Parental behaviour of captive Willow Grouse
*Lagopus l. lagopus*

H. M. ALLEN, C. BOGGS, E. NORRIS & M. DOERING


The parental behaviour of four wild pairs of Willow Grouse, maintained in captivity near Tromsø in northern Norway, is described. Two pairs bred normally in outdoor enclosures in June, while two, maintained indoors under artificial light, bred successfully in late autumn and early spring, respectively. All four hens laid full clutches, and all but one incubated them. Her eggs were incubated and the chicks subsequently brooded by the cock. The incubating birds were more active, and called more, just before hatching. In some cases they left the nest while individual chicks hatched. Hatching success was relatively low, but the chicks which did hatch were brooded effectively, usually by the hen. The results are discussed in relation to other studies of grouse breeding.


Introduction

In Norway, Willow Grouse hens *Lagopus l. lagopus* usually nest in a scrape in dense vegetation on rough moorland. Cock Willow and Red Grouse *L. l. scoticus* vigorously defend the area around the nest (Johnsgard 1973, Watson & Jenkins 1964), and it can be difficult to approach or observe the birds closely without flushing them. The hen incubates a clutch of about ten eggs for some 22 days. The chicks are precocial, and they temporarily leave the nest to feed within a very few hours of hatching, although they are completely dependent on the hen for warmth until they are at least a week old (Aulie & Moen 1975).

At the University of Tromsø’s Wildlife Research Station, near Tromsø in northern Norway, most grouse eggs are removed from the hen soon after they are laid, and are incubated in large batches by machine. However, captive Willow Grouse will, if allowed to do so, court, mate, and lay a normal clutch of eggs, incubate them, and care for the chicks, if left undisturbed with food, water, and nesting materials, under long day-length conditions.

Of the several successful breeding pairs already studied, we describe four, paired under widely varying conditions, which allowed us to concentrate on different stages of the breeding cycle in the different pairs.

Methods

Observations were made between May 1974 and June 1976 at the Wildlife Research Station on Tromsø Island, nearly 70°N on Norway’s coastal strip, where the climate is relatively mild for the latitude.

The subjects were four pairs of healthy, wing-clipped wild Willow Grouse, either trapped in the vicinity of Tromsø or first-generation offspring of trapped birds. In their home cages all had had continuous access to a specially developed pelleted feed, water, and grit.

The conditions under which the various observations were made varied with the season and climatic variations, and according to which aspect of behaviour was to be studied in a particular pair. The methods employed with the various pairs are summarized in Table I.
Table I. Comparison of methods used in a study of captive Willow Grouse

<table>
<thead>
<tr>
<th></th>
<th>PAIR 1</th>
<th>PAIR 2</th>
<th>PAIR 3</th>
<th>PAIR 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Age of birds</td>
<td>1 year</td>
<td>2 years</td>
<td>2 years</td>
<td>1 year</td>
</tr>
<tr>
<td>3. Holding conditions</td>
<td>Outdoor enclosure fenced with fishing net</td>
<td>Room with concrete walls, floor. Lit continuously, heated</td>
<td>As pair 2</td>
<td>Outdoor cage with wire mesh walls and wooden floor &amp; roof</td>
</tr>
<tr>
<td>4. Area available</td>
<td>255 m²</td>
<td>6.25 m²</td>
<td>13–16°C</td>
<td>3 m²</td>
</tr>
<tr>
<td>5. Ambient temperature</td>
<td>9–18°C</td>
<td>10–15°C</td>
<td></td>
<td>6–15°C</td>
</tr>
<tr>
<td>6. Food provided</td>
<td>Natural vegetation, grouse pellets</td>
<td>Grouse pellets, blueberry twigs</td>
<td>Grouse pellets</td>
<td>As pair 2</td>
</tr>
<tr>
<td>7. Nest materials provided</td>
<td>None</td>
<td>Fishing net pile on floor</td>
<td>Fishing net in car tyre</td>
<td>Turf-lined open nest box</td>
</tr>
<tr>
<td>8. Other materials provided</td>
<td>Water dishes &amp; hose</td>
<td>Water, grit, pine and birch twigs</td>
<td>As pair 2</td>
<td>As pair 2</td>
</tr>
<tr>
<td>9. Choice of mate</td>
<td>Chose each other from total of 4 birds together</td>
<td>T.V. camera and videorecorder. Microphone under nest</td>
<td>As pair 2</td>
<td>Rank-matched pair of 10 birds</td>
</tr>
<tr>
<td>10. Method of observation</td>
<td>Direct, from hide in enclosure. Also T.V.</td>
<td>3–7 hr/day during incubation, hatching and brooding</td>
<td>Daily inspection, T.V. during hatching and brooding</td>
<td></td>
</tr>
<tr>
<td>11. Times of observations</td>
<td>2 days before hatching; 7–10 hr. 8 days after; 19–24 hr.</td>
<td>9 hr during hatching – 2 hr/day, first 3 days of brooding</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Taping of observations</td>
<td>Video only</td>
<td>Audio &amp; video</td>
<td>As pair 2</td>
<td>Audio only</td>
</tr>
</tbody>
</table>

Observations

Table II summarizes certain of the results which are strictly comparable between the four pairs.

Pair one

Laying, incubation, and hatching

Before egg-laying, the hen made three nest scrapes, but spent little time near the eventual nest, which consisted of excess netting which had not been trimmed off the bottom of the fence. Nine eggs were laid in the nest, of which eight were incubated by the hen.

Incubation was uneventful and the pair was disturbed as little as possible. All eight eggs hatched between 0330 and 0845 hrs. on June 26. Slightly more than twelve hours before hatching, the hen began periodically rocking sideways on the nest, arching her back, and poking her head underneath her breast as she turned the eggs. The frequency of the action increased until after hatching, when the hen moved every three to four minutes.

Almost four hours after the first dry chick was seen, the hen left the nest, returned, and tossed out egg shells before settling down on the chicks.

Before and immediately after hatching, the cock roamed at large through the enclosure. The hen and the chicks left the nest about 15 hours after hatching was completed; thereafter the cock remained within two or three metres of them.

Brooding

Before brooding, until all the chicks were under, the hen called softly every three to five seconds. The chicks approached from the front, and looked up at her head. She looked down at the chick and raised her body slightly as the chick crawled under. If the hen did not notice the chick or would not let it under, the chick pecked at her breast. When all the chicks were under, she stopped calling for about a minute, and then called periodically. During
Table II. Comparison of results of observations of captive Willow Grouse

<table>
<thead>
<tr>
<th></th>
<th>PAIR 1</th>
<th>PAIR 2</th>
<th>PAIR 3</th>
<th>PAIR 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Days to 1st egg</td>
<td>Not known</td>
<td>6</td>
<td>15</td>
<td>Not applicable</td>
</tr>
<tr>
<td>2. Number of eggs laid</td>
<td>9</td>
<td>7</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td>3. Removed by observer</td>
<td>–</td>
<td>6</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>4. Eggs incubated</td>
<td>8</td>
<td>13 (12 infertile, later partly exchanged)</td>
<td>12 (4 infertile, added by observer)</td>
<td>10</td>
</tr>
<tr>
<td>5. Interegg laying interval</td>
<td>About 1 day</td>
<td>Fishing net</td>
<td>As pair 1</td>
<td>1 day</td>
</tr>
<tr>
<td>6. Nesting material used</td>
<td>Hen</td>
<td>Hen</td>
<td>Cock</td>
<td>Hen</td>
</tr>
<tr>
<td>7. Which bird incubated</td>
<td>22</td>
<td>21</td>
<td>25</td>
<td>1 day</td>
</tr>
<tr>
<td>8. Days of incubation</td>
<td>0.30–8.45</td>
<td>23.30–early morning</td>
<td>Night</td>
<td>21–22 (start date uncertain)</td>
</tr>
<tr>
<td>9. Time of hatching</td>
<td>No</td>
<td>Yes</td>
<td>Not observed</td>
<td>Yes</td>
</tr>
<tr>
<td>10. Did bird leave nest during hatching</td>
<td>8</td>
<td>5</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>11. Number of chicks hatched</td>
<td>Not checked</td>
<td>Hen only</td>
<td>Cock &gt; hen</td>
<td>Hen only</td>
</tr>
<tr>
<td>12. Brood patch</td>
<td>Hen</td>
<td>Hen</td>
<td>Cock</td>
<td>Hen</td>
</tr>
<tr>
<td>13. Which bird brooded</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>14. Brooding initiation pattern noted</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

the first few days, if chicks did not come when
the hen began brooding, she continued the
soft calls, and on five occasions rose and ap-
proached the chicks that were still out.

After brooding for several minutes, one or
more chicks usually left the hen, which would
start to call more and more loudly as she rose
and moved from the remaining chicks. For
several minutes after leaving the brood site,
the hen continued to call loudly. Three times
all the chicks left the hen before she got up,
and twice she rose before any of the chicks
had appeared. The chicks dispersed in search
of food when not brooding.

Both adults used the brooding periods for
brief naps. Normally the cock remained within
two metres of the brooding hen, but he would
rise and forage during the longer brooding
periods. As the length of the brood period
decreased, the cock either sat through the fol-
lowing non-brood period, or got up shortly
after the hen.

On about twenty occasions one or two chicks
approached the cock, looked up at him and
tried to crawl under. Usually, the cock either
turned away or moved slightly off and settled
again, often with a rocking motion similar to
the hen's. If the chick persisted, this was
repeated, usually ending with the chick ap-
proaching the hen. However, the cock was
seen brooding chicks five times.

The mean time between brooding periods
increased from 5 to 18 minutes during the
chicks' first week of life, and the maximum
time increased from 15 to 248 minutes. Am-
ient temperature and other conditions af-
fected both the average time between brooding
periods and the total time the chicks spent
brooding. The longer intervals between
brooding periods occurred around mid-day,
and brooding periods were longest between
2200 and 0300, when temperature was lowest,
although it was still bright day. Variations in
individual chicks' brooding times became more
marked with age, until by five days of age,
some chicks occasionally missed short brood
periods. Twice, when the chicks were six days
old and air temperature was 16–18°C, the hen
refused to let chicks crawl under her.

Diverse aspects of behaviour

The chicks began feeding the first time they
crawled out and pecked at the leaves and
blossoms of almost every plant they encoun-
tered. They also ate small insects on plant
leaves, including lepidopteran larvae, and to-
wards the end of the first week occasionally
cught small flying insects. By their fourth
day, the chicks were following the adult and
attempting to peck simultaneously at what it
was eating. After the first two days, the group
foraged throughout the whole enclosure, with
the chicks accompanied by the cock when
they were far from the hen.
Chicks were first seen preening about 24 hours after hatching, and were dust-bathing by the end of the first week.

Reactions to disturbances depended on their type and frequency. If the hen was approached, she flattened when brooding, calling softly. When not brooding, she usually stretched her neck, approached the intruder and gave loud open beak calls and occasional open beak hisses. The cock always threatened intruders with tail feathers spread, wings dropped, neck extended, neck feathers ruffled, eye combs exposed, and a loud warning call. After the disturbance was over the family moved to another location and the hen brooded, whether or not she had previously been brooding. The chicks responded to avian intruders by ‘freezing’ only when warned by call from the hen, which reacted only to Magpies *Pica pica* and Crows *Corvus c. cornix*. They took no notice of a neighbouring Willow Grouse hen which gave brooding calls.

**Pair two**

On her first day indoors, the hen was found sitting on the net, and a rough-surfaced egg lay on the floor. No more eggs were laid for six days, then she laid seven in eight days. Since this was the first pair studied indoors, it was not known whether the hen would incubate, and the eggs were removed one by one and each was replaced by two marked, infertile eggs. The seventh egg was not removed, as the hen immediately started incubating the thirteen eggs she now had.

Each egg-laying was marked by a period of calling, and this re-occurred frequently during incubation, when the hen turned the eggs. The nest was not made more elaborate by the hen, although she did occasionally tug at strands of netting, and rearrange pine twigs on the netting. In the twenty days of irregular observations, the hen was seen off the nest, feeding, on very few occasions. The cock stood alert one to two metres from the nest during incubation, except when disturbed. He called very little, and was never seen courting or copulating with the hen. Nevertheless, courting and mating must have taken place, as five of the six eggs which were placed in an incubator were fertile. Quiet calling continued to occupy much of the hen’s time until hatching. As the hen appeared to be incubating normally, turning them about hourly, eight of the infertile eggs were replaced by fertile eggs from the incubator. The hen returned to the nest within a few minutes and immediately resumed incubation.

On the night before day 21, the hen’s calling was almost continuous. Cheeping could be heard occasionally, and then more frequently, via the microphone under the nest, as the eggs approached hatching.

At about 2330, after looking down at the eggs a number of times and calling loudly, the hen left the nest. One egg could be seen moving back and forth as the chick struggled to get out. This activity continued for some minutes, while both the cock and the hen several times approached the nest, looked around, and left. The chick cheeped regularly, apparently every time it breathed, and both adults called irregularly. After seven minutes off the nest the hen returned, when the chick was almost clear of the egg. The hen pecked at both the empty shell and the chick, presumably clearing it of shell membranes. Settling down, the hen partially covered the chick, which soon started to work its way rearward, almost under the hen. About two hours later the chick appeared to be dry and fluffy, and it lay on the nest beside the hen. At this point there was almost continuous duetting between the hen and the chick which also spent some time looking at each other while the hen pecked gently at the chick’s face. When the chick returned these pecks, the hen raised herself enough to let it crawl under its breast feathers.

Some three hours after the first chick hatched, a second began to cheep regularly and loudly. Once again the hen left the nest while the chick struggled free of the shell. Returning after a few minutes, she settled down and allowed the newly hatched chick under when it had pecked at her face. Three more chicks hatched much later in the night.

The following day, while the hen was brooding, the cock approached several times and pecked either at the hen’s head or at something in the nest she was pecking at. Each time he was forced to leave or at least turn away by a peck or a gape display.

The chicks always approached the hen’s head and looked up at her before crawling under her breast feathers to brood. Occasionally hen
or chick would peck at the other or the chick would flap its wings and cheep. During the first three days the chicks spent most of the time under the hen, but spent more time wandering about, eating and drinking, after the hen started brooding at another nest site in the room.

Pair three

The pair soon settled down; the cock began to react to outside disturbances with aggressive calls and perched on one of the intended nests, a van tyre filled with fishing net. The hen found a regular place on the floor, and after fifteen days started to lay her eggs there. Copulation was never observed. Another pile of netting was placed in the room and the first eggs placed on it by the experimenter; soon the hen was laying her eggs with these.

By mid-October the hen had laid nine eggs, one of which was broken; two were removed for machine incubation so that in case nothing happened on the nest, we would at least know whether fertilization had taken place. The hen laid two more eggs, bringing the total in the nest to eight, but did not begin to incubate. Four days after the last egg was laid, the cock was found on the nest, and he had evidently been there some hours, as the eggs were warm. When disturbed he left the nest and did not return that day. In order to encourage the hen to take up incubation, four infertile eggs were added to the clutch, but two days later, it was again the cock who was found on the nest.

This time he stayed, and for the next twenty-five days he left the nest only for short periods when disturbed or in order to defecate, eat and drink. Within a couple of hours of the first observation, he was seen turning the eggs, poking his beak between them and drawing one back under him.

As the cock gradually pulled the netting closer round the eggs in an attempt to cover them, they became less easy to see. He did not turn the eggs in any particular pattern or order, but rose slightly and pulled the foremost egg backwards under himself, rolling it over several other eggs. He repeated this, often roughly, with several eggs, and then turned in the nest as he settled down, finally fluffing his feathers and rocking sideways for some seconds. He began calling before turning the eggs, and his calls, which were similar to a hen’s egg-turning calls, though lower in pitch, increased in rate as turning began and continued for a minute or so after the cock had settled again. Egg-turning took place about every one and a half hours.

The hen’s behaviour throughout incubation gave no indication that she was interested in the eggs. She either sat on the tyre, formerly the perch of the cock, or lay beside the nest, her original place. Not until the last two days before hatching did she climb on the nest when the cock was away, and poke around among the eggs, in what might have been a preliminary to turning them. Once she made ineffectual covering movements. On several occasions, when the cock returned, she remained near the nest and was chased away either by a clucking call or simply by a gape display, probably a hiss.

From the afternoon of day 20, sounds were picked up by the microphone under the eggs. Some originated with the cock (sounds of digestion, heart-beat), and some with the eggs (clicking, low-frequency sounds, and movements). The cock’s heart-rate was similar to the click rate (respiration rate) of the embryos. At 0220 on day 21, embryo sounds had become intense and rapid, and cheeping was heard. Bursts of activity were answered by the cock turning the eggs. In one case when the embryos continued active after turning, the cock rose and turned them again, after which the sounds diminished in intensity. On other occasions that day, calling by the cock appeared to increase the activity of the embryos for some seconds.

By day 22, the rate and intensity of sound production by the embryos had diminished, and it was found that none of the eggs had pipped; in fact, only one appeared to be alive. On day 24, two eggs from a batch in an incubator, due to hatch on the following day, were placed in the nest, in the hope that the cock would remain long enough on the nest to hatch them, as it was of interest to see whether he would respond to chicks.

When the nest was checked the following morning (day 25), four chicks were found. Two of them were from the eggs which had been added the previous day, and two from eggs which had been under the cock all the time. All four chicks appeared healthy and lively and they brooded under the cock, re-
turning to him for warmth, both voluntarily and when called. The cock's call was the one he had used when turning the eggs. One chick died two days later, and the others continued to brood under the cock, ignoring the hen, until they were removed at seven days of age. The hen did not appear to attempt to attract the chicks.

The cock had an extensive brood patch, much larger than the hen's, whose patch was similar to those of other hens which had laid eggs but not incubated them.

Pair four

In May the hen began to lay and her first ten eggs were immediately removed for another experiment. She continued to lay, and in mid-June began to incubate a clutch of ten eggs. Meanwhile the cock perched either on top of the nest box or on the highest pine branch in the cage, calling in answer to other cocks and at passing humans. The hen's response to the approach of people was an almost inaudible call, and crouching. On July 5 at 1800, several eggs were found pipped. At this point the hen could be flushed simply by reaching into the nest box, while the cock threatened the observer but did not attack.

At 2200, the hen appeared to be sitting higher than usual on the eggs, and she frequently called and resettled on the clutch. She also poked around among the eggs though without rising from them. At 2300 the nest was checked. As the hen would not rise from the eggs she was lifted enough to reveal that one chick was in process of cutting round the eggshell. The hen's behaviour continued in the same pattern of partially rising and poking with her beak among the eggs from time to time. She also called frequently, and cheeps could be heard from the eggs, though these were not correlated with the hen's vocalizations. Just after 0100 she rose and left the nest. Two damp chicks could then be seen and a third chick was struggling free of the eggshell. The hen returned and settled again after five minutes although the chick had not yet managed to free itself. The ambient temperature at this time was 6°C. When she once again left the nest less than an hour later, three chicks were hatched and a fourth was emerging. At 0230 a chick crawled out from under the hen and wandered around in the vicinity of the nest for several minutes before approaching the hen's breast and crawling under her. The chick, which could not have hatched more than three and a half hours previously, appeared quite dry, and it pecked at the cage floor. No vocalizations were heard from the chick or the hen.

No further activity was seen; at 0900, five chicks had hatched and were out foraging in the cage. They scattered and hid under branches when the cage was approached, and were called in and brooded under the hen when the intruder left.

Discussion

These observations of four grouse pairs confirm and amplify much of our knowledge of Willow Grouse parental behaviour, complementing the studies of Jenkins et al. (1963), Watson & Jenkins (1964), and Watson (1970) on Red Grouse in Scotland. The Scottish studies were primarily descriptions of the behaviour of large numbers of wild birds observed in the field over a period of many years, and to some extent observed in the course of other studies. This paper deals with limited aspects of the behaviour of captive, wing-clipped birds, living on an artificial diet in a restricted space. Their parentage, upbringing, age, and state of health were known, and they were partially tamed to humans. Secondly, Red Grouse and Willow Grouse are two varieties of the same species, adapted to different conditions and behaving in some respects differently.

After a period of about one week in the observation areas, eggs were laid at a rate of about one a day, about normal for tetraonids (Johnsgard 1973), until a clutch of about ten had been assembled. Myrberget (1972) gives a mean clutch size of 9.8 on Tranøy, an island just south of Tromsø.

In the small observation areas, the choice of nest sites was limited, especially as hens would not incubate on the bare concrete observation room floor, and were therefore constrained to nest on the pile of fishing net provided. This limitation did not apply to the hen of pair 1, which tried several sites in some 255 m² of natural vegetation. Eventually she chose a site which provided some shelter from aerial pre-
dators, under a corner of the fishing net fence, and on a pile of net, a good insulator from the cold earth but not a typical feature of the grouse environment. Similarly, the other hens preferred to lay in whatever shelter was provided, no matter how inadequate. This habit corresponds to field-workers' reports on site preferences; eggs are usually laid in a primitive scrape on the ground, in the lee of a heather clump or an earth tussock. Red Grouse nesting as described by Jenkins, Watson & Miller (1963) is similar to Willow Grouse. Nests of gallinaceous species appear to be generally very primitive, as far as anything is known about them (Wood-Gush 1975, Johnsgard 1973). Hens seldom laid during observation periods, even though these took place at nearly all times of day. They seemed to need to be undisturbed during laying, perhaps because they call loudly while doing so and must avoid attracting predators. Some of the hens reported here began to lay in different parts of the observation area, perhaps indicating that no nest site was satisfactory, or simply that they were stressed by the abnormal surroundings and the proximity of humans. Jenkins et al. (1963), however, reported instances of Red Grouse incubating and successfully hatching their clutches close to and even on farm roads. Hens of other indoor pairs, not reported here, have continued laying as many as 25 eggs in one place without beginning to incubate, again suggesting a stress-induced breakdown of the normal sequence of maternal activities. Except where the hen refused to incubate at all, incubation began as soon as the clutch was complete.

Normally in grouse species, only the hen incubates (Johnsgard 1973), but the cock of pair 3 showed that the process of incubation can be carried out equally well by either bird, while the cock of another pair, reported by Allen (in press) actually started incubating in competition with the hen who had been incubating adequately for several days. In the latter case, the cock's behaviour was as adequate as that of the cock of pair 3. These observations suggest that Willow Grouse parental behaviour may not always have been as rigidly sex-defined as now. The hen's absences were normally the only occasions on which the cock approached the nest. However, if a pair was disturbed by the observer, the cock would threaten from a distance and often mount the nest and poke around the eggs as the observer left the room. In the confined spaces of these observation areas, there was no room for the cock to display any of the types of diversionary behaviour described by Watson & Jenkins (1964). Occasional rudimentary attempts were made to cover the eggs, using pine-twigs and the string from the heather bundles. This happened only after disturbances and it is not clear whether the birds would cover the eggs if appropriate materials were available. Watson & Jenkins (1964) describe Red Grouse as sometimes covering their nests so well during the laying period that the eggs are invisible, and similar behaviour has been observed in other indoor pairs nesting on turfs.

All the incubating birds turned their eggs about hourly. First they called quietly and shifted restlessly several times on the nest before poking around the eggs with the beak and shuffling the eggs in random order. Only occasionally did the bird completely rise from the clutch, and it seems unlikely that all the eggs were moved every time. Drent, in a review (1973), lists the three known functions of egg-turning; first, the equalization of temperature among eggs lying in different positions; secondly, prevention of extraembryonic membrane adhesions; and thirdly, freeing the growing embryo to adopt the position of equilibrium dictated by its weight asymmetry. It is possible that a fourth function is that of increasing the arousal level of the developing C.N.S. so that the embryos will be more reactive to the calls of the incubating bird. Although the hen is nearly always silent on the nest, the calling which precedes egg-turning also accompanies it and continues for some minutes after. It is possible that calling sensitizes the embryos to the individual hen's voice. While hen-incubated grouse chicks ignore the calls of a strange hen, incubator-reared chicks approach the calls of any grouse hen.

The hens' increase in restlessness, which indicated the approach of hatching, may have been due to increased activity on the part of the embryos. For some time before hatching, the noises of heart-beats, respiration, clicking, body movements, as well as calls can be detected from grouse embryos (Allen, unpublished), and Vince (e.g. 1969) has shown that in many species, some of these sounds function as signals between the eggs. In pairs 2 and 4, where some of the eggs hatched during ob-
ervation periods, the chicks' calls during hatching seemed to cause the hen to sit higher on the eggs, to move them around, and eventually to leave the nest while individual chicks escaped from the egg. These were not distress calls; their rising inflection is associated with comfort, while the call emitted by a cold, lost, or hungry chick falls sharply in pitch.

The chicks' difficulties in getting out of the shell may have been due to the artificial nest material, which probably had a good deal more 'give' in it than a natural nest bottom of leaves, grass, twigs, and feathers, on bare earth. How normal it was for the hen to leave the nest during hatching is impossible to say without field observations, but it is remarkable that they did so in view of the temperature (measured at 6°C in the case of pair 4), and the emerging chicks' poor ability to either retain or generate warmth at that age (Aulie & Moen 1975).

Although all of pair 1's eggs hatched, the success rate of the other clutches was much lower. There are several possible reasons for this. The unhatched eggs were not subsequently examined, so it is not possible to say what proportion of the eggs were fertile. Only the first and fourth pairs were given any choice of mates, while the others were paired at random. Gjesdal (in press) has shown that such arbitrary mating of grous leads to lower fertility, as grouse appear to choose mates on the basis of similarity of social rank. At the Wildlife Research Station, where it is not practicable to allow birds a choice of mate, healthy and well-fed production hens manage only some 75–80 percent fertility. Johnsgard (1973, p. 67) suggests that, on the basis of field experience, 'the incidence of infertility and embryonic death is probably so low among wild populations as to be almost insignificant'. Factors which may have reduced hatchability, as opposed to fertility, are the low relative humidity of the observation rooms, the abnormal and possibly inappropriate material of the nests, and the disturbance and handling to which the birds were subjects.

Most of the detailed observations on brooding were made on pair 1, as the normal behaviour of the other pairs was too easily interrupted by necessary human activity to make systematic observations possible. Theberge & West (1973) point out that chicks of the closely related Ptarmigan Lagopus mutus are no longer brooded at six days of age; the observation that the hen of pair 1 refused to let six-day old chicks crawl under her when the temperature was high, suggests that the mother may unilaterally end brooding as the chicks approach homeothermy. Aulie & Moen (1975) found that five- to seven-day old Willow Grouse chicks became only slightly hypothermic after 20 minutes exposure to 19°C, so homeothermy is evidently well advanced at one week of age. A feature of brooding common to all four pairs was that immediately after disturbance by the observer, the hen (in one case, the cock) called in the chicks and brooded them.

Only the first grouse family was observed feeding on insects; the others were fed a specially developed artificial diet, plus a supplement of blueberry heather which the chicks ate avidly from the first day. Although grouse are primarily vegetarian, several papers make it clear that insects are an important component of the diet, at least for chicks. Butterfield & Coulson (1975) reported that Red Grouse on an English moor ate tipulid insects especially in May and June, and that the faces of chicks contained higher proportions than those of adults. Høst (1938) found a 'fly-factory' a necessary device for successful raising of Willow Grouse chicks in southern Norway, and Kolb (1971, p. 62) found that his captive Red Grouse chicks readily ate what insects they could catch in the breeder house. In this study the artificial diet plus heather but without insects appeared to be adequate.

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