I (2) assessed the effect of wind on the abundance of flying insects. Finally, I (3) tested for effects of wind speed on reproduction and adult survival rate of an insectivorous bird species, the barn swallow *Hirundo rustica*. I relied on a long-term study of insectivorous barn swallows during 1971–2011, with extensive information on reproduction for the entire study period, adult survival during 1984–2011 and food availability during 1997–2011.

Barn swallows live on flying insects whose abundance is determined by agricultural land use and weather (Turner 1980, 2006, Møller 2001). Climate effects on barn swallows appear as a consequence of responses of individuals to local weather condition. Even at the scale of hundreds of meters or a few kilometers individuals can differ

dramatically in timing of breeding, but also in response to changes in climatic conditions (Møller 2008). Because individuals in superior condition breed at sites where breeding date has advanced the most, such sites produce a disproportionate contribution to the next generation (Møller 2008). Møller (2002) showed that the North Atlantic Oscillation (NAO) through its effects on local climate affected the relative importance of second over first clutches of barn swallows. The size of first clutches increased with increasing NAO, and offspring produced in years with high NAO were of better quality in first than in second clutches. This resulted in greater immigration thereby increasing the size of the barn swallow population. Advancing spring is associated with a higher number of degree-days with consequences for emergence and abundance of organisms including flying insects (Ambrosini et al. 2012). The number of degree-days increased over time suggesting that barn swallows become increasingly decoupled in their breeding phenology relative to spring events. Indeed the size of second clutches decreased with number of degree days, indicating that barn swallows are now experiencing a delay in reproduction relative to spring phenology with negative consequences for annual reproductive output (Ambrosini et al. 2012).

However, conditions in Africa outside the breeding season may have equally large or even larger effects on migratory birds. European barn swallows winter in Sub-Saharan Africa with a tendency to winter further north in recent years (Ambrosini et al. 2011). Conditions during winter affect timing of spring migration, laying date, reproduction, morphology and many other characteristics of barn swallows (Saino et al. 2004a, b, Møller and Szép 2005). Møller et al. (2011) showed for barn swallows wintering in South Africa that although arrival in the African winter quarters advanced in recent years as a consequence of earlier breeding, this did not translate into earlier spring migration because the annual molt was delayed. Thus migration and molt may act as a constraint on response to climate change.

MATERIAL AND METHODS

Study area

This study was conducted at Kraghede (57°12' N, 10°00' E), Denmark, during 1971–2011, as part

of a long-term study of barn swallows (Møller 1994). This study site originally consisted of 12 km², but was subsequently expanded to 45 km² in 1987 to account for decreasing populations of barn swallows. Barn swallows breed inside barns and other buildings in an open agricultural landscape with scattered plantations, hedgerows and trees. Most crops are grain followed by maize and grass.

Meteorological information

I obtained monthly estimates of temperature (°C), precipitation (mm) and wind speed (m/sec) for April–August for Aalborg, Denmark, provided by the Danish Meteorological Institute, which recorded daily wind speed and averaged these to monthly mean estimates that were reported in public weather bulletins. This meteorological station is situated 25 km south of the study area. Wind speed was measured at a height of 2.0 m, which is well within the altitude range of foraging by barn swallows (Turner 1980, 2006). When sampling insects I recorded wind speed on the Beaufort scale because no wind speed monitor was available.

Sampling insects

I sampled insects on the same 1.2 km transect with a car on a road that passes through the study area between mid May and mid August 1997–2011. The number of samples per day ranged from none to three. A car was driven at constant speed of 60 km/h, and the number of insects killed on the front window was counted at the end of each transect. The window was perfectly cleaned at the start. Following recording of insects, I noted exact time of day, temperature, cloud cover (estimated as the proportion of the sky that is covered by clouds, to the nearest unit of one eighth) and wind speed (on the Beaufort scale). The surface of the front window was 1.5 m² with little variation among models (1.4–1.6 m²).

I tested whether the number of insects sampled on the 1.2 km transects was repeatable among sampling events made multiple times on the same day by calculating the intra-class correlation (Falconer and Mackay 1996). The abundance of flying insects was significantly repeatable among transects on the same day ($F = 6.58$, $df = 76, 676$, $r^2 = 0.43$, $P < 0.0001$, $R = 0.36$ (SE = 0.02)).

In addition, I used an insect sweep net to sample insects at a height of 1.5 m within a distance of 100 m from breeding colonies during the nestling period 15–30 June 1985–2011 (see Møller 1987 for further details). Mean insect abundance per sweep for each of the years 1997–2011 was strongly positively correlated with insect abundance recorded with car transects during 15–30 June 1997–2011 ($F = 71.01$, $df = 1, 14$, $r^2 = 0.84$, $P < 0.0001$, slope (SE) = 0.221 (0.026)).

Finally, I made a cross validation of the reliability of insect samples as an index of food abundance for barn swallows by recording feeding rates during one hour observation periods at least twice for 126 nests during May–August 1997–1998 after controlling for the potentially confounding effects of brood size, age of nestlings, time of day, time of day squared, air temperature, wind speed and cloud cover. Feeding rates were recorded on the same dates as insect samples were collected using car transects. I used in a GLM log₁₀-transformed feeding rates as the response variable and nest identity, the abundance of insects, brood size, age of nestlings, time of day, time of day squared, air temperature, wind speed and cloud cover as predictor variables. The partial effect of food abundance as sampled by car transects on feeding rate after accounting for the potentially confounding variables listed above was positive and statistically significant ($F = 11.56$, $df = 1, 119$, $r^2 = 0.09$, $P < 0.0001$).

Recording reproductive biology of the barn swallow

All nests were checked at least weekly. Laying date was estimated as the date when the first egg was laid. This was based on clutches in the process of being laid where laying date was the number of days after May 1 (where May 1 was set equal to 1) minus the number of eggs minus 1 because an egg in a clutch in the process of being laid was laid on the focal date. For eggs in the process of hatching laying date was estimated as the number of days after May 1 minus clutch size (to account for the fact than one egg is laid per day) minus 1 (because the last egg is assumed to be laid on the focal date). For clutches that had hatched I subtracted 14 days for the mean duration of incubation, the number of eggs

(because one egg is generally laid per day) and the age of the nestlings in days. Laying date was estimated as the number of days after May 1 minus clutch size (because one egg is generally laid per day) minus 14 days for the mean duration of incubation minus the age of the nestlings in days. These calculations were based on the assumption that one egg is laid daily, incubation lasts 14 days, and nestlings spend 21 days in the nest before fledging (Møller 1994).

Clutch size was recorded as the maximum number of eggs recorded before incubation started, while brood size at hatching and fledgling was recorded as the number of live nestlings after hatching and on the last visit before fledging. Hatching success was brood size at hatching divided by clutch size averaged across individual nests, fledging success brood size at fledging divided by brood size at hatching averaged across individual nests, and breeding success brood size at fledging divided by clutch size averaged across individual nests. All adults that reached the stage of egg laying for the second clutch were assumed to have a second clutch. All reproductive parameters were averaged to obtain an estimate for each year.

Adult survival rate

Barn swallows were captured with mist nets once a week at the breeding sites during April–August, measured and weighed, parasites recorded, feather and blood samples taken, and all individuals were provided with an individually numbered aluminum band and a combination of color bands for individual identification. Annual survival estimates were calculated as the proportion of adults present at the end of the previous breeding season that were present at the beginning of the next breeding season. Capture-mark-recapture studies have revealed that more than 98% of all adults are captured annually (Møller and Szép 2002). Therefore, simple recapture combined with re-sightings of banded birds suffices for obtaining reliable estimates of adult survival rate. All adults were assigned to nests by using binoculars to identify adults at nests.

Statistical analyses

The abundance of insects recorded during car transects was square-root transformed to normalize the data. Values reported are means (SE)

and the significance level was set to 5%. I tested if there were trends across years in mean wind speed for the different months April–August. In addition, I tested if all months tended to be windy the same year by investigating if average wind speed in different years was positively correlated for pairs of months. Strong correlations above 0.50 for mean wind speed between pairs of months across years would make it difficult to isolate any effects of wind in a particular month on insect abundance or barn swallow reproduction and survival. General linear models of the relationship between abundance of insects as a response variable and date, time of day and weather variables as predictors were conducted in JMP version 10 (SAS 2012). I constructed 14 a priori models, seven related to abundance of insects and seven related to adult survival rate. I used date as a predictor on the assumption that insects increase in abundance over time in temperate climate zones (e.g., Turner 1980, Møller 1994). Subsequent candidate models included Date + Wind, Date + Cloud cover, Date + Temperature, Date + Time of day, and Date + Time of day + Time of day squared (the latter to account for non-linear effects of time). A final model included Date + Wind + Cloud cover + Temperature + Time of day + Time of day squared.

I investigated seven candidate models of adult survival rate in Table 3. The first model included Sex only because sex effects on barn swallow survival rate are repeated in several studies (Møller 1994, Møller and Szép 2002, Turner 2006). The second candidate model included Wind + Sex to test for an additional negative effect of wind on the basic model. The third model included Wind + Body mass to test for any effect of Wind in addition to mass that has been shown to correlate positively with adult survival prospects (Møller 1994). The fourth model included Wind + Sex + Body mass to test for independent main effects. The fifth model included Wind + Sex + Body mass + Wind × Sex on the assumption that wind would have a differential negative effect of the sex that invests the most in reproduction (Turner 1980, Møller 1994), i.e., females. The sixth model included Wind + Sex + Body mass + Wind × Body mass on the assumption that wind had a differential negative effect on the flight cost of heavy individuals. The

Table 1. Information on candidate models explaining variation in insect abundance, their AICc, Δ AIC relative to the best model (in bold) including date, wind, cloud cover, temperature, time of day and time of day squared, the number of parameters, model weight (w), adjusted r^2 and the associated P value.

Model	AICc	Δ AIC	No. parameters	Model weight (w)	Adjusted r^2	P
Date	2037.33	1437.49	2	0.000	0.09	<0.0001
Date + Wind	1933.77	1333.93	3	0.000	0.18	<0.0001
Date + Cloud cover	1887.56	1287.72	3	0.000	0.22	<0.0001
Date + Temperature	664.49	64.65	3	0.000	0.31	<0.0001
Date + Time of day	1931.39	1331.55	3	0.000	0.15	<0.0001
Date + Time of day + Time of day squared	1930.25	1330.41	4	0.000	0.15	<0.0001
Date + Wind + Cloud cover + Temperature + Time of day + Time of day squared	599.84	0.00	6	0.999	0.41	<0.0001

final model included the three main effects of Wind + Sex + Body mass with the two interaction terms Wind \times Body mass and Wind \times Sex, with the justifications being presented above.

RESULTS

Temporal patterns of wind

When mean wind speed was high in a particular month of a year this tended only partially to be the case in other months as well with the strongest correlations being between mean wind speed in July and August (Pearson correlation $r = 0.46$, $t = 3.24$, $df = 41$, $P = 0.0025$) and between mean wind speed in April and May ($r = 0.38$, $t = 2.58$, $df = 41$, $P = 0.014$). All other correlations were less than 0.20. Mean wind speed for the months April-August varied significantly among years, although only wind speed in July showed a significant decrease during 1971–2011 (Fig. 1; $F = 5.02$, $df = 1, 39$, $r^2 = 0.11$, $P = 0.031$, slope (SE) = -0.020 (0.009)). There was no overall significant temporal trend in mean wind speed for the period April-August

for 1971–2011 ($F = 1.32$, $df = 1, 39$, $r^2 = 0.03$, $P = 0.26$, slope (SE) = -0.005 (0.004)).

Abundance of flying insects and wind

The abundance of flying insects during transects decreased with increasing mean wind speed (Fig. 2; $F = 157.48$, $df = 1, 1002$, $r^2 = 0.14$, $P < 0.0001$, slope (SE) = -0.192 (0.015)). Indeed, the estimated abundance of flying insects decreased from 1.3 to 0.3, or by a factor 4.3 across the six-fold increase in wind speed. A list of the seven candidate models, the associated AICc, Δ AIC, number of parameters, model weight (w), adjusted r^2 and P values is provided in Table 1. The model including date, weather variables, time of day and time of day squared had the highest model weight, and none of the other models had any support. This best candidate model is reported in Table 2. Because different components of weather covary, the abundance of flying insects was related to wind speed, date, cloud cover, temperature, time of day and time of day squared (the latter to account for the hump-shaped abundance of flying insects during the

Table 2. Insect abundance during transects with a car in relation to wind speed, date, cloud cover, temperature, time of day and time of day squared. The model had the statistics $F = 108.61$, $df = 6, 982$, adjusted $r^2 = 0.41$, $P < 0.0001$.

Variable	Sum of squares	df	F	P	Estimate (SE)
Wind	42.53	1	136.59	<0.0001	-0.173 (0.015)
Date	22.08	1	70.92	<0.0001	0.006 (0.001)
Cloud cover	32.69	1	104.98	<0.0001	-0.061 (0.006)
Temperature	29.17	1	93.67	<0.0001	0.062 (0.006)
Time of day	33.75	1	108.37	<0.0001	0.071 (0.007)
Time of day squared	12.52	1	40.22	<0.0001	-0.008 (0.001)
Error	306.10	982			

Table 3. Information on candidate models explaining variation in adult survival rate, their AICc, Δ AIC relative to the best model (in bold) including wind, sex, body mass, wind \times body mass and wind \times sex, the number of parameters, model weight (w), adjusted r^2 and the associated P value.

Model	AICc	Δ AIC	No. parameters	Model weight (w)	Adjusted r^2	P
Sex	-125.70	25.74	2	0.000	0.15	0.0021
Wind + Sex	-147.55	3.89	3	0.108	0.45	<0.0001
Wind + Body mass	-142.51	8.93	3	0.009	0.39	<0.0001
Wind + Sex + Body mass	-145.78	5.66	4	0.044	0.44	<0.0001
Wind + Sex + Body mass + Wind \times Sex	-144.76	6.68	5	0.027	0.45	<0.0001
Wind + Sex + Body mass + Wind \times Body mass	-146.10	5.04	5	0.061	0.46	<0.0001
Wind + Sex + Body mass + Wind \times Body mass + Wind \times Sex	-151.44	0.00	6	0.752	0.53	<0.0001

day with minima in the morning and the evening (Table 2)). The partial correlation between insect abundance and wind speed was still negative and significant after controlling statistically for these potentially confounding factors (Table 2). There were additional significant correlations between insect abundance and the other variables (Table 2). The abundance of insects during the pre-laying period of the second clutch in July decreased with increasing wind speed during July ($F = 12.70$, $df = 1, 13$, $r^2 = 0.48$, $P = 0.0043$, slope (SE) = -1.860 (0.538)). This analysis was based on data from the period 1997–2011.

Breeding biology of barn swallows and wind

Laying date of second clutches was on average 17 July (SD = 10 days), $N = 2303$. Thus breeding was relatively synchronous with most pairs laying eggs in the second clutch during a period of three weeks. Fledging of second clutches of

barn swallows decreased with increasing wind speed during July among years (Fig. 3; $F = 10.01$, $df = 1, 39$, $r^2 = 0.20$, $P = 0.003$, slope (SE) = -2.491 (0.787)), and there was also a decrease for breeding success of second clutches ($F = 5.93$, $df = 1, 39$, $r^2 = 0.13$, $P = 0.020$, slope (SE) = -3.099 (1.273)). In contrast, there was no significant relationship between wing speed in May during the pre-laying period of the first clutch and fledging success or breeding success of first clutches (fledging success: $F = 1.44$, $df = 1, 39$, $r^2 = 0.04$, $P = 0.24$; breeding success: $F = 0.07$, $df = 1, 39$, $r^2 = 0.00$, $P = 0.80$).

Body mass, adult survival rate and wind speed

Annual mean estimates of body mass were 18.23 g (SE = 0.09) for males and 19.09 g (0.01) for females, being highly significantly different (paired t-test, $t = 12.41$, $df = 1, 26$, $P < 0.0001$). Mean annual body mass of males and females decreased with increasing wind speed during

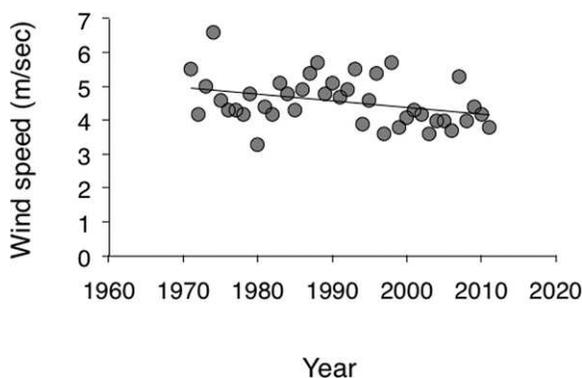


Fig. 1. Mean wind speed (m/sec) for July 1971–2011 at Aalborg, Denmark. The line is the linear regression line.

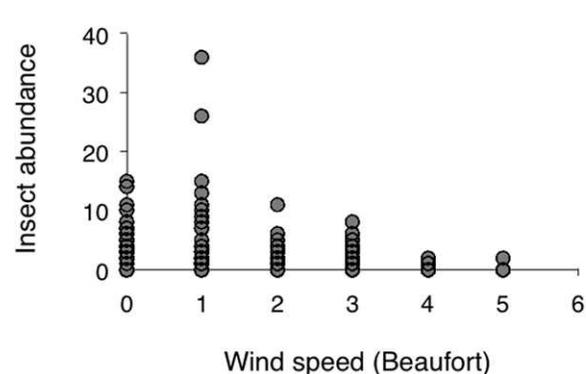


Fig. 2. Abundance of flying insects in relation to wind speed on the Beaufort scale based on transects at the study site May–August 1997–2011.

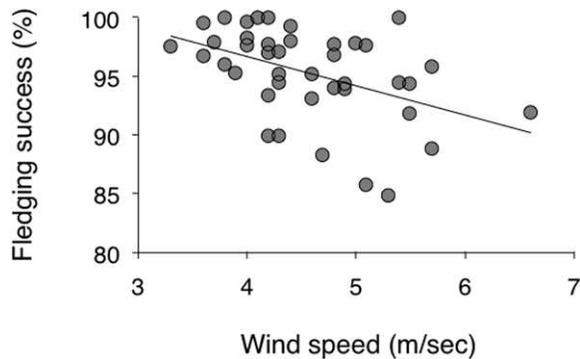


Fig. 3. Fledging success of second clutch of barn swallows during 1971–2011 in relation to mean wind speed (m/sec) during July 1971–2011. The line is the linear regression line.

April–August (Fig. 4). There were a significant negative correlation between body mass and wind speed ($F = 21.62$, $df = 1, 52$, $r^2 = 0.29$, $P < 0.0001$, slope (SE) = -1.080 (0.0233), with an additional effect of sex ($F = 49.28$, $df = 1, 52$, $r^2 = 0.49$, $P < 0.0001$).

Adult survival rate was on average 0.338 (SE = 0.014), $N = 27$ years, for male barn swallows and on average 0.274 (SE = 0.014) for females, being highly significantly different (paired t -test, $t = 6.42$, $df = 1, 26$, $P < 0.0001$). Annual adult survival rate decreased with increasing wind speed for both adult males and females (Fig. 5). For males survival rate decreased by a factor 1.6 across the range of annual mean wind speeds (4.3

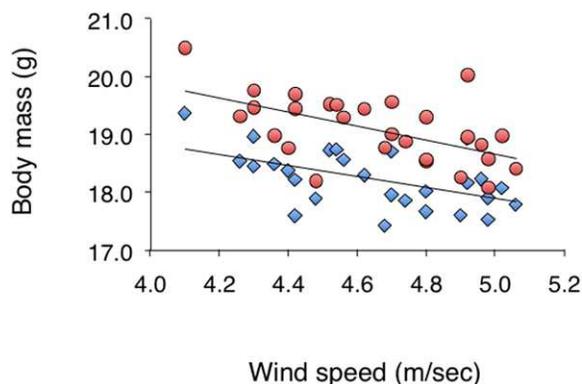


Fig. 4. Mean body mass (g) of male (squares) and female adult barn swallows (circles) in relation to mean wind speed for April–August 1971–2011. The lines are the linear regression lines.

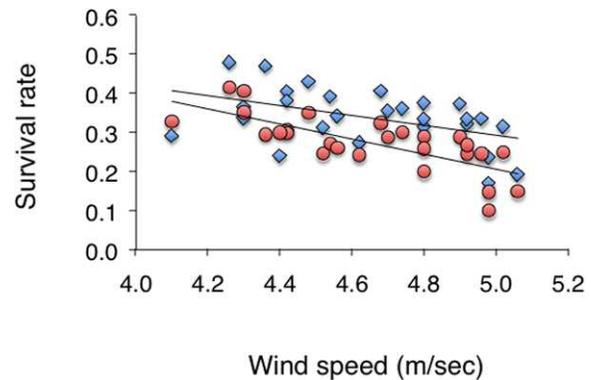


Fig. 5. Annual adult survival rate for male (squares) and female barn swallows (circles) in relation to mean wind speed for April–August 1971–2011. The lines are the linear regression lines.

to 5.1 m/sec), while in females there was almost a two-fold difference in survival, with survival in both sexes increasing in recent years when low wind speeds during July prevailed. The best-fit model explained 53% of the variance in adult survival rate among years with adult survival rate and sex, wind speed, body mass and their interactions as predictors (Table 3). The ΔAIC relative to the basic model were all >2.0 . Model weight was the largest for the seventh model, with the other models except the one that included sex having some support (Table 3). The single-most important predictor of adult survival rate was wind speed during April–August accounting for 53% of the variance (Table 4). Survival rate also differed significantly between the sexes, while there was no significant main effect of body mass. Body mass interacted significantly with wind speed, implying that for a given wind speed, survival rate increased with increasing body mass (Table 2). Finally, wind speed interacted significantly with sex, implying that survival decreased more with increasing wind speed in females than in males (Table 2).

DISCUSSION

The main findings of this study were that wind speed during summer varied considerably among years, with a clearly decreasing trend for July only during 1971–2011. Abundance of flying insects decreased with increasing wind speed. The abundance of insects during the pre-

Table 4. Annual adult survival rate in relation to wind speed, sex, body mass, body mass by wind speed interaction and sex by wind speed interaction. The model had the statistics $F = 12.73$, $df = 5, 48$, adjusted $r^2 = 0.53$, $P < 0.0001$.

Variable	Sum of squares	df	<i>F</i>	<i>P</i>	Estimate (SE)
Wind	0.097	1	33.05	<0.0001	-0.191 (0.033)
Sex	0.019	1	6.42	0.015	-0.026 (0.010)
Body mass	0.001	1	0.46	0.50	-0.011 (0.017)
Body mass × Wind	0.027	1	9.05	0.0042	0.140 (0.046)
Wind × Sex	0.023	1	7.65	0.0080	-0.093 (0.034)
Error	0.141	48			

laying period of the second clutch in July increased during 1997–2011, and fledging and breeding success decreased with increasing wind speed. Adult body mass increased considerably and adult survival rate increased by 50% as wind speed was reduced, showing that wind speed through its effects on food availability has fitness consequences for adult barn swallows.

Wind speed is known to affect the abundance of flying insects with insect abundance decreasing drastically with increasing wind (Turner 1980, 2006). Here I used the abundance of insects sampled with a car as a relative estimate of the abundance of insects. These estimates were repeatable among sampling events, albeit only weakly as demonstrated by a repeatability of 0.36. Such a low repeatability is partly caused by confounding effects of differences in time of day and changes in weather conditions among transects. Furthermore, mean annual estimates of insect abundance during the nestling period of barn swallows based on sweep netting were strongly positively correlated with mean annual abundance of insects assessed from the car transects, providing important cross-validation for the insect sampling method. The estimated abundance of flying insects was biologically meaningful because the feeding rate of nestlings increased as the estimated abundance of insects increased during transects. Thus there were reasons to believe that these relative estimates of the abundance of flying insects reflected the true abundance. Mean predicted abundance of flying insects decreased by 77% across the range of wind speeds recorded (Fig. 2). Therefore, the abundance of insects shows dramatic changes in response to environmental conditions, and wind speed is a factor accounting for this effect. In fact, the negative effect of wind speed on the abundance of flying insects remained indepen-

dent of statistical control for potentially confounding variables such as date, time of day, time of day squared and other weather variables such as ambient temperature and precipitation. The model including date, weather, time of day and time of day squared had most support, while the other models had little support as reflected by model weights being close to zero.

There was no evidence of temporal change in mean wind speed for April–August 1971–2011, when barn swallows are present in the study area. Mean wind speed for different months varied mainly independently, with the largest correlation coefficient between months being 0.46. There was only a significant decline in wind speed during July, when second clutches are laid, incubated and reared, but not during the other months of spring and summer. Thus, the effects of wind speed on the first clutch, when there is no temporal trend may serve as a control for the effects on the second clutch, when there is a temporal trend. Indeed, there were significant effects of mean wind speed on abundance of flying insects during the pre-laying period of second clutches with negative consequences for fledging and breeding success, while there was no similar trend for wind speed, insect abundance or fledging and breeding success of first clutches.

Mean wind speed appeared to have an indirect effect on reproductive success of the second clutch through effects on the abundance of food. Indeed, the abundance of flying insects decreases with the increasing wind speed, as shown here and in previous studies of other barn swallow populations (Turner 1980, 2006). This effect was mediated by a trend in wind speed and abundance of food during the pre-laying period of the second clutch in July. There were negative relationships between fledging and breeding

success of second clutches only, respectively, and mean wind speed during July and these effect sizes were intermediate to large, with the overall trend depending on years with strong wind and poor reproductive success. Effects of wind speed on reproductive success are mainly related to starvation of nestlings, with nest predation being close to zero in the study population (Møller 1994), as in other populations of barn swallows (Turner 1980, 2006).

The body mass of adult males and females was negatively correlated with wind speed in July, with around 30% of the variance in mean annual body mass being accounted for by wind speed (Fig. 4; where r^2 was derived from F-statistics and denominator degrees of freedom). Furthermore, adult survival rate decreased with increasing wind speed at a similar rate in males and females, accounting for 37% of the variance in annual survival estimates (Fig. 5). I explicitly tested whether adult survival rate was explained by sex, mean wind speed, body mass and their interaction. There were several candidate models with weak support, although the model that included wind, sex, body mass and the two-way interactions between wind and body mass and between wind and sex had the highest support (Table 3). The support for the best model on adult survival was less than the support for the best model on insect abundance, which is not surprising given that weather directly affects insect abundance, whereas adult survival is directly and indirectly affected by many different variables. Because the effect of body mass was not significant (although body mass was retained in the model because the two-way interaction between wind and body mass was significant), elimination of body mass from the model only resulted in a slightly different adjusted $r^2 = 0.48$, with the effects of sex, wing and sex by wind interaction being qualitatively similar as in the model reported in Table 4. Although there were no main effects of body mass, survival rate increased with increasing body mass for a given wind speed. Thus, there was evidence of an indirect effect of wind speed on survival rate through the effect of wind speed on body mass. Finally, survival rate differed between the sexes, decreasing more with increasing wind speed in females than in males.

Because the abundance of insects is so strongly

affected by wind speed, it seems likely that natural and sexual selection on morphology will be modified by wind. Although the temporal trends in wind speed were not consistent, with July being the single exception, we can expect that patterns of selection will be divergent except for selection on morphology related to the rearing of a second clutch. It is already known that climate warming has resulted in the interval between first and second clutches of barn swallows now being almost ten days longer on average than in 1971 (Møller 2007). This has had consequences for reproductive decisions for the second clutch, the quality of offspring and the effects of rearing a second clutch on survival prospects of adult males and females (Møller 2007).

In conclusion, mean wind speed varied considerably among months and years with the temporal pattern of wind speed only showing a decreasing trend for July. The abundance of flying insects decreased with increasing wind speed, and this in turn affected reproductive success of second clutches that were initiated during July. Annual mean body mass of adult barn swallows decreased with increasing wind speed in both sexes. Likewise, annual adult survival rate declined with increasing wind speed, and this correlation was linked to a direct effect of wind speed, but also an indirect effect of wind speed on body mass. If wind speed changes as a consequence of climate change, we can expect that such change will affect animals susceptible to the effects of wind such as insectivores, marine seabirds and others relying heavily on flight.

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