Journal of Animal Ecology 2001
70, 47–61

Climate change and breeding success: decline of the capercaillie in Scotland

ROBERT MOSS*, JAMES OSWALD† and DAVID BAINES‡

**Centre for Ecology and Hydrology, Banchory Research Station, Glassel, Banchory, Kincardineshire AB31 4BW, UK; †Newton Farm House, Dinnet, Aboyne, Aberdeenshire AB34 5PE, UK; and ‡The Game Conservancy Trust, Upland Research Group, Middle End Farm, Middleton-in-Teesdale, Co. Durham DL12 0SA, UK*

Summary

1. The number of capercaillie in Scotland has fallen since the 1970s. Previous work showed that low breeding success, exacerbated by deaths of fully grown birds flying into forest fences, was the primary cause of the decline. The hypothesis that climate change caused the lower breeding success was investigated in this study.

2. Temperature usually rose during April. There was no trend in mean April temperature during the study (1975–99) but there was a progressive cooling in mid-April relative to the rest of the month, such that the normal April warming was increasingly delayed.

3. Hens reared more chicks when the temperature rose more in early April. It is suggested that this stimulated timely plant growth, so improving the laying hens' plane of nutrition and the viability of their chicks.

4. Hens also reared more chicks when late May was warmer and early June was warmer and had fewer rain days. Young chicks may have foraged more successfully in warm dry conditions. However, neither temperature nor rain days in late May or early June showed any trend during the study.

5. Increasingly protracted spring warming seems to have been a major cause of the decline of the capercaillie in Scotland.

Key-words: April temperature, maternal nutrition, phenology, protracted spring warming, *Tetrao urogallus*.

Journal of Animal Ecology (2001) **70**, 47–61

Introduction

Capercaillie (*Tetrao urogallus* L.) numbers in Scotland have fallen greatly since the mid-1970s. By 1992–94 there were estimated to be 2000–3000 (Catt *et al.* 1998) and by 1998–99 about 1000 (N.I. Wilkinson, R.H.W. Langston, R.D. Gregory, R.W. Summers, D.W. Gibbons & M. Marquiss, unpublished manuscript). The primary reason for the decline has been low breeding success, exacerbated by deaths of fully grown birds flying into forest fences (Moss *et al.* 2000). This study examined the hypothesis (Moss 1994) that changes in climate caused the lower breeding success. If so, some aspect of weather should be related to breeding success and should have changed during the study (1975–99).

Many factors affect year-to-year and forest-to-forest variations in the breeding success of capercaillie. A widespread comparison among forest areas in Scotland showed that breeding was more successful where ground cover of blaeberry was optimal (about 15%) and predators fewer (D. Baines, R. Moss & R.W. Summers, unpublished manuscript). In Norway (Slagsvold & Grasaas 1979) and Scotland (Moss 1985) annual variations in breeding success were correlated with the number of days with rain in the first 10 days of June. In another Scottish study (Picozzi, Moss & Kortland 1999), broods of chicks that had eaten more moth larvae survived better, and hens reared more chicks when the available larvae were bigger.

The nutrient requirements of tetraonids seem to be critical twice a year (reviewed by Moss & Hanssen 1980; Moss 1997). The most detailed evidence is from *Lagopus lagopus* and *Lagopus mutus*, but we presume that the following generalizations apply also to capercaillie. First, in spring, earlier availability of newly growing plant food to gravid hens improves the quality of their diet, and so increases egg quality and chick viability. Secondly, in their first 2–4 weeks the chicks have a high requirement for protein, and usually supplement their mostly plant diet with arthropods (Savory 1989). Weather can affect the timing and rate of plant growth in spring, and the availability of arthropods to chicks in early summer. Hence we anticipated that any effects of

Correspondence: R. Moss (fax 01330 823303; e-mail rmoss@ceh.ac.uk).

weather on capercaillie reproduction would be most apparent in spring or early summer.

Materials and methods

STUDY AREAS

The main study area was in Glen Tanar (59°2′N, 2°52′W) in the Dee valley, Aberdeenshire, UK (Moss & Oswald 1985; Picozzi *et al.* 1999). For here, there were data on capercaillie breeding success and weather (daily maximum and minimum temperatures and rainfall) from 1975 to 1999, the latter recorded by estate staff using standard UK Meteorological Office protocols. There was also a more heterogeneous set of data from six forest areas in the Spey valley, Inverness-shire (Table 1).

CAPERCAILLIE COUNTS

Measures of breeding success were based on counts of hens and well-grown chicks, made with the aid of trained dogs, in July and August each summer. Counts at Glen Tanar were done between 5 July and 20 July, and in the Spey valley between 15 July and 25 August. The chicks with a hen were her 'brood'. The 'proportion of hens with broods' (broods/hens) was the proportion of hens with at least one chick. Hens with no chicks included subadults that had not attempted to breed (some first-year birds and a small proportion of second-year birds; Romanov 1979; Borchtchevski 1993; Picozzi *et al*. 1999) and hens that had lost all eggs or chicks. 'Brood size' (chicks/broods) was the mean number of chicks per successful hen. Most successful hens had fewer chicks than eggs laid (average clutch size about seven, usual range 5–11; Cramp & Simmons 1980), partly because some eggs failed to hatch but mostly because some chicks had died. The number of 'chicks per hen' (chicks/hens) was an overall measure of reproductive rate equal to the proportion of hens with broods multiplied by brood size, unless there were no chicks and so no brood size.

Capercaillie are polygynous birds that mate at leks. From 1981 numbers of cocks and hens attending the leks in Glen Tanar during the second half of April were counted (J. Oswald & R. Moss, unpublished data). There were two main leks, where birds were counted several times each season, and a few other sites where birds displayed in some years only. The lekking season is short and hen numbers peaked for a few days only. The median date of peak hen numbers at the main leks was used to indicate the timing of breeding.

ANALYSIS OF DATA

Spurious correlations with weather become increasingly likely as more meteorological data are considered. The number of weather measurements investigated was therefore minimized. First, the analysis was restricted to seasons when there were prior biological reasons to expect an effect of weather on breeding success (see the Introduction). Hens begin to lay their eggs in late April or early May. Most clutches hatch in early June (Moss & Oswald 1985) and chicks depend partly on arthropods, especially lepidopterous larvae, for 3–4 weeks (Kastdalen & Wegge 1985; Picozzi *et al*. 1999). Most chick mortality occurs before the end of June (Moss & Oswald 1985; Moss 1985) and counts began on July 5, so July weather was not considered. Hence the analysis was confined to weather measurements from April, May and June. Secondly, from Slagsvold & Grasaas (1979) and Moss (1985) it seems that 10 days is long enough for sums or averages of meteorological measurements to be biologically meaningful for capercaillie, and short enough to capture relevant weather patterns that might be lost in monthly averages. The analysis was therefore based solely on summary weather measurements from 1–10, 11–20 and 21–30 (or 21–31 for May) of each month and other summary periods were not investigated.

Weather measurements from the same or successive 10-day periods might be confounded with each other. For example, greater rainfall was likely to go together

Table 1. Study areas, years of counts and forest type. Glen Tanar counts involved a total of 320 observations of hens in 1975–98 (mean 13 per count, range 6–26); the 61 Spey valley counts included 492 hen observations (mean 8, range 1–34). Most of the Spey valley observations (420) came from 1989–98. See Table 8 for 1999 sample sizes. The Spey valley weather data were provided to the Natural Environment Research Council by the UK Meteorological Office. Most of the data came from Aviemore (59°12′N, 2°49′W) but no single station had relevant records for the entire study. The Aviemore data were therefore supplemented with data from stations within 20 km [Lagganlia (temperature and rain 1975–82), Insh (rain 1995–98) and Dorback (rain 1999)] to compile a single composite set

Valley	Forest area	Count years	Predominant habitat type
Dee	Glen Tanar	1975–99	Semi-natural Scots pine*
Spey	Abernethy	1989–99	Semi-natural Scots pine
	Castle Grant	1991–93	Scots pine plantation
	Reidhaven	1977, 1979–99	Scots pine plantation
	Inverlaidnan	1979–89, 1992–99	Scots and lodgepole pine† plantation
	Craigmore	1990–99	Scots pine plantation
	Rothiemurchus	1992–99	Semi-natural Scots pine

**Pinus sylvestris.*
†*Pinus contorta.*

with more rain days, and a spell of warm weather might extend from one period to the next. Independence among weather variables was ensured by using principal component (PC) scores (PRINCOMP procedure; SAS Institute 1996). However, measures that were not simultaneous or successive were unlikely to be confounded. Also, PC based on widely separated measurements might have no physical meaning. Therefore, separate principal component analyses (PCA) and scores were calculated for each subset of simultaneous or successive measurements. In the event (below) there were two such subsets.

When PCA are used to identify the chief sources of variation in data, it is customary to discard PC with eigenvalues of less than 1·0. However, we used PCA to ensure independence among explanatory variables. There was no reason to assume that the PC that explained most of the variation in the weather would best explain variations in breeding success. Hence there was no reason to discard PC with small eigenvalues.

We anticipated that one or more weather measurements would be related to breeding success and would show a trend over the study period. However, spurious correlations could arise if breeding success and weather each showed a trend despite no causal relation. We therefore included year as a continuous explanatory variable in some analyses. The parameter estimates (SAS GENMOD procedure) and significance levels used here were derived using partial (SAS type 3) sums of squares. Consequently, the inclusion of year controlled for any linear trends in the explanatory data but not for deviations about such trends.

Generalized linear models (GLM; SAS GENMOD procedure) were used to investigate the effects of weather measurements or PC scores on the three aspects of breeding success. GLM for the number of chicks per hen were Poisson regressions with chick numbers as the dependent variable and $\log_e$(hens) as an offset (Poisson distribution, log link). GLM for the proportion of hens with broods were logistic regressions with broods/hens as the dependent variable (binomial distribution, logit link). GLM for brood size were Poisson regressions with the number of chicks as the dependent variable and $\log_e$(broods) as offset (Poisson distribution, log link). Overdispersion in the data was corrected for by estimating the dispersion parameter as the Pearson's χ^2 statistic divided by its degrees of freedom. Deviances were from SAS type 1 analyses. *F*-statistics from SAS type 3 analyses estimated the significance of each effect, after controlling for all other effects. Postdictions ('predictions' made after the event) and likelihood-based confidence intervals were estimated using the SAS GENMOD procedure.

The category ('class' in SAS terminology) 'valley' was used in some GLM to distinguish Glen Tanar (Dee valley) from Spey valley data. The latter came from six forest areas (Table 1) and so the class 'forest' was also used. Data from different forest areas covered different sets of years (Table 1) and so 'valley' and 'forest' effects were due partly to differences among years, which in turn must have been due partly to differences in weather. It was therefore conservative to include valley or forest classes when testing for effects of weather on breeding success. Year could not be included as a class effect because it would then have been confounded with weather effects.

SELECTION OF WEATHER VARIABLES

Temperature (mean of daily maximum and daily minimum temperatures, °C), rainfall (mean daily rainfall in mm) and rain days (the number of days with rain during each 10-day time period) were considered as a basis for explaining variations in breeding success at Glen Tanar. Hence there were 27 potential explanatory weather measurements (three types of measurement × three months × three 10-day periods). The first stage in selecting useful ones was stepwise regressions (SAS REG procedure) that retained all measurements related ($P < 0·1$) to any of the three aspects of breeding success.

The next stage was backward elimination using GLM. The least significant explanatory measurements were discarded one by one until all remaining were significant ($P < 0·05$). These were then scrutinized to see if their sign was consistent with the birds' biology, and one was discarded (see below). The weather measurements finally selected were each significantly related to at least one aspect of breeding success. Henceforth GLM with breeding success explained by the selected weather measurements, or by PC scores derived from them, are referred to collectively as the model.

VERIFYING AND SIMPLIFYING THE MODEL

The model was developed with Glen Tanar data from 1975 to 1998. It was tested with Spey valley data. The selection procedure was not repeated and only the seven weather measurements previously selected for Glen Tanar were used. Testing was done in two ways. First, eigenvectors from the Glen Tanar weather PCA were used to calculate two sets of PC scores, from the Glen Tanar and from the Spey valley weather data, respectively. These scores were directly comparable between valleys but took no account of possible differences in weather patterns. Secondly, eigenvectors from the Spey valley weather PCA were used to calculate another set of Spey valley PC scores. These were not directly comparable with the Glen Tanar PC scores but did take account of differences in weather patterns.

Subscripts are used to distinguish PC scores derived in different ways: SCORE_{gg} signifies Glen Tanar eigenvectors applied to Glen Tanar weather measurements; SCORE_{ss}, Spey valley eigenvectors applied to Spey valley weather measurements; SCORE_{gs}, Glen Tanar eigenvectors applied to Spey valley weather measurements. For clarity, subscripts are dropped when more than one type of score is being considered simultaneously.

A reduced model represented the main conclusions from the PC GLM analyses. Its explanatory variables were based on the original weather measurements and not on PC scores. It was therefore easier to interpret and should facilitate future comparisons with other studies. We used it to postdict breeding success for 1999.

Results

SELECTION OF WEATHER VARIABLES USING GLEN TANAR DATA

The preliminary stepwise regressions retained 14 of the 27 original weather measurements (Table 2) and the backward selection by GLM retained seven of these. This involved discarding rainfall in early June, despite its statistical significance, because it was positively related to brood size. This made no sense because previous work (Slagsvold & Grasaas 1979; Moss 1985) showed that the number of rain days in early June was negatively related to brood size.

The seven retained measurements included two subsets of simultaneous or successive measurements. So two PCA were done. One involved the three April temperatures, the other temperature and rain days in late May and early June (Table 3). PC scores ($\mathrm{APRIN1}_{gg}$-3_{gg} and $\mathrm{MJPRIN1}_{gg}$-4_{gg}, respectively) were then used as explanatory variables in three separate PC GLM, one for each aspect of breeding success.

Table 2. Weather variables related to capercaillie breeding success, selected from Glen Tanar data. Left, preliminary selection by stepwise regressions (retention level $P < 0·1$) from the original set of 27. Right, final backward selection from the preliminary set, by GLM (retention level $P < 0·05$). T_i is average daily temperature (°C) in period i (1, early; 2, mid; 3, late month), RD_i rain days, and RF_i average daily rainfall (mm)

	Stepwise regressions			Backward GLM		
Weather variable	Chicks per hen	Proportion broods‡	Brood size	Chicks per hen	Proportion broods‡	Brood size§
Apr T_1	*	*		*	*	
Apr T_2	*	†		*	*	
Apr T_3	*	*	*	*	*	
May T_1	*					
May T_3	†			*	*	
Jun T_1	*			*		
Apr RD_1			†			
Apr RD_2		*				
May RD_3	†	*	*	*		
Jun RD_1			*			*
Jun RD_2	†					
Jun RD_3	*	*				
May RF_1			*			
May RF_2	*		*			

†$P < 0·1$, *$P < 0·05$
‡Proportion of hens with broods.
§Includes one removal on grounds of biological implausibility (see text).

Table 3. Principal components analyses of (a) April temperatures (APRIN) and (b) temperature and rain days in late May and early June (MJPRIN) at Glen Tanar. Weather abbreviations are as in Table 2

(a)	APRIN1	APRIN2	APRIN3
Eigenvalues	1·308	0·926	0·767
Proportion*	0·44	0·31	0·26
Eigenvectors			
Apr T_1	0·500	0·785	0·366
Apr T_2	0·656	–0·067	–0·752
Apr T_3	0·565	–0·616	0·548

(b)	MJPRIN1	MJPRIN2	MJPRIN3	MJPRIN4
Eigenvalues	1·824	1·374	0·607	0·194
Proportion*	0·46	0·34	0·15	0·05
Eigenvectors				
May T_3	0·238	–0·653	0·712	–0·095
Jun T_1	0·676	0·222	0·070	0·699
May RD_3	–0·119	0·711	0·669	–0·178
Jun RD_1	–0·687	–0·131	0·200	0·686

*Proportion of variance accounted for.

Table 4. Total and residual deviances from GLM (Table 5) explaining three aspects of breeding success, with and without year as a continuous explanatory variable, for Glen Tanar and the Spey valley separately

Deviance	Chicks per hen	Proportion broods*	Brood size
Glen Tanar			
Total	216·65	72·98	42·24
Residual, no year†	55·94	20·08	15·31
Residual, with year	55·93	19·80	15·30
Spey valley‡			
Total	529·95	248·43	79·04
Residual, no year†	325·86	124·63	49·22
Residual, with year	324·49	123·83	45·07§

*Proportion of hens with broods.
†Not including year as an explanatory variable.
‡Total and residual deviances for Spey valley GLM using PC scores calculated with Glen Tanar (Table 3) or Spey valley (Table A1) eigenvectors were necessarily identical.
§The parameter estimate for year was positive, so the deviance reduction due to year (0·05 < P < 0·1) does not help to explain any decline in brood size.

Weightings (eigenvectors; Table 3) showed that high APRIN1$_{gg}$ scores reflected warmer Aprils, APRIN2$_{gg}$ Aprils that were warmer early but colder late, and APRIN3$_{gg}$ Aprils that were warmer early and late but colder in the middle. Temperature usually rose during April, so a high APRIN3$_{gg}$ score meant that the rise was delayed. High MJPRIN1$_{gg}$ scores reflected warmer and drier early Junes, MJPRIN2$_{gg}$ colder and rainier late Mays, MJPRIN3$_{gg}$ warmer and rainier late Mays, and MJPRIN4$_{gg}$ warmer and rainier early Junes.

GLEN TANAR WEATHER AND BREEDING SUCCESS

The model (PC GLM) explained 74% of the total deviance (Table 4) in the number of chicks per hen at Glen Tanar. Three PC scores, APRIN3$_{gg}$ (–, negative parameter estimate), MJPRIN1$_{gg}$ (+, positive parameter estimate) and MJPRIN2$_{gg}$(–) had significant explanatory value (Table 5). Hence hens reared more chicks in years when the main rise in April temperature was earlier, and when late May and early June were warmer and drier.

The role of April temperature was illustrated by classing it according to breeding success: high, middling or low (Fig. 1). Hens reared most chicks when temperature peaked in mid-April and, if anything, fell (NS) between mid- and late April.

The model (PC GLM) explained 72% of the total deviance in the proportion of hens with broods and 74% of that in brood size (Table 4). APRIN3$_{gg}$(–) was

Table 5. Parameter estimates (± SE) for explanatory variables (weather PC scores) in GLM explaining breeding success for Glen Tanar and the Spey valley, separately and with data combined. The Spey valley data came from six forest areas (Table 1) and so forest was included as a class variable. F-values are from SAS type 3 analyses. Parameter estimates for models with year included as an explanatory variable (not shown) were very similar, the same parameters were significant, and year was never significant

Variable	Chicks per hen	Proportion broods‡	Brood size
Glen Tanar			
APRIN1$_{gg}$	–0·098 ± 0·092	–0·159 ± 0·149	–0·021 ± 0·049
APRIN2$_{gg}$	0·109 ± 0·114	0·057 ± 0·168	0·043 ± 0·064
APRIN3$_{gg}$	–0·727 ± 0·137***	–1·204 ± 0·227****	–0·217 ± 0·080**
MJPRIN1$_{gg}$	0·234 ± 0·069**	0·193 ± 0·112†	0·137 ± 0·037***
MJPRIN2$_{gg}$	–0·299 ± 0·083**	–0·558 ± 0·144***	–0·082 ± 0·049†
MJPRIN3$_{gg}$	0·050 ± 0·119	0·324 ± 0·228	–0·038 ± 0·067
MJPRIN4$_{gg}$	0·277 ± 0·205	0·428 ± 0·328	–0·027 ± 0·119
Spey valley			
APRIN1$_{gs}$	–0·150 ± 0·192	0·004 ± 0·287	–0·163 ± 0·071*
APRIN2$_{gs}$	–0·115 ± 0·192	–0·437 ± 0·296	0·083 ± 0·080
APRIN3$_{gs}$	–0·440 ± 0·219*	–1·210 ± 0·382**	0·084 ± 0·099
MJPRIN1$_{gs}$	0·305 ± 0·128*	0·420 ± 0·220†	0·159 ± 0·052**
MJPRIN2$_{gs}$	0·041 ± 0·176	–0·147 ± 0·271	0·129 ± 0·066†
MJPRIN3$_{gs}$	0·266 ± 0·196	0·762 ± 0·281**	–0·096 ± 0·076
MJPRIN4$_{gs}$	0·006 ± 0·533	–0·065 ± 0·799	–0·084 ± 0·186
FOREST§	$F_{5,48}$ = 1·79, NS	$F_{5,48}$ = 3·57**	$F_{5,41}$ = 1·85, NS
Both valleys (seven forests)			
APRIN1	–0·106 ± 0·103	–0·042 ± 0·153	–0·059 ± 0·040
APRIN2	–0·081 ± 0·106	–0·224 ± 0·160	0·011 ± 0·045
APRIN3	–0·530 ± 0·129****	–1·097 ± 0·209****	–0·077 ± 0·056
MJPRIN1	0·243 ± 0·072***	0·248 ± 0·111*	0·139 ± 0·029****
MJPRIN2	–0·147 ± 0·085†	–0·365 ± 0·135**	0·015 ± 0·036
MJPRIN3	0·118 ± 0·113	0·481 ± 0·174**	–0·072 ± 0·048
MJPRIN4	–0·028 ± 0·216	0·094 ± 0·342	–0·128 ± 0·086
FOREST	$F_{6,71}$ = 2·23*	$F_{6,71}$ = 4·64***	$F_{6,63}$ = 1·93†

†P < 0·1, *P < 0·05, ** P < 0·01, ***P < 0·001, **** $P \leq$ 0·0001.
‡Proportion of hens with broods.

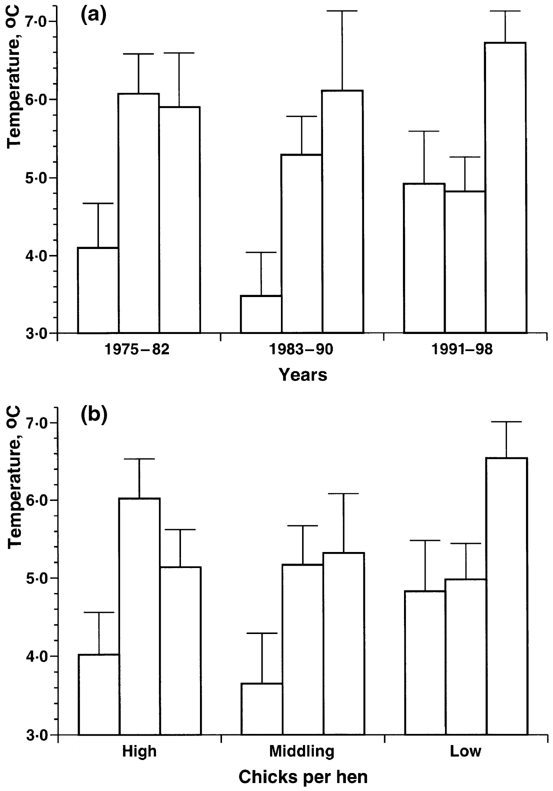

Fig. 1. (a) April temperatures at Glen Tanar in 1975–82, 1983–90, 1991–98; (b) April temperatures at Glen Tanar in years of high (chicks per hen > 1·95), middling and low (chicks per hen < 0·9) breeding success. Columns represent means, bars SEM, *n* = 8 for early, middle and late April. Temperature profiles were similar (though not shown) for the proportion of hens with broods (category thresholds 0·48, 0·67) and brood size (category thresholds 1·0, 3·05).

significant for each aspect, as for chicks per hen (above). However MJPRIN1$_{\rm gg}$(+) was significant for brood size but not (0·05 < P < 0·1) for the proportion of hens with broods, while MJPRIN2$_{\rm gg}$(–) was significant for the proportion of hens with broods but not (0·05 < P < 0·1) for brood size.

In 1981–99 (no data 1992) the mean date when the peak number of hens was seen at Glen Tanar leks was 23 April (range 17–27). Hens attended leks earlier as the years passed (parameter estimate –0·23 ± 0·07 days year^{-1}; SAS GENMOD procedure, normal distribution, identity link χ^2_1 = 6·94, P = 0·008, total deviance 90·5, residual deviance 61·5). Peak hen date, however, was not significant when entered as an explanatory variable into the GLM for breeding success.

TESTING THE MODEL WITH SPEY VALLEY DATA

The first Spey valley capercaillie data were from 1977 but most were from 1989 onwards (Table 1). This section uses Spey valley weather PC scores derived using Glen Tanar eigenvectors. Results from PC scores using Spey valley eigenvectors (Table A1) are in the Appendix (Table A2).

The model (PC GLM) explained 39% of the total deviance in chicks per hen in the six Spey valley forest areas (Table 4). APRIN3$_{\rm gs}$(–) and MJPRIN1$_{\rm gs}$(–), but not forest, had significant explanatory value (Table 5). Hence, as at Glen Tanar, hens reared more chicks when April temperature rose earlier, and when early June was warmer and drier. A difference was that MJPRIN2(–), reflecting colder, wetter, late May weather, had no significant effect in the Spey valley.

The model (PC GLM) explained 50% of the total deviance in the proportion of hens with broods (Table 4). APRIN3$_{\rm gs}$(–), MJPRIN3$_{\rm gs}$(+) and forest each had significant explanatory value (Table 5). Hence, as at Glen Tanar, a greater proportion of hens had chicks when April temperature rose earlier. Although the effect of warmer, wetter, late May weather [MJPRIN3(+)] was not significant at Glen Tanar, the parameter estimates were in the same direction in both valleys.

The model (PC GLM) explained 38% of the total deviance in brood size. APRIN1$_{\rm gs}$(–) and MJPRIN1$_{\rm gs}$(+) had significant explanatory value, so that colder Aprils and warmer, drier, early Junes were followed by bigger broods.

In short, the main conclusions for Glen Tanar were validated by the Spey valley results: the number of chicks per hen was enhanced by an earlier rise in April temperature (APRIN3) and by warmer, drier, weather in early June (MJPRIN1). There were, however, some apparent differences between valleys. Also, in both valleys, there was a hint that the proportion of hens with broods and brood size were each influenced by somewhat different factors. Data from the two valleys were combined to explore such differences.

COMBINED DATA

The combined data were first analysed with forest (Glen Tanar and the six Spey valley forest areas) and the PC weather scores as main effects in three GLM (Table 5) without interactions. We then checked for differences between valleys by using valley (Dee, Spey) as an additional class variable, entering forest as a main effect as before and valley × PC scores as interactions.

The main effects significant in Table 5 were also significant in the GLM with valley × PC score interactions. The only exception was that the main effect APRIN1(–) was insignificant in the former but significant ($F_{1,56}$ = 4·51, P = 0·038) in the latter. Even so, the parameter estimates (–0·059 ± 0·040 and –0·163 ± 0·069, respectively) were not significantly different. The rest of this section reports results from the GLM with interactions. Insignificant PC scores are not mentioned.

Although warmer Aprils (APRIN1) were probably followed by depressed brood sizes (previous paragraph), the main effect APRIN1 had no significant effect on chicks per hen ($F_{1,64}$ = 1·25, P = 0·27) or the proportion of hens with broods ($F_{1,64}$ = 0·21, P = 0·65). No valley × APRIN1 interaction was significant.

Table 6. Trends in breeding success, weather measurements and weather PC scores during 1975–78. PC scores were derived using Glen Tanar eigenvectors (slopes from scores using Spey valley eigenvectors are in Table A3). Slopes were from least squares linear regressions, or (Spey valley breeding success only) analyses of covariance with forest as a class variable. Weather abbreviations are as in Table 2. The April T index is the April warming index defined in Table 7

	Glen Tanar			Spey valley		
Breeding	Slope ± SE	P	R^2	Slope ± SE	P	R^2
Chicks per hen	–0·095 ± 0·026	0·001	0·39	–0·049 ± 0·033	0·14	0·24
Proportion broods*	–0·021 ± 0·006	0·002	0·38	–0·022 ± 0·008	0·009	0·32
Brood size	–0·065 ± 0·026	0·018	0·24	–0·009 ± 0·033	0·79	0·16
Weather						
Apr T_1	0·065 ± 0·050	0·21	0·07	0·113 ± 0·048	0·028	0·20
Apr T_2	–0·073 ± 0·039	0·078	0·13	–0·029 ± 0·044	0·52	0·02
Apr T_3	0·055 ± 0·050	0·28	0·05	0·048 ± 0·064	0·46	0·03
May T_3	–0·012 ± 0·051	0·81	0·00	0·021 ± 0·049	0·67	0·01
May RD_3	0·009 ± 0·082	0·92	0·00	–0·002 ± 0·008	0·82	0·00
Jun T_1	–0·098 ± 0·064	0·14	0·10	0·039 ± 0·064	0·55	0·02
Jun RD_1	0·029 ± 0·068	0·67	0·01	–0·006 ± 0·005	0·29	0·05
Apr T (month)	0·016 ± 0·032	0·63	0·01	0·044 ± 0·033	0·19	0·08
Apr T index	–0·133 ± 0·040	0·003	0·33	–0·109 ± 0·038	0·01	0·27
PC scores						
APRIN1	0·003 ± 0·035	0·93	0·00	0·035 ± 0·037	0·35	0·04
APRIN2	0·013 ± 0·029	0·66	0·01	0·035 ± 0·036	0·34	0·04
APRIN3	0·070 ± 0·022	0·004	0·32	0·055 ± 0·022	0·023	0·21
MJPRIN1	–0·040 ± 0·040	0·32	0·05	0·002 ± 0·037	0·95	0·00
MJPRIN2	–0·004 ± 0·035	0·91	0·00	–0·012 ± 0·031	0·70	0·01
MJPRIN3	–0·004 ± 0·024	0·88	0·00	–0·011 ± 0·023	0·64	0·01
MJPRIN4	–0·022 ± 0·013	0·096	0·12	0·030 ± 0·014	0·033	0·19

*Proportion of hens with broods.

The main effect APRIN3(–) was significant for chicks per hen ($F_{1,64}$ = 17·93, $P \le 0·0001$) and for the proportion of hens with broods ($F_{1,64}$ = 29·99, $P \le 0·0001$). For brood size, the main effect was not significant ($F_{1,56}$ = 1·09, P = 0·30) but a significant ($F_{1,56}$ = 5·65, P = 0·02) APRIN3 × valley interaction occurred, such that the timing of the rise in April temperature was related to brood size in Glen Tanar but not in the Spey valley.

The main effect MJPRIN1 was significant for chicks per hen ($F_{1,64}$ = 12·17, P = 0·0009), for the proportion of hens with broods ($F_{1,64}$ = 5·85, P = 0·019) and for brood size ($F_{1,56}$ = 21·49, P = 0·0001). There was no significant valley × MJPRIN1 interaction. Warmer, drier, early Junes were followed by higher breeding success in all its aspects.

The main effects MJPRIN2 and MJPRIN3 had no significant influence on chicks per hen (respectively $F_{1,64}$ = 1·61 and 1·63, P = 0·21 and 0·21) or brood size ($F_{1,56}$ = 0·32 and 1·71, P = 0·58 and 0·20), although for brood size there was a significant MJPRIN2 × valley interaction ($F_{1,56}$ = 6·56, P = 0·013). MJPRIN2(–) and MJPRIN3(+), however, had significant but opposite effects on the proportion of hens with broods ($F_{1,64}$ = 4·82 and 6·92, P = 0·03 and 0·011). Hence colder, rainier, late May weather (MJPRIN2) was associated with a smaller proportion of hens with broods, and warmer, wetter, late May weather (MJPRIN3) with a greater proportion. It follows that warmer temperature in late May, and not fewer rain days, enhanced the proportion of hens with broods.

In brief, the combined data confirmed that APRIN3 and MJPRIN1 influenced the number of chicks per hen. APRIN3 had its greatest effect on the proportion of hens with broods, while MJPRIN1 was the strongest influence on brood size. Temperature in late May seemed to affect the proportion of hens with broods but not brood size. Also, significant interactions indicated that the effects on brood size of APRIN3 and MJPRIN2 differed between the two valleys.

YEAR AS AN EXPLANATORY VARIABLE

At Glen Tanar, all three aspects of breeding success showed significant declines during 1975–98 (Table 6). We checked for non-linearity in these declines, and those of the seven relevant weather measurements and PC scores, by trying up to five extra polynomial year terms as explanatory variables (SAS RSQUARE and GENMOD procedures). None but year was significant, suggesting that each decline was adequately described by a simple linear trend. In the Spey valley, where most of the data were from 1989 to 1998 (Table 1), only the proportion of hens with broods showed a significant decline, although the slopes of the regressions of chicks per hen and brood size upon year were each negative.

Year was entered into the model as a continuous explanatory variable, to check whether associations between weather and breeding success were artefacts of two causally unrelated linear trends. After the effects of weather had been taken into account, year explained

Table 7. Reduced model, GLM parameter estimates ± SE, explaining breeding success in terms of an index of April warming [(Apr T_2 – Apr T_1) – (Apr T_3 – Apr T_2)]/2, late May temperature, early June rain days and forest (Glen Tanar and the six Spey valley areas; Table 1). Weather abbreviations are as in Table 2. Parameter estimates (not shown) from GLM including year (effect not significant) were very similar

Variable	Chicks per hen	Proportion broods‡	Brood size
April T index	0·282 ± 0·064****	0·582 ± 0·105****	0·061 ± 0·028*
May T_3	0·159 ± 0·051**	0·355 ± 0·078****	0·034 ± 0·029
June RD_1	–0·098 ± 0·042*	–0·051 ± 0·061	–0·077 ± 0·017****
Forest	$F_{6,75}$ = 2·33*	$F_{6,75}$ = 5·03***	$F_{6,61}$ = 2·10†
May T_3 × forest	–	–	$F_{6,61}$ = 2·32*
Deviances§ from GLM			
Total	793·4	338·2	125·0
April T index	652·0	274·5	117·8
May T_3	571·1	230·3	115·3
June RD_1	518·8	225·4	92·1
Forest	426·7	160·4	79·4
May T_3 × forest	–	–	65·2

†P < 0·1, *P < 0·05, **P < 0·01, ***P < 0·001, ****P ≤ 0·0001.
‡Proportion of hens with broods.
§Total deviance, with no explanatory variables, and residual deviances after the explanatory variable on the left was added to the model.

little extra deviance (Table 4) and had no significant negative effect upon any aspect of breeding success in either valley. Parameter estimates (Table 5 and Table A2) were very similar with and without year as an explanatory variable. All this suggested that weather was sufficient to explain the decline in breeding success. If so, the relevant aspect of weather should also have changed over the years (Table 6).

APRIN3 scores (APRIN3$_{gg}$, APRIN3$_{gs}$, APRIN3$_{ss}$) were each related to breeding success (Table 5 and Table A2). They increased significantly during 1975–98 (Table 6 and Table A3), not because of any change in mean monthly April temperature but because more of the April rise in temperature occurred later in the month. Mid-April temperature declined over the years when early and late April temperatures were held constant in partial correlations (Glen Tanar, partial Pearson $r = -0·497$, $P = 0·019$; Spey valley, partial $r = -0·432$, $P = 0·045$).

The changing pattern of April temperature was illustrated by classing Glen Tanar data according to date: early (1975–82), mid- (1983–90) or late (1991–98) study (Fig. 1). Early on, average temperature rose most between early and mid-April. Late in the study, temperature rose most between mid- and late April. Temperature was also classed according to breeding success (Fig. 1). The temperature profiles were similar when temperature was classed according to year (early, mid- and late study) or to breeding success (high, middling and low, respectively).

In the Spey valley, as at Glen Tanar, the rise in April temperature (APRIN3$_{ss}$) occurred progressively later in the month during the study (Table A4). An apparent difference between valleys was that early April temperature increased significantly in the Spey valley but not in Glen Tanar (Table 6). The slopes of the regressions from the two valleys, however, were not significantly different.

REDUCED MODEL

For simplicity, a reduced set of explanatory variables (Table 7, Fig. 2 and Fig. 3) was devised. These were an index representing the timing of April warming, late May temperature, and rain days in early June. The index, resembling APRIN3 but with opposite sign, was half the difference between the temperature rise in the first half of April and that in the second half, [(Apr T_2 – Apr T_1) – (Apr T_3 – Apr T_2)]/2.

To check whether the effects of weather differed among forests, data from Glen Tanar and the Spey valley were combined, and interactions between forest and each weather variable entered into the reduced model. Insignificant interactions were dropped one by one, so retaining the three main effects and, for brood size only, the forest × late May temperature interaction. The main effect, late May temperature, was not significant for brood size, and so this interaction indicated that warmer late Mays were associated with bigger broods in some forest areas but not in others.

Postdictions of breeding success (Table 8), made with the reduced model, involved all data up to 1998 but only weather data for 1999. Despite low sample sizes, the model postdicted the low number of chicks per hen and brood size quite accurately. Postdictions for the proportion of hens with broods were even lower than observed. This was because the April warming index was much lower than previously recorded: April 1999 began and ended with relatively high temperatures but was cold in the middle. Hence the postdictions involved extrapolations outside the range of index values upon which the model was based.

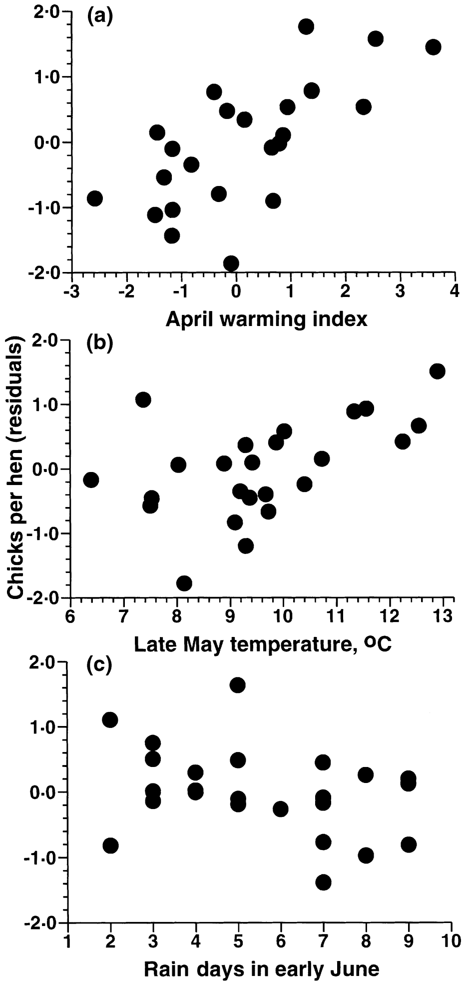

Fig. 2. Partial plots, from the reduced model (Table 7), of breeding success at Glen Tanar in relation to (a) the April warming index, (b) late May temperature and (c) early June rain days.

A prediction was made for breeding success at Glen Tanar before the counts were done (Table 8). It used an early version of the model, which was based on Glen Tanar data only and did not include late May temperature, but nonetheless correctly predicted low breeding success.

OUTLIERS – EXAMPLES OF HIGH BREEDING SUCCESS IN INCLEMENT WEATHER

Two outliers, included in all versions of the model, showed capercaillie having locally higher breeding success than postdicted from weather, and higher than capercaillie in other forests nearby. At Inverlaidnan in 1992 the three hens seen had 15 chicks between them (reduced model postdiction 5·7 chicks; 95% confidence level for mean, 4·0–8·3) while the other 55 Spey valley hens had 102 chicks ($\chi_1^2 = 10{\cdot}08$, $P = 0{\cdot}0015$). At Craigmore in 1997, 10 hens had 27 chicks (postdicted 12·0 chicks; 95% confidence level 9·2–15·5), while the other 45 Spey valley hens had 12 chicks altogether ($\chi_1^2 = 48{\cdot}73$, $P \leq 0{\cdot}0001$). The reduced model used here included forest as a class effect, and so these outliers were not simply the result of Inverlaidnan and Craigmore being consistently better habitat. Both outliers were associated with much green brash from ongoing forestry operations that had started in previous years. However, silvicultural operations in other forest areas were not always associated with better breeding.

Discussion

MODEL SELECTION AND VERIFICATION

The retrospective selection of explanatory weather variables is perilous. The danger of spurious correlations was reduced by considering only variables with a prior biological rationale. Also, the 10-day period for weather averages was fixed before the analysis. In the event, seven explanatory weather measurements were selected from a potential set of 27. In addition, the model was developed on one set of data (Glen Tanar) and tested on another (Spey valley). Finally, the model was developed using data from 1975–98 and then used

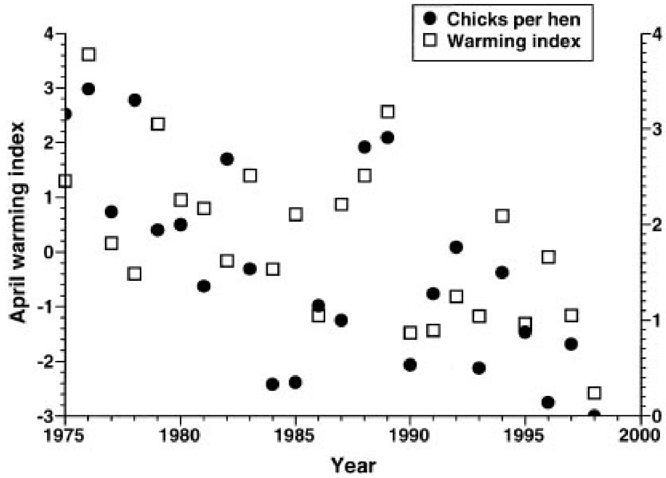

Fig. 3. The April warming index (Table 7) and breeding success declining together at Glen Tanar.

Table 8. Breeding success postdicted for 1999, from the reduced model with main effects only. At Castle Grant no count was done, at Reidhaven no hens were seen. Column heading Observation means observed, P'dict postdicted. The 95% confidence limits (CL) are for the postdictions. Predictions for Glen Tanar, based on an earlier version of the model, were made on 2 July, 1999: chicks per hen 0·0 (95% CL 0·0–0·5); proportion of hens with broods 0·13 (CL 0·04–0·37); brood size 1·2 (CL 0–2·4)

		Sample size		Chicks per hen			Proportion broods*			Brood size		
Vakkey	Forest	Hens	Broods	Observation	P'dict	95% CL	Observation	P'dict	95% CL	Observation	P'dict	95% CL
Dee	Glen Tanar	7	1	0·3	0·3	0·1–0·6	0·14	0·03	0·01–0·12	2·0	2·1	1·4–3·1
Spey	Abernethy	15	0	0·0	0·1	0·03–0·3	0·00	0·01	0·001–0·03	–	2·3	1·4–3·6
Spey	Craigmore	9	3	0·9	0·2	0·07–0·5	0·33	0·03	0·01–0·09	2·7	1·6	1·1–2·5
Spey	Inverlaidnan	5	0	0·0	0·3	0·1–1·0	0·00	0·06	0·01–0·23	–	2·5	1·6–3·8
Spey	Rothiemurchus	7	3	0·7	0·3	0·1–1·0	0·43	0·02	0·05–0·11	1·7	2·3	1·4–3·7

*Proportion of hens with broods.

successfully to predict and postdict low breeding success in 1999 (Table 8).

WEATHER AND BREEDING SUCCESS

At Glen Tanar and in the Spey valley hens reared more chicks when April temperature rose earlier (Table 5, Fig. 1 and Fig. 2), when late May was warmer (Tables 5 and 7 and Table A2), and when early June was warmer and drier (Tables 5 and 7, see the Appendix). Spring weather is critical for the nutrition of gravid hen tetraonids and can indirectly affect the viability of chicks (Introduction). Plant growth in April depended upon rising temperature. We suggest that, when this rise occurred mainly between early and mid-April, gravid hens had enough newly growing plant food just when they needed it. If so, the hens' plane of nutrition and thereby chick viability would have been enhanced.

The increase in early April (1–10 April) temperature during 1975–98 (Table 6), significant in the Spey valley, was obviously not sufficient to induce higher breeding success. Indeed, high temperatures in March or early April might not increase breeding success, for any nutritious flush of new plant growth might then pass before the birds need it. Also, slow spring growth associated with protracted warming might be less nutritious than a burst of growth due to sudden warming. We speculate further below.

Capercaillie are single-brooded but some hens renest if their eggs are robbed by predators (Cramp & Simmons 1980). In Norway, about a third of robbed hens renested, although the proportion varied greatly from year to year (Spidsø, Wegge & Storaas 1985; T. Storaas, P. Wegge & L. Kastdalen, unpublished manuscript). The diet of late renesters and their offspring may not conform to our generalizations about phenology but, to judge from the estimated age of chicks seen during counts (unpublished data), most broods would have been from first nests.

Most chicks hatch in early June and are still in the egg in late May. Hence the main effects of late May weather on capercaillie chicks are likely to operate through phenology. Capercaillie plant foods, such as blaeberry (Spidsø & Stuen 1987; Storch 1993), are in full growth by late May and so the most relevant effects are likely to be on the number and size of arthropods, such as moth larvae (Picozzi *et al.* 1999).

Early June weather too may influence arthropod size and abundance, and is likely also to affect the chicks' ability to forage for arthropods (Moss 1985). Such effects are likely to have their biggest impacts on chicks, up to about 20 days of age, that are still eating many arthropods (Picozzi *et al.* 1999). In short, the main associations observed between weather and breeding success are consistent with the birds' biology.

Some minor variations occurred on the main themes above. Factors affecting the proportion of hens with broods may have differed somewhat from those affecting brood size. First, more rain days in early June preceded lower brood sizes (Table 7) but not lower proportions of hens with broods. Perhaps rainy weather caused attrition of chicks without necessarily causing deaths of entire broods. Secondly, warmer late Mays preceded higher proportions of hens with broods but had no consistent effect on brood size (Table 5 and Table 7). Perhaps effects of late May temperature on arthropods predominantly influenced the proportion of total failures shortly after hatching. This could happen, for example, if a brood's early survival depended on it locating a patch rich in big arthropods.

Despite no overall effect of late May temperature on brood size, there was a significant forest × late May temperature interaction (Table 7). Hence any influence of late May temperature on brood size varied among forests. If so, this might have depended on how habitat interacted with temperature, perhaps by influencing the availability or size of arthropods.

HABITAT AND BREEDING SUCCESS

Management of forests affects capercaillie, partly through its impact on habitat and predators (D. Baines, R. Moss & R.W. Summers, unpublished manuscript). During the study, the main change at Glen Tanar, a semi-natural Caledonian forest remnant, was due to a perimeter fence erected in 1968–69. This excluded red deer and subsequently the ground vegetation, predominantly heather (*Calluna vulgaris* L.) with blaeberry, became taller and ranker. The Spey valley data came from six different forest areas, each with different management, and in some big changes occurred during the study. This included, for example, thinning and felling of trees, changes in drainage, and changes in the number of predators being killed by gamekeepers and wardens. The valley and forest terms in the model assumed constant differences among forests and did not allow for changes in suitability for capercaillie. Also, the runs of data were from different years in different forests, so that valley and forest terms would have included some effects due to differences among years. Consequently, statistically significant effects involving valley and forest as classes must be interpreted with caution.

The very heterogeneity of the data, however, argues against the decline in breeding success being due mostly to habitat change. We noted no such change common to all the forest areas. Also, the inclusion of year as a continuous variable in the model scarcely increased the deviance explained by weather, suggesting that changes in weather were a sufficient explanation for the decline. In these circumstances, the similarity of the results from the two valleys is consistent with a pervasive influence of weather.

Even so, the unpostdictedly high breeding success at Inverlaidnan in 1992 and Craigmore in 1997 may mean that weather is not always an overriding influence. We used a single set of weather data for all six Spey valley forest areas (Table 1) and so unconsidered local variations in weather may have affected capercaillie breeding success. Alternatively, factors other than weather may have varied locally. For example, an unusually rich source of large arthropods might overcome any depressing effect of a rainy early June upon arthropod size and abundance. Such sources might include wet ground (Stuen & Spidsø 1988), decomposing brash, or a ground flora and fauna invigorated by the extra light that follows thinning or felling of trees. The effects of silvicultural operations upon the abundance of arthropods suitable for capercaillie chicks deserve investigation.

CLIMATE CHANGE AND BREEDING IN BIRDS

It is adaptive for herbivores to grow and reproduce at times when their plant foods are most nutritious. New plant growth in spring is rich in nutrients and highly digestible to herbivores adapted to its defensive toxins (Moss 1997), but becomes tougher and less digestible as it matures (Dury *et al.* 1998). The hatching of winter moth (*Operophtera brumata*) larvae (Buse *et al.* 1999), for example, seems timed to take advantage of this short spring feast and the same probably applies to egg laying by hen capercaillie.

The onset of plant growth, however, varies from year to year. Experimentally elevated temperatures caused earlier budburst in pedunculate oaks (*Quercus robur*), a food of winter moths, and shortened the time between budburst and leaf maturation (Buse *et al.* 1999). Winter moth larvae in the same experimental conditions hatched earlier and grew faster, so that peak larval biomass was earlier and shorter but no smaller. Tetraonids, however, seem to respond less flexibly to variations in the onset of spring growth, laying poorer quality eggs when springs are later (see the Introduction).

Tetraonids have another apparent constraint on their fitness. Winter moth larvae are a staple diet for chicks of both capercaillie and great tits (*Parus major*) and, for each bird species, hatching is timed such that the growing chicks' need for larvae more or less coincides with peak larval abundance (Perrins 1991; Baines, Wilson & Beeley 1996; Picozzi *et al.* 1999). Hence a long-term advance in plant phenology might lead to mismatches between larval abundance and chick requirements, lower breeding success or recruitment, and selection for an earlier laying date.

Visser *et al.* (1998) gave evidence that warmer springs in the Netherlands have led to mistimed reproduction in great tits. Plant phenology and the date of peak larval abundance advanced in 1973–95 and there was selection for earlier egg laying by adults. The mean laying date of great tits could, under selection, change by 0·5 days per generation (van Noordwijk, van Balen & Scharloo 1981). In the Netherlands, however, selection was ineffective and the date of egg laying did not change. In an English study of great tits (McCleery & Perrins 1998), by contrast, the date of egg laying advanced during 1970–97.

The date of peak hen numbers at capercaillie leks advanced during our study, consistent with the generalization (Crick *et al.* 1997; McCleery & Perrins 1998; Crick & Sparks 1999) that UK birds are breeding earlier. That early April tended to become somewhat warmer during the study, significantly so in Speyside (Table 6), is consistent with the explanation that earlier breeding is due to advanced plant phenology (Myneni *et al.* 1997). However, the date of the main April warming (indicated by APRIN3 or the April warming index; Table 6 and Fig. 3) became later through our study. Under these complex conditions, it is not clear whether earlier breeding by capercaillie was adaptive.

If spring came earlier but was otherwise the same, capercaillie hens might get a better quality diet by mating and laying earlier. If spring simply came later, they might get better food by delaying breeding. But the rate of plant growth, and not just its onset, depends on temperature. A spring that started earlier but warmed more slowly, for example, might involve a reduced plant growth rate, reduced food quality, and a decline in the laying hens' plane of nutrition. In this case, hens breeding earlier could not offset a consequent decrease in chick viability.

Perhaps warmer Aprils were followed by earlier peaks in larval abundance. If so, the association between warmer Aprils (APRIN1) and smaller broods (see combined data in the Results) might be explained by peaks in larval abundance coming too early to satisfy the chicks' requirements. In Glen Tanar in 1991–96 larvae were abundant during the first 2–3 weeks of June but then many pupated and became unavailable to the chicks, which turned more to other, presumably less nutritious, invertebrates (Picozzi *et al.* 1999). In the same study, chicks that ate more larvae survived better. It is not known, however, whether peak larval abundance advanced during our study. Although the hens' earlier breeding would seem to have reduced any mismatch between larval availability and the chicks' requirements, the date of peak hen numbers at leks had no significant effect upon breeding success.

In short, as the years passed hens attended leks earlier and reared fewer chicks. It is not clear whether earlier breeding was adaptive. There is insufficient evidence to decide whether a mismatch between the chicks' needs and the availability of larvae contributed to the fall in breeding success.

CLIMATE CHANGE AND THE DECLINE IN CAPERCAILLIE NUMBERS

The decline of capercaillie in Scotland has been due primarily to lower breeding success (Moss *et al.* 2000). Suggested mechanisms, reviewed by Moss (1994), include habitat destruction through changed silvicultural practices, reductions in the quality of chick-rearing habitat through overgrazing by red deer *Cervus elaphus* (Baines, Sage & Baines 1994), increased predation, climate change and widespread pollution.

Glen Tanar was a Caledonian forest remnant, with effective predator control by keepers, little active habitat management, and light grazing by large herbivores throughout the study. Here, therefore, habitat destruction, increased predation and overgrazing cannot explain the lower breeding success. Progressively delayed spring warming during 1975–99 was sufficient to account for the fall in breeding success at Glen Tanar and in the Spey valley (Tables 4, 7 and Table 8 and Fig. 3). A trend in a weather pattern lasting for 25 years can reasonably be called climate change, and so the present evidence supports the suggestion that climate change has been a major factor causing the decline of Scottish capercaillie.

Climate change is outwith our immediate control, but this does not mean that the decline in capercaillie numbers cannot be reversed. Habitat management and predator control can probably contribute to improved breeding success (D. Baines, R. Moss & R.W. Summers, unpublished manuscript). In addition, deaths of fully grown birds flying into forest fences (Catt *et al.* 1994; Baines & Summers 1997) have contributed to the decline, which might not have occurred had such deaths been substantially fewer (Moss *et al.* 2000).

Acknowledgements

The work was funded partly by the Natural Environment Research Council, the Royal Society for the Protection of Birds, the Forestry Commission, Scottish Natural Heritage, the Scottish Forestry Trust, Eagle Star and Horsens Folkeblad A/S. R.A. Parr, D.C. Catt, N. Picozzi, A. Stolte, L. Rattray, D. Dugan, D. Clements, S. Franks, R. Moncrieff, D. Gladwin, M. Andrew, R. Proctor, P. Baker, N. Cobley, R. Hawley, Y. Sheldon and many others helped with field work. Numerous landowners gave permission to work on their land and many keepers, rangers, foresters, factors and students gave invaluable assistance. M. Marquiss and N. Picozzi made helpful comments on the manuscript, D. Elston and P. Rothery advised on statistics.

References

Baines, D. & Summers, R.W. (1997) Assessment of bird collisions with deer fences in Scottish forests. *Journal of Applied Ecology*, **34**, 941–948.

Baines, D., Sage, R.B. & Baines, M.M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology*, **31**, 776–783.

Baines, D., Wilson, I.A. & Beeley, G. (1996) Timing of breeding in black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. *Ibis*, **138**, 181–187.

Borchtchevski, V.G. (1993) *Population Biology of the Capercaillie, Principles of the Structural Organization*. Central Laboratory of the Management of Hunting and Nature Reserves, Moscow, Russia [in Russian with English summary].

Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G. (1999) Effects of elevated temperature on multi-species interactions: the case of pedunculate oak, winter moth and tits. *Functional Ecology*, **13**, 74–82.

Catt, D.C., Baines, D., Picozzi, N., Moss, R. & Summers, R.W. (1998) Abundance and distribution of capercaillie *Tetrao urogallus* in Scotland 1992–94. *Biological Conservation*, **85**, 257–267.

Catt, D.C., Dugan, D., Green, R.E., Moncrieff, R., Moss, R., Picozzi, N., Summers, R.W. & Tyler, G.A. (1994) Collisions against fences by woodland grouse in Scotland. *Forestry*, **67**, 105–118.

Cramp, S. & Simmons, K.E.L. (1980) *The Birds of the Western Palearctic*, Vol. II. Oxford University Press, Oxford, UK.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg-laying trends. *Nature*, **399**, 423–424.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.

Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A. & Kaye, T. (1998) The effects of increasing CO_2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology*, **4**, 55–62.

Kastdalen, L. & Wegge, P. (1985) Animal food in capercaillie and black grouse chicks in south-east Norway – a preliminary report. *Proceedings of the Third International Grouse Symposium* (eds P.J. Hudson & T.W.I. Lovel), pp. 499–513. World Pheasant Association, Lower Basildon, UK.

McCleery, R.H. & Perrins, C.M. (1998) ... temperature and egg-laying trends. *Nature*, **391**, 30–31.

Moss, R. (1985) Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. *Ibis*, **128**, 65–72.

Moss, R. (1994) Decline of capercaillie (*Tetrao urogallus*) in Scotland. *Gibier Faune Sauvage*, **11** (Special number), 217–222.

Moss, R. (1997) Grouse and ptarmigan nutrition in the wild and in captivity. *Proceedings of the Nutrition Society*, **56**, 1137–1145.

Moss, R. & Hanssen, I. (1980) Grouse nutrition. *Nutrition Abstracts and Reviews*, **50B**, 555–567.

Moss, R. & Oswald, J. (1985) Population dynamics of capercaillie in a north-east Scottish glen. *Ornis Scandinavica*, **16**, 229–238.

Moss, R., Picozzi, N., Summers, R.W. & Baines, D. (2000) Capercaillie *Tetrao urogallus* in Scotland – demography of a declining population. *Ibis*, **142**, 259–267.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

van Noordwijk, A.J., van Balen, J.H. & Scharloo, W. (1981) Genetic variation in the timing of reproduction in the great tit. *Oecologia*, **49**, 158–166.

Perrins, C.M. (1991) Tits and their caterpillar food supply. *Ibis*, **133**, 49–54.

Picozzi, N., Moss, R. & Kortland, K. (1999) Diet and survival of capercaillie *Tetrao urogallus* chicks in Scotland. *Wildlife Biology*, **5**, 11–23.

Romanov, A.N. (1979) *Capercaillie*. Nauka, Moscow, Russia [in Russian].

SAS Institute (1996) *SAS/STAT Software: Changes and Enhancements Through Release 6.11*. SAS Institute Inc., Cary, NC.

Savory, C.J. (1989) The importance of invertebrate foods to chicks of gallinaceous species. *Proceedings of the Nutrition Society*, **48**, 113–133.

Slagsvold, T. & Grasaas, T. (1979) Autumn population size of the capercaillie in relation to weather. *Ornis Scandinavica*, **10**, 37–41.

Spidsø, T.K. & Stuen, O.H. (1987) Food selection by capercaillie chicks in southern Norway. *Canadian Journal of Zoology*, **66**, 279–283.

Spidsø, T.K., Wegge, P. & Storaas, T. (1985) Renesting in capercaillie in southern Norway. *Proceedings of the Third International Grouse Symposium* (eds P.J. Hudson & T.W.I. Lovel), pp. 278–288. World Pheasant Association, Lower Basildon, UK.

Storch, I. (1993) Habitat selection of capercaillie in summer and autumn: is bilberry important? *Oecologia*, **95**, 257–265.

Stuen, O.H. & Spidsø, T.K. (1988) Invertebrate abundance in different forest habitats as animal food available to capercaillie *Tetrao urogallus* chicks. *Scandinavian Journal of Forest Research*, **3**, 527–532.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lesells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceeding of the Royal Society of London B*, **265**, 1867–1970.

Received 4 March 2000; revision received 13 May 2000

Appendix

SPEY VALLEY WEATHER

In the main text we used eigenvectors from Glen Tanar PCA to calculate Spey valley PC scores. Here, we give PCA for the Spey valley weather data (Table A1), calculated using the same basic weather measures over the same period (1975–98) as at Glen Tanar. Eigenvectors from the two valleys (Table 3 and Table A1) were similar for PC APRIN3, MJPRIN3 and MJPRIN4 and so their interpretation (main text) is similar. High APRIN1$_{ss}$ scores (Table A2), however, reflected warmer weather in mid- and late April. High APRIN2$_{ss}$ scores reflected warmer early Aprils. High MJPRIN1$_{ss}$ scores reflected colder and rainier weather in late May and early June. High MJPRIN2$_{ss}$ scores reflected colder and wetter weather in late May followed by a warmer and somewhat dry early June.

Like APRIN3$_{gs}$, APRIN3$_{ss}$ increased significantly during the study (Table A3). This was because, as at Glen Tanar, the April warming occurred later in the month as the study progressed (Table A4).

Table A1. Principal components analyses of (a) April temperatures (APRIN) and (b) temperature and rain days in late May and early June (MJPRIN) in the Spey valley. Weather abbreviations are as in Table 2

(a)	APRIN1	APRIN2	APRIN3
Eigenvalues	1·129	1·185	0·521
Proportion*	0·43	0·40	0·17
Eigenvectors			
Apr T$_1$	0·502	–0·654	0·566
Apr T$_2$	0·785	0·070	–0·616
Apr T$_3$	0·363	–0·753	0·548

(b)	MJPRIN1	MJPRIN2	MJPRIN3	MJPRIN4
Eigenvalues	1·985	1·078	0·660	0·277
Proportion*	0·50	0·27	0·16	0·07
Eigenvectors				
May T$_3$	–0·402	–0·562	0·711	–0·128
Jun T$_1$	–0·573	0·438	0·145	0·677
May RD$_3$	0·391	0·605	0·663	–0·202
Jun RD$_1$	0·597	–0·355	0·183	0·696

*Proportion of variance accounted for.

Table A2. Parameter estimates for explanatory variables (weather PC scores based on Spey valley eigenvectors; Table A1) in GLM explaining breeding success for the Spey valley. Parameter estimates for models with year included as an explanatory variable were almost identical, the same parameters were significant, and year was never significant

	Chicks per hen	Proportion broods†	Brood size
APRIN1$_{ss}$	–0·087 ± 0·208	0·190 ± 0·315	–0·181 ± 0·078*
APRIN2$_{ss}$	–0·005 ± 0·201	0·225 ± 0·296	–0·114 ± 0·082
APRIN3$_{ss}$	–0·520 ± 0·244*	–1·330 ± 0·421**	0·055 ± 0·108
MJPRIN1$_{ss}$	–0·234 ± 0·094*	–0·375 ± 0·158*	–0·086 ± 0·037*
MJPRIN2$_{ss}$	0·114 ± 0·181	–0·043 ± 0·273	0·159 ± 0·068*
MJPRIN3$_{ss}$	0·278 ± 0·192	0·755 ± 0·275**	–0·079 ± 0·074
MJPRIN4$_{ss}$	0·005 ± 0·466	–0·085 ± 0·698	–0·058 ± 0·162
FOREST‡	$F_{5,48}$ = 1·79, NS	$F_{5,48}$ = 3·57**	$F_{5,41}$ = 1·85, NS

*P < 0·05, **P < 0·01, ***P < 0·001, ****P ≤ 0·0001.
†Proportion of hens with broods.
‡The Spey valley data came from 6 forest areas (Table 1) and so forest was included as a class variable.

Table A3. Trends in weather PC scores in the Spey valley during 1975–78. Scores were calculated using the eigenvectors in Table A1

Score	Slope ± SE	*P*	R^2
APRIN1_{ss}	0·025 ± 0·034	0·48	0·02
APRIN2_{ss}	–0·026 ± 0·032	0·43	0·03
APRIN3_{ss}	0·060 ± 0·018	0·002	0·35
MJPRIN1_{ss}	0·001 ± 0·043	0·98	0·00
MJPRIN2_{ss}	–0·015 ± 0·031	0·64	0·01
MJPRIN3_{ss}	0·013 ± 0·024	0·60	0·01
MJPRIN4_{ss}	0·034 ± 0·014	0·024	0·18

Table A4. Mean temperatures (°C ± SE) for early, mid- and late April in the Spey valley. Weather abbreviations are as inTable 2

	Years			
Period	1975–98	1975–82	1983–90	1991–98
Early (Apr T_1)	4·64 ± 0·36	4·12 ± 0·67	4·18 ± 0·58	5·64 ± 0·56
Mid (Apr T_2)	5·69 ± 0·30	6·01 ± 0·55	5·61 ± 0·54	5·47 ± 0·51
Late (Apr T_3)	6·75 ± 0·44	6·19 ± 0·59	6·81 ± 1·14	7·24 ± 0·39