ENVIRONMENTAL LIMITATIONS OF PHEASANT EGG HATCHING SUCCESS

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THE Ring-necked Pheasant, *Phasianus colchicus*, was first introduced into the United States from China in the late 1700s. Attempts have been made to establish reproducing populations in nearly every state, but have usually failed south of 40° N (Fig. 1).

The latitudinal boundary points to temperature as a factor that may restrict pheasant range. Rainfall temperature climographs (Graham and Hesterberg 1948) show temperature and rainfall to be similar in April and May in areas that had maintained pheasant populations. This information suggested a possible sensitive period to temperature or humidity during the nesting period or soon after the chicks hatch. If this is so, a limiting constraint on these bird populations would lie in the thermal physiology of the egg or chick rather than in the adults where most physiological studies are conducted. Yeatter (1950) found a significant reduction in hatchability after exposing pheasant eggs to high temperatures during the preincubation period (the laying period). Later attempts to correlate high air temperatures in the field with reduced hatchability yielded conflicting results (Ellis and Anderson 1963, Martinson and Grondall 1966, Nelson 1969). In these observations, general climatological data were supplied by nearby weather stations. Air temperature from these general measurements was used to estimate egg temperatures. Geiger (1966) demonstrated the necessity of using microclimatological measurements rather than gross climatological measurements. Francis (1968) demonstrated that temperature and humidity were significantly higher at 10 cm than at 1 m in potential nesting habitats.

In an effort to explore the relationship between egg temperature and the physical environment, we: (1) measured the physical parameters in pheasant nests to determine the heat load on the eggs, (2) developed a thermal model of a nest situation that would predict egg temperature for any set of micrometeorological data, and (3) predicted hatchability on the basis of pheasant egg temperatures during the preincubation period, as a function of air temperature and solar radiation.

METHODS

A. CONSTRUCTING THE MODEL

A steady state energy balance model (Porter and Gates 1969) was constructed. The model equated the energy flows into the pheasant egg and heat production by the egg with energy flows from the egg.



Fig. 1. Past and present distribution of the Ring-necked Pheasant in the United States (Map from Fish and Wildl. Serv., Circ. 34, 1955).

The equation describing this balance is

$$\mathbf{M} + \mathbf{Q}_{abs} = \mathbf{R}_n + \mathbf{C}_v + \mathbf{C}_d + \mathbf{E} \tag{1}$$

where,

M = metabolic heat production $Q_{abs} = solar radiation absorbed by the egg$

- $= s \cdot A \cdot \alpha \cdot Q_{inc}$
 - s = fraction of the total surface area exposed
 - to the sun (0.25 for a sphere)
 - α = absorptivity of the shell to solar radiation
 - A = total surface area of the egg
 - $Q_{inc} = solar radiation measured in the nest$

 R_n = net infrared radiative exchange between the egg and the vegetation $= 0.7 \cdot A \cdot \epsilon \cdot \sigma (T_{egg}^{4} - T_{veg}^{4})$

- $T_{egg} = temperature of the egg, ^{\circ}K$
- $T_{veg} =$ temperature of the vegetation, °K
 - $\varepsilon = \text{emissivity of the egg}$
 - σ = the Stefan-Boltzmann constant (8.132 \times 10⁻¹¹ cal/cm²-min)
- $C_v =$ convective heat exchange between the egg and the surrounding air $= 0.7 \cdot A \cdot h_c (T_{egg} - T_{air})$
 - $T_{air} = air temperature in the nest, °C$
 - $h_e =$ convection coefficient for the pheasant egg in the nest
- C_d = conductive heat exchange between the egg and the ground

= k · 0.3 · A (T_{egg} - T_{grd})/dx

- k = thermal conductivity of the vegetative mat
- $T_{grd} =$ temperature of the ground, °C
 - dx = depth of the vegetative mat
- E = energy loss due to evaporation from the egg

 $= \dot{m} \cdot L$

m = mass of water lost from the egg

L = latent heat of vaporization of water.

Several simplifying assumptions and approximations have been made in this model:

1. The pheasant egg was regarded as spherical with a diameter = (length + breadth)/2, and a surface area of $4 \cdot \pi \cdot \text{radius}^2$. The convection coefficient used for pheasant eggs in the field is given by the equation

$$(h_{c} \cdot d)/k_{f} \equiv .37 ((u \cdot d)/\upsilon_{f})^{.6}$$
 (2)

where

d = radius of the egg

 $k_f = conductivity of air$

u = local wind velocity

 $u_f =$ kinematic viscosity

Equation (2) is valid for spheres with Reynolds numbers between 17 and 17,000 (Holman 1963).

2. The egg was visually approximated to have a radiating and convecting area of 70% of the total area when on a vegetative mat.

3. It was assumed that the egg was radiating entirely to the vegetation, which was taken to be at the same temperature as the air.

4. The temperature of the eggs was taken to be uniform, as the range of Biot numbers for pheasant eggs in the nests observed was 0.05 to 0.09. For an explanation of Biot Moduli, see Holman (1963).

5. The thermal conductivity of the vegetative mat was taken to be equivalent to that of air, and the thermal conductivity and specific heat of the egg were assumed to be the same as water.

6. Both the eggs and vegetation were assumed to have an emissivity of 0.98 (Gates 1962).

7. Metabolism was disregarded in the model as the amount of heat generated in the early stages of development of the pheasant egg is minute when compared with the other modes of heat transfer. A fresh infertile hen's egg generates only 0.005 cal/g-min (Romanoff and Romanoff 1949).

8. Evaporation was also disregarded as an avenue of significant heat loss. The amount of water lost by a freshly laid egg is very small (Schulte 1972), and accounts for an energy loss of approximately 0.003 cal/minute.

With these approximations, the energy balance reduces to

$$Q_{abs} \equiv R_n + C_v + C_d \tag{3}$$

Solar radiation is the only significant energy input. The absorptivities of the pheasant eggshells to solar radiation was measured with a Beckman spectrophotometer over a spectral range of 290–2600 nm. Absorptivities ranged from 0.46 to 0.56. The average value, 0.51, was used in the energy balance. Despite the fact that pheasant nests are difficult to locate, Hamerstrom (1936) found that 30.2% of 503 pheasant nests were completely exposed above. In the nests observed, there was often considerable exposure of the eggs to the sun, accounting for heating of the eggs substantially above local air temperature—one by 15° C. Conduction becomes the least important energy loss as the vegetative mat measured under the eggs was 2.5 to 8.0 cm deep, providing good insulation from the ground. Conductive heat losses reached maximal values of 0.01 cal/minute. Wind velocity



Fig. 2. Comparisons of pheasant egg temperatures *predicted* for meteorological data obtained at pheasant nesting sites, with *measured* temperatures of eggs in the nest.

in the nest was anticipated to be small so the magnitude of natural vs. forced convection were compared in the ratio, Grashof number/(Reynolds number)². This quantity was never larger than 1.0, consequently only forced convection was considered (Kreith 1965). Despite average wind speeds of only 0.2 mph in the nests, convection accounted for a significant heat loss as shown below. Thermal radiation from the egg to the surrounding vegetation was also important whenever the egg was under a radiant load from the sun.

B. STUDY AREAS

Egg temperatures can now be predicted by using micrometeorological data from actual pheasant nests and substituting these variables into equation (3). The nests used were in the Waterloo Wildlife Area in Dodge and Jefferson County, Wisconsin. The area is glaciated, well supplied with calcium, and is characterized by rolling topography. The lowland soils are poorly drained and high in organic matter. Approximately 40 nests were located as part of a long-term project (Dept. of Nat. Res., P.R. W-141-R) that is investigating methods of radio-equipping pheasants, mortality factors, growth of pheasant populations, and pheasant nesting behavior. Five nests were used to obtain micrometeorological data after predators had destroyed the eggs, or the eggs had hatched. Hourly data were

Nest No. 1 Nest No. 3 1 1230 8.68 4.90 3.74 1 1300 3.03 1.86 1.16 2 7.46 4.15 3.27 2 2.88 1.77 1.11 1 1330 8.68 4.12 4.52 4 2.74 1.67 1.06 2 7.46 3.48 3.94 1 1400 2.76 1.69 1.02 1 1430 1.69 1.51 3 2.63 1.60 1.02 2 2.77 1.43 1.31 1 1500 3.23 1.98 1.24 1 1530 3.03 1.55 1.45 2 3.07 1.88 1.19 3 2.60 1.31 1.26 4 2.92 1.79 1.10 0.69 1 1300 4.61 1.83 2.76 3 1.79 1.10 0.69 2 2.60 1.31 2.63 <th>Egg No.</th> <th>Time</th> <th>Qabs</th> <th>Rad</th> <th>Conv</th> <th>Egg No</th> <th>Time</th> <th>Qabs</th> <th>Rad</th> <th>Conv</th>	Egg No.	Time	Qabs	Rad	Conv	Egg No	Time	Qabs	Rad	Conv
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Nest No. 1					Nest No.	3			
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1230	8.68	4.90	3.74	1	1300	3.03	1.86	1.16
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		7.46	4.15	3.27	2		2.88	1.77	1.11
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		7.46	4.15	3.27	3		2.88	1.77	1.11
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1330	8.68	4.12	4.52	4		2.74	1.67	1.06
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		7.46	3.48	3.94	1	1400	2.76	1.69	1.07
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		7.46	3.48	3.94	2		2.63	1.60	1.02
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$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		2.77	1.43	1.31	4		2.50	1.51	0.98
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		2.77	1.43	1.31	1	1500	3.23	1.98	1.24
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1530	3.03	1.55	1.45	2		3.07	1.88	1.19
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		2.60	1.31	1.26	3		3.07	1.88	1.19
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$\begin{array}{c ccccccccccccccccccccccccccccccccccc$						1	1600	1.88	1.16	0.72
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Nest No. 2					2		1.79	1.10	0.69
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1300	4.61	1.83	2.76	3		1.79	1.10	0.69
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		4.85	1.93	2.89	4		1.71	1.04	0.66
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		4.38	1.73	2.63	-				
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	4		4.38	1.73	2.63	Nest No.	4			
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1400	4.48	1.83	2.63	2	1230	3.29	1.82	1.44
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		4.71	1.93	2.75	3		3.46	1.93	1.50
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		4.26	1.72	2.51	2	1330	1.77	0.89	0.85
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	4		4.26	1.72	2.51	3		1.86	0.94	0.89
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1500	1.28	0.68	0.57	2	1430	1.04	0.51	0.50
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		1.35	0.72	0.60	3		1.09	0.54	0.52
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	3		1.22	0.64	0.55	2	1530	1.22	0.60	0.59
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	4		1.22	0.64	0.55	3		1.28	0.63	0.62
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1	1600	1.28	0.53	0.73					
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2		1.35	0.56	0.76	Nest No.	5			
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3		1.22	0.50	0.69	1	1300	2.50	1.25	1.22
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	4		1.22	0.50	0.69	2		2.63	1.32	1.27
$\begin{array}{cccccccccccccccccccccccccccccccccccc$						3		2.63	1.32	1.27
$\begin{array}{cccccccccccccccccccccccccccccccccccc$						4		2.63	1.32	1.27
$\begin{array}{cccccccccccccccccccccccccccccccccccc$						1	1400	1.40	0.69	0.68
$\begin{array}{cccccccccccccccccccccccccccccccccccc$						2		1.47	0.73	0.71
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1 1500 0.24 0.11 0.11 2 0.26 0.11 0.12 3 0.26 0.11 0.12 4 0.26 0.11 0.12						4		1.47	0.73	0.71
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3 0.26 0.11 0.12 4 0.26 0.11 0.12						2		0.26	0.11	0.12
4 0.26 0.11 0.12						3		0.26	0.11	0.12
						4		0.26	0.11	0.12

 TABLE 1

 Energy Fluxes in Outdoor Nests

taken on given days in May and June between 1200 and 1600. The egg temperatures were determined using a thermocouple inserted into the center of each intact egg. Ground temperature was measured under the vegetative mat, at the surface of the soil. Air temperature was measured with several thermocouples at 3 to 5 cm above the ground in the nest. An Eppley pyrheliometer was used to measure direct and scattered sunlight in the nest. A Hastings anemometer was used to measure wind velocity in a cleared area in the adjacent grass at approximately 10 cm above the soil surface.

Inserting these data into the energy balance equation (3) leaves egg temperatures appearing several times as an unknown. To solve this equation, a computer program was set up using the Regula-Falsi method of solving roots (Stanton 1961). The egg temperatures that would be predicted to satisfy the energy balance with



Fig. 3. Pheasant egg temperatures predicted by equation (4) vs. pheasant egg temperatures measured for 13 different values of $Q_{\rm abs}$ and four pheasant eggs.

each set of micrometeorological data were plotted against the actual measured egg temperatures (Fig. 2). The wide scatter of data points is thought to be due to two causes. The eggs in the same nest sometimes had very different temperatures as some were more exposed to the sun than others. In one instance two eggs had temperatures of 30° C and 43° C; one was totally shaded from the sun and the other was totally exposed. Additional measurement difficulties were caused by the wind shifting the grasses and the difficulty of making good solar radiation measurements under partially cloudy skies. Both these situations changed the radiation load on the eggs in an unpredictable fashion. The data points, however, are evenly distributed about the line and 60% of them fall within $\pm 3^{\circ}$ C of the predicted value. At steady state (when the energy entering the egg is equal to that leaving the egg), each of the terms of the energy budget has been evaluated. These values are given in Table 1.

C. TESTING THE MODEL

Because of the difficulty in making meteorological measurements in the field and to test the model further, the accuracy of the predicted egg temperatures was checked with laboratory experiments in which thermal radiation and wind speed could be measured accurately.

The experiment was set up with a pheasant egg mounted on a flat piece of styrofoam to minimize conductive heat loss and to maximize the convecting and radiating areas.



Fig. 4. Solar radiation: air temperature relationships that yield pheasant egg temperatures of 5°-30° at wind speeds of 138 cm/min and 1320 cm/min. Ground temperature = 25° C, pheasant egg diameter = 4 cm, pheasant egg mass = 29 g, --- = maximum values of Q_{inc} anticipated.

The eggs were subjected to long-wave radiation from infrared bulbs painted black. The radiation was measured with an Eppley pyrgeometer. Egg temperatures were monitored with a recorder and a value was taken when a steady state was achieved. The energy balance describing this experiment is

$$Q_{abs} = C_v + R_n \tag{4}$$

The radiating and convecting areas were visually approximated as 95% of the total area. In this experiment the convection coefficient was empirically determined using a gold-plated aluminum casting of a pheasant egg (Tibbals et al. 1964, Wathen et al. 1971). A value of 0.0114 cal/cm²-min- $^{\circ}$ C was obtained for the convection coefficient under these conditions, and this value was used in equation (4).

The computer program was used to solve equation (4) and obtain predicted egg temperatures. These were compared to the measured egg temperatures in Fig. 3. Of the measured temperatures 77% were within $\pm 3^{\circ}$ C of the predicted temperatures.

D. PREDICTING CLIMATE SPACE

The chief value of constructing a model lies in its predictive capabilities. As we know that high egg temperatures decrease the hatchability of pheasant eggs, insight into the climatic relations that might produce a reduced hatch can be gained by means of a climate diagram similar to those presented by Porter and Gates (1969). The two most important physical variables that determine egg temperature



Fig. 5. Solar radiation: air temperature relationships that would result in various hatchabilities for a preincubating pheasant egg.

are solar radiation and air temperature. These are varied in Fig. 4 while wind velocity is held at 138 cm/min and 1320 cm/min, representing the two extremes likely to be encountered in pheasant nesting situations. The enclosed areas represent the climate space the egg must occupy in order to be in temperature environments between 5°C and 30°C at air temperatures greater than 0°C and levels of solar radiation up to 1.2 cal/cm²-min. As is obvious from the graph, situations that drive egg temperature over 30°C can be easily foreseen in much of North America. For example when wind speed is 1320 cm/min, solar radiation is 0.4 cal/min, and air temperature is greater than 25°C, egg temperature will be greater than 30°C. Unfortunately hatchability cannot be predicted so easily as egg temperature as no experiments have been done on how the duration of high temperature affects it. A degree-minute approach as Russell (1972) used to measure microclimate could be applied in attempting to find a relationship between time, temperature, and hatchability. Air temperature and solar radiation values that would result in lines representing constant egg temperatures were constructed. Predictions of a percent hatch in the field are made below on the basis of hatchability values obtained from eggs that were preincubated for 10 days at various constant temperatures (Schulte 1972) and then incubated. If pheasant eggs experienced these conditions of air temperature and solar radiation for 10 days during their preincubation period, they should approximate the hatchability predictions of Fig. 5.

RESULTS

We can see from the model that the only important input to the egg is solar radiation, and the two important energy outputs are convection and radiation (Table 1). This indicates that pheasant egg temperatures in a nest are chiefly dependent on two parameters of the environment: (1) air temperature in the nest, and (2) the amount of solar radiation received by the eggs.

Parameters such as ground temperature, air temperature above the vegetation, and humidity have little relative influence on egg temperatures other than their indirect effects on air temperature in the nest, and on the vegetation shielding the eggs from the sun. During midday, meteorological measurements of air temperatures above the vegetation had little relevance to the temperatures of 30° C and more, which if prolonged may contribute to a reduced hatch.

CONCLUSIONS

The examination of the heat fluxes affecting the egg's temperature points out the necessity of obtaining microclimatological data rather than extrapolating egg temperatures from measurements outside the vegetation.

The modeling technique points out the relative importance of the various environmental parameters and the functional dependence of the most important heat inputs and outputs upon vegetation density and structure. Convective heat loss is a function of wind velocity above the vegetation and the vegetation density. Air temperature in the nest is a function of air temperature above the nest, solar radiation, and vegetation structure and density. The amount of solar radiation impinging on the egg is also a function of vegetation structure and density. Possibly if we are to look for a single factor limiting the range of the pheasant, it is to be found in the ameliorating or exacerbating effects of vegetation on the physical environment of the pheasant egg—that is, how the vegetation restricts the climate space available to the pheasant for successful nesting.

This study suggests that further investigation be directed to: (1) discovering how various vegetational types influence the modes of heat transfer for the egg, (2) noting whether hens are able to select vegetation that offers the best thermal conditions for the eggs, (3) predicting hatchability from microclimatological data after determining precisely how time and temperature interact to reduce hatchability, and (4) modeling other sensitive periods in the pheasant's life.

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