

# Variation in temperature increases the cost of living in birds

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## Summary

The effect of temperature variability on laying birds was studied experimentally, using Japanese quail. Two aspects of temperature variability were investigated: the effects of regular daily variation in temperature, and of a sudden change in temperature. Both of these may become more common as a consequence of climate change. These manipulations were carried out at two levels of food supply. Energy expenditure increased with higher daily temperature variation, and also after a sudden change in temperature, taking several days to settle to a constant

level. Manipulating daily temperature variation also resulted in smaller eggs being laid under more variable temperatures, when food quality was also low. The results demonstrate that day-to-day variation in temperature, as well as mean temperature, affects energy expenditure, which can have consequences for egg production.

Key words: Japanese quail, *Coturnix japonica*, temperature variability, energy expenditure, egg production.

## Introduction

There has been much interest in the impact on ecosystems of recent climate changes (McCarty, 2001; Parmesan and Yohe, 2003; Penuelas and Filella, 2001; Walther et al., 2002). Rising temperatures, driven by this climate change, have been fundamental in causing these ecological impacts (Penuelas and Filella, 2001). Correlations with increased temperatures, and changes in range, migratory pattern, reproductive success and over-winter survival, have been demonstrated for a range of animals (reviewed in McCarty, 2001). These temperature changes have included increases of annual mean temperatures by up to 3°C in northern latitudes over the last 30 years (IPCC, 2001). The range of daily temperatures has also been altered as a result of climate changes, with increases in some areas and decreases in others (Easterling et al., 1997; IPCC, 2001). However, although the effects of mean temperature on energy expenditure have been studied previously, the effects of temperature variability have received very little attention.

This paper investigates the impacts of temperature variability on energy expenditure, and the consequences for reproduction, using Japanese quail *Coturnix japonica* as the model species. Costs of living, which are clearly important for breeding due to their impact on reproductive decisions, can be affected by changes in thermoregulation and foraging costs (Bryant, 1997; Feist and White, 1989; Kendeigh et al., 1977). Temperature can be important in determining the amount of time and energy that can be allocated to the different stages of reproduction. For birds, this has been demonstrated for egg production (Stevenson

and Bryant, 2000; Ward, 1996), incubation (Bryan and Bryant, 1999) and brood-rearing (Spencer and Bryant, 2002). Food supply is also important for breeding birds, as the levels of available nutrients are important in determining resource allocation to egg production (Houston, 1997).

Manipulation of roosting temperatures of breeding wild birds has demonstrated the effects of mean temperature on egg quality (Nager and van Noordwijk, 1992), timing of laying (Meijer et al., 1999), the ability to maintain a daily laying schedule (Yom-Tov and Wright, 1993), and incubation behaviour (Bryan and Bryant, 1999). This implies that temperature can alter thermoregulatory costs, leading to a reallocation of energy resources available for reproduction. In this way, mean temperature could directly influence fitness *via* the quality of eggs (Both et al., 1999; Christians, 2002; Perrins, 1996; Williams, 1994) and the pattern of laying (Nilsson and Svensson, 1993).

Temperature variability is less commonly investigated than the effects of mean temperature. However, an experiment involving captive Japanese quail found that rapid sinusoidal temperature fluctuations resulted in an increase in metabolism (Prinzinger, 1982). Another experiment involving captive turkeys (*Meleagris gallopavo*) showed that, when they were transferred from a low to a high temperature, metabolic rate decreased slowly during an acclimatisation period of several days (MacLeod et al., 1980b).

These experiments suggest that temperature variability, as well as mean temperature, may be important in determining

daily living costs. This may then have consequent effects on egg-laying ability (Perrins, 1970; Stevenson and Bryant, 2000) and fitness more generally. This paper uses two experiments to investigate independently the effects on egg production and energy expenditure of: (i) daily variation in temperature and (ii) a sudden change in temperature.

## Materials and methods

### *Study population*

The study took place at the Roslin Institute, Scotland, using Japanese quail *Coturnix japonica* Temminck and Schlegel reared from stock. These quail are from a population that have not been subject to any intentional selection pressures, allowing comparisons to be made with wild birds. The first experiment was carried out from February to April 2002, and the second from September to December 2002. Two different sets of birds were used: 20 females for the first experiment, and 16 for the second. The birds were aged 14 weeks at the start of each experiment.

Four weeks prior to the experiments, each bird was randomly allocated to one of four large chambers (1 m×1 m×1.2 m high). During this time, the chambers were kept at a constant temperature of approx. 20°C, with a lighting cycle of 14 h:10 h light:dark. The birds were provided with standard quail layer feed (Savory and Gentle, 1976) and water *ad libitum*.

### *Experiment 1 – Daily variation in temperature*

A 2×3 factorial design was used for the experimental treatments. This involved two levels of food quality and three levels of temperature variation. The two levels of food quality were 'high' ('HQ'; 100% standard food) and 'low' ('LQ'; 50% standard food, 50% cellulose). These were alternated each week, with the aim of minimising changes in intestinal architecture (Starck, 1999). The three levels of temperature variation were 'constant' ('C'; set at 18.3°C), 'low' ('L'; set at 25°C during the day and 15°C at night) and 'high' ('H'; set at 31.7°C during the day and 11.7°C at night). These treatments aimed to provide the same mean daily temperature. The temperature changes took place at 09:00 h and 17:00 h each day. The shorter warm-cycle than light-cycle gave conditions with cooler dawns and dusks, compared to the rest of the day.

Each treatment, run for a 7 day period, was randomly allocated to each chamber. This was then repeated. The experiment therefore lasted for 12 weeks. The 7 day period included an acclimatisation period of 3 days prior to measuring egg mass or gas exchange for that treatment. At the end of each 7 day period, all the birds were weighed to 0.1 g using an electronic balance (Sartorius UK, Epsom, Surrey, UK). Eggs were weighed on the day of laying to 0.01 g using an electronic balance. In each of the eight chambers, temperature was measured every 10 min using data loggers (Gemini Data Loggers Ltd., W. Sussex, England).

Each week, two pairs of birds (at different times; the same

birds were used each week) from each of the four groups, were moved into smaller calorimeter chambers (600 mm×600 mm×450 mm high) for 2 days at a time. Here they were provided with the same food, temperature and lighting conditions as found in the larger chamber from which they came. Gas exchange was measured on the second day, using the system described by Lundy et al. (1978) and MacLeod et al. (1985).

### *Experiment 2 – Sudden temperature change*

A 2×4 factorial design was used for the experimental treatments. This involved two levels of food quality and four temperature-change treatments. The same two levels of food quality were used: 'high' (100% standard food) and 'low' (50% standard food, 50% cellulose). The four temperature-change treatments were changes from 'high to medium' ('HM'), 'medium to high' ('MH'), 'medium to low' ('ML') and 'low to medium' ('LM') temperatures, where 'high' was set at 28°C, 'medium' at 20°C, and 'low' at 12°C.

Two females were kept in each of the smaller calorimeter chambers. The birds were subjected to a temperature change every 7 days, and the effects on gas exchange were measured over the subsequent days. At the end of each week, all the birds were weighed to 0.1 g using an electronic balance. In each of the chambers, temperature was measured every 10 min using data loggers (Gemini Data Loggers Ltd., W. Sussex, England). After 8 weeks, each bird had been subjected to each of the treatments. The experiment was then repeated with another eight birds.

### *Indirect calorimetry*

Indirect calorimetry was used to measure energy expenditure for both experiments. Metabolic rate was calculated from the rates of oxygen consumption and carbon dioxide production. This was done by comparing the air from the calorimeter chamber with ambient air. Energy expenditure ( $\text{kJ h}^{-1}$ ) was calculated using the equation of Romijn and Lokhorst (1961):

$$\text{Energy expenditure} = 16.18V_{\text{O}_2} + 5.02V_{\text{CO}_2}$$

where  $V_{\text{O}_2}$  and  $V_{\text{CO}_2}$  are the volumes of oxygen consumed and carbon dioxide produced ( $\text{l h}^{-1}$ ). Mean energy expenditures were calculated for both day (10:00 h–16:00 h) and night (23:00 h–05:00 h).

### *Statistical analysis*

All data were analysed using Genstat for Windows, 5th edition. The effects on egg mass and energy expenditure were analysed using a linear mixed model using restricted maximum likelihood (REML) to control for the use of different chambers for each group, and the repeated measurements on individual birds (Patterson and Thompson, 1971). Values quoted in the text and tables are means  $\pm$  S.E.M. Vertical bars in graphs represent S.E.M. The effect sizes for factors, presented in tables, are relative to the reference group.

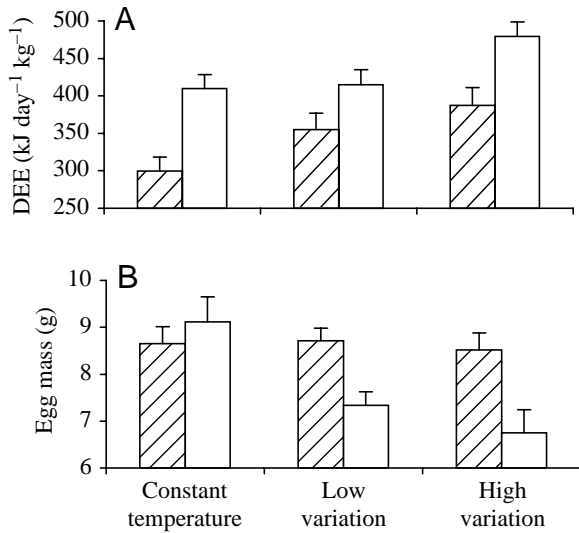


Fig. 1. The effects of the temperature variation and food quality treatment groups (Experiment 1) on (A) daily energy expenditure (DEE) and (B) mean egg mass. Values are means  $\pm$  S.E.M. ( $N=20$ ). Hatched columns, high-quality food; open columns, low-quality food.

**Results**

*Effects of daily variation in temperature*

*Temperature treatments*

There was a significant difference in the range of temperatures for the three temperature treatment groups (C,  $1.9 \pm 0.7^\circ\text{C}$ ; L,  $11.9 \pm 0.6^\circ\text{C}$ ; H,  $19.8 \pm 0.6^\circ\text{C}$ ;  $\chi^2=846.46$ ; d.f.=2;  $P<0.001$ ). There was also an unplanned but significant difference in mean temperature for these three groups (C,  $19.7 \pm 0.3^\circ\text{C}$ ; L,  $18.5 \pm 0.2^\circ\text{C}$ ; H,  $19.6 \pm 0.3^\circ\text{C}$ ;  $\chi^2=14.57$ ; d.f.=2;  $P<0.001$ ), but this difference was small ( $<1.3^\circ\text{C}$ ). To control for any effects of mean temperature on energy expenditure (Godfrey and Bryant, 2000; Spencer and Bryant, 2002) or egg mass (Nager and van Noordwijk, 1992; Nager and Zandt, 1994), mean temperature was included in the analysis as a covariate.

*Energy expenditure*

Energy expenditure is shown for the six treatment groups in Fig. 1A. Energy expenditure was significantly affected by the food quality treatment, temperature variation, mean temperature and time of day (Table 1). Energy expenditure was higher for the low-quality, compared to the high-quality food treatment, and increased with higher temperature variability; and increased with a decrease in mean temperature.

*Egg production*

Birds fed on the high-quality food laid significantly larger eggs than birds fed the low-quality food (Table 2). There was also a significant interaction between food treatment and temperature treatment (Table 2). Under the low-quality food treatment, significantly larger eggs were laid under the constant-temperature treatment compared to both the low and

Table 1. Linear mixed model (REML) of energy expenditure (from Experiment 1) in terms of food quality, temperature variation, mean temperature and time of day

Term	d.f.	Effect	Energy expenditure	
			Wald statistic ( $\chi^2$ )	P value
<b>Minimal model</b>				
<b>Food quality</b>				
HQ		0		
LQ	1	$89.0 \pm 12.3$	52.48	$<0.001$
<b>Temperature treatment</b>				
C		0		
L	2	$29.7 \pm 15.0$	14.83	$<0.001$
H		$58.2 \pm 15.2$		
Mean temperature	1	$-3.98 \pm 1.38$	8.29	0.004
<b>Time of day</b>				
Day		0		
Night	1	$-172.2 \pm 19.8$	75.28	$<0.001$
<b>Excluded terms</b>				
Egg mass	1		2.82	0.093
Week	1		0.78	0.376

A random term of ‘bird identities and calorimeter chamber’ was used ( $\chi^2=37.24$ ; d.f.=1;  $P<0.001$ ) to account for the non-independence of conditions from different chambers, and repeated measures of the same birds.

For definitions of HQ, LQ, C, L and H, see text.

Table 2. Analysis of egg mass (from Experiment 1), in terms of food quality, temperature treatment, maximum temperature, and interactions between food quality and temperature treatment, and food quality and maximum temperature

Term	d.f.	Egg mass	
		Wald statistic ( $\chi^2$ )	P value
<b>Minimal model</b>			
<b>Food quality</b>			
Food quality	1	41.05	$<0.001$
<b>Temperature treatment</b>			
Temperature treatment	2	1.65	0.439
Maximum temperature	1	2.17	0.140
<b>Interactions</b>			
Food quality $\times$ Temperature treatment	2	9.24	0.010
Food quality $\times$ Maximum temperature	1	5.65	0.017
<b>Excluded terms</b>			
Mean temperature	1	2.03	0.154
Week	1	0.93	0.336
Minimum temperature	1	0.63	0.427
Female mass	1	0.03	0.872

A random term of ‘bird identities and calorimeter chamber’ was used ( $\chi^2=14.45$ ; d.f.=1;  $P<0.001$ ) to account for the non-independence of conditions from different chambers, and repeated measures of the same birds.

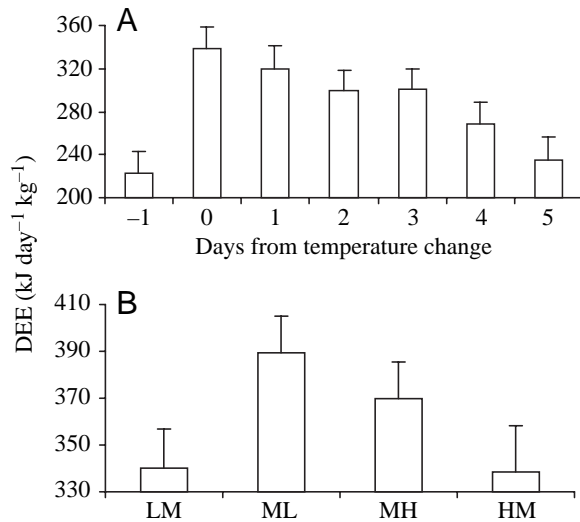


Fig. 2. Daily energy expenditure (DEE) (Experiment 2) (A) following a sudden change in temperature; and (B) for the sudden temperature-change treatment groups (LM, low to medium; ML, medium to low; MH, medium to high; HM, high to medium). Values are means  $\pm$  S.E.M. ( $N=16$ ).

high temperature-variation treatments (Fig. 1B). Under the high-quality food treatment there was no such difference in egg mass between the treatments. Also, under the low-quality food treatment only, egg mass increased with maximum temperature by  $0.23 \pm 0.10$  g °C<sup>-1</sup>.

#### Effects of sudden temperature change

##### Temperature

There was a significant difference in mean temperature between the three temperature levels (H,  $29.4 \pm 0.1$  °C; M,  $19.8 \pm 0.1$  °C; L,  $12.5 \pm 0.1$  °C;  $\chi^2=10399.76$ ; d.f.=2;  $P<0.001$ ). This gave a difference of mean temperature between 'medium' and 'low' levels of  $7.4 \pm 0.02$  °C, and  $9.6 \pm 0.02$  °C between 'medium' and 'high' levels.

##### Energy expenditure

Energy expenditure was highest on the day after the change in temperature and decreased over the next 6 days (Fig. 2A), when controlling for temperature treatment, time of day, and week (Table 3). Highest energy expenditures occurred when temperature was changed from 'medium' to 'high' or 'low', compared to 'high' or 'low' to 'medium' (Fig. 2B).

## Discussion

### Temperature variability and energy expenditure

Both high daily temperature variation, and a sudden change in temperature, resulted in an increase in energy expenditure. A previous experiment has shown that rapid temperature fluctuations also increase energy expenditure (Prinzinger, 1982). In this latter experiment, temperature cycled between 7 °C and 13 °C, and metabolic rate increased between treatments as the cycle-time decreased from 4 h to 1 h

Table 3. Linear mixed model (REML) of energy expenditure (from Experiment 2), in relation to temperature treatment, day from temperature change, time of day and week

Term	d.f.	Energy expenditure		
		Effect	Wald statistic ( $\chi^2$ )	P value
<b>Minimal model</b>				
Day from change	1	$-19.81 \pm 3.10$	45.85	<0.001
<b>Temperature treatment</b>				
HM		0		
MH		$31.09 \pm 17.64$	15.11	0.002
ML	3	$58.91 \pm 17.88$		
LM		$2.40 \pm 18.93$		
<b>Time of day</b>				
Day		0		
Night	1	$-135.32 \pm 12.34$	120.27	<0.001
Week	1	$-31.01 \pm 3.10$	100.21	<0.001
<b>Excluded terms</b>				
Food quality	1		1.02	0.313
Mean temperature	2		4.25	0.120
Female mass	1		3.29	0.070

A non-significant random term of 'bird identities and calorimeter chamber' was used ( $\chi^2=3.51$ ; d.f.=1;  $P>0.085$ ) to be consistent. The analysis was similar without this random term, and also if the close-to-significant term of 'female mass' was controlled for.

For definitions of HM, MH, ML, LM, see text.

(Prinzinger, 1982). These results suggest that temperature variability can be important in determining daily living costs. Day-to-day constancy, as well as the mean value, should therefore be studied when investigating the effects of temperature. Since the daily range of temperatures may be changing as a result of climate change (Easterling et al., 1997; IPCC, 2001), the effects of temperature variability should be investigated when studying the impacts of these changes.

The increase in energy expenditure during more variable temperatures, or after a sudden change in temperature, could be caused by the feedback system controlling metabolism 'overshooting' while adjusting to new temperatures (Prinzinger, 1982). This is thought to be more important than the energy expenditure required by the increase in activity in the neurological centres of the measuring and feedback control systems, which is believed to be negligible (Prinzinger, 1982). Other possible reasons include the inefficiency of changing from fat synthesis/deposition during cold temperatures, and fat-catabolism at higher temperatures, and more variable conditions resulting in increased physical activity or feeding during warmer temperatures to compensate for increased energy expenditure during cold temperatures.

The increase in energy expenditure following a sudden change of approx. 8 °C suggests that acclimatisation to such a change can take several days. This was also found for growing turkeys when temperature was changed from low to high, but not *vice versa* (MacLeod et al., 1980b). Nevertheless, the period

of acclimatisation may be shorter for wild animals that are more familiar with variable temperatures, compared to the quail and turkeys used in these experiments. Energy expenditure also tended to be higher when the temperature was changed from 'medium' to either 'high' or 'low', compared to a change from 'high' or 'low' to 'medium'. This suggests that it is easier to adjust to average rather than more extreme temperatures.

Energy expenditure also showed circadian rhythmicity, being higher during the day than at night (Lundy et al., 1978; MacLeod et al., 1980a). This has been shown to be due mainly to increased activity (MacLeod et al., 1982), controlled by the lighting cycle (MacLeod et al., 1980a). Basal metabolic rates are also higher during the day than the night (Aschoff and Pohl, 1970).

#### Food supply

Energy expenditure was also affected by food quality, with birds fed low-quality food having higher energy expenditures than birds on high-quality food. This is likely to be due to the greater time required for feeding under the low quality food treatment, and the increased processing in the gut required for a high-cellulose diet.

Food quality also had a major influence on egg mass. A positive effect of food on egg mass has previously been found from: experiments with captive birds (Yamane et al., 1979); observations of wild birds over years of differing food availability (Bryant, 1978; Hiom et al., 1991; Järvinen and Vaisanen, 1984); and supplementary feeding experiments of wild birds (Hill, 1988; Hiom et al., 1991; Högstedt, 1981; Källander and Karlsson, 1993; Ramsay and Houston, 1997). Food is therefore likely to directly affect the amount of resources available for egg production.

#### Temperature variability and egg mass

Under the low-quality food treatment, significantly larger eggs were laid when temperature was constant compared to when it was varied during the day. The increased thermoregulatory costs imposed by higher temperature variability may have therefore reduced resources available for egg production. Since an increase in energy expenditure is required for egg production (Stevenson and Bryant, 2000; Ward and MacLeod, 1992), smaller eggs may therefore be produced under more variable conditions. Under the high-quality food treatment, egg mass was not influenced by temperature variability, suggesting that under good food conditions any negative effects of temperature variation can be fully compensated. Since food conditions can vary between years and areas (Bolton et al., 1992; Dijkstra et al., 1982), and within a breeding season (Birkhead and Nettleship, 1982; Gibb, 1950), our results suggest that temperature variation is likely to be more important in some situations compared to others. Alternatively, since foraging costs are higher for wild birds than captive birds provided with food *ad libitum*, birds in the wild may invariably experience relatively 'poor' conditions, so temperature variation may be more likely to affect energy expenditure.

This effect of temperature variability on reproduction is unlikely to be limited to just birds. Similar effects could also be expected for other animals.

#### Conclusions

We have demonstrated an effect on energy expenditure of temperature variability, in terms of daily variation and the effect of a sudden temperature change. This had subsequent effects on the resources allocated to egg production. Since daily temperature ranges have increased in some areas due to climate change (Easterling et al., 1997; IPCC, 2001), temperature variation is likely to become more important in determining daily living costs in these areas. Where day-to-day variation in temperature is decreasing, by contrast, daily living costs may also be reduced. Although recent increases in mean temperatures (IPCC, 2001), and a reduction in energy expenditure with temperature would be expected to reduce daily living costs (Kendeigh et al., 1977; Walsberg, 1983), our results suggest that increasing temperature variability might counteract this affect. The effect of the exact pattern of temperature change is thus likely to be important in predicting biotic responses to future climate change.

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