Breeding success and survival in the common swift *Apus apus*: a long-term study on the effects of weather

D. L. Thomson*, H. Douglas-Home, R. W. Furness and P. Monaghan

Applied Ornithology Unit, Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Glasgow University, G12 8QQ, Scotland

(With 3 figures in the text)

In an analysis of data collected between 1954 and 1993, the breeding success of swifts *Apus apus* was found to have been positively related to temperatures in June, especially in recent years. Adult survival until the next breeding season, by contrast, was found to have been more vulnerable to low temperatures in July, at the end of the breeding season. In addition to the effects of changes in June and July temperatures, both breeding success and survival have shown further long-term trends, increasing and then decreasing through the study period. A simulation integrating all these effects suggests that lifetime reproductive success (LRS) is influenced more by changes in lifespan than annual breeding success, and so fluctuations in July temperatures, but not June temperatures, would have important effects.

Introduction

While environmental change clearly influences the behaviour and population ecology of birds (e.g. Furness & Greenwood, 1993), the biological effects of long-term changes in weather patterns may be difficult to evaluate (Marquiss & Newton, 1990). Aerially feeding birds, such as swifts *Apus apus*, are unusually sensitive to weather changes (Lack & Lack, 1951; Bryant, 1975; Martins & Wright, 1993c). Over five years, Lack & Lack (1951) found that chick survival had been poor in the years when the breeding season had been cold, wet, windy or overcast. Over a shorter time scale, they found higher chick growth rates on warm, sunny, dry or calm days. In a three-year study, Martins & Wright (1993a, b, c) enlarged broods, but in only one year of harsh weather did they find greater brood reduction or depressed body condition of adults or of chicks. They also found different effects at distinct stages of the breeding season. Brood reduction happened soon after hatching, while critically low adult body condition occurred later in the breeding season. Swifts suffer higher predation during harsh weather particularly at the end of the breeding season (Kuhk, 1948; Klass, 1953).

Many of these results have been inferred from studies of relatively short duration. To date, it has not been possible either to follow the effects of long-term weather changes, nor to ascertain whether the different effects of weather at different stages in the season persist over several separate years. No studies have looked directly at the effects of weather on adult survival, or explored the implications of weather change for lifetime reproductive success. Using the results of a study of breeding swifts commenced in 1954 (Douglas-Home, 1977; Thomson & Douglas-Home, 1993), we examine the effects of weather on breeding success and survival and consider

* Present address: British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU

whether each might be affected at different periods in the season. We also look at whether other factors have produced further long-term trends ('temporal effects') in breeding success and survival. By combining the statistical regression models derived from these analyses, we explore the influence of these weather factors on lifetime reproductive success (LRS).

Methods

Study site and fieldwork

With a view firstly to marking and identifying individuals, and secondly to measuring their breeding performance, 15 nest-boxes located near Coldstream, southern Scotland (Douglas-Home, 1977; Thomson & Douglas-Home, 1993) were visited once annually in all years from 1954 to 1993 except 1963 and 1964. These visits generally took place in July, and were timed to coincide with the late chick-rearing stage. Adult swifts often roost nocturnally in their nest-boxes and can thus commonly be caught by hand. Not all breeding birds were caught each year, however, and individuals were trapped in only just over 50% of the years between their first and last capture. When caught, the identity of ringed adults was noted, and metal rings were attached to unmarked adults. Breeding success is defined as the number of large feathered young present, and ringed, in each nest at the time of the visit, and the database covers 236 breeding attempts over 38 years. Though adults were not caught in all years, survival rate was determined from the patterns of captures and recaptures following standard methods (Clobert, Lebreton & Allaine, 1987; Pradel, 1989; Lebreton *et al.*, 1992).

Weather records

In order to examine the effects of weather on both chick production and adult survival, we analysed records of temperature and rainfall collected from the Floors Castle station, 13 km from the study site. Temperature and rainfall have been found to be important for breeding performance in other studies, and although there is some evidence that other meteorological variables can also have effects (Lack & Lack, 1951; Gory, 1987; Cucco *et al.*, 1992), records of local sunshine and wind speed are not available here, and data from more distant stations are not representative. For each of the 3 months of the breeding season (May, June, and July) we used 2 standard meteorological variables. We considered first the monthly means of daily maximum temperature, and secondly the number of days each month with rainfall in excess of 1 mm. Long-term trends in these variables have been found (Thomson & Douglas-Home, 1993).

Analyses

The analysis sought firstly to test which weather variables affected breeding performance and adult survival. We further looked for additional temporal changes in breeding and survival that might indicate other unidentified environmental changes. Having tested the significance of each of the effects, we constructed regression models of breeding success and adult survival which contained all the significant effects. Using a simulation, we then combined these 2 regression models and examined the implications of the weather variables for lifetime reproductive success.

Environmental factors such as weather have simultaneous effects on large numbers of birds, so individuals breeding under the same conditions cannot be assumed to yield statistically independent observations. Thus, using *mean annual* breeding success as the dependent variable, we tested the significance of temporal effects and weather variables in a multiple linear regression. We examined the change in the variance accounted for when each independent variable was dropped from the regression model containing all the other significant variables. Having thus established which variables were significant, we then went on to build a model describing 'individual' rather than 'mean annual' breeding performance.

Because studies of LRS have often found effects of experience on survival and annual breeding performance (Clutton-Brock, 1988; Newton, 1989), it was important to take these into account. Although breeding age could be measured, it was not possible to determine true age because age of first breeding was estimable for only 12 birds which returned to breed in the natal colony and there was no fixed age of first breeding. Five birds were first recorded breeding at age 1 year, 1 at 2, 2 at 3, 1 at 4, 1 at 5, and 2 at 6. We did not attempt to estimate true age, but focused instead on breeding age. An adult caught breeding for the first time was given a breeding age '1', etc. Where both adults of a pair were caught, we used the age of the older bird. Individual breeding success increased and then decreased with breeding age, and could be described by a quadratic equation (ordinal logistic regression: $z = 2.73$, $d.f. = 227$, $P < 0.01$ for the linear component, and $z = 2.41$, $d.f. = 227$, $P < 0.02$ for the quadratic component). This significant effect of age on breeding success persisted after controlling for the weather and temporal effects and was therefore incorporated into the simulation. Conversely, the other effects also persisted after controlling for the effects of age. Long-term changes in the performance of the colony were not due to changing age structure, even though average breeding age was inevitably lower during the early years of the study.

Although repeated observations of individual birds were used in the analysis, this did not violate assumptions regarding the independence of data. All variables being tested were characteristics of particular years or particular breeding ages. Any individual can breed only once in any particular year or at any particular age. Spurious associations between the consistent performance of individuals and the particular conditions of any year or age do not therefore arise.

Because individual breeding performance is a discontinuous variable, the technique of ordinal logistic regression (McCullagh, 1980; Cole & Lane, 1989), rather than multiple linear regression, was used in the final analysis of individual breeding success. This is analogous to logistic regression but the dependent variable can take more than 2 ordinal values. It is also similar to multiple linear regression, but acknowledges that individual breeding success can take only whole numbers rather than being continuous. With this technique, it was possible to determine the probabilities of producing 0, 1, 2, or 3 chicks, given the year, the weather conditions, and the bird's breeding age. The ability to make these predictions using ordinal logistic regression is clearly preferable to making predictions from a multiple linear regression model in which breeding performance is assumed to be continuously and normally distributed. Ordinal logistic regression could not, however, be used to examine the effects of annual conditions on mean annual performance because mean annual performance is a continuous, not an ordinal, variable.

Regression models of adult survival rate were constructed using the SURGE4 technique (Clobert et al., 1987; Pradel, 1989; Lebreton et al., 1992). The significance of weather, temporal, and age effects could be tested, combining and controlling each as independent variables in a manner akin to multiple regression analysis. The technique estimates both survival rate and capture rate simultaneously by integrating all the information from captures and recaptures and so has more power than conventional techniques (Cormack, 1964; Jolly, 1965; Seber, 1972; and see North, 1987). With the SURGE4 regression model, and with information on the year and weather conditions, it was possible to calculate the probability of an individual surviving to the next year.

Although several variables were found to affect survival rate, none was found to affect capture rate as well, and there was no evidence that capture rate was affected by the weather during the month of the visit. Accordingly, except for the years 1963 and 1964 where no field records were available, and where capture rate was therefore fixed to zero, capture rate was otherwise assumed to be constant in the final analysis.

Simulation to investigate the implications for life-time reproductive success

Since individual breeding adults were captured in only just over 50% of their breeding years, LRS could not be studied directly but only indirectly by means of a simulation based on the regression models of breeding success and adult survival. After establishing the statistical significance of the weather, temporal, and age effects on survival and annual reproductive success, the biological importance of each was examined

by considering the relative impact on LRS, and by looking at whether LRS would itself show long-term temporal trends under the conditions of the simulation. The simulation was not performed to test the significance of the various effects, but to explore their possible implications. It provided a means of estimating the numerical magnitude of the effects and the fractions of variance accounted for. It could thus be used as a way of quantifying the biological importance of effects whose significance had already been established.

For the simulation, a GENSTAT program (Lane, Galwey & Alvey. 1987) was used to follow 24 putative cohorts each of 400 birds starting breeding in the years 1954–1977. We set the maximum breeding lifespan to 16 years (the highest recorded in this colony), thus necessitating the omission of cohorts commencing breeding during 1978–1993. In the simulation, we followed the effects of conditions around the study site in the years 1954–1993. Real values for all the significant weather, temporal, and age variables were thus known for each individual throughout the simulation period.

In the simulation, each bird commencing breeding was randomly assigned a breeding success of either 0, 1, 2 or 3 chicks, using the probabilities generated from the ordinal logistic regression model. With the analogous probabilities derived from the regression models of survival rate, each bird was then randomly assigned either survival to the next year or mortality. The same procedure was then repeated successively for the birds which survived each time, and a lifetime total of reproductive success was determined for each individual by summing the assigned annual successes. For each cohort, the mean breeding lifespan, the mean annual breeding success, and the mean lifetime reproductive success were determined by averaging the values for the individuals.

In order to compare the importance of factors affecting annual breeding success and adult survival, the results of the simulation were analysed in 2 ways. First, we examined the fractions of variance in LRS which could be accounted for by mean annual breeding success and breeding lifespan. Secondly, we looked at whether the different components of the weather in the first breeding year influenced LRS via effects on either mean annual reproductive success or breeding lifespan.

Results

Empirical results

Factors affecting annual reproductive success

On average, throughout the study period and for all age classes, the birds produced an average of 1.63 ($\pm$ S.E. 0.069) large feathered young per breeding attempt.

Mean daily maximum June temperatures were positively related to mean annual reproductive success (regression coefficient = 0.613, $F_{1,34} = 8.51$, $P < 0.01$, $R^2 = 0.23$, Fig. 1a), and there was a significant interaction between June temperatures and time such that June temperatures have become more important for breeding success in recent years ($F_{1,34} = 6.68$, $P < 0.05$, $R^2 = 0.16$, Figs 1b and c). June will generally have coincided with the first stages of chick-rearing. There was no evidence that annual reproductive success was influenced by mean daily maximum temperatures during the months of May or July, nor by the number of days with rainfall in excess of 1 mm, in any of the months of the breeding season.

After controlling for June temperature effects, there was a significant temporal effect. The residual breeding success increased before it decreased and could be described by a quadratic equation ($F_{1,34} = 7.73$, $P < 0.01$, $R^2 = 0.20$, for the linear component, and $F_{1,34} = 7.54$, $P < 0.01$, $R^2 = 0.20$, for the quadratic component) (Fig. 2). The cause of this temporal effect is not clear, but it may be due to weather variables which were not measured at the station or to other factors influencing the abundance of aerial insects.
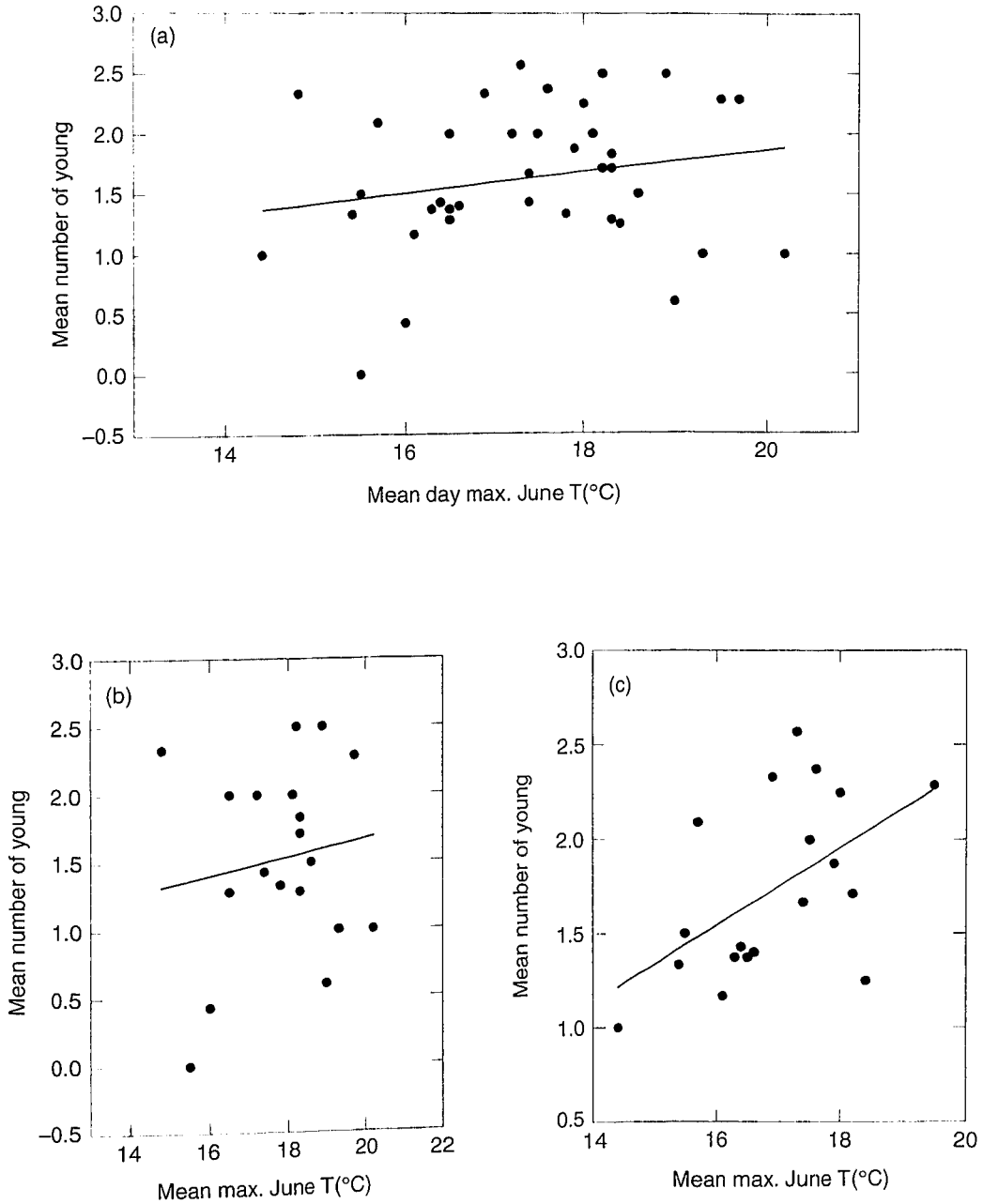
FIG. 1. (a) The relationship between mean daily maximum June temperatures and breeding success. (b) The relationship between mean daily maximum June temperatures and breeding success in the period 1954–1974. (c) The relationship between mean daily maximum June temperatures and breeding success in the period 1975–1993.

All the significant effects persisted when each of the others was first controlled, and remained when the average fitted annual productivity, predicted from the age function, was used as a term to contend with possible changes in the age structure of the population. Any correlations between the independent variables themselves could not therefore produce spurious effects.
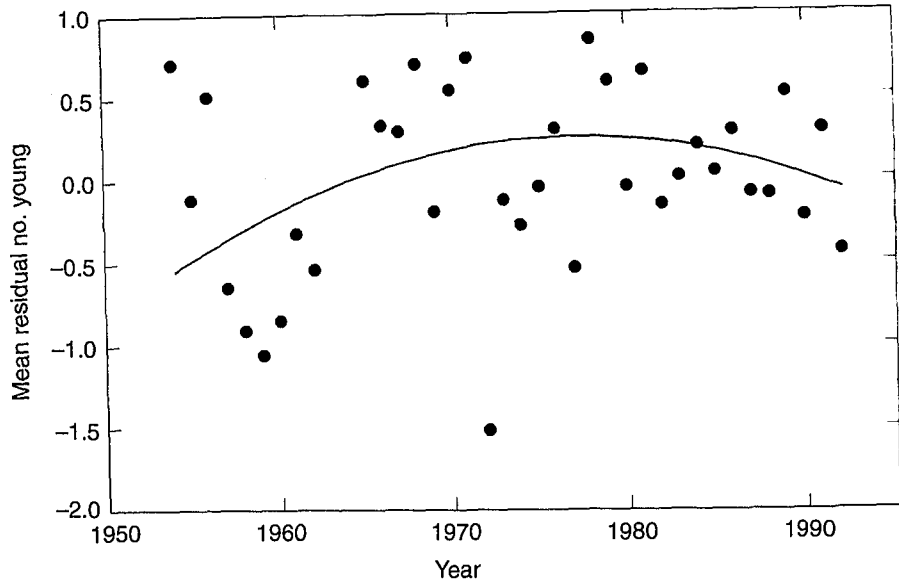
Fɪɢ. 2. (a) Long-term quadratic temporal trend in annual breeding success, after controlling for the effects of June temperatures.

Factors affecting annual adult survival rates

Overall, the average annual adult survival was estimated at 76.16% (95% confidence interval (C.I.) = 72.2–79.70%).

At the end of the breeding season in any one year, increasing July temperature significantly improved the chances of swifts surviving to the following year (regression coefficient = 0.653, 95% C.I. = 0.2834–1.0224, $P < 0.05$). No significant effects of any other weather variables or age on survival could be detected. A significant temporal effect, resembling that shown by breeding success, was detected; after controlling for the other effects, residual survival rate increased before decreasing (regression coefficient for linear component = 0.176, 95% C.I. = 0.0461–0.306, $P < 0.05$, and for regression coefficient for quadratic component = −0.00456, 95% C.I. = −0.00764 − −0.00149, $P < 0.05$). Each significant effect persisted even when the others were controlled.

Simulation results

Will changes in weather have affected lifetime reproductive success?

The simulation indicated that lifetime reproductive success would not be constant, but would show long-term changes. The trend in cohort average lifetime reproductive success indicated by the simulation could be described by a long-term sine model, and this accounted for 52% of the variance (Fig. 3a). Under this scenario, birds commencing breeding at the peak of the trend would have over twice the lifetime reproductive success of birds starting in the trough. The most productive cohort in the simulation had an average reproductive success of 11.58 (S.D. = 8.345) offspring, while the least productive achieved only 3.04 (S.D. = 5.052). Cohort effects could account for 14.2% of the variance in simulated individual LRS.
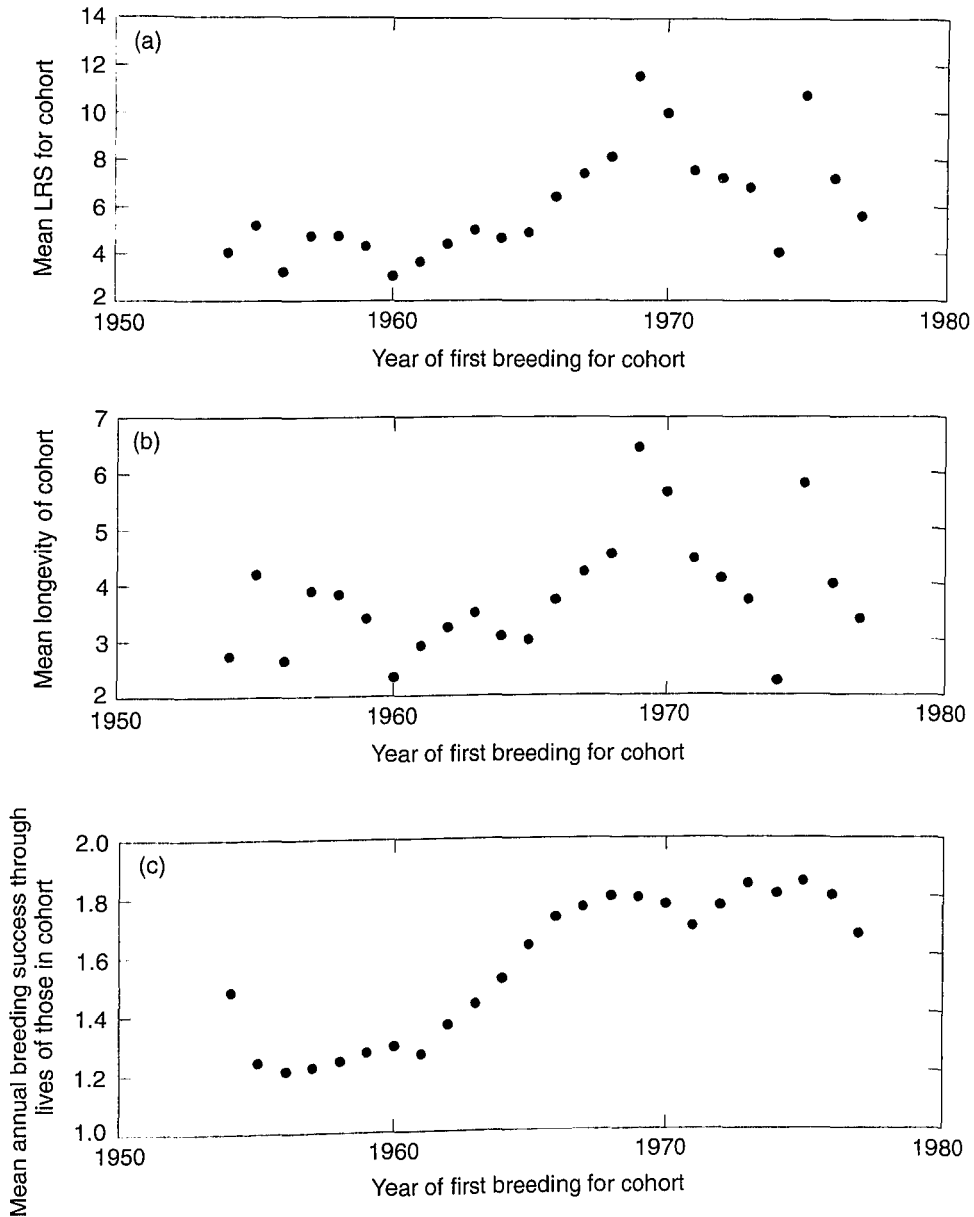
FIG. 3. Long-term trends in: (a) average cohort lifetime reproductive success; (b) breeding lifespan; and (c) cohort mean annual breeding success, as determined from the simulation.

The potential implications of longevity and annual breeding success for lifetime reproductive success

Figure 3b shows that the long-term trends in breeding lifespan are strikingly similar to those of LRS shown in Fig. 3a. Figure 3c shows long-term trends in mean annual reproductive success for comparison. Although both survival and breeding success were influenced by similar temporal effects, their potential implications for LRS might differ partly because each was influenced by

different weather variables. In the simulation, after allowing for the effects of mean annual breeding success, 81.5% of the variance in LRS could be uniquely accounted for by the number of breeding years. By contrast, mean annual breeding success was much less important and accounted uniquely for only 11.4% of the variance after allowing for the number of breeding years. A further 7.1% of the variance was shared between the two variables because mean annual breeding success is correlated with number of breeding years and because annual breeding success changes with age.

Although mean daily maximum June temperatures had a significant effect on breeding success in any year, the simulation indicates that June temperatures in the first breeding year would have no detectable effect on the average annual breeding success of a cohort ($F_{1,22} = 0.0167$, ns). Clearly then, the results also indicate that June temperature would have no detectable effect on the average LRS of a cohort ($F_{1,22} = 0.559$, ns).

By contrast, under the conditions of the simulation, July temperature in the first breeding year could account for 16.6% of the variance in breeding lifespan ($F_{1,22} = 5.56$, $P < 0.05$), and this has clear implications for LRS, accounting for 11.8% of the variance. Through their effects on adult survival, conditions in July at the end of the breeding season would have an appreciable influence on lifetime performance.

Discussion

Lack & Lack (1951) suggested that chick mortality was higher in poor weather, and that chick growth rates and feeding rates were influenced by temperature, rainfall, wind speed, and sunshine. Thomson & Douglas-Home (1993) found that the timing of fledging was affected by both temperature and rainfall in all months of the breeding season. Here, however, only temperatures during June, the period of hatching and early chick-rearing, were found to have any significant influence on the number of large feathered chicks ultimately produced by swifts. These results are consistent with Martins' & Wright's (1993a) suggestion that breeding success is strongly influenced by brood reduction soon after hatching. Weather throughout the season clearly has marked effects on the breeding patterns of swifts. However, apart from brood reduction which may tailor brood size to annual weather conditions and food abundance, swifts have a suite of responses which serve to buffer breeding success from the effects of weather. These include plasticity in laying dates, incubation duration, chick growth rates and the allocation of food between parents and chicks (Lack & Lack, 1951; Martins & Wright, 1993a, b, c).

In contrast to breeding success, it is the temperature in July at the end of the breeding season that most influences adult survival to the next year. This may be because body condition is low at that time and the birds may be more susceptible to weather and to predators (Kuhk, 1948; Lack & Lack, 1951; Klass, 1953; Martins & Wright, 1993a, b, c). The percentage of swifts in the diet of predatory birds can increase by more than 10-fold at the end of breeding seasons or after harsh weather (Kuhk, 1948; Klass, 1953). This shows that both the strain of breeding and harsh weather expose the birds to predation. Martins & Wright (1993b, c) showed that in poor weather food was limited and that parents allocated food to their brood and sacrificed their own self-feeding. Towards the end of the breeding season, this led to vulnerable adults in critically low body condition. Conditions in July at the end of breeding may also influence the birds' ability to prepare for and cope with migration, though Martins & Wright (1993b) found that adults could quickly recover body condition after they stopped feeding chicks.

Both annual breeding success and adult survival showed long-term trends during the period

1954–1993, increasing before decreasing. Although the cause is unclear, this indicates that, in addition to the effects of the measured weather variables, other changes in the aerial environment around the study site may have occurred. These may have been due to factors such as other weather variables not measured around the study site, or changes in levels of aerial pollution. That both survival and breeding success have shown comparable trends suggests that conditions around the study site, rather than in the wintering areas or on migration, are important. Long-term trends in adult survival could arise through changes in wintering or migration conditions, and could reflect climate change, changing land-use, desertification, or other processes that influence the abundance and availability of aerial insects.

The results indicate that different components of the weather differ in their importance for LRS. Swifts are long-lived birds with relatively low annual reproductive output (Perrins, 1971), and LRS appears to be influenced more by breeding lifespan than by average annual reproductive performance. Our simulation thus shows that the temperatures in July towards the end of the breeding season will have been more important for LRS than temperatures in June during the earlier stages of the chick-rearing period. Weather affecting adult survival is more important than weather affecting annual breeding success. Though survival was marginally lower than for other populations (Perrins, 1971; Baillie & Green, 1987; Lebreton *et al.*, 1992), our estimate of 76.16% translates into an average breeding lifespan of 4.47 years, and this opportunity to breed in several years may lessen the impact of poor breeding conditions in any one year.

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