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Analysis of Ovulation–Oviposition Patterns in the Domestic Fowl by Telemetry Measurement of Deep Body Temperature

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Abstract

Continuous temperature records in relation to time of oviposition and behaviour associated with it are summarized for 13 laying strain pullets with a regular pattern of oviposition and for a further 10 pullets which were either 'internal layers', or natural or induced layers of membranous-shell eggs. The records of five pullets, in which the most recently ruptured follicle was excised within 2–5 h after ovulation, and of four control pullets are also included.

The previously reported finding that a temperature peak normally occurs at oviposition is confirmed. However, no evidence could be found for the regular occurrence of twin temperature peaks (for ovulation and oviposition), or for other direct temperature indicators of time of ovulation.

The 'oviposition' temperature peak is always accompanied by characteristic pre-laying behaviour, even in the absence of the oviposition due to occur at that time. Like the pre-laying behaviour, the temperature peak is shown to be a consequence of the ovulation event of the previous day; more precisely it is shown to depend on the presence of the intact ruptured follicle from which the ovum was shed.

It is concluded that the timing of a sequence of ovulations may be inferred, therefore, from the pattern of temperature peaks and this method is being used to study unusual ovulation–oviposition patterns occurring in some of our selection lines.

Some preliminary observations are also reported on the effects of injection of oxytocin, vasopressin or progesterone on body temperature.

Introduction

Changes in ovulation–oviposition patterns brought about by selection for reduced interval between eggs in an environment of continuous light (Sheldon *et al.* 1969; Sheldon and Podger 1972, 1974*a*, 1974*b*; Bobr, unpublished data) have for a long time highlighted the need for a precise and simple method of determining the time of ovulation, which would aid analysis and interpretation of these results of selection. Study of changes in deep body temperature in relation to the egg laying cycle was an obvious possibility. The report by Winget *et al.* (1965), suggesting twin temperature peaks for ovulation and oviposition, encouraged us to pursue the approach of radiotelemetry measurement of deep body temperature. Cain and Wilson (1971) reported an oviposition temperature peak but found no evidence of twin ovulation–oviposition peaks. After establishing the basic temperature–oviposition relationship in 'normal' pullets laying regular sequences of eggs, we have concentrated our studies, reported in this paper, on birds with abnormal patterns of oviposition such as chronic or intermittent 'internal layers', and chronic or sporadic layers of membranous-shell (*ms*) eggs, i.e. prematurely laid eggs having shell membranes with little or no apparent calcification. We also report some preliminary observations on

the effects of injecting progesterone, oxytocin and vasopressin. A brief preliminary report of our early results has already been published (Bobr 1974).

Methods

Telemetry System

For the first four birds studied the telemetry system used was based on a conventional thermistor-pulsed oscillator combination (Winget *et al.* 1965; Fryer *et al.* 1966; Mackay 1968; Riley 1970; Cain and Wilson 1971) but with some variations designed to reduce implant size and increase service life and sensitivity. This system was provided for us by Mr B. H. Ridley. For the remaining 19 birds a quartz crystal temperature transducer (Ridley, unpublished data) was used because of radio frequency interference problems and other considerations of less than optimal stability and resolution in the first system. The new system is narrow band, reducing the radio frequency interference problem, and inherently stable.

The first transducer implants used were circular [as in Winget *et al.* (1965)] and, after being sealed with beeswax, were 2 cm in diameter and 0·8 cm thick. Later ones were oblong in shape [as used by Cain and Wilson (1971)] and about 3 cm long, 1·8 cm wide and 0·8 cm thick. In the first system temperature was recorded continuously on a single-channel chart recorder, and in the second system every 10–12 s on both a single-channel chart recorder and a digital display. Both systems have been subject to considerable background 'noise', i.e. momentary but sizeable increases or decreases in temperature caused by outside interference. In presenting the temperature graphs the noise spikes or more prolonged effects, obviously due to such external factors, have been removed. The correct calibration of each implant in use was checked by regular recording of the bird's rectal temperature.

The effective life of the implants averaged 6–8 weeks, varying from 1 week in extreme cases up to 6 months, failure of the very short-lived ones being usually due to faulty moisture-proofing with beeswax and Silastic 382 (Dow Corning Co.). However, the lifetime of the battery powering the transmitter was the main factor affecting the life of the implant.

Surgery

The temperature transducers were surgically implanted in the abdominal cavity under nembutal anaesthesia. Initially they were sutured to the right side of the sternum (Winget *et al.* 1965), the liver overlaying the implant very closely. Later, for ease of surgery, they were implanted under the tip of the sternum (Cain and Wilson 1971). The latter position was also more convenient for replacement of transmitters.

Management of Test Birds

The birds were housed in single wire cages, the egg tray fronts of which were equipped with a light wire gate and mercury switch circuit for recording time of oviposition on the chart recorder. Room temperature did not fall below 18°C (day–night fluctuation 18–22°C), and rarely exceeded 24–26°C. No obvious effects of extremes of temperature on the results were observed. Most birds were recorded under constant 14 h light : 10 h dark. As far as possible birds under test were observed daily for varying periods to record changes in behaviour, particularly those associated with the oviposition temperature peak. Initially such observations of behaviour were made in relation to 90–95% of ovipositions and/or temperature peaks for each bird; later the proportion observed was about 60–70%.

Results

Birds with a Regular Pattern of Oviposition

Data were obtained from four birds in 1972 and confirmed subsequently in a further nine birds over the next $2\frac{1}{2}$ years. Pullets aged 6–14 months and laying regular sequences (clutches) of at least 5–6 eggs were used. Except for one bird which was a White Leghorn × Australorp crossbred, these birds came from four related strains of White Leghorns and two related synthetic strains, derived originally (some 15–16

generations previously) from a White Leghorn × Australorp crossbred population. For most birds the period of testing and data collection ranged from $2\frac{1}{2}$ to $7\frac{1}{2}$ weeks but two extreme cases were recorded for 11 and 21 weeks.

As it is not possible to present detailed data for all or even a few of the birds observed, the following is largely a schematic, generalized outline of typical features of temperature and behaviour changes associated with the oviposition cycle. It should be stressed that there are characteristic differences both between and within individual birds but these will be referred to only when they affect the general picture and its interpretation in a significant way.

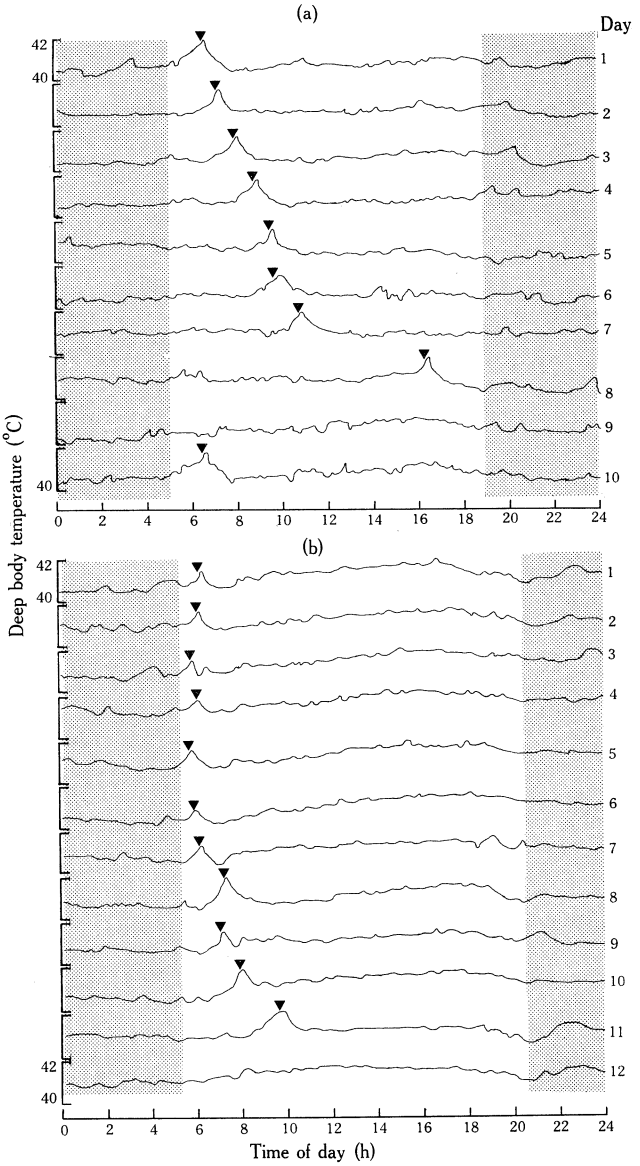

Fig. 1. Sample of temperature records of two pullets (*a* and *b*) with a regular pattern of oviposition. ▼ Time of oviposition. Dark periods are shown shaded. The temperature records on all days are between 40 and 42°C.

(i) *Body temperature*

The basal temperature during the dark phase (night) is usually 0·3–0·7°C lower than that during the light phase (day). A fairly typical pattern is that it begins to rise just before or at first light and continues to rise very slowly until mid to late afternoon. It may remain at this level for 1–2 h but in the last 1–2 h before darkness it drops to the night time level where it tends to remain throughout the night. However, there are considerable departures from this pattern both during the day and during the night. In contrast, the temperature peak related to oviposition is consistent and repeatable both within and between birds—typical sequences for two different birds are shown in Figs 1*a* and 1*b*, and Fig. 2 shows some individual temperature peaks in more detail. These results confirm that a rise in temperature normally occurs at the time of oviposition.

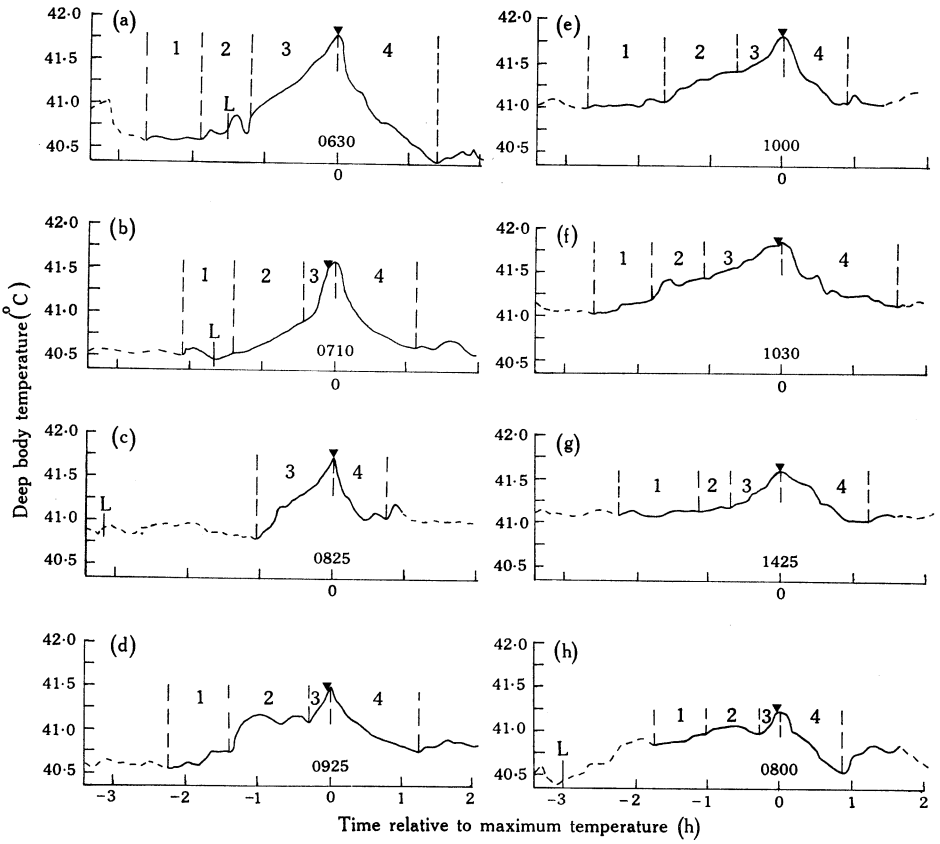

Fig. 2. Examples of detailed individual temperature peaks of four pullets (two per pullet—*a* and *b*; *c* and *d*; *e* and *f*; *g* and *h*). ▼ Time of oviposition. Stages 1, 2, 3 and 4 are shown above the graphs. *L*, Beginning of the light phase in those cases where the full period shown was not in the light phase.

The body temperature begins to rise 1–2½ h before oviposition. Typically it starts from a point slightly below the preceding basal level, and initially rises very slowly (stage 1). Then the rate of increase accelerates gradually (stage 2) and this stage is usually terminated by a relatively short period (up to 20 min) of levelling off or even

fall of temperature. In the next stage (stage 3) the temperature increases rapidly to the maximum—the peak. It then falls to a minimum (stage 4) and then rises to a more or less stable basal level. These defined stages, especially 1 and 2, are somewhat arbitrary descriptions of a variable situation, but they serve to facilitate the exposition of the results in the following sections.

The decrease of temperature in stage 4 is usually more rapid than the rise in stage 3, and the minimum reached in stage 4 is usually slightly below the level in stage 1 at which the rise started. As a rule, the egg is expelled by the bird 2–8 min before the maximum temperature is reached, although rather infrequently the expulsion of the egg may coincide exactly with the temperature maximum. The peak itself usually persists for 2–10 min but it may be a 'momentary' one, i.e. of 10–12 s duration (the shortest interval of temperature sensing in our system). Delayed expulsion of the egg, i.e. 1 h or more after the temperature peak, was observed only rarely. Only a few isolated occurrences of twin peaks within the period of elevated temperature, of the type reported by Winget *et al.* (1965), have been observed among the total of several hundred temperature peaks we have recorded. The total temperature rise to the oviposition peak is usually within the range 0·5–0·8°C, the highest recorded being 1·2°C and the lowest 0·2°C. The usual duration of the oviposition temperature change, from the start of the rise to the post-peak minimum, is 2–3 h, although shorter (1½ h or less) and longer periods (up to 4 h) were also recorded.

(ii) *Behaviour*

The onset of pre-laying behaviour is usually signalled by soft continuous vocalization ('talk'), the pullet standing quiet but alert and facing the front of the cage. The talk may be interrupted occasionally or frequently, depending on the bird, for various lengths of time by eating, drinking or preening and then resumed again to become continuous and gradually increasing in intensity. Vocalization in one form or another (talk, short calls, etc.) usually persists until oviposition. After a variable period (30–90 min) of quiet talk the pullet enters the phase of restless activity reported by Wood-Gush and Gilbert (1969). She moves around in the cage with increasing frequency and occasional brief interruptions for nervous attempts at picking up food or drinking. The initial pacing of the cage develops into, or may be intermittent with, 'escape' movements, sometimes violent. 'Nest-building' or 'dust-bathing' may be present also, particularly in the final stages. Some pullets may have periods of preening or resting (sitting quietly, no vocalization) between bouts of restlessness. The majority cease their activity rather abruptly, assume the laying stance, facing the back of the cage, and then expel the egg. Some have a period of rest before oviposition; they then get up quietly, make a few preparatory movements to get themselves into a laying stance and expel the egg. After the expulsion of the egg, the bird immediately becomes relaxed, pauses for a while (2–8 min) and, in a very characteristic manner, turns abruptly to the food trough and eats avidly for quite a time as if very hungry.

(iii) *Relation of body temperature changes to behaviour*

The body temperature starts to rise about the time of the onset of the pre-laying behaviour. The stage of the slow rise and fluctuating temperature (stage 1, Fig. 2) corresponds to the period of quiet talk with interruptions for eating, drinking or preening. The gradual acceleration in temperature rise, terminated by the temporary

levelling off or decrease (stage 2), followed by the rapid rise up to the peak (stage 3) parallels the increasing intensity and frequency of restless activity, the overall continuity in temperature rise being not affected either by periods of rest or by other breaks between bouts of vigorous activity. The start of temperature fall (stage 4) coincides with the sudden commencement of eating. The pause in activity between expulsion of the egg and eating includes the short post-expulsion continuation in temperature rise and the duration of the peak. In cases when expulsion of the egg coincides exactly with the temperature peak, the latter is of the 'momentary' type and the pullet usually begins to eat immediately. In the rare case of oviposition being delayed 10–15 min beyond the peak, eating was also delayed.

The overall pattern of temperature changes and behaviour was similar in all pullets investigated. It was relatively constant from one oviposition to another for an individual bird, particularly with respect to the behaviour pattern. Nevertheless, differences in the duration and rate of temperature increase, in the size of the total increase and in the intensity of a bird's activity were observed between ovipositions within pullets. But no relationship between these differences and the position of the egg in the clutch or the clutch length could be detected. Differences *between* pullets were more pronounced. Differences occurred with respect to the duration, frequency and sequence of the various components of the restless behaviour and/or in the absence of some of the activities like nest-building, dust-bathing and rest period. The shapes of the temperature curves reflected, to some extent, these differences (e.g. Fig. 2). Some birds, on rare occasions, did not have the initial 'quiet' stage of behaviour, but suddenly exhibited intense restlessness of relatively short duration (as low as 20 min in an extreme case), i.e. only the usual stage 3 was present. The temperature curve in such instances consisted only of a short steep rise followed by a similar decrease.

Birds with Abnormal Patterns of Oviposition

It is evident from the data presented so far that the two events known to be associated with oviposition, namely (1) the temperature peak (Winget *et al.* 1965; Cain and Wilson 1971), and (2) the pre-laying behaviour (Wood-Gush and Gilbert 1969; Woodard and Wilson 1970) occur simultaneously which suggests a common cause for both events.

That ovulation is a prerequisite for the pre-laying behaviour occurring some 24–26 h later and that the pre-laying behaviour is a reliable indicator that ovulation occurred, whether the egg is laid or not, is unequivocally documented for hens kept in floor pens (Wood-Gush and Gilbert 1965*a*, 1965*b*, 1970). Confirmatory evidence that the same relationship is operative in the case of the temperature peak, i.e. that the temperature peak is a reliable indicator of ovulation on the previous day, was obtained from the following sources.

(i) *Birds with a natural tendency to lay* ms *eggs*

The premature laying of an *ms* egg occurs occasionally in almost all pullets and frequently in some. It is quite common in the White Leghorn selection line reported by Sheldon and Podger (1974*b*). Observations of sporadic *ms* events in most birds studied and of the more frequent events in a few birds with this tendency have shown that the *ms* egg is *always* followed by a typical 'oviposition' temperature peak in the

absence of oviposition some 12–20 h after the *ms* egg was laid, i.e. when that *ms* egg should have been laid as a complete hard-shelled egg if development had proceeded normally (Fig. 3).

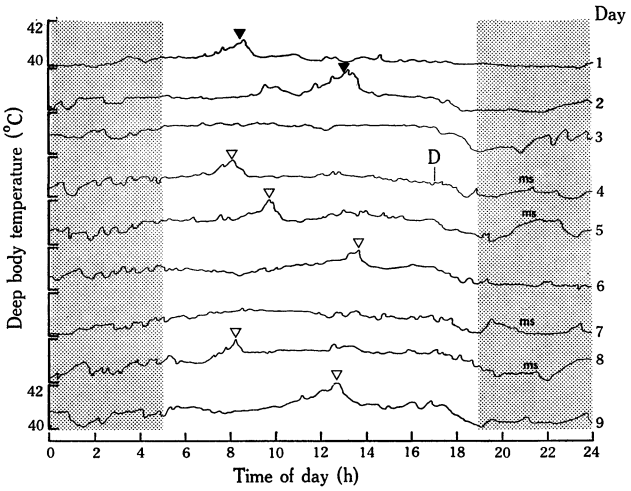

Fig. 3. Sample of temperature record of a pullet with a tendency to lay *ms* eggs. ▼ Time of oviposition of a normal hard-shelled egg. ▽ Temperature peak without an oviposition. *ms*, Approximate time of oviposition of an *ms* egg. *D*, Time of delayed oviposition of a normal hard-shelled egg.

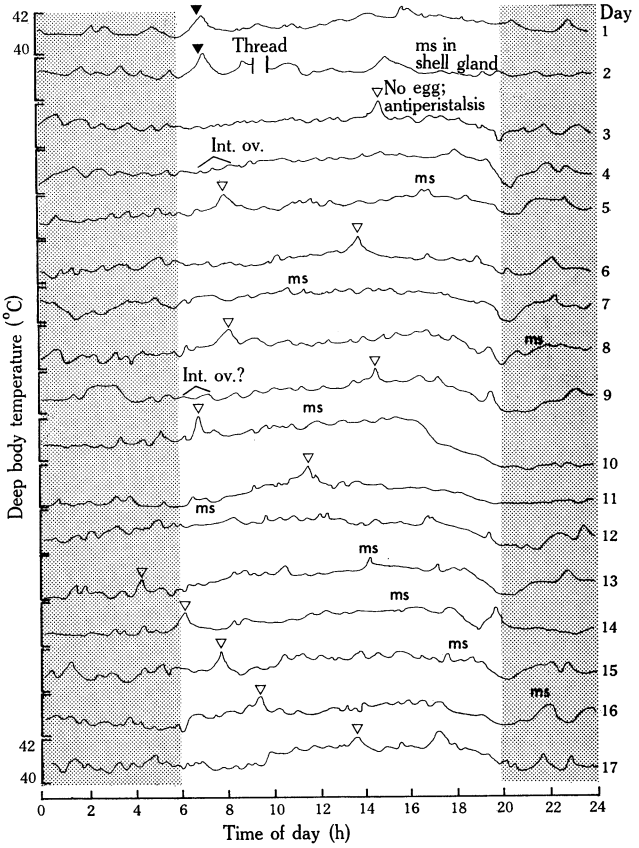

Fig. 4. Sample of temperature record of a pullet induced to lay *ms* eggs by insertion of a thread in the shell gland. Symbols as in Fig. 3 legend. Int. ov., a probable internal ovulation.

(ii) *Obligatory layers of* ms *eggs*

This condition is induced in normal layers by the insertion of a thread through the walls of the shell gland [the technique was introduced by Sykes (1953) and used by Wood-Gush (1963) and Lake and Gilbert (1964)]. One pullet was under observation for 7 weeks following the insertion of the thread (see Fig. 4). As in a further three birds studied for shorter periods the temperature peaks (and associated pre-laying behaviour), unaccompanied by oviposition, formed a regular pattern as in a clutch sequence, with no peak on a 'miss' ('clutch-break') day. The *ms* eggs were dropped 12–20 h before each temperature peak, i.e. on the previous afternoon or during the night. All *ms* eggs laid were at approximately the same stage of development—well plumed and with hardly any trace of calcification, i.e. they were laid 7–8 h after ovulation. The *ms* egg which originated from the first ovulation of a clutch was laid in the early afternoon, successive *ms* eggs in the clutch being laid later in the day and early in the night. There was no temperature peak at the time an *ms* egg was laid, but a very brief rise of 0·05–0·10°C occurred usually at the same time and was hardly distinguishable from the background noise of the temperature graphs. About 10 min and sometimes up to 30 min before dropping an *ms* egg, the pullet assumes a peculiar, motionless posture with wings slightly lowered and the feathers on the top of the head, particularly along the sides of the comb, distinctly raised. She remains in this position for up to 5 min after dropping the egg, giving the impression of being puzzled.

The antiperistalsis shown on day 3 of Fig. 4 indicates that the *ms* egg palpated in the shell gland the previous day must have moved back up the oviduct and into the abdominal cavity because laying of that egg, as membranous or hard-shelled, did not occur. A similar event (temperature peak but no oviposition and no *ms* egg the previous day) had been observed previously in the same bird. When laparotomy was performed a few weeks after this observation to insert the thread into the shell gland, an aged *ms* egg (liquified but still within the shell membrane) was identified in the abdominal cavity. Membranous eggs have also been found occasionally in the abdominal cavity at autopsy of other birds with an irregular pattern of oviposition, in our various selection or inbred lines.

(iii) *Autopsy of suspected 'internal layers', performed immediately after an eggless temperature peak occurred*

'Internal' laying was confirmed by autopsy in three pullets that had eggless temperature peaks (accompanied by pre-laying behaviour). Fig. 5 shows the temperature pattern for an intermittent internal layer and Fig. 6 for a chronic internal layer. In both pullets no egg could be palpated before the expected oviposition (checked both on the previous afternoon and about 1 h before the temperature peak). At autopsy of two intermittent internal layers (the one in Fig. 5 and a similar one) it was confirmed that the number of follicles apparently ruptured over the previous 3 days exceeded by one the number of eggs laid during that period but corresponded to the number of temperature peaks. In the experience of one of us (LWB) follicles ruptured earlier than 3 days previously cannot be distinguished from each other by graded size and appearance. The chronic internal layer in Fig. 6 had an impacted oviduct as a result of ovulating for 3 or 4 weeks without normal egg development and oviposition. This bird also had a relatively fresh bit of unabsorbed yolk, probably the remains of the previous day's ovulation, and a freshly ovulated ovum in the abdominal

cavity. Extensive experience of one of us (LWB) with habitual internal layers has shown that bits of unabsorbed yolk accumulate in the abdominal cavity.

Effect of Excising the Post-ovulatory Follicle

To specify further the relationship between the ovulation event and the temperature peak on the following day, the role of the post-ovulatory follicle was investigated.

Five pullets had their most recently ruptured follicle removed, by the technique of Wood-Gush and Gilbert (1964), within 2–5 h after a presumed mid-clutch ovulation.

Four control pullets were subjected to the same surgical procedure after ovulation but without excision of the follicle. All birds were autopsied 2–5 days later.

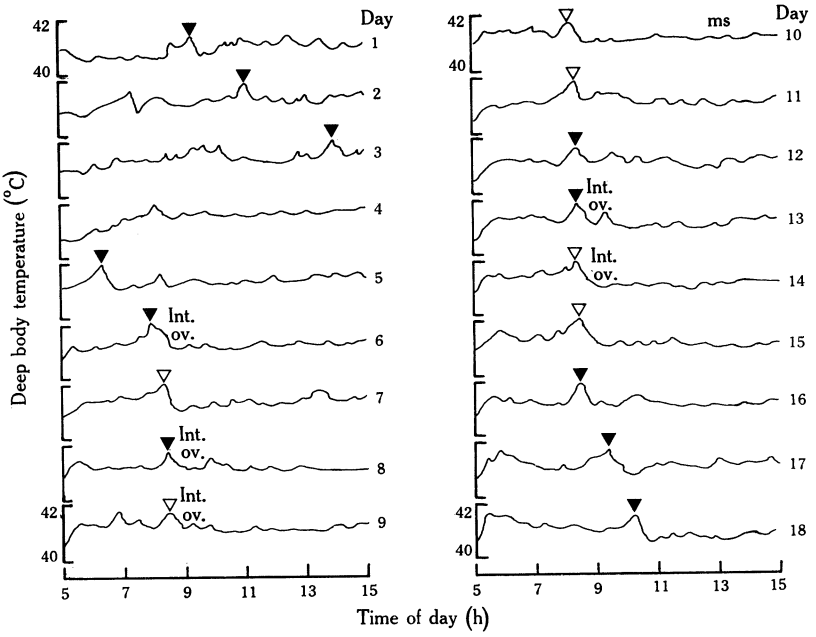

Fig. 5. Sample of the temperature record of an intermittent internal layer. Symbols as in legends for Figs 3 and 4.

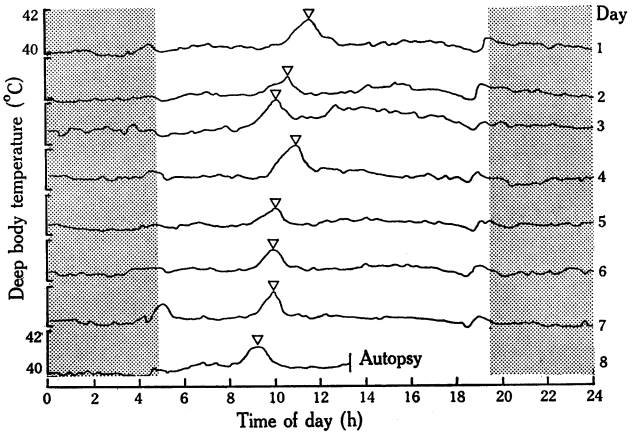

Fig. 6. Sample of the temperature record of a chronic internal layer. Symbols as in legends for Figs 3 and 4.

In all treated pullets the pre-laying behaviour was abolished [as shown by others (Wood-Gush and Gilbert 1964)] and the temperature peak was also absent during the day of expected oviposition and at the time a delayed egg was laid (Fig. 7). In one pullet the egg was delayed for 3 h, and in another pullet for 3 days, i.e. until the day of next ovulation. The remaining three pullets dropped the eggs prematurely as *ms* eggs several hours after surgery. No particular posture or behaviour was associated with the laying of the delayed eggs.

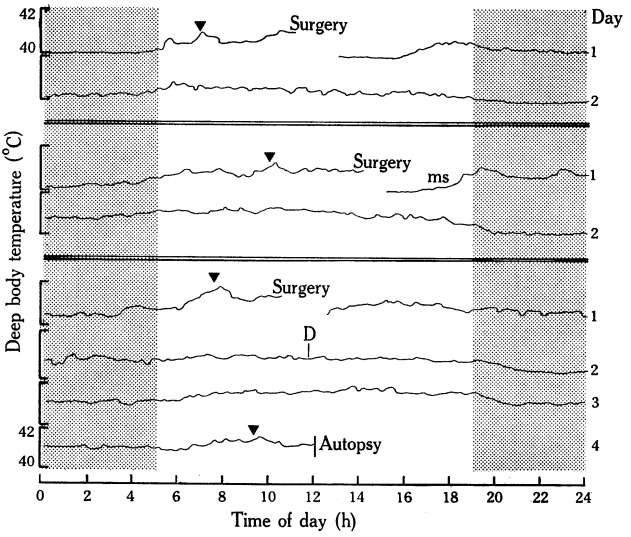

Fig. 7. Temperature record of three pullets immediately before and after excision of the most recently ruptured follicle. Symbols as in Fig. 3 legend.

In all control pullets the pre-laying behaviour and the accompanying temperature peak were consistently present at the same time as oviposition on the following day. In one pullet oviposition was delayed by 3 h, and in another it was delayed by 5 h; these eggs became the last of the clutch. The remaining two pullets laid their eggs at the expected time.

In all birds in treated and control groups the ovulation sequences were interrupted or terminated following surgery. At autopsy it was observed that at least one follicle became atretic, including the one due to ovulate on the day following surgery (see also Rothschild and Fraps 1944). Consequently, the ovulation immediately preceding surgery, which would normally have been a mid-clutch ovulation, became the last of the sequence. In two cases, one in each group, where the postovulatory follicle was in fact the last of the clutch, the next follicle due to ovulate (i.e. the first of a new sequence) was not affected and ovulation occurred at the expected time. A decreased body temperature and 'subdued' general behaviour on the day following surgery were very evident in the treated birds and to a lesser extent in the controls.

Effect of Some Hormones on Body Temperature

To throw some light on the possible mechanism of the temperature peak some attempts were made to induce it with hormones, namely posterior pituitary principles (oxytocin and vasopressin) which cause premature expulsion of an egg (Gilbert

1971*a*), and progesterone, known to be related to ovulation and oviposition (Brard 1961; Gilbert 1971*b*) and pre-laying behaviour (Wood-Gush and Gilbert 1975).

Oxytocin and *vasopressin* (Pitocin and Pitressin, Parke-Davis) were used in single intravenous injections of 2 i.u. at different stages of the egg cycle (arginine vasotocin, the most potent oxytocic principle in the fowl, was unobtainable). Oxytocin was injected into one of the obligatory layers of *ms* eggs during stage 4, 10 min after the last temperature peak of the clutch sequence. It caused an immediate and rapid temperature rise of 0·5°C within 10 min, and a similarly rapid fall to the pre-injection level from where the temperature continued its postpeak downward course. By comparison, in stage 3 of this peak the same rise of 0·5°C occurred after 20 min. The effect of oxytocin injected in another bird 3 h before the expected oviposition peak, also the last of the clutch sequence (an egg being present in the shell gland), was somewhat ambiguous because inadvertently the injection was partly subcutaneous and the expected premature oviposition (Gilbert and Lake 1963) did not occur. Nevertheless, as in the previous bird, a very rapid, almost instantaneous, temperature rise of 0·5°C occurred 10 min after the injection (0·4°C in the first minute and 0·1°C in the remaining 9 min). The elevated temperature remained constant for 2½ h, rising further to the oviposition peak by the time the egg was laid (0·7°C within 45 min). The oviposition peak occurred at the time expected as if there had been no injection.

Vasopressin was similarly injected, but into only one bird at intervals of 6 days: (1) 80 min after the presumed last oviposition peak of the sequence (no egg in the shell gland later in the day) at the postpeak minimum temperature; (2) late afternoon on a 'miss' or clutch-break day, about 10 h after ovulation (*ms* egg in shell gland); and (3) 9 h after the first oviposition peak of the sequence (slightly calcified egg in the shell gland). The temperature changes following vasopressin injection were rather similar in all three cases and the temperature rises were similar to those obtained with oxytocin: 0·44°C in 14 min, 0·55°C in 13 min and 0·3°C in 7 min in the three cases. Following the temperature rises the decrease to pre-injection level was slow and gradual (40–50 min), unlike the case in the first oxytocin-injected bird. The overall picture of these temperature graphs was that of a somewhat scaled down oviposition temperature peak with a relatively shorter ascending part and rather typical descending part. When an egg was present in the shell gland at the time of injection a premature *ms* egg ensued within 1–3 min.

Injection of either oxytocin or vasopressin was followed immediately by a stance and abdominal muscular efforts of short duration typically associated with the expulsion of an egg, irrespective of the presence or absence of an egg in the shell gland. Symptoms of heat stress, panting, and blanching of the comb lasted for a longer period, particularly the latter. Similar effects were observed by Gilbert and Lake (1963) who reported a transitory increase in respiration rate following injection of oxytocin or vasopressin.

Progesterone was injected intravenously in one bird 6 h after oviposition when an *ms* egg was already present in the shell gland. The dose was 1 mg progesterone in propylene glycol–ethanol solution [this dose was used for inducing premature ovulation by Gilbert (personal communication)].

The temperature peak the following morning appeared to be delayed by about 3 h and the oviposition was delayed by a further 7 h. When twice this dose of progesterone was given to another bird 4½ h after oviposition (an *ms* egg also being detectable in the oviduct) the temperature peak the following morning occurred at

the expected time but the oviposition was delayed by about 6½ h. In neither bird was there any immediate effect of the injected progesterone on body temperature, beyond an insignificant momentary rise of 0·1°C. Control injection of propylene glycol–ethanol solution had no effect on temperature. On the second day after injection both birds returned to the normal pattern of oviposition accompanied by a temperature peak.

Discussion

(1) The results presented for birds with a regular pattern of oviposition confirm and extend the main result of Winget *et al.* (1965) and Cain and Wilson (1971), i.e. an unmistakable rise in deep body temperature normally coincides with the laying of an egg. However, the results presented above for birds with abnormal patterns of oviposition, either natural or induced, show unequivocally that the usual association of the temperature peak with oviposition is brought about by the dependence of both on the preceding ovulation; furthermore, the absence of a temperature peak after excising the immediate post-ovulatory follicle shows that this association depends on the presence of the intact ruptured follicle from which the egg was shed.

That no obvious simultaneous temperature rise occurs and is due to a specific ovulation event, is confirmed by the universal absence in our results of a temperature peak at the appropriate time on the day before the first egg of a clutch sequence, when an ovulation is certain to have occurred (e.g. Figs 1 and 3). Thus the original aim of being able to determine time of ovulation directly from simultaneous change in body temperature was not realized. Nevertheless, the dependence of the temperature peak on the ovulation event of the previous day presents a way of inferring, within reasonable limits, the timing of a sequence of ovulations, since the time an egg spends in the oviduct in birds with a regular pattern of oviposition is reasonably well known and has a relatively narrow range (Warren and Scott 1935; Gilbert and Wood-Gush 1971; Melek *et al.* 1973). Taken in conjunction with accurate recording of the timing of the related sequence of ovipositions, the continuous recording of deep body temperature therefore provides a reasonably powerful technique for discriminating between ovulation and oviduct function as the causes of unusual ovulation–oviposition patterns, such as occur in some selection lines (e.g. Sheldon and Podger 1974*b*). It is now being used for this purpose in our laboratory.

(2) The weight of all the evidence summarized in this paper, as well as that of Cain and Wilson (1971), does not support the possibility of twin temperature peaks for ovulation and oviposition reported by Winget *et al.* (1965). The frequency of twin temperature peaks in our data was less than 1% of all temperature peaks recorded.

In addition, in our results oviposition nearly always occurs relatively very late in the period of elevated temperature, rather than early as indicated by Winget *et al.* (1965). They reported further that the temperature peak was different for the last egg of the clutch, whereas in our results there is no difference in the form of the temperature peak for the last egg of the clutch and for the others. No satisfactory explanation is available for these differences between our results and those of Winget *et al.*

(3) The close relationship of the *pre-laying and laying behaviour* and the 'oviposition' peak in body temperature suggests that the *muscular activity* involved may be mainly responsible for this peak, as already pointed out by Cain and Wilson

(1971). However, the situation is clearly more complex than this. The total increase in temperature is not simply correlated with the overall duration or intensity of muscular activity. High, steep peaks seem to be equally associated with low as with high intensity of pre-laying behaviour. In Fig. 2 the second bird (recordings *c* and *d*) shows an example of steep and high temperature rises (0·8–1°C) consistently associated in this bird with extremely limited muscular activity which was restricted to infrequent quiet vocalization followed by several pacing movements just before oviposition.

Secondly, the birds from the synthetic strains and the single Leghorn × Australorp crossbred (heavier, more placid birds) had a definite tendency for less strenuous muscular activity than the lighter White Leghorns. Similar observations were reported by Wood-Gush and Gilbert (1969) and Wood-Gush (1972). However, the heavier birds did not exhibit patterns of temperature change different from those of the White Leghorns.

Furthermore, two instances of oviposition temperature peak without any increase in muscular activity were observed. It should also be added that occasional bursts of muscular activity, comparable to that in pre-laying behaviour, occur at times other than oviposition (disturbance by presence of strangers, sudden noise, etc.) and do not cause a rise in body temperature more than about 50% of the times. Conversely, neither the rise in body temperature nor the muscular activity (pre-laying behaviour) are necessary conditions for the expulsion of an egg. Both are absent when either *ms* eggs occur (Figs 3 and 4) or there is a delay in oviposition, whether naturally occurring (Fig. 3 and additional observations) or due to the excision of the ruptured follicle (Fig. 7).

(4) The role of posterior pituitary hormones in raising the body temperature and of progesterone in delaying oviposition without affecting temperature warrants further investigation. Our failure to induce a complete, typical oviposition temperature peak by single injections of oxytocin or vasopressin may have been due to their relatively short-lived biological activities in the blood. The half-lives are reported to be 10 and 20 min for oxytocin and vasopressin respectively (Hassan and Heller 1968). A slow infusion instead of single injections might have been more effective. In the absence of experimental evidence we can only speculate on the role of vasotocin, the other posterior pituitary hormone identified in the fowl and related to oviposition (Gilbert 1971*a*). It is conceivable that it may be the major hormone (singly or in combination with the others) responsible for the rise in body temperature associated with oviposition. It seems particularly significant in this respect that changes in the blood level of vasotocin [marked increase prior to oviposition and subsequent fall to resting level (Sturkie and Lin 1966)] run parallel to similar changes in body temperature at that time. Reports that prostaglandins can induce premature oviposition in the quail and hen (Hertelendy 1972, 1974) suggest another line of investigation into the mechanism of oviposition and associated events.

Although progesterone injection had no effect on body temperature in our pilot experiment, further observations of possible temperature effects of progesterone may help towards an understanding of the effects of progesterone on ovulation and oviposition. In our results there was delayed oviposition following progesterone injection [as shown by Brard (1961) and Wilson and Sharp (1976)] and no effect on the time of the temperature peak and associated pre-laying behaviour in one case, although the temperature peak was apparently delayed somewhat in the other case. However, there was no disruption of the ovulation pattern following our progesterone

treatment. In both cases the clutch pattern of ovulations subsequent to progesterone injection occurred at the times normally expected, indicating no interference by progesterone. In contrast to this Brard (1961) and Wilson and Sharp (1976) showed significant and variable effects of progesterone on time of ovulation, i.e. delaying, advancing or blocking completely. Because of the small number of our tests we cannot put much weight on the difference between our results and those of the above authors. It is possible that different technique influenced the results. In both the above reports progesterone was given by intramuscular injection whereas we injected intravenously.

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