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Long term changes in weather and in the breeding schedule of Common Swifts *Apus apus*

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Abstract At a small colony in Southern Scotland, long term changes in weather, have been associated with correponding changes in the date at which the chicks of Common swifts *Apus apus*, have reached the later stages of development. The dates at which the young have reached a suitable stage for ringing, have been significantly influenced by rainfall and temperatures in May and June. All of these variables have shown regular changes through time. There is also some evidence that July temperatures may also have changed through time and had additional effects. While the strong effects of weather in the early part of the season are consistent with there being effects of laying date and incubation period on changes in the breeding schedule, the changes in June and July weather during the later stages of breeding, may have had effects on chick growth rates which are known to be highly flexible in this species.

Introduction

In addition to the effects of environmental conditions on laying date (e.g. Perrin and Birkhead 1983, Cucco *et al.* 1992, Gory 1987) and incubation period, swifts are subject to strong environmental influences on chick growth rate (Lack and Lack 1951, Thibault *et al.* 1987). They may thus be expected to show considerable variance in fledging date depending on annual weather conditions. Weather around a small colony of swift in the Eastern Scottish Borders has shown long term changes over the period 1954 to 1992, and these have had significant effects on the breeding performance of the birds (Thomson and Douglas-Home in prep.). Using data collected on these swifts over this period (Douglas-Home 1977), we examine the prediction that the breeding schedule is variable and has been altered by changes in the weather, and we resolve where possible the effects of weather during the three months of the breeding season in order to identify at which breeding stage the effects upon breeding chronology are most marked.

Methods

In 1954, nest boxes for swifts were erected beneath the windows of a large country house, the 'Hirsel' near Kelso in the Borders of Scotland. These proved successful, and the number of boxes was increased quickly to a final total of 15. The data cover a total of 37 years, and over 220 breeding attempts. In only 1963 and 1964 were records not collected. During single visits in July of each year, it has been possible to ring adults and young, and note the productivity of each nest. Using observations of the birds before the selected date, as well as the habits and impressions established in the preceding 1 or 2 years, it was possible to time the visit to coincide with the presence of large feathered young of suitable age for ringing. Throughout this paper 'date' refers to the time of this visit. Clearly, though most chicks were large, feathered and close to fledging, this developmental stage is somewhat arbitrary, and is not equivalent to fledging date or laying date. Despite the statistical noise which may be generated by this, no confounding biases can be identified. Standard measures of temperature and rainfall are available locally from 'Floors Castle', Kelso, and cover the entire period. Sunshine and wind speed records have not been collected at this station. Long term trends in these weather patterns have been identified, and have been found to have significant effects on the breeding productivity of the birds in the colony (Thompson and Douglas-Home in prep.). These weather changes are thought to be a local rather than a widespread phenomenon (R. Tabony, Meteorological Office, Pers. comm.). To contend with noise around the long term trends, and to acknowledge the inevitable effects of date in year 'n' upon the date chosen in year 'n+1', running means over periods of 3 years were calculated (c.f. Aebischer *et al.* 1990, Digby *et al.* 1989). Although sine functions were fitted, the duration of the study was not long enough, to use stan-

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dard time series approaches such as 'ARIMA' to investigate whether the patterns were genuinely cyclical. As well as fitting functions to model each variable in time, multiple regression was used to examine and separate the effects of several weather variables on ringing date (Lane *et al.* 1987). The origin of the years was moved to 1953 to avoid computing errors associated with very large sums of squares. Where multiple linear regression was used, variables were added into the model in various orders, and full models were constructed using all variables which had at least one significant effect. The significance of these variables was then tested by examining the change in explained variance, when each was dropped from the full model. The significance of other variables was tested by examining the changes when they were added to the full model.

Results

Graphs of 3-year running means for July chickringing date, and the number of days with rainfall in excess of 1 mm during the months of May and June, are given in Figure 1. Trends in mean daily maximum temperatu-res for the months May, June, and July are given in Figure 2. Multiple regression (Lane *et al.* 1987, Digby *et al.* 1989) was used to compare the fit of sine or quadratic functions with that of simple linear fun-ctions. The results of fitting these functions are given in Table 1. A multiple linear regression model was con-structed to examine all the effects of the weather vari-ables on ringing date. (see Table 2. for these results).

The model can be expressed as:

July date = -38.1-(1.422 x No. June days with rain fall >1mm)
+(3.67 x Mean daily max May temperature)
+(1.056 x No. May days with rainfall >1mm)
+(1.372 x Mean daily max June temperature)
-(1.112 x Mean daily max July temperature).

This accounts for 58.1% of the variance in running means of the date selected for ringing.

The ringing date has been later in years when there have been lower temperatures in May and June, lower May rainfall, higher June rainfall, and higher July temperatures. The signs of the May rainfall effect and the July temperature effect would seem counter intuitive, though the latter effect is weak.

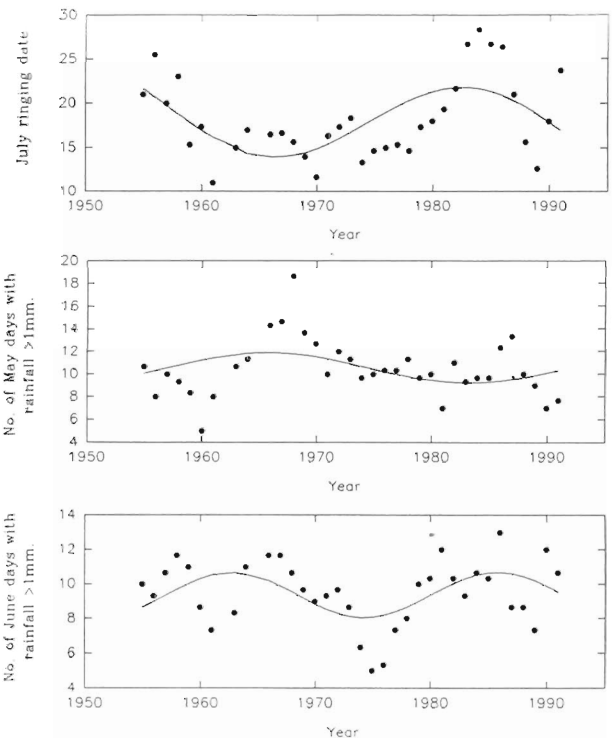

Figure 1.Graphs showing trends in the 3 year running means for the date at which chicks reached the large feathered stage, and the number of days in May and June with rainfall greater than 1mm. Lines show fitted sine functions.

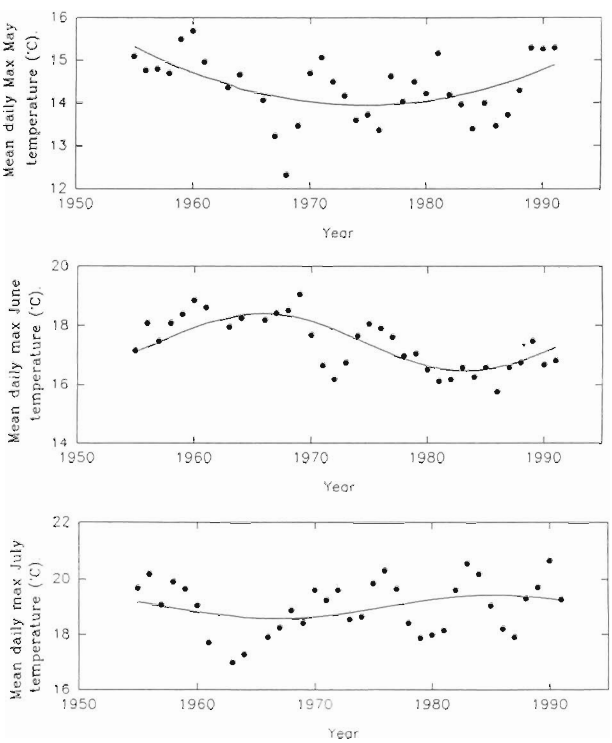

Figure 2. Graphs showing trends in the 3 year running means of mean daily maximum temperature during the months of May, June, and July. Lines show fitted quadratic or sine functions.

Table 1. Functions describing trends in weather and ringing date. All variables are 3-year running means.

Variable	Function type	Statistics.
July ringing date.	Sine	$F_{1,33}$=14.451, P<0.01, explained S^2 =28.4%.
No. May days, rain >1mm	Sine	$F_{1,33}$=4.872, P<0.05, expl. S^2=10.2%.
No. June days, rain >1mm	Sine	$F_{1,33}$=9.361, P<0.01, expl. S^2=19.7%.
Mean daily max May T.	Linear and quadratic	Linear: $F_{1,33}$=9.178, P<0.01 quadratic: $F_{1,33}$=8.501,P<0.01, explained S^2=23.6%
Mean daily max June T.	Linear and sine	Linear: $F_{1,33}$=4.472,P<0.05 Sine: $F_{1,33}$=9.297,P<0.01 expl. S^2=58.4%.
Mean daily max July T.	(Sine)	$F_{1,33}$=3.785,P<0.1, expl. S^2=7.6%.

Table 2. Results from multiple linear regression models for the effects of weather variables on the date at which Common Swifts reached a suitable age for ringing. All variables are 3 year running means.

Variable dropped from full model.	Significance of change.
Mean daily maximum June temperature.	$F_{1,30}$=4.375, P<0.05.
Mean daily maximum May temperature	$F_{1,30}$=8.504, P<0.01.
Mean daily maximum July temperature	$F_{1,30}$=3.517, (P<0.1).
No. June days with rainfall >1mm.	$F_{1,30}$=13.050, P<0.01.
No. May days with rainfall >1mm.	$F_{1,30}$=7.612, P<0.01.
Variable added to full model.	
No. July days with rainfall >1mm.	$F_{1,28}$=0.541, N.S.

Discussion

The mechanisms behind the relationship found in this study may not be simple. At least four components of weather - temperature, sunshine, wind speed, and rainfall - have been found to be important for chick growth rates in Swifts (Lack and Lack 1951) and weather in the prelaying stage has been found to affect the laying date of Common and Pallid Swifts Apus pallidus (Cucco *et al.* 1992, Gory 1987, Thibault *et al.* 1987). No sunshine or wind speed records are available for this colony, but additional long term trends in breeding success, after controlling for temperature and rainfall, suggest that other features of the environment, such as sunshine, wind speed, or insect availability, may have changed in tandem with measured weather variables (Thomson and Douglas-Home in prep.) Thus although the meteorological variables for which data are available do show marked and significant associations with ringing date, it cannot necessarily be concluded that these variables have caused direct or independent changes in the breeding schedule. The patterns are however largely consistent with predictions from the species biology (Lack and Lack 1951). The mechanism may include a direct effect on feeding conditions and an indirect effect on the abundance of aerial insects (e. g. Bryant 1975). While low rainfall in May and higher temperatures in July may be directly detrimental to the birds, these associations with late ringing date may also be due to a more complex indirect relationship with other weather variables or insect abundance.

Since chicks were often ringed within the first two weeks of July, weather during the whole month would naturally be expected to have smaller effects than that during earlier months. The importance of May weather may have influenced laying and hatching dates, but the effects of weather during the later parts of the breeding season suggest that the considerable flexibility in growth rates may also be an important source of variance in the timing of fledging.

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Riassunto- In una piccola colonia di Rondone comune *Apus apus*, situata nel Sud della Scozia, si è evidenziata una relazione tra cambiamenti a lungo termine del tempo atmosferico e i corrispondenti cambiamenti della data di involo dei giovani nidiacei. Le date in cui i giovani hanno raggiunto uno stadio adatto per l'inanellamento sono state significativamente influenzate dalla piovosità e dalle temperature di maggio e giugno. Tutte queste variabili hanno presentato cambiamenti regolari nel tempo. Vi sono inoltre alcune evidenze che le temperature di luglio possono essere cambiate negli anni ed avere influenzato ulteriormente la riproduzione. Nella prima parte della stagione riproduttiva il clima ha influenzato fortemente la data di deposizione e il periodo di deposizione, mentre i cambiamenti climatici di giugno e luglio, che coincidono con gli studi finali dello sviluppo, possono avere avuto effetto sulla velocità di accrescimento dei piccoli.

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