THE UNIVERSITY OF MANITOBA

A radio telemetry study of the incubation behavior
and egg temperatures of the Canada goose (Branta
canadensis interior) in the Hudson Bay Lowlands

by

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Bachelor of Arts, 1977

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A RADIO TELEMETRY STUDY OF THE INCUBATION BEHAVIOR

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GORDON BRUCE STENHOUSE

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF ARTS

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This thesis is dedicated to a friend of seventeen years, who did not live to see the final manuscript of this research.

The Quitter

When you're lost in the Wild, and you're scared as a child,

    And Death looks you bang in the eye,

And you're sore as a boil, its according to Hoyle

    To cock your revolver and ... die.

But the Code of a Man says: "Fight all you can",

    And self-dissolution is barred.

In hunger and woe, oh, it's easy to blow ...

    It's the hell-served-for-breakfast that's hard.

"You're sick of the game!" Well, now, that's a shame.

    You're young and you're brave and you're bright.

"You've had a raw deal!" I know -- but don't squeal,

    Buck up, do your damnedest, and fight.

It's the plugging away that will win you the day,

    So don't be a piker, old pard!

Just draw on your grit; it's so easy to quit:

    It's the keeping-your-chin up that's hard.

It's easy to cry that you're beaten -- and die;

    It's easy to craw fish and crawl;

But to fight and to fight when hope's out of sight --

    Why, that's the best fame of them all!

And though you come out of each gruelling bout,

    All broken and beaten and scarred,

Just have one more try -- it's dead easy to die,

    It's the keeping-on-living that's hard.

                         by Robert Service.

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Foreword

A master's thesis is an academic exercise. It's emphasis
is not so much an original thought as it is on methodology
and adherence to scientific principles. It is also an oppor-
tunity for a professor and a student to work together on a
research project. Too often the student's thesis becomes an
exercise in the commonplace for the professor. It becomes a
relatively simple matter of providing guidelines within which
research can be done with some probability of achieving re-
peatable, though not necessarily meaningful, results. Occa-
sionally, hwoever, a thesis is done which exemplifies the
true spirit of research and allows the student the opportunity
to demonstrate the true mettle of his worth. This thesis is
a good example of that situation. I have added this preface
to Gordon's thesis because I felt that his performance during
the course of this project warranted further comment on my
part. The obstacles he encountered would have defeated lesser
students and many professionals as well.

Originally, Gordon's thesis was to have been conducted at
the field station of the Avian Behavior Laboratory. As such,
he would have been able to study the incubation patterns of
a captive flock of Canada geese under relatively comfortable
conditions albeit still under field conditions. In the spring
of 1979 the Red River flooded and completely covered the field
station with several feet of water. Gordon's options were to
postpone his field research for at least one year or to move

the location of his thesis further north, where the spring
nesting season would occur several weeks later.

Some of Gordon's experiences have been recounted in this
thesis but his own modesty and the dictates associated with
writing a thesis prevented him from recounting some of the
problems he had to overcome. The same may be said of the
profound hardships and dangers he encountered during his
lonely vigil of almost two months on the tundra. His per-
formance during this period of physical strain, emotional
turmoil, and periods of utter frustration cannot be recounted
in mere words. Only those who have experienced field research
conditions with many months of preparation and a great deal of
funds can adequately appreciate the wonder of his achievement.
The latter is especially so given the extremely short period
of time he had to plan this venture (18 days) and the shortage
of funds available for such a major, unexpected undertaking.

The setbacks Gordon experienced in the conduct of this
research would have disappointed many other researchers in
a similar situation. Disappointments however, only became
setbacks Gordon never gave up and tried again, again, and
yet again. It is with extreme pride that I publicly con-
gratulate this young man for his determination, courage, and
inner fortitude. He has learned lessons that I could never
teach him - and he has learned them well. Unlike the campus
situation, where the classroom is too frequently a place of
ritualized oratory, stupefying boredom, and enormous apathy,
his classroom was the natural environment. Under the severe

tutelage of the arctic weather, he learned the true meaning
of the predator prey relationship as he realized just how
small and insignificant he was in nature's overall scheme
of things. He realized how he had to fit into nature's scheme
of things or he would be eliminated, just as any other animal
would be under similar conditions. His classroom was anything
but boring and at the smallest sign of apathy he would be
rudely slapped to frightening attention as he became aware of
his potential danger.

When Gordon returned to Winnipeg, I could only marvel at
the stories he had to tell. Safely back in his hometown, I
could sense the feeling of tremendous satisfaction he had as
a result of his experience. Part of life's tragedy is what
dies inside a man while he lives. Gordon's experiences in
the arctic provided him with an experience that made him live
that part of his life to its fullest. His memories are the
richer for it and his ability to lead others in similar under-
takings has been greatly enhanced. More important, perhaps
is that the experience has stimulated, excited and exalted
Gordon in a way that I never could in a campus setting.

During Gordon's stay in the arctic he never allowed the
severity of the climate or the frustrations of his self-
imposed privation to compromise his dedication to excellence
and his devotion to his research. He learned that when you
take the time to look, the commonplace becomes wonderous and
the wonderous becomes commonplace. He saw the beauty of the
empty space before him and he identified with the other forms

of animal life living with him as he began to understand the
forces being imposed on all of them. Reality, in all of its
phases, was no longer a term in a book but a very real force
that had to be reckoned with.

To understand the arctic's reality Gordon had to come to
grips with a personal philosophy. He learned that to reject
any hypothesis on purely ideological grounds is to argue that
static ignorance is preferable to increasing our knowledge
of reality. Gordon's thesis, more than anything else, repre-
sents an example of a young scientist willing to examine
nature on her own terms, under her own conditions, at her
convenience. There was no approximating natural conditions
here, i.e., there was no attempt to conduct an experiment in
the laboratory and then to generalize results to the natural
environment. This research was done in the natural environ-
ment of the organism in which he is interested. As such, his
thesis provides answers to questions that have only been ap-
proximated before. Sooner or later, someone had to do this
type of research to see what the real answers were to the
questions previously raised.

After Gordon returned to Winnipeg, he worked on his data
for one year before any results could be tentatively discussed.
During that time he learned that one's research does not lead
to old answers but to new puzzles, new problems, new models
of experience, new perspectives, and subsequently may pro-
vide a possible - though not guaranteed - footing from which
one may reach for new answers and new skills. I would hope

that in the future the North will find Gordon a frequent visitor. There are very few scientists who can live in a hostile environment and also appreciate that environment for its own sake.

The results of Gordon's research will eventually be published. At that time Gordon will learn that any scientist's communication is modified, amplified, and fused with the ideas and results of others. The tremendous importance each scientist associates with his own work is diluted when his results melt into the stream of knowledge and ideas which form our culture. Hopefully, however, the future will see additional research from this bright young man whose enthusiasm and dedication to field work is catching and inspiring.

It has been said that those who scorn perfection for the sake of travel go nowhere, slowly. Those who put travel aside for the sake of perfection go anywhere instantly. Gordon's thesis is a good example of someone who has dedicated himself to perfection and who has travelled at the same time. He has seen a part of this planet's real world as it really exists. He has survived the conditions imposed upon him and he has marvelled at the wonders he has witnessed. As such, he becomes a fine candidate for tomorrow's teacher. Such an individual will have to have the ability to communicate, to listen, to light a little fire under a lad, to teach not what to think, but how to wonder. I am sure he is equal to the task.

Working with Gordon has been a pleasure and a real in-

spiration for me. I hope that future students of mine emulate his example and aspire to the levels he set for himself. Gordon's education was more than just reading and writing. It was a part of living; that part, in fact, which makes life full, alive, and exciting. Gordon would be the last person to claim that his work is the final word on his subject matter. It does provide much valuable data but it also raises many new questions. I hope that he decides to try to answer some of these new questions. And my best wishes go with him in his future endeavors.

L. James Shapiro

Acknowledgments

In order to successfully complete a field study of this nature, it was necessary to call upon many individuals and agencies for assistance and advice. Without their support this research would not have been possible.

First of all I would like to thank the Canadian Wildlife Service whose University Support Research Fund grant #KL229-9-4134 provided financial support for this study. Additional financial support was graciously provided by Mr. D. G. Mulder, president of Mulder Bros. Ltd.

Equipment necessary for the operation of the radio telemetry systems and the field communication equipment was generously donated by; Union Carbide Canada Ltd., E S B Canada Ltd., and General Motors of Canada Ltd. Additional equipment was loaned to me for the duration of the study period by; Varta Batteries Ltd., and the Atmospheric Service Branch of Environment Canada. To the aforementioned agencies and companies I express my deepest thanks.

Mr. Phil Gerson provided invaluable expertise in designing and constructing the radio telemetry system used in this research. I also wish to thank Mr. Les Bell who provided constructive criticism and technical expertise during the construction of the monitoring system. Without the help of these two gentlemen this research venture might not have proceeded past an idea.

Mr. Bryn Easterbrook deserves a word of praise and a great deal of thanks for designing, modifying, redesigning

of incoming solar radiation on the incubation behavior of female geese.

To thank all the individuals that helped along the way would take many pages. I'm sure that even if I attempted to thank each individual, I would forget someone. For this reason I will simply say thank-you to all the people who assisted me. Without the help of these people I might not have completed this thesis.

As I will never forget my stay on the tundra, I will also never forget the help and encouragement I received during this study.

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Abstract

This study was conducted to investigate the incubation behavior of female Canada geese, as well as to determine the care provided to the eggs during undisturbed incubation.

Contradictory or no data exists on several facets of incubation in the Canada goose. The principle reason for this problem is the methodological difficulties involved in trying to obtain data in the field without disturbing the nesting females.

During the spring of 1979 five Canada goose (Branta canadensis interior) nests were studied on the Hudson Bay Lowlands in northern Manitoba. Five radio telemetry goose eggs were designed and constructed to monitor three egg temperatures (shell, core, and air cell), nest attendance, and egg turning, on a 24 hour basis for the entire incubation period. The first egg laid was removed and replaced with a telemetering egg in each study nest. Behavioral observations were made on the focal females in three time periods between 07:00 and 22:00 hours throughout the entire incubation period, with the aid of a 20-60 X spotting scope.

Data on environmental factors was gathered during this study to determine if they exerted any influence on incubation behavior.

Two of the five study eggs were lost to predators during the study. A total of 2,012 hours of data was collected by the telemetering eggs, with an additional 305 hours of behavioral

observations being recorded.

Behavioral data indicated that there were five readily distinguishable postures seen while the female was incubating. The sitting posture constituted 93.2% of all positions occurring during incubation sessions. Female's spent 4.3% of their time during incubation sessions engaged in a hide posture. Results indicated that the time of the observation period had a significant effect on the amount of time spent in each of the five postures. Nesting females spent the majority of time (31.1%) feeding while on an incubation recess.

Nest attendance for the successful nests averaged 95.03% over the entire incubation period. Nest attentiveness was high on the day the first egg was laid, and increased steadily for the rest of the egg laying period. This data contradicts past research which indicates incubation did not begin until the clutch was complete.

Females averaged 2.15, 20.97 minute recess periods per day. Multiple regression analysis showed no significant effects of the weather variables, time of day, or day of incubation on recess period length. Recess periods were taken at all hours of the day and there was no change in the frequency or duration of recess periods over the incubation period.

Mean incubation session length was 10.45 hours for the successful nests. Multiple regression analysis showed that ambient temperature, humidity, solar radiation, temperature x humidity interaction and a temperature x solar radiation

interaction all had a significant effect on session length.

The average egg air cell temperature was 34.45°C. This egg temperature was low early in the egg laying period, but increased steadily during egg laying. There was a 5.71°C temperature gradient found between the females breast and the bottom of the nest cup. Egg air cell temperature dropped an average of 3.59°C during a recess period, while the egg core temperature dropped 2.49°C during this time. There was a significant effect of stage of incubation on all three egg temperatures, but only a small percentage of the observed variance was accounted for by the stage of incubation.

The regression equations for air cell, core, and shell temperatures accounted for 48.5%, 60.8% and 48.3% of the respective variances. Although statistically significant, no weather variable accounted for more than 1% of the variance in the three egg temperatures. The nest variable accounted for 20.6%, 24.4%, and 17.1% of the respective variability in air cell, core, and egg shell temperatures.

The data on egg turning did not support previous research which stated that egg turning was directly related to the weight characteristics of the eggs. The present study showed a great deal of variation in the number of turns each study egg received. Egg turning was carried out at all times of the day and the mean time between turns was 3.14 hours. Incubating females turned their eggs without rising from the nest. Multiple regression analysis showed a significant effect of stage of incubation on egg turning. Egg turning

fell off sharply preceding hatching. Further regression analysis showed a significant effect of egg air cell temperature, nest, egg core temperature x humidity, egg air cell temperature x humidity, and egg core temperature x solar radiation on the time between egg turning. While these results were statistically significant, the amount of variance accounted for was very low.

The results indicate that incubating female Canada geese have a high degree of nest attentiveness, provide a relatively stable thermal and physical environment for their eggs, and feed little over the course of incubation. These results suggest that the physical condition of nesting female geese plays an important role in determining nesting success.

Introduction

Reproduction is one of the most important periods in any
animals life. Activities occurring during the reproductive
period determine whether or not the species will continue, or
whether it will become extinct.

The reproductive period of birds can be divided into three
general categories. They are 1) courtship and mate selection,
2) the reproductive process, and 3) caring for the young.

An incubating bird is faced with a very complex task. In
incubation the parent must adequately provide for itself, as
well as for its eggs. The egg requires a temperature range
which will allow optimum development, mechanical shifting
and rotation provided by the parent bird, and protection from
predators. The parent, meanwhile, must maintain its normal
body metabolism during the period of incubation, while under
the added physiological stress of supplying the necessary
incubation temperature to its eggs.

The relative responsibilities of the attending birds
ranges from sharing of the incubation task, to total involve-
ment by one parent for the entire incubation period. The
former case is called bisexual incubation, and the eggs of
birds who engage in this mode of incubation are attended at
all times by one or the other parent. Most marine birds,
as well as most nonpasserine birds engage in bisexual incuba-
tion. Ducks and geese, on the other hand, engage in single
sex intermittent incubation. In this system a single parent,

most often the female, divides her time between caring for the eggs and gathering food for herself. Between these two incubation strategies there are a number of other strategies. For example, in some birds the non-incubating member of the pair may feed the incubating mate to some extent, depending on the species. For a more complete review of the incubation process see Drent (1970, 1973, 1975).

It is important to understand the way in which most incubating birds conduct the incubation process. The requirements of incubation may sound quite simple. When one considers the task in greater detail, however, the complexity is very apparent.

Proper egg temperature in natural incubation is achieved by the incubating bird applying its incubation patch/es to its eggs. "An incubation patch consists of a feather-free area with thickened skin and a rich supply of blood vessels to facilitate the transfer of heat from the body of the incubating bird to its eggs" (Pettingill, 1970, p. 355). In this case, the incubating bird uses its own body heat to provide the proper incubation temperature for its eggs.

While most avian species incubate their eggs by applying their body heat directly to their eggs through incubation patches, there are some exceptions to this typical form of incubation. The megapodes of Australasia (Frith, 1956) lay their eggs in holes in the ground or in mounds of rotting vegetable matter and thus use the natural heat from this decomposition process for incubation. The pelecaniform birds

(eg. northern gannet <u>Morus</u> <u>bassanus</u>), which lack brood patches, cradle their eggs in the webs of their feet during incubation (Nelson, 1966). To what extent the ventral body surface contributes to heating these eggs is still a matter of debate (Howell & Bartholomew, 1962). It is interesting to note that the average incubation temperature in nests of 37 species of birds of 11 orders is very similar, $34.0^{O}C \pm 2.38^{O}C$ (Huggins, 1941).

Drent (1975) commented on this narrow range of incubation temperature for proper embryonic development:

> The range for optimum development is narrow;
> death through overheating is uncomfortably
> close at all times; a slight fall in internal
> temperature, if long maintained, will lead to
> abnormal development, and an internal egg
> temperature between physiological zero (25° –
> $27^{O}C$) and freezing can be tolerated for long
> periods, the most important limitation being
> that tolerance declines with age (p. 352).

Under natural conditions, egg temperature is regulated by adjusting the time pattern of an incubating bird's attentiveness, which is usually defined as the percentage of a twenty four hour day that a bird spends incubating the eggs.

Besides requiring a specific thermal input from the parent bird, the eggs also require mechanical shifting and rotation. New (1957) showed that absence of egg turning

results in an abnormal degree of adhesion between the chorion and shell membranes during the first week of incubation. Kaltofen (1961) and Robertson (1961) have also shown the beneficial effects of egg turning during the course of incubation. It is generally agreed that turning is most critical during the first half of incubation. The parent bird, therefore, has to provide the proper egg shifting and turning for the entire course of incubation, while paying particular attention to the first half of incubation.

As well as actively influencing the physical environment of the eggs, the parent must also attend to the eggs' other needs, as well as to its own needs. The parent must protect the eggs from predators and at the same time reach some compromise between obligations to the eggs and its own nutritional demands. This compromise can be accomplished if the incubating bird adjusts its time pattern of nest attentiveness. In a species which follows a single sex intermittent mode of incubation, incubation strategies have evolved where the incubation period is divided between attentiveness and food gathering, somehow adjusting attentiveness against fluctuations in environmental conditions to regulate egg requirements (temperature and turning). Time for food gathering must be of sufficient length to allow the female to acquire enough food to support her metabolism.

The Canada goose is a single sex intermittent incubator. Each spring, after a northward migration from the wintering grounds, the female goose selects a nest site, lays approxi-

mately five eggs, and begins incubating them. For the next
24 to 28 days the female goose shows a high degree of nest
attentiveness and maintains her clutch of eggs at approximately
$34^{\circ}C$ (Cooper, 1978). The female maintains her eggs at this
temperature by transferring her body heat to the eggs. In the
order Anseriformes (ducks, geese, and swans), however, this
heat transfer does not occur through a "true" incubation patch.
Geese, as do most waterfowl, pluck down from their breast to
line their nests and this behavior results in a bare region
of skin on the ventrum (Hanson, 1959). A "true" incubation
patch is formed by a localized molt (Jones, 1971). During
the incubation period the male goose guards his mate and the
region around her (Cooper, 1978). The goslings hatch in a
precocial state and the parent birds share the duties of
caring for their offspring.

Species of birds which nest in the arctic have to contend
with the environmental conditions which prevail in this region.
There have been numerous studies which have attributed reduced
annual production to factors associated with weather. (Barry,
1962; Eisenhauer & Kirkpatrick, 1977; Hanson, Queneau, &
Scott, 1956; MacInnes, 1968; MacInnes, Davies, Jones, Lief
& Pakulak, 1974; Mickelson, 1975; Ryder, 1972). The arctic
nesting period is short and each breeding phase (egg laying,
incubation, rearing of young, moult, etc.) is so timed that
the final phase is completed just prior to the drop in temper-
ature at the end of the season (Ryder, 1967). Anything which
upsets or delays the precise timing of this schedule can re-

duce reproductive success.

Environmental factors which have to be contended with in the arctic range from low temperatures and unpredictable weather to large diurnal temperature cycles. Birds that nest in the areas affected by these factors have to have a very efficient incubation pattern. Geese which nest in the arctic have this restricted and precisely timed reproductive period as a result of specific environmental adaptations. Every species of bird breeds at the time of the year during which it can raise young most efficiently. Young birds hatched at less advantageous times suffer a heavier mortality and rarely survive to reproductive age.

Little information exists on the process of incubation in arctic nesting geese. This study was conducted to investigate the incubation behavior of female Canada geese, as well as to determine the care provided to the eggs during undisturbed incubation.

One goal of the present study was to determine the way in which incubating female Canada geese manage to meet the requirements of incubation (egg temperatures, egg turning, as well as the female's nutrient requirements) during a brief arctic nesting season. These incubation requirements are met through a certain rhythm of nest attentiveness. As White and Kinney (1974) pointed out, "the precise relationship between attentiveness and environmental temperature has remained unclear" (p. 186). The literature contains little data on the complete incubation schedules of arctic nesting geese. This

situation is primarily caused by the difficulties involved in trying to obtain a complete record of nest attendance in unpredictable and often harsh arctic conditions.

Another goal of the present study was to provide answers to questions of incubation in Canada geese for which contradictory evidence exists. For example, the egg temperature data for the Canada goose presented by Huggins (1941), Kossack (1947), and Cooper (1978), differ somewhat from one another. The reason for these different results may be attributable to methodological differences in data collection. No researcher to date has collected egg temperature data for the Canada goose from the time the first egg was laid until hatching occurred.

The literature also contains conflicting data on the length of incubation for Canada geese. Kossack (1950) reported that the incubation period varied from 25 to 28 days with 26 days being average. Dow (1943) reported incubation periods of between 28 and 33 days. Most researchers have considered 28 days as the normal incubation period (Brakhage, 1965; Collias & Jahn, 1954; Cooper, 1978). It is not known whether different subspecies of Canada geese have different incubation period lengths. Once again, methodological problems may account for the conflicting data reported for incubation period length in Canada geese.

No research has yet been conducted to study egg turning in Canada geese or the incubation postures of female geese over the course of undisturbed incubation. The reason that

no information or contradictory information exists on these
facets of incubation is that collecting data of this nature
has proved to be quite difficult methodologically.

The present research developed a new technique with which
to study the thermal and physical requirements of Canada goose
eggs unobtrusively during incubation. The techniques used to
study the incubation process in past field situations are
presented in the next section.

Previous Techniques

Thermistors or thermocouples. In the past, various tech-
niques have been used to collect data on the nest attendance
and incubation temperatures of different avian species.
Typically, thermistors or thermocouples have been used to
study incubation temperatures. Researchers have placed these
devices in nests to obtain readings on nest air temperatures
(Baldwin and Kendeigh, 1927; Kendeigh, 1963; and Norton,
1972). This procedure provides nest air temperature data
but has the drawback of errors occurring during the data
collection state. Norton (1972) states:

> nest air temperature sensors were more sensitive to
> slight motions of the incubating adult, which produced
> sharp, temporary rises in temperature, probably as a
> result of momentary contact between eggs and thermistor.
> (p. 165)

Thermistors have also been placed inside viable eggs
(Caldwell and Cornwell, 1975; Cooper, 1978; Derksen, 1977;

Huggins, 1941; Kossack, 1947; Norton, 1972; Schulte and Porter, 1974; Snelling, 1972). Huggins (1941) placed thermistor probes through the shell and albumen layers so that they lay just under the embryo. Using this procedure he had to drill a hole through the shell to the albumen at the midle of the egg. Kossack (1947) also used this procedure as one of his techniques but stopped it because of "the probability that it killed the embryo" (p. 121).

Since Kossack's (1947) research was published, the typical procedure for thermistor implantation in a viable egg has been to drill a hole in the blunt end of the egg and to insert the thermistor into the air space. The hole is then sealed with either epoxy glue or collodion, a liquid plastic (Caldwell and Cornwell, 1975; Cooper, 1978; Drent, 1970, 1975; Kossack, 1947; Norton, 1972, Snelling, 1972). The problem with this method is that wires have to be connected to the egg. These wires may interfere with normal egg turning behavior. In addition, they may be dislodged or torn loose from the egg during incubation. These wires may also interfere with normal movements of an incubating bird which shift the eggs. As Huggins (1941) suggests, "if the egg is in the middle of the nest the maximum temperature will be recorded. Under ordinary conditions, however, the egg does not stay in one place in the nest but is constantly being moved around" (p. 136). Caldwell and Cornwell (1975) speculated on the importance of this shifting. They said that "egg billing moves the presumably colder peripheral

eggs to the centre of the bowl and the centre eggs to the cooler bowl edges, thus assuring more uniform heat distribution and uniform embryonic development" (p. 718). It seems reasonable, therefore, to assume that by permitting the eggs to be moved around, unencumbered by wires, the temperatures obtained would be more typical of actual conditions in the nest.

Photocells or photoresistors. Photocells or photoresistors have been used to study nest attendance in incubating birds (Weeden, 1966). This technique, however, has definite disadvantages. For example, if the photocell is covered by a piece of down, a feather, some nest material, an egg, a young bird, etc., then the data will suggest that the incubating bird is on the eggs when, in fact, this is not the case. The photocell system used by Schwartz, Weaver, Scott and Cade (1977) was only sensitive to nest absences longer than ten minutes. This system would only be practical in measuring recess periods longer than ten minutes.

Mechanical nest platforms. Nest attendance has also been studied with the use of weight activated nest platforms (Breckenridge, 1956; Cooper, 1978). The problem with this method is that it only gives an approximation of nest attendance since the data will only indicate that a bird is standing on the platform, and may not be applying heat necessary for embryonic development.

Observational methods. A review of the literature revealed little comprehensive data on egg turning during nat-

ural incubation in field research. This situation is probably due to the difficulties of trying to obtain reliable data on egg turning.

To date, egg turning data on Canada geese has been limited to observational reports of the number of times the female turns her eggs each day, as well as the amount of time she invests in this activity (Balham, 1954; Collias and Jahn, 1959; Cooper, 1978; Kossack, 1950). Previous researchers have assumed that the eggs were being turned when the female was seen "poking" at the eggs. Whether this was actually occurring remains to be determined.

Beer (1961) and Drent (1970) watched the effects of the actions of an incubating bird on egg position while they were underneath nests fitted with transparent perspex plates. The difficulties involved and the endurance required by this observational technique deserve little comment but a great deal of praise.

Flushing. By far the most common technique used to study egg turning under natural conditions has been to either flush the incubating bird from the nest or to wait until the female is off the nest on a recess period and then to record egg positions (Bergman, 1946; Drent, 1970; Dircksen, 1932; Lind, 1961; Tinbergen, 1948). This method has provided some interesting data (Lind, 1961) but requires a great deal of experimenter interference to collect a complete record of changes in position over the course of an incubation period. This interference may affect the pattern of nest at-

tendance of the species under investigation.

Time activated camera systems. Recently, advancements in instrumentation have led to new approaches in studying egg turning in the field. Caldwell and Cornwell (1975), for example, collected data on egg turning in mallards with the use of a time activated camera system. Their data was "collected at approximately six day intervals until the eggs hatched. The data collection lasted for seven to twenty-four hours and consisted of a nest photograph taken every hour. The female was lifted or coaxed from the nest before taking each photograph" (p. 708). Apart from the problems associated with trying to quantify the amount of egg rotation from these photographs, there are other problems associated with this procedure. A strobe light going off every hour, day or night, could conceivably alter the pattern of egg turning. Furthermore, collecting data at six day intervals (only 4 of the 28 days of incubation were studied) may not reflect the egg turning of the entire incubation period. The effects of these intrusions on the incubating female and her egg turning behavior remain unknown and the data obtained may not be a true indication of natural incubation conditions.

Radio telemetry. Schwartz et al. (1977) studied egg turning and egg temperatures in captive falcons. With the use of a radio telemetry egg they analyzed egg turning by changes in the thermal cycle of their study egg. When the shell temperature dropped and the internal temperature re-

mained stable in their study egg, these authors concluded the egg had been turned. This technique would certainly pick up thermal changes as a result of an egg being turned 180° but it would prove less useful in smaller rotations. For example, the female bird may adjust her brood patch so that it is no longer directly against the same spot on the egg shell. The data would then indicate a fall in the shell temperature as a result of this change in position of the female's brood patch. One could conclude (from this thermal change) that the egg had been turned, when in fact this would not be the case.

The equipment designed and constructed for the present research also used radio telemetry techniques to try to overcome the problems of nest disturbance and egg modification while gathering data on the incubation patterns of Canada geese under natural conditions.

Previous Research

Egg turning. New (1957) showed that turning of the hens' egg is particularly important during the latter half of the first week of incubation. He showed that absence of turning results in an abnormal degree of adhesion between the chorion and shell membranes during the first week of incubation. New (1957) also states that "turning is not a device to prevent adherance altogether, but to prevent it from occurring too soon" (p. 228).

The first field study to look at egg turning in the wild

was conducted by Lind (1961). He discovered an unexpected finding in his study of egg turning in the Black-tailed Godwit (_Limosa limosa_). He found that each egg assumed a stable position as incubation progressed. Lind (1961), and others since Lind's work (Caldwell and Cornwell, 1975; Drent, 1970), correlated this finding with the progressive development of weight asymmetry of the egg as the embryo develops. All of these researchers have also shown that the egg, when placed in a dish of water, will settle in a fixed position as incubation progresses. The reasons for this progressive weight symmetry in the egg are related to developmental changes of the embryo. In early incubation the yolk mass is free to revolve within the shell, but as incubation progresses the extraembryonic membranes and the shell membranes fuse, and approximately midway in incubation, embryo position is fixed in relation to the shell and the egg becomes asymmetrical (Drent, 1975). This fixed egg position may be vital for attainment of the proper prehatch and hatching positions. Since the egg is asymmetrical in the later stages of incubation it has been assumed that the frequent egg turning behavior of the parent allows the egg to assume its position of gravitational equilibrium.

This "gravitational theory" of egg turning holds that egg shifting by the sitting bird reduces the friction between the eggs of the clutch and hence allows each egg to assume its characteristic position as dictated by the force of gravity. The data presented by Caldwell and Cornwell

(1975), Drent (1970) and Lind (1961) showed (after the extra-embryonic membranes and the shell membranes fuse and thus the embryo position is fixed) that the heaviest side of the egg was not facing the nest bottom 100% of the time. In fact, the other, lighter, sides spent some time facing the bottom of the nest. This suggests that some other factor may be affecting the egg turning. Perhaps the shape of the nest bowl or contact with the other eggs in the clutch influences the position of the egg. Gravity may be the vital factor but it is unlikely that it is the only one. As Chattock (1925) states, "the usual explanation is that the turning prevents the germ from sticking to the shell. If this is the only function its effect should vanish after the first ten days or so of incubation" (p. 409).

Inner shell temperature. Few researchers have attempted to ascertain the shell temperatures of eggs during incubation. Kossack (1947) cemented a thermo-couple junction on the outer shell surface of Canada goose eggs. Along with the problems of lead wires radiating from the egg he found an additional problem with this technique. When the egg shell temperature of an egg with the thermo-couple facing the breast of an incubating female was compared to the egg shell temperature when the thermo-couple was facing the bottom of the nest, there was a $10^{\circ}F$ ($-12.2^{\circ}C.$) difference in temperature. This data was confounded by the fact that the position of the egg in the nest was influencing the shell temperature data. Kossack (1947) also had no way of telling exactly

what position each egg was in other than inferring a position from the egg shell temperatures. Norton (1972) also faced these problems when he measured egg shell temperatures in paraffin filled eggs in four species of sandpipers.

Varney and Ellis (1974) placed the thermistor used to record egg shell temperature under the shell surface at the small end of their telemetering egg. This positioning of the thermistor would definitely affect the shell temperature data since the eggs in a nest are tilted at an angle such that the air cell (blunt end) is uppermost during incubation (Drent, 1970). The egg shell temperatures recorded by Varney and Ellis (1974) would definitely be lower than if the thermistor had been placed closer to the blunt end of the egg. This is true for several reasons:

1. since the breast of the incubating bird is against the uppermost portions of the eggs (blunt end), and heat diffuses across a surface, the small end of an egg would receive a smaller amount of heat.

2. the small end of the egg (housing the thermistor) is in contact with the nest material, which would absorb some of the heat reaching the small end of the egg, resulting in a lower shell temperature being recorded from the egg.

Therefore, it seems that Varney and Ellis's (1974) thermistor placement would provide a lower shell temperature than would be experienced by the shell surface at the middle of the egg.

<u>Air cell and core temperatures</u>. Typically, the term egg temperature is synonymous with egg air cell temperature (Caldwell and Cornwell, 1975; Cooper, 1978; Kossack, 1947). In fact, however, as Cooper, (1978) points out, "Ideally, egg temperature should represent the temperature at the centre of the egg. But egg centre probe implantation causes embryo death, and because embryo thermogensis occurs during development (Drent, 1970) readings from infertile eggs or those with dead embryos cannot be considered representative" (p. 46).

For these reasons, researchers concerned with egg temperatures have taken temperature readings in the air cell of viable eggs. The technique used, however, does cast some doubt on the results obtained. This doubt is chiefly due to the change in the air cell size as incubation progresses (Romanoff, 1949). Caldwell and cornwell (1975), as well as Cooper (1978), inserted a thermistor so that it rested against the air cell membrane and cemented the lead wire in place where it passed through the shell. This implantation was performed shortly after the eggs had been laid. Since the air cell gets progressively larger as incubation proceeds, the air cell membrane drops down lower in the egg. When this happens the thermistor no longer lays on the air cell membrane. So, in fact, the data being collected with this technique may start out being air cell <u>membrane</u> temperatures and, then, as incubation progresses, change to air cell temperatures. Therefore, this data would not only be a func-

tion of the actual air cell temperature, but would also depend on whether the termistor was in contact with the air cell membrane at the time.

Kossack (1947) did not rest his thermistor on the air cell membrane. He inserted the thermistor two-thirds of the way into the air cell. This technique would not be affected by a change in the position of the air cell membrane.

While little data has been collected on the actual inner egg temperatures during incubation, there have been several attempts to obtain this information. Since the insertion of a probe into a viable egg results in embryonic death (Cooper, 1978; Kossack, 1947) this procedure is no longer used. Instead, some researchers have attempted to simulate a natural egg. Granted, it is next to impossible to simulate a living, developing organism. The goal of the researchers involved has been to approximate a viable egg. Eklund and Charlton (1959) injected albumen back into the penguin eggs they were studying after inserting a radio transmitter and sealing the egg. Norton (1972) filled dummy eggs with paraffin and then sealed them. These researchers not only did not leave an air space of any nature but did not provide data concerning the finished weights of their eggs. Although these researchers were not concerned with egg movement but rather egg temperatures, no concern was expressed for the weight characteristics of the eggs involved. It is quite possible that the weight properties of the eggs affected the treatment provided to them by the incubating

birds. This affect may be in the form of egg turning or perhaps egg shifting in relation to the other eggs in the clutch.

Purpose. Given the numerous attempts to study incubating eggs and the array of techniques used, this study was conducted to more accurately determine the thermal and physical requirements of Canada goose (B. c. interior) eggs and to investigate the incubation patterns of incubating geese.

Method

Subjects

The present research used Canada geese (Branta canadensis interior) for subjects. Before 1945, most writers referred to Canada geese in the Churchill area as Branta canadensis or Branta canadensis canadensis. In 1945 the American Ornithologists' Union recognized Branta canadensis interior as a race (Wetmore, 1945). Hanson and Smith (1950) state that the Canada geese which breed inland from Hudson Bay and James Bay as far north as Churchill conform to the description given by Todd (1938) for Branta canadensis interior. Jehl and Smith (1970) and Johnsgard (1975) also classified the Canada geese which breed in the Churchill region as Branta canadensis interior. Vaught and Kirsh (1966) found that the Canada geese of the Churchill region winter in Missouri and South Dakota.

Study Area

This study was conducted in the vicinity of Knights Hill at approximately 59°45'N and 94°33'W. The map presented in Figure 1 shows the province of Manitoba. The area enclosed by the circle on the Hudson Bay coastline in this figure is presented in greater detail in Figure 2. The location of the study area is shown in Figure 2 as well as its relation-ship to Churchill and Cape Churchill. Figure 3 is an aerial photograph of the study area. This photograph illustrates Knights Hill, the esker (a long narrow ridge of gravel formed
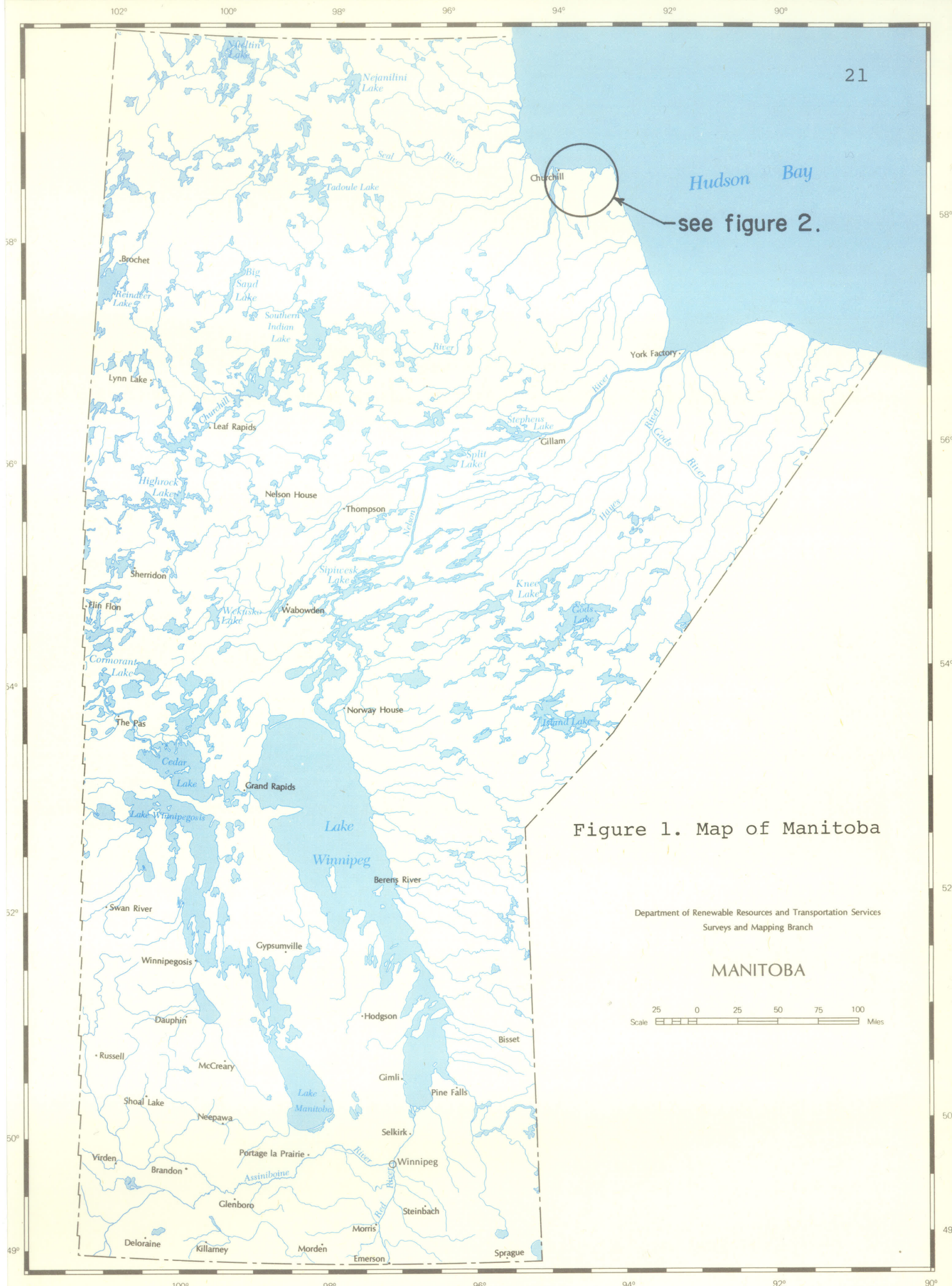
Figure 1. Map of Manitoba

Department of Renewable Resources and Transportation Services
Surveys and Mapping Branch

MANITOBA

Scale [25 0 25 50 75 100] Miles
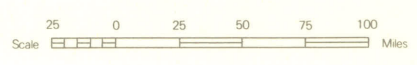
Figure 2. Map of Churchill - Cape Churchill
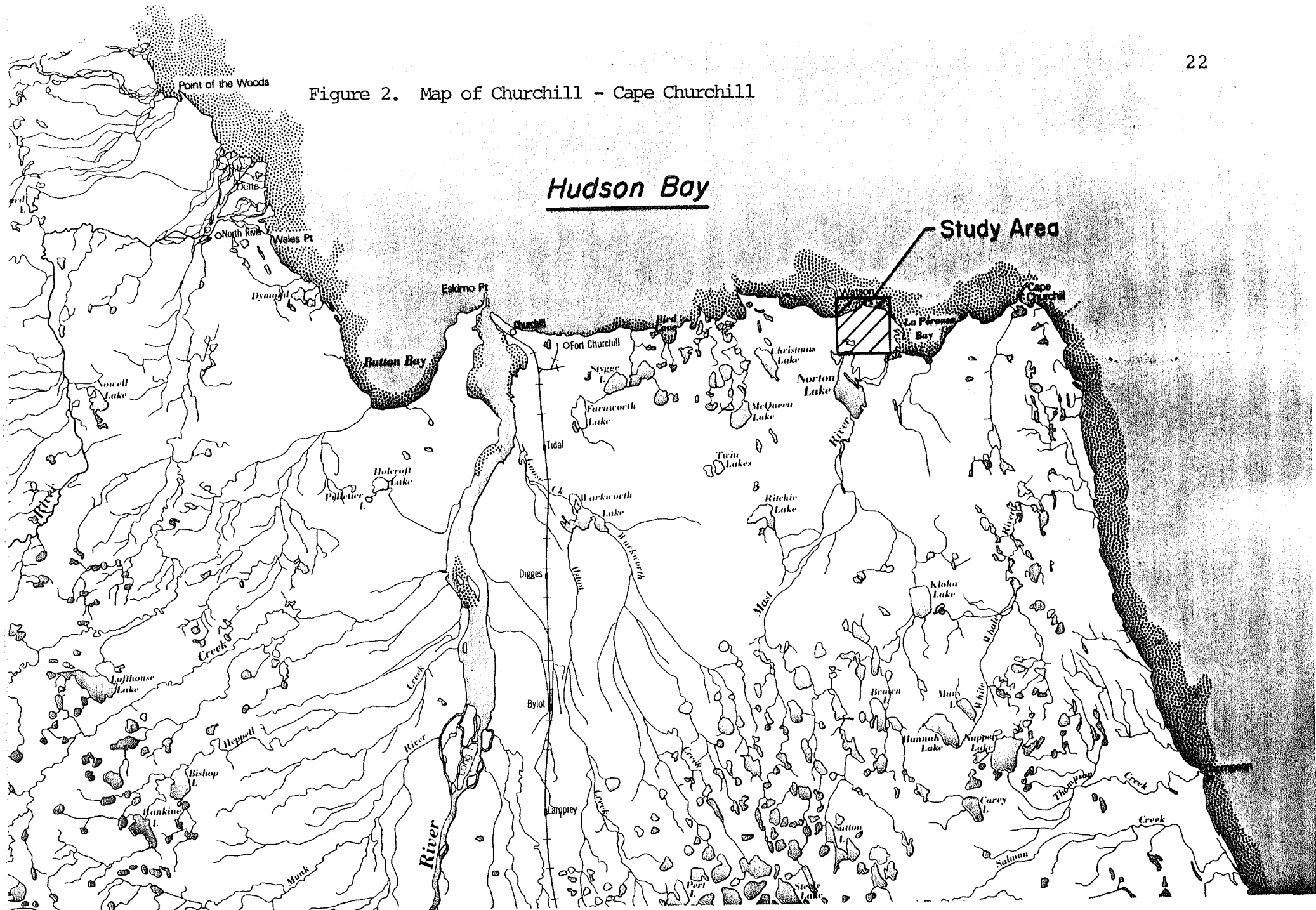
Hudson Bay

Figure 3. Aerial photograph of the study site.

Hudson Bay

Esker

Knights Hill

Norton Lake

in a tunnel-like channel within a glacier), Norton Lake, and
the large number of small ponds and lakes in the area. The
study area lies within the northern sub-arctic and is part
of the tundra ecotone. An airplane was used to travel to
and from the study site.

Vegetation

The soil, cold weather and strong winds of this area
have resulted in lichens, grasses, sedges and shrubs domina-
ting the flora of this region. The species which predomin-
ated the study area were: willows (<u>Salix spp.</u>), dwarf birch
(<u>Betula glandulosa</u>), water sedge (<u>Carex aquatilis</u>), crow-
berry (<u>Empetrum nigrum</u>), labrador tea (<u>Ledum spp.</u>), red
bearberry (<u>Arcostaphylos spp.</u>), lichen species (<u>Cladonia</u>,
<u>Parmelia</u>, and <u>Cetraria</u>), mosses (<u>Musci spp.</u>), rhododendron
(<u>Rhododendron lapponicum</u>), and cotton grasses (<u>Eriophorum
spp.</u>).

Apparatus

<u>Study eggs</u>. The telemetry system used in the present
study was a modification of one originally designed by Varney
and Ellis (1974). These modifications entailed: changing
the electronic circuitry of the telemetry system, increasing
the number of sensors so that more dependent variables could
be measured, cutting down the number of components as well as
the cost of the system, and correcting the problem of lost
signals, previously cited by Varney and Ellis (1974).

The telemetry system was composed of a transmitter
(housed in an egg), a nest loop antennae, a receiver and

heat sensor unit, and a chart recorder.

Each egg contained eight sensors; three thermistors were used to measure core temperature, air cell temperature, and shell temperature, a photocell monitored nest attendance, and four sensors monitored egg turning (a mercury switch), as well as switch and timing circuits and a blocking oscillator pulse-transmitter. Each of the sensors was sampled in sequence for periods of eight seconds. The complete sampling sequence was repeated every 64 seconds. Changes in the sensor resistance caused variations in the pulse repetition frequency of the transmitter, which in turn sends out a series of short (10 μ sec.) pulses to the loop antennae which surrounds the nest. Figure 4 shows a circuitry diagram of the transmitter. Two NOR-gate logic circuits form an astable multivibrator which generates a 1-second period square wave. This signal is divided by 64 in a seven stage binary counter. The three output lines from the binary counter control the multiplexer output, thereby selecting the eight sensors. The blocking oscillator period is controlled by the resistive value of the sensor. The pulses are then radiated to the loop antennae which surrounds the nest. CMOS (Complementary Metal-Oxide Semiconductor) was used to minimize the current drain of a 5.6V (23 gm) mercury battery which powers the transmitter unit. The total transmitter and logic circuit drain averages 20mA which is considerably less than the drain reported by Varney and Ellis (1974). With this current drain the transmitter was expected to run for at least 2.5 years

Figure 4. Schematic diagram of the transmitter unit

TRANSMITTER
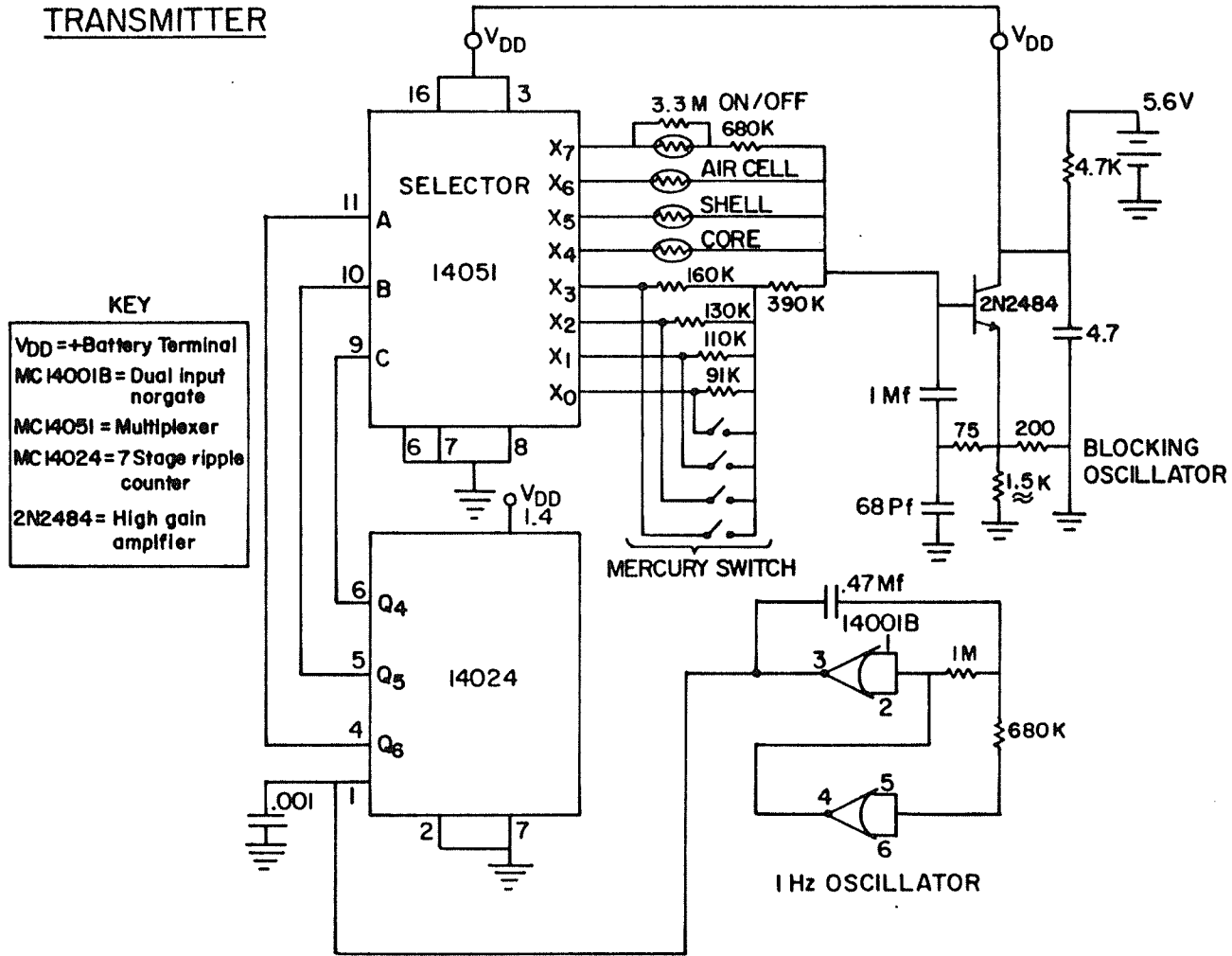
KEY

V_{DD} = +Battery Terminal
MC14001B = Dual input norgate
MC14051 = Multiplexer
MC14024 = 7 Stage ripple counter
2N2484 = High gain ampifier

after being connected to the mercury battery.

Receiving and recording equipment. Due to the low power level of the transmitter signal an egg had to be within 2 m. of the receiving antennae. The antennae was placed around the outside of the nest cup and covered with moss (Musci spp.). The antennae was a 50-turn loop of #24AWG wire about 60 cm. in diameter. The antennae was wrapped with electrical tape to protect it from inclement weather.

A 50 m. connection was made with unshielded two conductor cable between the nest antennae and the receiver.

The receiver was composed of a high gain amplifier, a one-shot multivibrator, an integrator, a voltage regulator, and a temperature controller. Figure 5 shows a schematic diagram of the receiver unit. While Varney and Ellis (1974) used a radio link in their receiver section, the present system incorporated a three stage transistor amplifier and filter in its place. The signal from the egg was picked up by the nest loop antennae which sent it directly to the three stage transistor amplifier. The amplifier output signal triggered the one-shot multivibrator which, in turn, generated a constant pulse width which determined the resistor-capacitor network. The pulses were integrated by an operational-amplifier integrator circuit to give a DC current proportional to the average input pulse rate. A light emitting diode (L. E. D.) flashed each time the circuit was triggered. This component proved useful while checking the system's operation in the field. A voltage regulator was incorporated

TEMPERATURE SENSOR & HEATER
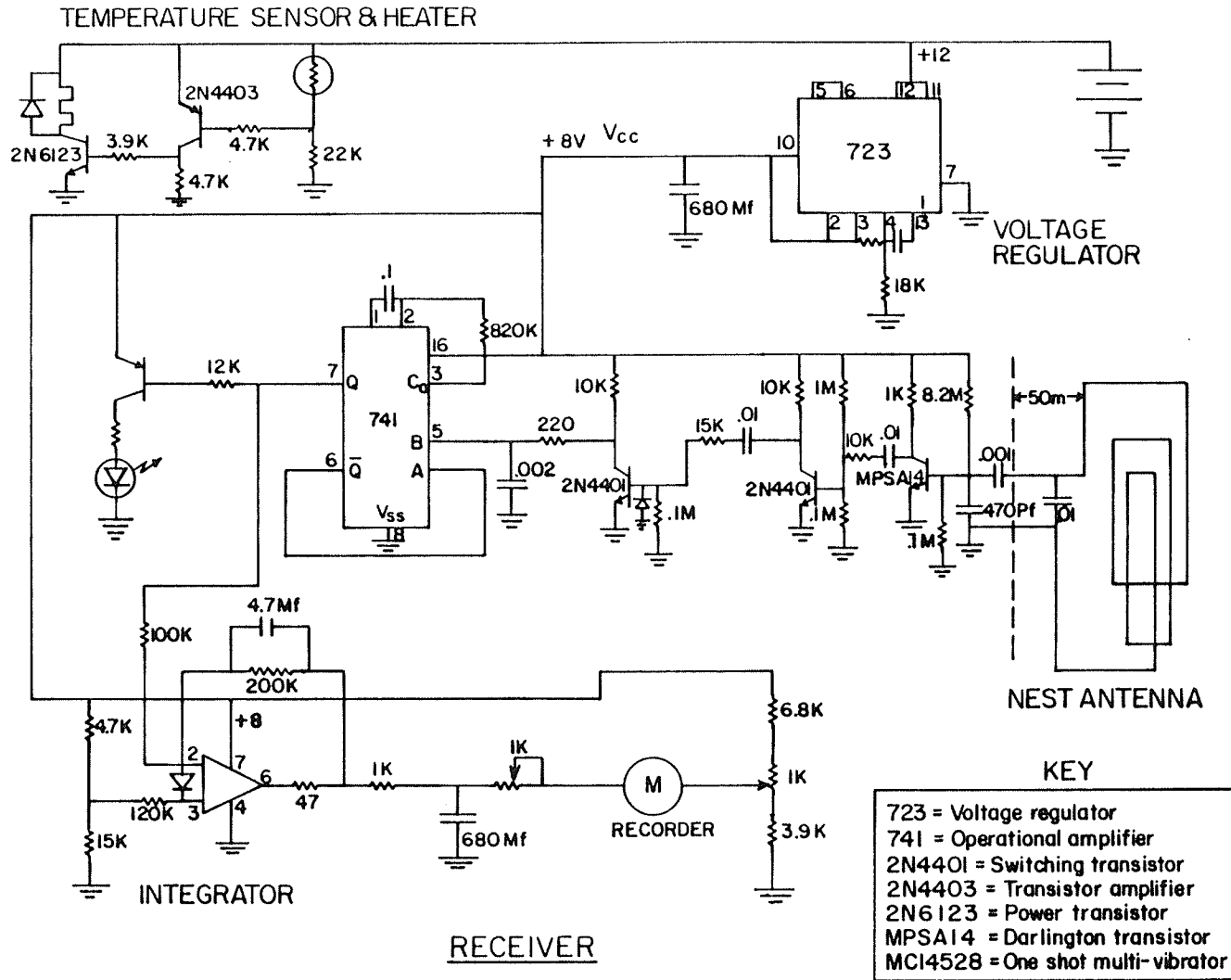
Figure 5. Schematic diagram of the receiver system

to make the receiver insensitive to changes in battery voltage.

A problem associated with the system designed by Varney and Ellis (1974) was that it had no signal being transmitted as specific couplings occurred between the egg and the nest-loop antennas. As a result, data was lost when an egg was turned in certain positions. The present system overcame the problem of loss of signal by using a high gain amplifier to boost the transmitted signal. Therefore, no data was lost as a result of the position of the study egg.

The D. C. output signal from the integrator was fed to a 1 milliampere (mA) battery-operated chart recorder (Rustrak Model 288). The chart recorders used in this study had a chart speed of one inch per hour which allowed 30 days of data to be collected on a single roll of chart paper (15.3 meters). The Rustrak chart recorders were chosen for their compactness and for the sensitized paper they used. A chart recorder using a pen and ink system would have been inoperable under the field conditions which were experienced during the course of this study.

The power requirements of the recording and receiving unit were 15 mA. for the receiver and 15 mA. for the recorder. The receiving and recording system was powered by a 12 volt lantern battery. These batteries were selected for their small size and light weight, which was a great advantage in field transportation of the equipment. A system's battery was changed when the output voltage dropped below 10 volts D.C.

Because of the harsh and unpredictable weather conditions in arctic and sub-arctic regions certain safeguards were incorporated into the receiver system. Specifically, a temperature controller was added to monitor the ambient temperature around the chart recorder. It was felt that the chart speed might possibly slow down at low temperatures. This temperature controller activated a battery powered heating unit when the ambient temperature around the chart recorder dropped below 0°C. The entire receiving and recording system was housed in an insulated-waterproof box (see pp. 39).

Egg construction. Canada goose (Branta canadensis interior) eggs were not available in the study egg construction phase of this research. For this reason domestic goose (Anser anser) eggs were used to house the transmitters in the present study, and were selected so that they fell into the egg dimensions reported by Cooper (1978). Each egg was measured with vernier calipers prior to the construction of the housing. These measurements are presented in Table 1. This table also lists two fresh egg weights associated with each egg. The first weight was calculated from an equation derived by Cooper (1978), who estimated Canada goose egg weights using a multiple regression equation generated from 1, 018 Canada goose eggs (B. c. maxima), whose fresh weights and physical dimensions were known. This equation was:

$$F = -29856 + 5.5w - 1.65L$$

where   F = fresh egg weight (grams)

              W = width of egg (millimeters)

              L = length of egg (millimeters)

TABLE 1.

Measurements of Study Eggs

	Egg Width (mm.)	Length (mm.)	Egg Weight 1*(gms.)	Egg Weight**(gms.)
A	59.1	85.2	166.22	163.08
B	58.3	90.0	169.69	167.63
C	58.6	87.1	166.58	163.09
D	59.1	88.2	171.14	168.82
E	59.1	87.3	169.66	167.09
$\overline{X}$ =	58.84	87.56	168.66	165.94
s^2 =	.37	1.75	2.15	2.68

* After Cooper (1978).

$$F= -298.56 + 5.5W + 1.64L$$

where F = fresh egg weight, W = width, L = length.

** After Hoyt (1979).

$$W= Kw \times L \times B^2$$

where W = fresh egg weight, Kw = .548 (constant),

L = length of egg, B = breadth of egg.

The second fresh egg weight presented was taken from Hoyt (1979), who derived a formula for calculation of fresh egg weights for a variety of avian species. His formula was:

$$W = Kw \times L \times B^2$$

where   W = fresh egg weight

Kw = .548 (constant)

L = length of egg

B = breadth of egg

Hoyt's (1979) equation is more generalizable and is presented for comparative purposes.

It can be seen from Table 1 that Cooper's (1978) formula predicts fresh egg weights which are between 2 and 3 grams heavier than the fresh weight calculated by Hoyt's (1979) equation.

To make each study egg as realistic as possible it was felt that an air cell should be included in each egg. Hence, each study egg was drained and cut open using a Moto-tool equipped with a cutting blade attachment. Prior to being opened, a pencil mark was made on the shell to indicate how to reassemble each egg after it had been cut. The cutting operation itself presented a problem: Where should each egg be cut open? Romanoff (1949) stated, "The volume of the air cell increases at a constant rate as time passes and is thus proportional to the loss of water from the egg" (p. 657). This statement indicates that the size of the air cell is not a stable entity. While I did want to make each study egg as realistic as possible, there was no way to mimic the

changes which would be occurring in an incubating egg. Furthermore, no data was found which showed the chronological development of air cell size during incubation in Canada goose eggs. Therefore, not even an "averaged" size dummy air cell could be made in each egg. Since there did not appear to be any accepted method to use, each study egg was cut open so that it had a 5 cm. air cell at its widest point. This size was arbitrarily chosen but it did allow the egg's transmitter to fit through this opening with a minimum of difficulty.

After the egg had been cut open each half of the shell had a thin layer of dental acrylic poured into it to provide strength for the housing. Care had to be taken at this stage not to make the layer of dental acrylic too thick. If this occurred, the heat generated by the acrylic, when hardening, would break the egg shell, as was discovered when preliminary work was done on spare eggs.

The large half of the shell had a 1 cm. lip of bee's wax attached to the outside of it prior to pouring in the dental acrylic. This lip followed the contours of the egg shell. This structure was used to bring a .5 cm. layer of dental acrylic past the shell edge to serve as an overlapping joint with which to fasten the two sections of the egg back together. The small half of the egg had the inside .5 cm. of the shell left uncovered by the dental acrylic so that it would fit smoothly against the lip of the large half of the shell. Once the dental acrylic had hardened the lip was re-

moved from the outside of the shell and the remaining residue was removed with a cloth dampened with rubbing alcohol. The .5 cm. extension of dental acrylic was then trimmed in certain areas so the two sections of the egg would fit together as they had prior to being cut in two. Once this was done the open space that remained between the two halves measured 1 mm. or less, which was the width of the cutting blade. The extending lip of dental acrylic, which was slightly visible through the 1 mm. opening, was painted with an off white plastic enamel which closely approximated the color of the egg shell.

After the egg was modified the transmitter was placed inside the housing. One temperature-sensing thermistor was epoxyed to a small acrylic free area, under the egg shell surface, midway between the equator and the blunt end of each egg. This probe was defined as the egg shell thermistor and it collected shell temperature data. A second thermistor was located in the centre of the egg and collected data on egg core temperatures. A third thermistor was positioned in the large end of the egg which was the air space for each egg. This probe collected data on the air cell temperature during the study. A photocell was also placed in the air cell portion at the large end of the egg to measure nest attentiveness. Figure 6 shows the placement of the egg's transmitter and the aforementioned probes. Diagram A in this figure is a cross sectional view of a study egg viewed from the blunt pole. Diagram B shows the sensors that were housed

A
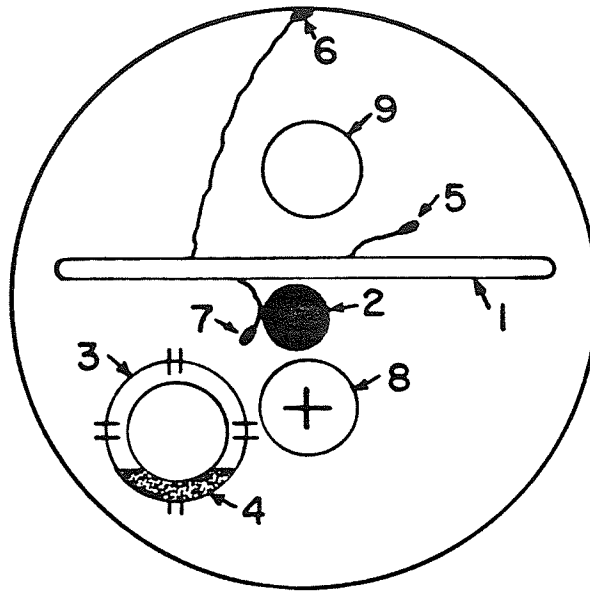
KEY

1. Transmitter
2. Photocell
3. Mercury Switch
4. Mercury

5. Core temperature thermistor
6. Shell temperature thermistor
7. Air cell temperature thermistor
8. Battery
9. Lead counter weight

B
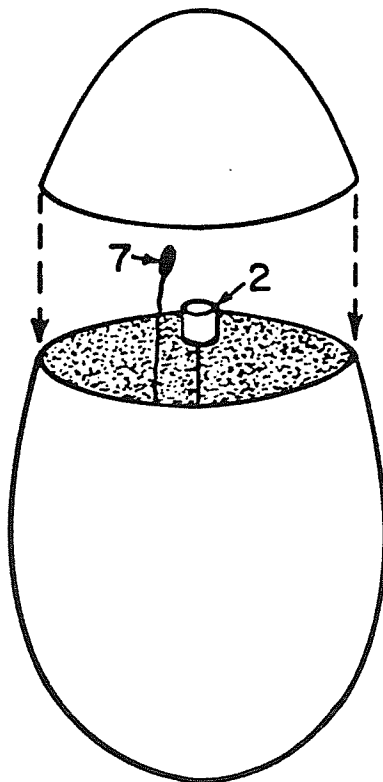
Figure 6. Major components in a study egg

in the blunt (air cell) end of the egg.

A specially designed glass structure was made in order to study egg turning behavior of the incubating female goose. This structure, shown in Figure 7, is a 2.2 cm. circle of 3 mm glass tubing. Four pairs of platinum wires were placed at 90° intervals around this structure. Even though platinum wire is quite costly, it had to be used in this case since it is one of the few metals that mercury will not travel through via capillary action. If the mercury were allowed to travel through the electrodes in the switch the solder joints would disintegrate and make the switch inoperable.

The glass tubing was partially evacuated and a small amount of mercury was placed inside it before the unit was sealed. This structure is a simple mercury switch with four sets of electrodes. Every time the switch is rotated 90° the mercury droplet makes a new contact with a different pair of electrodes. Thus the data will indicate changes in position with reference to these four electrode pairs (see pp. 41 and Figure 8). It should be noted that because of the design of this switch it was not possible for two pairs of electrodes to be contacted by the mercury at any one time.

The glass mercury switch was placed horizontal to and just under the joint where the two egg shell halves fit to-gether. The large half of the egg was then filled with paraffin and allowed to harden. Paraffin was used because its specific heat is closer to egg albumen than is any other readily available encapsulating material (Varney and Ellis,
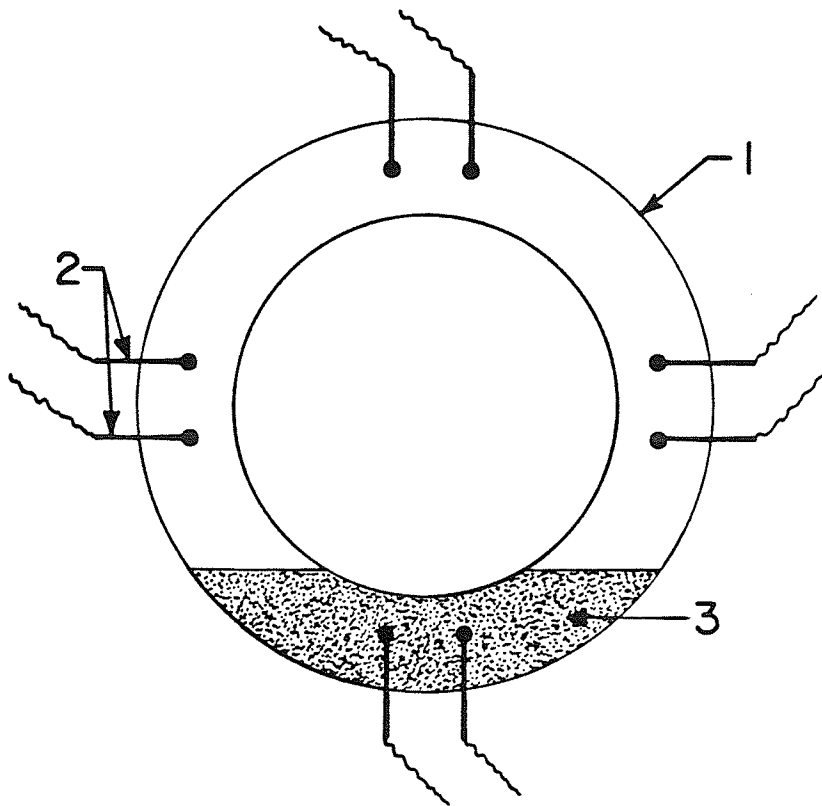
Mercury Switch

1. Glass tubing
2. Platinum wire electrodes
3. Mercury

Figure 7. Mercury switch used to monitor egg turning
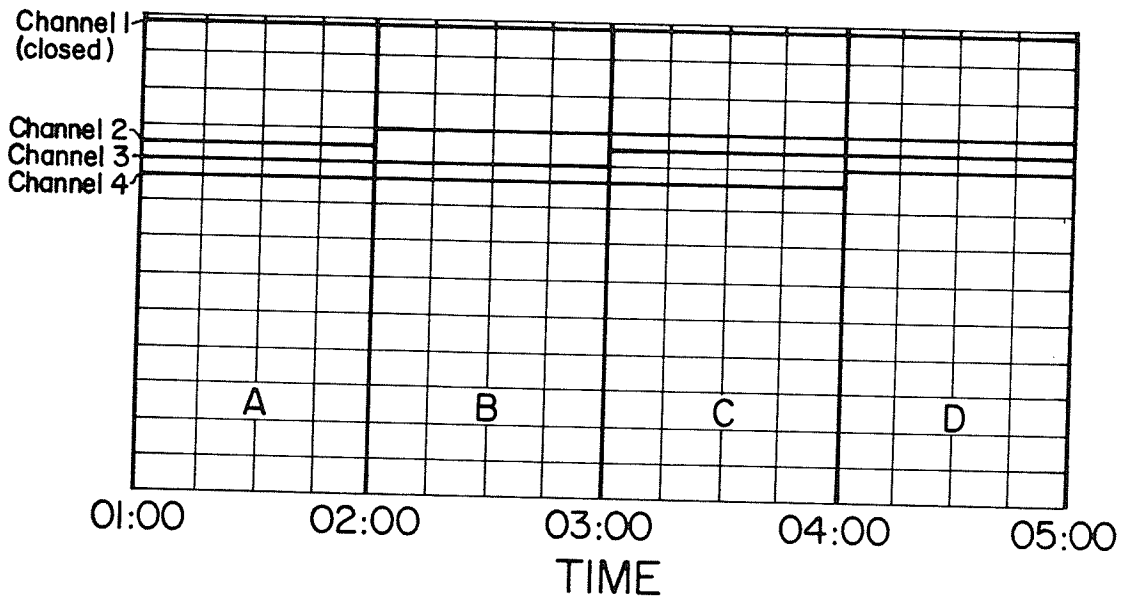
Turning Channels of Mercury Switch

A. —— Channel 1 closed = shell thermistor facing female's breast.

B. —— Channel 2 closed = shell thermistor facing bottom of nest.

C. —— Channel 3 closed = shell thermistor facing the right side.

D. —— Channel 4 closed = shell thermistor facing the left side.

Figure 8. Turning channels of mercury switch

1974). Each egg was then weighed to make sure it met its required "fresh" weight (#1) as previously determined. Cooper's (1978) equation was used since his equation dealt directly with Canada goose eggs.

Once each egg was the correct weight, the two halves of the shell were fastened together using clear dental acrylic. The 1 mm. space between the two halves was filled with collodion so that no ridge or indentation was evident to the human touch. After each egg was completed it was calibrated in a constant temperature water bath, which provided a temperature scale template for each egg. This template was later used to read data from the completed record.

Housing Units for Recording and Receiving Systems. The only other piece of equipment built for this study was an insulated waterproof box to house the receiver, recorder, and power supply for each study nest. A 30.5 x 30.5 x 30.5 cm. frame of 3.8 x 3.8 cm. strapping was covered with a layer of 6.3 mm. plywood. The base, on which the equipment rested, was lined with R-20 rigid styrofoam insulation as was the entire interior of the box. The box had a stand on its base to keep it about 6 cm. above the ground. The box was covered with a grey marine enamel paint to waterproof its exterior. A small hole was drilled through the bottom of the box so the lead wires from the nest antennae could be connected to the receiver.

These boxes were built to keep the electronic equipment they housed dry and to provide some protection for them from

the harsh environment where this study was conducted. There was also some concern for the Rustrak 288 chart recorder since the unit had only been tested by Gulton Industries to $0^{\circ}C$. For this reason the waterproof boxes were insulated and a heating system was installed inside each box. This heating system was built onto the receiver unit (see Figure 5) and consisted of a thermistor to measure the temperature inside the box. Once the temperature inside the box reached $0^{\circ}C$ the thermistor closed the circuit which supplied a 12 volt current to a heat lamp (a 40 watt clear light bulb). This system kept the temperature in the waterproof boxes above the critical level for the chart recorders.

Weather Data

A Lambrecht TH 252C hygrothermograph was used to collect data on the ambient temperature and humidity at the study site. The hygrothermograph was placed at a height of .3 meters above the ground. It was felt that the data collected by this in- strument in this location would be similar to the conditions experienced by the incubating geese. Both Greiger (1966) and Schulte and Porter (1974) have demonstrated the necessity of using microclimatological measurements rather than gross climatological measurements.

Wind speeds during the study period were provided by the Churchill weather station, in the town of Churchill. The Climatological Research Station, operated by McMaster University, provided data on incoming solar radiation (K↓) for the study period. The solar radiation data was measured by pyronometers.

These consist of a glass dome covering a thermopile. These measurements were made approximately 20 miles west of the study site. Since incoming solar radiation is affected by cloud cover, two hour K↓ totals were used in all of the final data analysis. It was felt that two hour totals would adequately reflect the incoming solar radiation at the study site (Note 1.).

Data Collected by the Study Eggs

Each egg gathered data on five separate factors. These included egg turning, inner shell temperature, air cell temperature, core temperature, and nest attendance.

Egg turning. Each egg was built to shed some light on the "gravitational theory" of egg turning. The diagram in Figure 6 shows the principal components of each study egg. The transmitter in each egg was contained on a piece of veroboard (6 x 4 cm.), which fit inside the large section of the prepared egg housing. Each transmitter was powered by a 5.6 volt mercury battery which, due to the size of the transmitter unit, could only be placed either above or below the transmitter. Once the battery and transmitter were positioned in the egg, it was obvious that its heaviest side would be the one containing the battery. With this construction it was felt that the "gravitational theory" would predict that the battery side of each egg should be facing the bottom of the nest for most, if not all, of the incubation period. Study eggs C and D were constructed in the aforementioned manner. The numerals above and below study eggs A, B, and E (51,49),

and below eggs C and D (100) in Figure 9 show the results of
100 water dish trials (Drent, 1970) for each "weight type"
of study egg. Eggs C and D had 100 trials in which the
heaviest side was always down in these trials. Eggs A, B,
and E were constructed so that they had two "heavy sides".
In these eggs a counterweight of lead, which was the same
weight as the mercury battery (23 gms.), was placed on the
opposite side of the transmitter from the battery (see diagram
1, Figure 9). Lead had to be used as a counterweight since
it is one of the few metals which does not affect radio sig-
nals. The water dish test results show that either side has
an equal probability of being down (51/100 vs. 49/100).

Shell temperature. An accurate means of recording shell
temperatures would be by placing thermistors at equal inter-
vals around the horizontal axis of an egg. With this tech-
nique one could see the effects of egg position with respect
to heat diffusion across the egg shell. This technique,
however, would require a large number of thermistors (and
lead wires) and hence a large number of input channels if
shell temperature was to be electroncially monitored in a
simultaneous fashion.

The present study attempted to solve the problem of egg
shell temperatures in relation to egg position in the follow-
ing manner. A thermistor was epoxyed, in an acrylic free
area under the shell, midway between the equator and blunt
end of each egg. Then the glass mercury switch was positioned
so that egg position and position of this shell thermistor

1

51

CW counter weight

transmitter

+ battery

49

Study Eggs A,B,E.

2

transmitter

+ battery

100
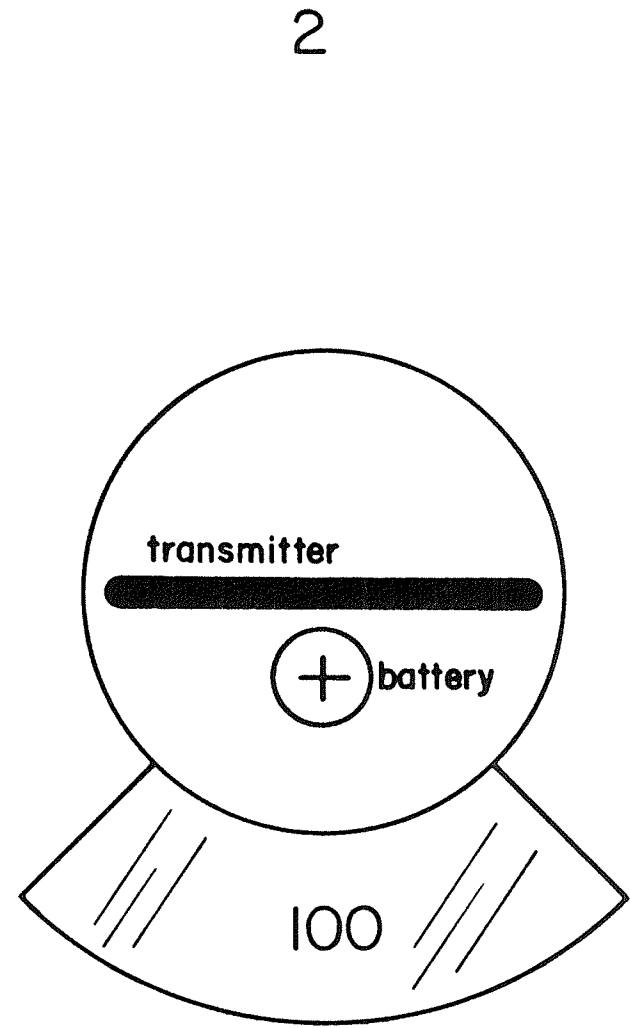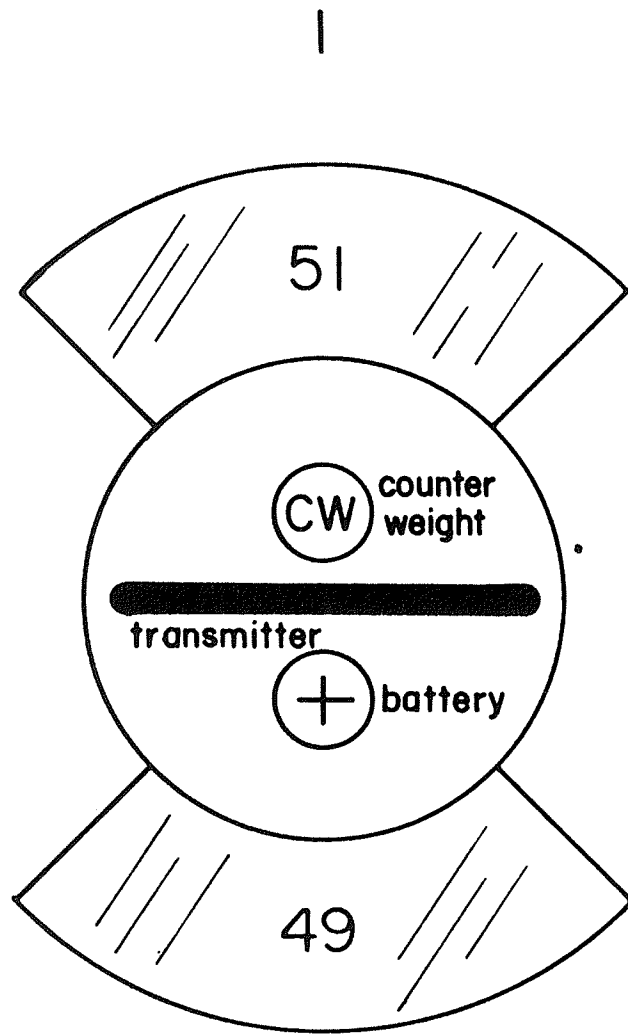
Study Eggs C,D.

Figure 9. Weight symmetry of the study eggs and the results of 100 water dish trials

could be simultaneously monitored. For example : if channel 1 is closed -- the shell thermistor is facing the female's breast; if channel 2 is closed -- the shell thermistor is facing the bottom of the nest; and if channels 3 or 4 are closed the shell thermistor is in an intermediate position. These alternative positions are shown in Figure 8. When a pair of electrodes made contact with the mercury, the channel these electrodes represented on the record was considered closed and was displaced to the top line of the chart paper. This system provides an average shell temperature and also provides data on shell temperature when the egg is in four different positions.

Air cell and core temperatures. The eggs designed and constructed for this study overcame some of the methodological problems cited in previous techniques (see p.8). First of all, care was taken to assure that each completed egg had the appropriate fresh egg weight according to its physical dimensions. Second, each egg contained a simulated (but fixed) air cell. This air cell housed a thermistor so air cell temperature data could be compared to existing air cell temperature data recorded from viable eggs by other researchers. Finally, the weight symmetry of each egg was fixed in one of two modes so egg turning could be studied as previously mentioned.

Procedure

Once a nest was found in the field the first egg was removed and replaced with a telemetering study egg. The first

egg was replaced so that data would be collected during the
egg laying period, as well as the incubation period. The
study egg was then covered with material from the nest cup
to hide it from potential predators. A loop antennae was
then placed around the outer periphery of the nest and cover-
ed with some of the surrounding vegetation. The two conductor
cable was connected to the nest antennae and unrolled 50
meters away from the nest to the insulated box which housed
the receiving and recording units. This wire was fed into
the box through its base and connected to the receiver. The
receiver was connected to the chart recorder and the 12 volt
battery which served as the power supply for this system.
The chart paper was set to the proper time. The LED indicator
on the receiver showed that the system was functioning pro-
perly. It should be noted that although each study egg was
covered with nest material before the nest was left, the
chart recorder indicated that the female was off the nest.
The entire procedure, from egg removal until closing the
waterproof box, took approximately five minutes.

The way in which the study nests were chosen deserves
some attention. First of all, only those birds which were
observed for one hour time periods had a possibility of being
selected. This means that only those birds seen on scouting
trips were "possibilities" for inclusion in this sample. The
location of geese which were seen engaging in nest building
activities but had no eggs at that time were plotted on a
map and checked again the following day. Finally, only those

nest sites were selected which could be seen clearly from some observation point at which the observer could position himself so that he would not disturb the nesting geese. Nests which were hidden in dense vegetation were omitted from the sample.

Each study nest was checked daily during the egg laying period to determine when the final clutch size was reached. If on two consecutive days the clutch size had not changed, the clutch was considered complete. The data on the egg laying period (see Table 5) supports this conclusion. This daily check resulted in the female being flushed from her nest. After examining the eggs the investigator covered the eggs with nest material to hide them from potential predators. Once each clutch had been completed, nests were visited every five days during the incubation period to check on the voltage of the power supply. Originally I had planned not to disturb (flush) the incubating geese when the 12 volt batteries had to be renewed. The 50 meters of cable running from the nest antennae to the receiver and recorder proved to be too short. Because of the topography of this area the incubating geese could see the researcher approaching when he was still a quarter of a mile from their nest. Therefore, the incubating geese would leave their nests when the batteries were changed. It should be noted that during the fourth week of incubation the incubating females did not leave their nests when the batteries housed in the insulated boxes were changed.

A heating system was designed to keep the air temperature around the chart recorder above 0°C. After four days of use this system had to be abandoned. The low temperatures at the study site caused the heat lamp to remain on for a large percentage of the day and this resulted in a large current drain on the 12 volt lantern batteries. If these "weakened" batteries had to be replaced at two day intervals, the supply of batteries would have been exhausted before the study was completed. Therefore, the chart recorders were not heated during this study. They worked at ambient temperatures. Fortunately, the chart speed did not suffer as a result of this change, as confirmed by my five day nest checks to change the 12 volt batteries and check on the system's operation. If other researchers plan to use this system in these environs, the design of the heater system should be modified so that it is activated at a lower ambient temperature and it should also have a timing mechanism to prevent constant battery drain.

The data from the study eggs were collected on a 24 hour basis for the entire study period. Behavioral observations were made of the activities of incubating females on the study nests. Females were observed with a 20-60x spotting scope and 7 x 50 binoculars. One hour sampling periods were picked at random during three separate time periods of the day, 07:00 - 12:00, 12:00 - 17:00 and 17:00 - 22:00 hours. Every 60 seconds the activity of the focal (Altmann, 1974) female at that time was recorded on a data sheet (see

Appendix A). A stop watch was used to monitor this one min-
ute time sampling technique (Altmann, 1974).

The typical procedure for the behavioral observations
was to proceed to the observation point and set up the nec-
essary equipment. After fifteen minutes the one hour observa-
tion period began. This procedure was followed in order to
minimize the likelihood of my arrival (albeit from a distance
of over 150 meters) affecting the behavior of the focal
female. The only situations in which observations were not
made during the three specified time periods were in periods
of dense fog, which made visual contact impossible, and in
times of severe weather (strong winds accompanied by freezing
rain and snow).

On June 5th and June 15th (between 24:00 - 02:00 hrs.)
all the focal females were flushed from their nests to check
on the reliability of the nest attendance data. Once the
incubating bird had been flushed her eggs were covered with
a layer of down and nest material and then the record was
checked to see if the data indicated the bird was off the
nest. The data on both days showed that the female was off
the nest, even though these tests were made during periods
of minimum light conditions (see Appendix B).

Data Analysis

In this study the telemetering eggs collected data on
the following five dependent variables: egg core temperature,
egg air cell temperature, egg shell temperature, nest attend-

ance, and egg turning. The independent variables in this study were: ambient temperature, wind speed, relative humidity, solar radiation $(K\downarrow)$, day of incubation, hour of the day, and nests (A-E).

Due to the continuous nature of the independent weather variables used in this study, multiple regression analysis was used in all analyses except those concerning behavioral observations and egg turning. Chi-square goodness of fit analyses were used to investigate the data on egg turning and behavioral observations.

The data collected during this study were analyzed at the University of Manitoba computer facilities using the Statistical Analysis System, 1979 (SAS) package. SAS (1979) was used in this thesis because of its superior data modification and programming capabilities as well as for its multiple file merging and date time functions.

Results

Arrival

On May 17, 1979, the study area was still snow covered except for Knights Hill and portions of the adjoining esker. This esker begins at the Hudson Bay coast, approximately 2.4 kilometers from Knights Hill, and continues 14.5 kilometers south west to Norton Lake.

Although there were single birds, pairs, and small groups (n=5) of Canada geese in the study area on May 17, nesting had not yet started. Canada geese were noted in this area on May 4, 1979 (Note 2).

Nest Initiation Observations

The following description of nest initiation activities comes directly from my field notes for a single nest. This description was almost identical for all the study nests.

Nest B. May 28 - at 16:00 I began observing a pair of Canada geese that were on a small peninsula of land which jutted out about 10 meters into a fairly large pond. The female (presumably) was sitting in the same area for quite some time. She then stood and poked about the area where she had been sitting. This same bird then began to pull up vegetation in her bill and placed it on the spot where she had been sitting. This bird then sat down and began to pull some of the surrounding vegetation up to her breast and around the periphery of her body. The other goose (presumably the male) was standing about 10 meters away the entire time. This latter bird was

constantly looking around and seemed to have his neck extended
for a large percentage of the time. Perhaps the presence of
herring gulls (Larus argentatus) flying over this general
area accounted for this situation. No vocalizations were
heard from either of these two geese during the one hour
observation period. At 17:00 hours I put on my pack and
flushed both geese from this area, in order to check for a
nest and/or eggs. At this time I discovered a single un-
covered egg, (not covered probably as a function of my flush-
ing this pair) in a nest cup that was made of allamus grass
and small willow twigs. This nest cup contained a small
amount of down and feathers. I removed this egg, replaced
it with a study egg, set up the rest of the telemetry system,
and left the area to continue searching for nests.

Weather

The overall mean temperature during the incubation period
was $3.23^{\circ}C$ with $-4.12^{\circ}C$ being the lowest daily mean recorded
and $14.1^{\circ}C$ the highest daily mean recorded. The mean relative
humidity during this period was 84.71% with a low daily mean
of 65.64% and 100% the mean daily high recorded.   An overall
mean daily windspeed of 19.4 Km/hour was recorded during the
incubation period. The lowest daily wind speed average was
9.17 Km/hour, however on some days there were wind gusts up
to 61.48 Km/hour.

Behavioral Observations

The automated study eggs and recording apparatus collected
incubation data on a 24 hour basis. A further 305 hours of

behavioral observations were made on focal female geese between 07:00 and 22:00 hours. The females from each of the five nests (A through E) were studied.

Various terminology has been used to describe the temporal patterns of avian incubation behavior (Beer, 1961; Drent, 1970; Kendeigh, 1952; Skutch, 1962). The present study used Skutch's (1962) terminology. Periods on the nest are sessions, while periods off the nest are recesses.

Incubation Sessions

A total of 294 hours were spent observing incubating geese during incubation sessions. Observations were recorded on a specially prepared data sheet (Appendix A). The results of the behavioral observations are summarized in Table 2. The activities listed in this table (sitting, alert, hiding, resting, and nest maintenance) were five separate and readily distinguishable behavior patterns. The results show that the majority of time (93.2%) on the nest was spent sitting on the eggs.

The typical sitting posture assumed by incubating geese is shown in Figure 10. The sitting activity may be slightly over represented in the data presented in Table 2. Other observers may have called portions of the sitting activity resting or sleeping since there have been reports of the white upper eyelids appearing when the female is in this stance (Pakulak, Note 3). Since I was quite a distance from the focal females, it was not possible to make this fine distinction based on the appearance of the white upper eyelids.

Table 2

Time engaged in Activities on the nest by Female Geese*

Time Period	Sitting	Alert	Hide	Resting Nest	Maintenance
0700-12:00	91.08 hrs.	.75 hrs.	7.42 hrs.	0 hrs.	.75 hrs.
100 hrs. of observations	(91%)	(75%)	(7.4%)	(0%)	(.75%)
12:00-17:00	88.46 hrs.	1.56 hrs.	1.86 hrs.	0 hrs.	1.9 hrs.
94 hrs. of observations	(94.1%)	(1.77%)	(2.1%)	(0%)	(2.14%)
17:00-22:00	94.4 hrs.	.4 hrs.	3.4 hrs.	.13 hrs.	1.67 hrs.
100 hrs. of observations	(94.4%)	(.4%)	(3.4%)	(.13%)	(1.67%)
TOTAL	273.95 hrs.	2.71 hrs.	12.68 hrs.	.13 hrs.	4.32 hrs.
294 hrs. of observations	(93.2%)	(.92%)	(4.3%)	(.04%)	(1.46%)

* It was assumed that incubating geese were females, since it is widely held that in-
cubation is done solely by the female (Balham, 1954; Brakhage, 1965; and Cooper, 1978).

Figure 10. Sitting posture

Incubating female geese would always face into the wind while on the nest, a phenomenon earlier reported by Drent (1970). The reason for this behavior may be related to the female attempting to conserve as much body heat as possible. If she was not facing into the wind her feathers may be blown out of place, thus allowing body heat to escape. Finally, the data collected by the study eggs show that during the sitting activity the female turns the eggs. Since observations revealed that the female did not rise from the nest to use her culmen for this turning, it is reasonable to conclude it was done with the use of her feet and/or abdomen. (For a more detailed description of egg movements see pp. 97).

Females spent .92% of the time engaged in the "alert" pose. This pose, shown in Figure 11, is characterized by the goose holding her head and neck nearly upright and vertical. This position is assumed when the female is startled by some noise or sees something that alarms her. Typically, the goose in the alert pose remains extremely vigilant and surveys the surrounding area while moving the head from side to side. This pose was usually seen when herring gulls (Larus argentatus) or parasitic jaegers (Stercorarius parasiticus) were flying between 200 and 300 meters away from the incubating goose or when a caribou (Rangifer arcticus) would pass by a nesting area. If these predators would approach too close to an incubating goose, the alert posture typically changed to a hide posture. The only other situation in which a female goose assumed this posture, was when another goose (presumably her

Figure 11. Alert posture
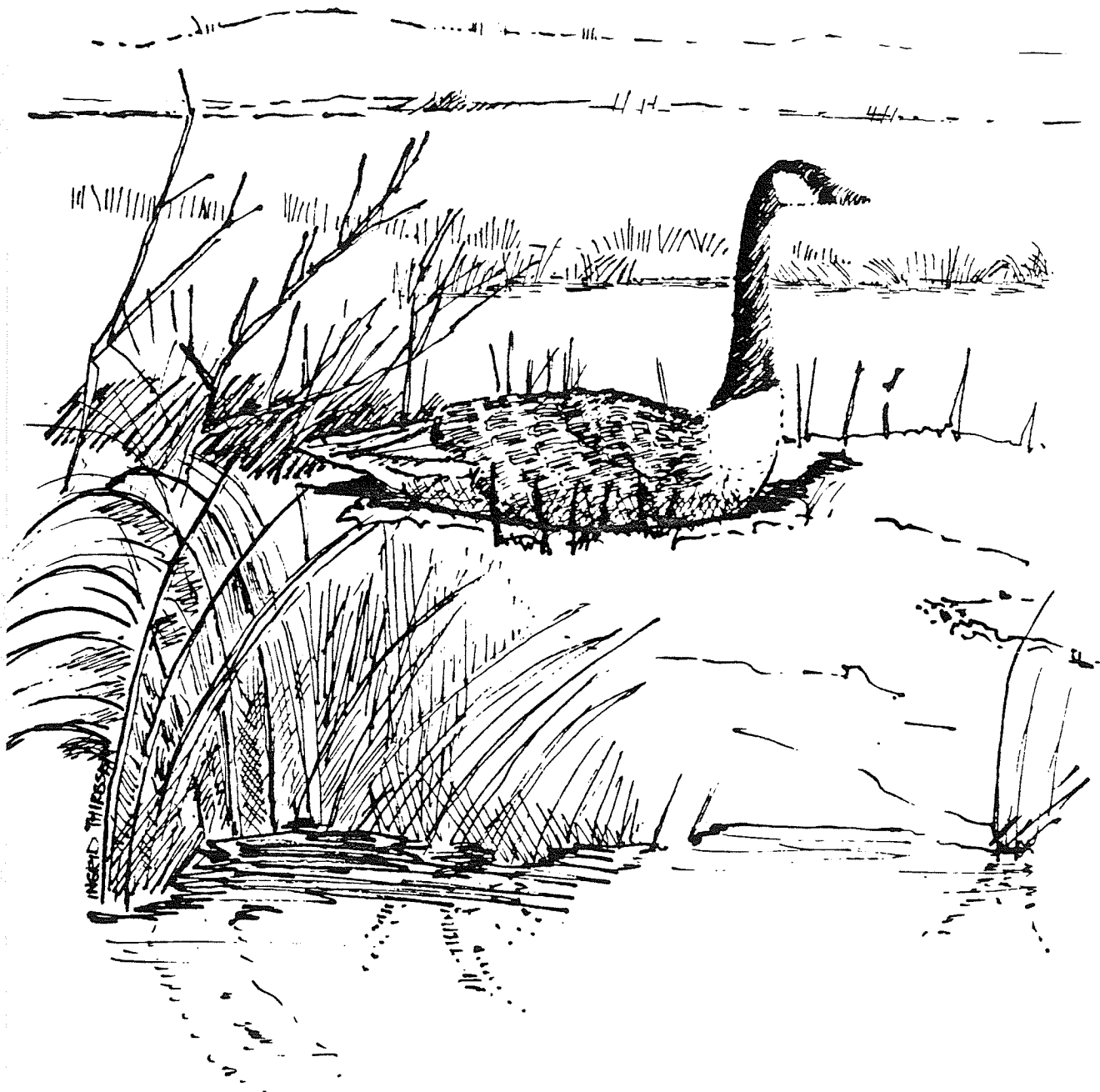
mate) was alarmed at something and began calling. Perhaps the alert pose is a time when the female evaluates the situation and decides whether or not she should leave her nest (fight or flight). I only saw females leave the nest after assuming the alert pose when I went to check on the telemetry system. Perhaps the female perceived she was in danger, not just her eggs, as would be the case with gulls.

The hide posture, shown in Figure 12, involves the female extending her head and neck outward, low to, if not on the ground. Once in this position she would remain motionless until the danger passed. It was extremely difficult to make out the incubating goose while she was in the hide position. This was a result of her cryptic coloration. When in this hide posture the only conspicuous features of the goose were her white cheek patches. The females observed during this study spent 4.3% of their sessions engaged in the hide posture. I feel this percentage is a direct function of the large number of herring gulls in this area. In fact, a large number of herring gulls were nesting in the same areas as the focal female geese. Nest E for example, had a herring gull nest less than 20 meters away from it.

There were additional displays which contained elements of both the hide and alert postures. Figure 13 shows an example of a mixture of these elements. I have termed the behavior pattern shown in Figure 13 as the "ready to hide" posture. This posture followed the alert posture and was most often seen when caribou were passing in the general area

Figure 12. Hide posture
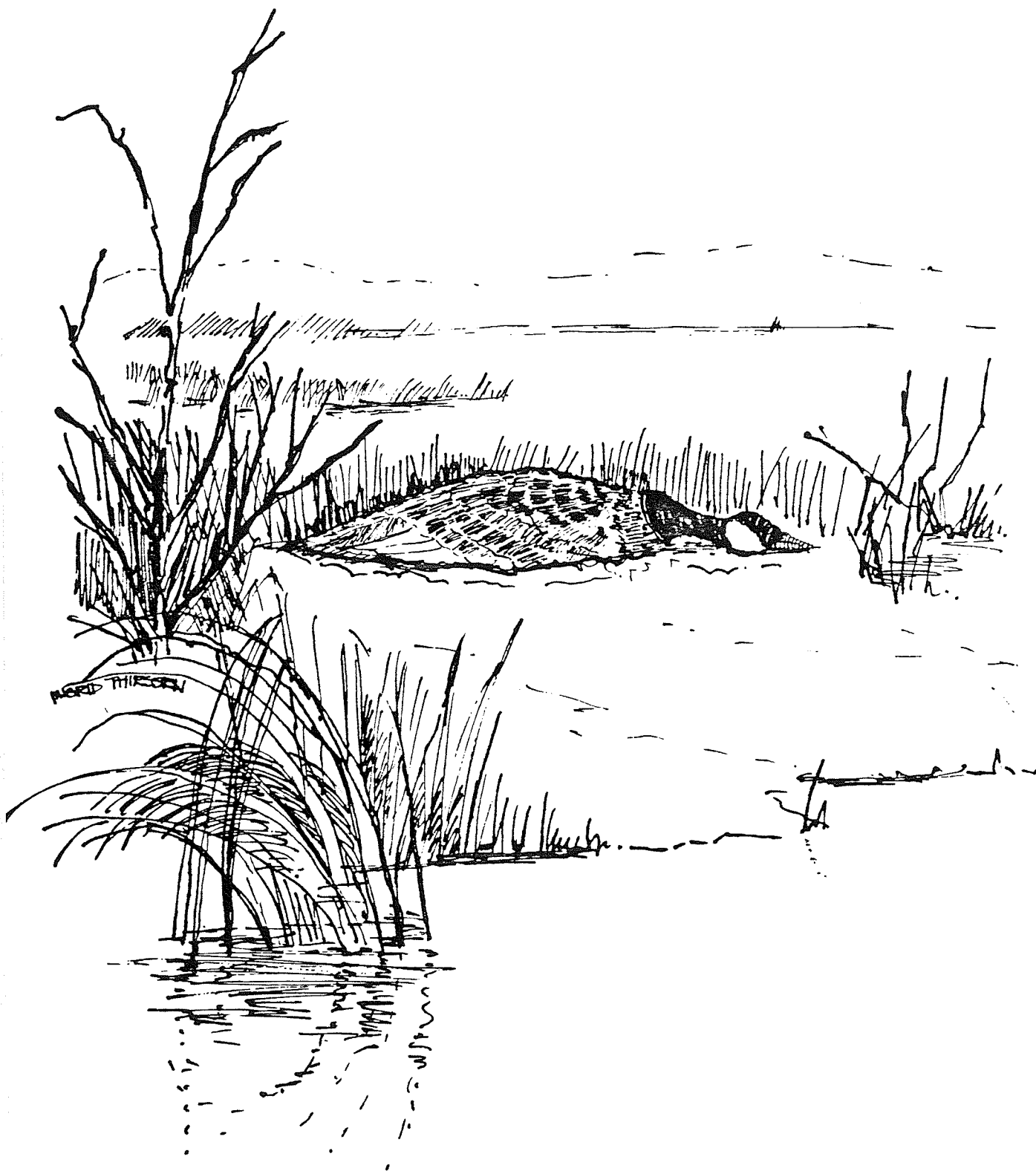
Figure 13. Ready to hide posture

of a nesting female goose. Perhaps the goose in this situation was aware of the possible danger, but was not certain exactly what path of travel the caribou were taking. Therefore, the goose would lower her head and neck and remain motionless while at the same time keeping her head high enough above the vegetation to see if the caribou were going to pass too near the nest site. I feel this ready to hide posture was a case of indecision or uncertainty on the part of the incubating goose.

There were only .13 hours out of 294 hours of observations when incubating geese were seen resting or sleeping (.04%). This activity consisted of the female either tucking her mandible between her wings on her back, or tucking it under one wing on her back. This data is probably not fully representative of the amount of time an incubating goose spends resting or sleeping. This is partly due to the fact that the closed eyes of the incubating geese could not be seen by the observer (as previously mentioned), and could be due to the fact that behavioral observations were only made between 07:00 and 22:00 hours.

Nest maintenance by incubating geese accounted for 1.46% of the total observation time. This activity consisted chiefly of repairing the nest and covering the eggs with down before leaving the nest on a recess period. In these cases, the females would pull in materials that were within reach and press them around the outside of their bodies. Females were also often seen replacing down and other nest materials

on windy days. Presumably the wind had blown this material
from around their bodies on these days. Incubating females
were also observed to put their culmens on the outer edge of
the nest cup and pull it back towards themselves. Females
sometimes stood briefly to undertake nest repairs. In these
cases the incubating female would pick up pieces of nearby
vegetation and "stuff" them into the nest. This action would
then be followed by some poking of the nest (and possibly its
contents) with the culmen. The situations where the female
was seen to stand over the nest, on the outer edge of her
nest cup, and undertake nest repairs were usually brief, last-
ing less than one minute. When an incubating female goose
would stand to leave on a recess period she would always cover
her eggs with a layer of down. The covering process was
usually a single movement in which the female would grasp a
section of the inner nest cup and pull it over the eggs. The
section of the nest which was used to cover the eggs was much
like a "blanket". This "blanket" consisted of a large amount
of down which had small pieces of willow twigs and dried moss
intertwined within it. This structure was a solid mat which
the female could manipulate as a single item.

The data collected on behavioral activities during sessions
revealed that the time of observation period had a significant
effect on the amount of time spent, across the five activities,
$x^2 = (10) = 324.1$, $p < .001$. The chi-square values for each
activity during incubation sessions for observation time per-
iod are presented in Table 3. These results show that the

Table 3

Chi-Square Analysis of Incubation Postures during Sessions

across Observation Periods.*

	Sitting	Alert	Hide	Resting	Nest Maintenance
x^2	11.64**	47.49***	233.08***	16.04***	30.8***

* Based on 294 hours of observations on incubation sessions.

** $\underline{p} < .01$

*** $\underline{p} < .001$

observational time period had a significant effect on the amount of time spent in each activity. The largest chi-square value was found for the hide posture indicating a large amount of variation in time spent in the posture over observational periods. From Table 2 it can be seen that the majority of hide postures were seen in the morning observational period, with a second peak in the evening observational period. This occurrence may be related to greater numbers of avian predators near focal nests during these periods.

Recess Periods. A recess period during this study was defined as an interval when the female left her nest. While the study eggs collected information on length of recess periods on a 24-hour basis over the course of the study, I spent 10.95 hours observing focal females during 36 recess periods. The sequence of the female's activities varied little during the 36 observed recess periods. The following account recorded on June 9, 1979, for female/nest C describes the typical sequence of activities during a recess period.

June 9, 1979, 10:07 : Female stood over her nest and covered her eggs. She then walked about five meters and entered the water. About forty meters from the nest she was joined by another goose (presumably her mate) who swam up beside her in the water. No greeting ceremony was seen at this time. The pair then swam another thirty meters toward the shore of another island. Here the female began to bath and preen herself. She continued these activities for about three minutes and then got onto the island and began to feed rapidly. The

male accompanied the female but did not engage in the same
activities. Instead, he kept looking about in all directions.
The female continued feeding for approximately seven minutes
and then stood beside the other goose. The pair remained like
this for another two minutes, at which time they re-entered
the water and began swimming back towards their nest site.
On the way back, however, the female spent some time drinking
and twice she "up-ended" and emerged with some acquatic
vegetation between her mandibles. When the pair was about 10
meters away from the nest site they split up. The male swam
away from the nest site, while the female continued toward it.
The female then walked onto the island on which her nest was
built, and walked over to the nest. Then, while standing
over her nest, she preened and stretched her wings. These
activities lasted for about one minute, after which she sat
down on her nest. The female then pulled nest material
around her body while settling herself on the eggs. This
settling was a gentle side to side rocking motion accompanied
by pokes of the culmen to the nest contents (possibly the
eggs). This settling behavior adjusts egg position within
the nest-bowl and hence ensures close contact with the brood
patch, as well as drawing the eggs tightly together (in com-
bination with the concave shape of the nest floor) allowing
the eggs to lie with the blunt pole highest (Drent, 1970).
The blunt pole facing the females brood patch allows the
maximum surface area of the egg to be in contact with the
heating source.

A few general points should be made about the observations of the recess periods of the incubating females. First of all, the females always covered their eggs with nest material before they vacated the nest. Females were never observed flying to or from their nests on a recess period. Instead, they walked from their nest and entered the water which was around the nest site. After leaving the nest site, the female was always joined by another goose (presumably her mate). The joining goose would accompany the female on her recess period and maintained a constant alert posture. The pair of geese would never go back to the nest site together. Instead, the male would leave the female as they approached the nest site. Finally, on returning to the nest after a recess period, females sat directly on the down covering without making any attempt to push it aside. During recess periods the females were always within sight of their nests.

Table 4 shows the summarized results of the behavioral observations which were made on focal females during their recess periods. It should be noted that while only 36 recess periods were observed directly by the researcher, there were a total of 170 recess periods taken over the study period (as recorded by the study eggs). Table 4 shows that more time during a recess period (31.1%) was spent feeding than at any other activity. This fact seems reasonable when it is remembered that recess periods were the only times when females left their nests/eggs to feed. These short periods of food intake had to assist the female in maintaining her body

Table 4

Time Engaged in Activities during Recess Periods of

Incubating Geese*

in H_2O	Bathing	Standing	Sitting	Preening	Aggression	Feeding
180 mins.	39 mins.	159 mins.	0 mins.	75 mins.	0 mins.	204 mins.
27.4%	5.9%	24.2%	0%	11.4%	0%	31.1%

* 657 minutes (10.95 hrs.) of observations, from 36 recess periods.

metabolism. It is doubtful whether these short periods of food intake would alone be sufficient to support the incubating female, and the body fat reserves of the incubating female undoubtedly played an important role in this matter. The time the incubating female spent in the water during her recess periods, should probably have been divided into two sub categories. These could have been ; feeding in the water and drinking. I feel if these subdivisions would have been used the total time spent feeding would have been much greater. The time spent in exterior body maintenance (bathing and preening) was relatively small (5.9% and 11.4% respectively). The other striking feature of the data in Table 4 is that no observations of aggression were seen during the study period. This is probably due to the low nesting density in the study area.

Additional Observations. On June 10, 1979, a group of five herring gulls attacked an incubating female Canada goose. At 07:59 that day, while walking through an area with a large number of islands, towards nest E it seemed that a group of five gulls were "following" me. A few minutes later a Canada goose flushed and flew about 200 meters west of my path of travel. Shortly thereafter the group of gulls, previously mentioned, began swooping down at an incubating female Canada goose about 50 meters behind me. Each gull swooped down and pecked, or attempted to peck at the incubating female in rapid succession. The female, meanwhile, was in the typical hide posture and remained motionless on her nest. The goose

which had previously flushed was now 30 meters behind me, calling vigorously, and alternating looking towards me and the attacking group of gulls. Realizing that this goose was probably the female's mate, and had been removed from his role as her defender, I hurried off and positioned myself behind a small clump of dwarf willows about 100 meters north of the harassed female goose. Through my binoculars I watched the presumed mate of this female fly into the air above the nest site and engage in an aerial battle with the five gulls. The gulls rapidly dispersed from the area and the male goose flew to a small island about 30 meters south of the incubating female where he stood scanning the area. Meanwhile the female goose on the nest had resumed her normal incubation posture.

My observations of this predatory behavior are similar to reports of other researchers working in arctic and sub arctic regions. Researchers collecting nest data in these regions have often had the impression that they were being followed by avian predators, such as gulls and jaegers (MacInnes & Misra, 1972). Recently Strang (1980) presented data supporting the view that avian predators are attracted to people searching for waterfowl nests. His data indicated that only parasitic jaegers were drawn to people, but his observations indicated that both jaegers and gulls sometimes take eggs from exposed waterfowl nests when people are nearby. It seems reasonable to assume that predators may learn to forage in the vicinity of field workers if such behavior increases feeding success.

Herring gulls in this area also showed another interest-
ing predatory technique. When caribou were walking through
a nesting area they would inevitably flush incubating geese
from their nests. These birds would not have time to cover
their nests with down, as was typical in a recess period.
Groups of herring gulls would fly behind these passing caribou
and once an incubating goose was flushed by the caribou, the
gulls would swoop down and predate the eggs in the nest.
Based on the observations during the 1979 nesting season in
the study area, it appears that herring gulls are the great-
est predatory threat to nesting geese.

Telemetry Data

Only three telemetering eggs survived the entire incuba-
tion period. Table 5 shows the number of eggs, dates of lay-
ing, and incubation periods for each study nest.

The telemetry equipment collected 2,012 hours of data
during this study.

The telemetry data was transcribed from the continuous
chart recorder records onto computer cards. The following
information was recorded onto these cards on a fifteen min-
ute sampling sequence : egg shell temperature, egg core
temperature, egg air cell temperature, whether the female
was on or off the eggs (nest attendance), and which of the
four sides of the egg was facing the top of the nest. If an
incubating female left her nest on a recess period the exact
time of departure was recorded along with the egg temperature
and egg position at that time. When the female returned to

Table 5

Laying and Incubation Schedules of Study Nests

Nest	Date 1st Egg Laid	Date Clutch Completed	Final Clutch Size	Date Hatched	Incubation Period (days)
A	May 29	June 1	4[a]	--	--
B	May 28	May 29	2	June 25	28
C	June 1	June 4	4[b]	June 27	24
D	May 29	June 1	4[c]	--	--
E	May 30	June 3	5	June 26	24

[a] Clutch predated June 3. Signal from telemetering egg lost at 23:05, June 3.

[b] Total clutch size = 4 eggs, however 1 egg lost between June 10, 07:50 and June 15, 20:00. Only the remaining 3 eggs hatched from this nest.

[c] Clutch predated by herring gull June 5, 20:15.

her nest this information was once again recorded. The weather data (ambient temperature, relative humidity, wind speed, and solar radiation) was then merged with each nest's data for the study period.

The day that the final clutch size had been reached in a nest was designated day 1 of incubation. The laying period was numbered consecutively backwards from day 1 of incubation (eg. -3, -2, -1, 1). This system of specifying day of incubation was adopted to conform with Heinroth's (1922) rule for determining the incubation period. He defined the incubation period as, "the time elapsed from the laying of the last egg until the last young has left its egg shell" (p. 174). This system has also been widely adopted by other researchers in this field (Caldwell and Cornwell, 1975; Cooper, 1978; Drent, 1970, 1975; and others). Once each nest was classified according to its day of incubation, it could be directly compared with other nests that had reached the same incubation day.

Two of the five telemetering eggs were lost during this study. On June 5th I was making behavioral observations at nest D. At 20:10 the incubating female stood over her nest, covered her eggs with nest material, and left on a recess period. At 20:15 a herring gull flew to the nest and started to peck at the eggs in the nest cup. Approximately two minutes later the gull flew into the air carrying an egg (presumably one which had been impenetrable, (the study egg)) and dropped it on a rock from a height of about 20 meters. This

rock was about 15 meters from the nest site, and was in a pond about one metre deep. I left my observation post and walked to the nest where I found the empty shells of three eggs, the study egg was not present.

The exact fate of nest A is unknown. The study egg, however, did transmit data until the time this nest was destroyed. This female (A) left her nest at 16:45 on June 3. She did not return before the nest was destroyed and the study egg lost at 23:00 on June 3. The egg temperatures when this female left her nest were in the average range (air cell temperature 34.1°C), egg core temperature 34.6°C, and egg shell temperature 37.4°C). The length of this recess period (6¼ hours) was most atypical. I feel that this was not, in fact, a recess period, but a nest desertion, since the female left her eggs for 6¼ hours and the egg temperatures at the time of nest predation were all 10.0°C (very low). The ambient temperature at this time was .9°C. These extremely low egg temperatures would probably have lowered the hatch rate for this nest since this clutch of eggs were in their third day of incubation. When nest A was checked on June 4th at 08:15 the nest loop antennae was found approximately 40 meters north of the original nest site on another island. The original nest site did not contain any egg shells or any sign that a nest cup had been there a day before. This nest's total destruction suggests that it may have been predated by a caribou.

Finally, nest C lost a single egg sometime between June

10, 07:50 and June 15, 20:00. Fortunately, the study egg was not lost from this nest. The loss of the egg reduced nest C's clutch size from 4 eggs to 3 eggs. While there is no information available concerning what happened to this lost egg, it is possible that it was eaten by avian predators. MacInnes and Misra (1972) hypothesized that the loss of part of a clutch to an avian predator might be the result of human disturbance forcing the parents from the nest. Gulls or parasitic jaegers would discover the nest before the parents returned and start feeding on the eggs. The parents may however return before all the eggs in the clutch were eaten. It is not known whether I caused any disturbance which may have resulted in the loss of this egg from nest C. On the other hand Strang (1980) reported that avian predators (gulls and jaegers) do not always destroy the entire clutch. He reports observing a pair of parasitic jaegers at a white-fronted goose (Anser albifrons) nest, who took turns feeding and keeping watch, and eventually left this nest after only consuming one egg of the clutch.

Nest Attendance

The three successful study nest (B, C, and E) showed an average nest attentiveness (% of incubation period on the eggs) of 95.03% over the course of the study period. Individually, the attentiveness figures for the successful nests were as follows: Nest B 92.79%, Nest C 97.27% and Nest E 95.66%. The attentiveness of the unsuccessful nests were 79.03% and 93.53% for nest A and D respectively. While the

figures on nest attentiveness for the unsuccessful nests are
not for complete incubation periods, they do provide material
for speculation. Specifically, the nest attendance for nest
D does fall into the range reported for the successful nests
while the figures for nest A do not. Nest attendance of only
79.03% does seem quite low when compared to the successful
nests. This finding indicates that female A took more recess
periods than any of the other four females studied from May
29 to June 1st. It is possible that the data gathered from
nest A represents the nest attendance patterns of a female
goose prior to nest desertion.

A total of 179 recess periods were taken by the three
successful females in this study. Recess periods for these
three nests were taken an average of 2.15 (s^2 = 2.06) times
per day. Females typically left their eggs twice daily, but
on some days they left five times, while on other days they
did not leave their eggs at all. No recess periods were
taken on 14.47% of the days, one on 22.36% of the days, two
on 26.31% of the days, three on 19.74% of the days, four on
11.84% of the days, and five on 6.57% of the days.

The length of the recess periods (N = 179) averaged
20.97 minutes with a range of 5 to 82 minutes. This maximum
recess period (82 mins.) represents 5.7% of the day. A mul-
tiple regression analysis was used to determine if there were
any linear relationships between the length of the recess
periods and weather variables, as well as day of incubation.
All possible two-way interactions were also tested in the

analysis. As can be seen from Table 6, the overall F value (1.45) is non significant. This indicates that overall, the variables used in this regression model do not affect the length of the recess periods in any significant way. These results indicate that the length of the recess periods were not affected by : (a) the time of day, (b) any of the weather variables measured, and (c) the day of incubation.

There was no statistically significant change in the frequency (x^2 = 25.85, df = 27, p>.05) or duration (F = .08, p>.05) of recess periods during the entire period monitored in this study, which included both the egg laying period and the hatching period. No recesses were taken within the 24 hour period preceding hatching in all the successful nests. This response of not leaving the nest, was probably the female's response to pipping eggs.

Recess periods were taken at all hours of the day (Figure 14). This figure shows that each individual focal female had two typical time periods when recesses were taken. For female B these time periods were 15:00 to 18:00 and 18:00 to 21:00, female E left her nest most of the time between 09:00 to 12:00 and 21:00 to 24:00, while female C took most of her recess periods between 03:00 to 06:00 and 18:00 to 21:00. While these patterns of recess periods do show a great deal of individual variation, all three females took a large percentage of recess periods in the hours between 18:00 and 21:00.

The length of the incubation periods, previously pre-

Table 6.

Multiple Regression Analysis of Recess Length [a]

Dependant Variable : Recess Period Length

Source	df	F value	sr^2
Nest	2	1.41	--
Hour of day	1	.00	--
Temperature	1	.08	--
Humidity	1	.06	--
Wind speed	1	.02	--
Solar radiation	1	.30	--
Day of incubation	1	.08	--
Hour of day X nest	2	6.72*	.043
Day of incubation X nest	2	7.36*	.047

---

[a] Only main effects and significant interactions are presented in this table.

* $p < .01$

N = 179 F ratio = 1.45 $p > .05$ at 32/147 df

r = .549 r^2 = .302
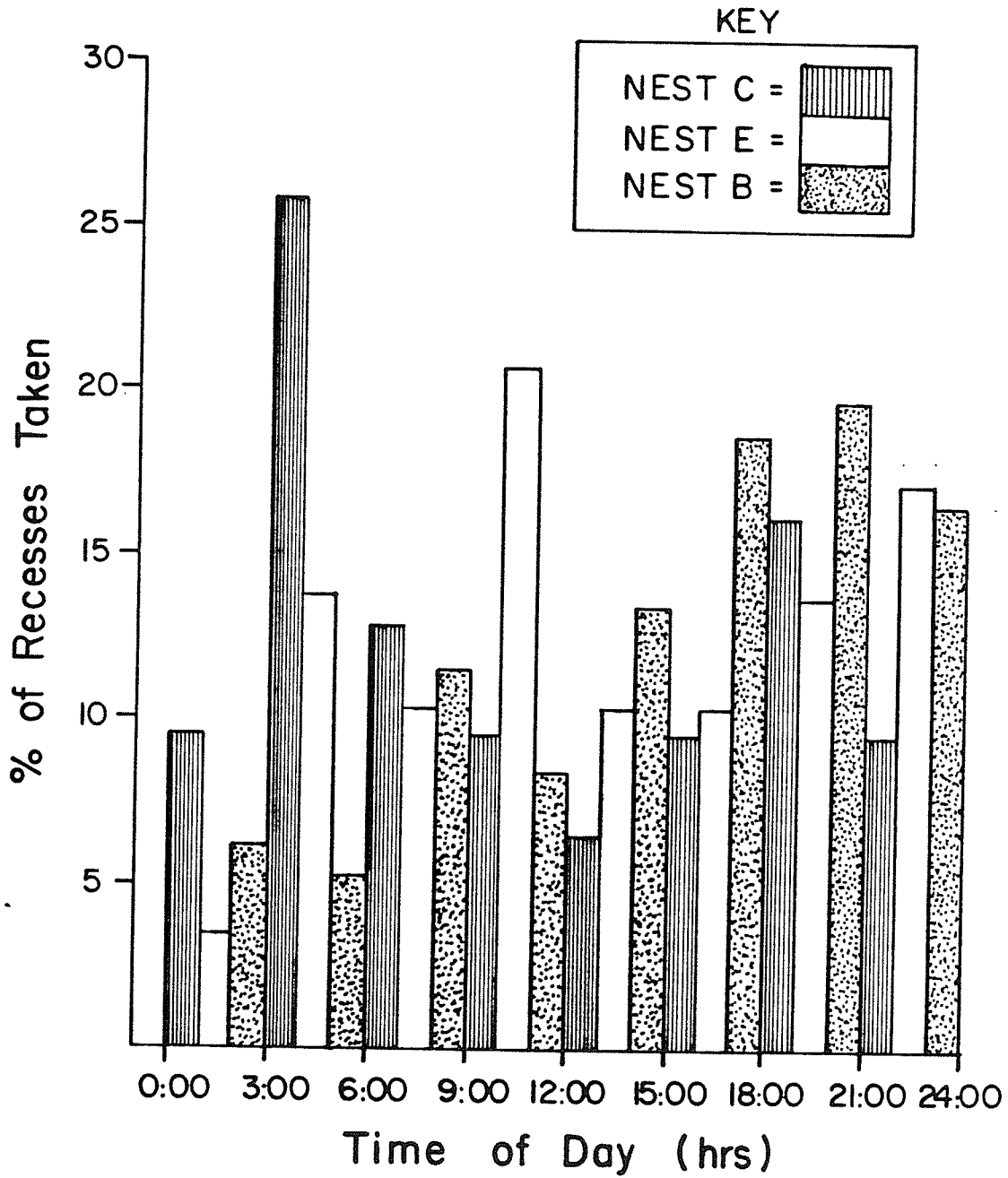
Figure 14. Time of day recess periods taken in successful nests

sented in Table 5 show that of the three successful nests
one hatched in 28 days (Nest B), while the other two hatched
in 24 days (Nests C and E). The difference in incubation
periods between nest B and nests C and E is somewhat surpris-
ing. From Table 7 it can be seen that female B took 96
recess periods over the course of the incubation period while
females C and E took 40 and 43 recesses, respectively.
Female B took more than twice the number of recesses as did
female C or female E. Table 7 also shows that although
females C and E took approximately the same number of recess
periods over the incubation period, female E was off her eggs
about 1.5 times as much as female C. Yet, both nests C and
E hatched in 24 days. It appears that since female B spent
such a large amount of time off her eggs, this fact accounted
for the 28 day incubation period. It is not so easy to ex-
plain, taking into account only the time off the eggs, the
hatching of nests C and E in 24 days despite the large
difference in time off their eggs between these two females.

Incubation sessions are the periods between recesses
when the female is on her eggs. The mean session length for
the successful nests was 626.95 minutes or 10.45 hours ($s^2 =$
9137.4 hrs., Range = .33 - 93.73 hrs.). The longest session
recorded was 5624 minutes and occurred in nest E. The session
length represents 93.73 hours of nest attendance or 3.9 days
without leaving the nest! The summary statistics for the in-
dividual nest incubation sessions are presented in Table 8.
The mean time between recesses for female B was 6.45 hours

Table 7

Recess Periods of Successful Nests

Nest	# of Recesses	Total time accumulated on Recess Periods
B	96	2865 (mins.)
C	40	972 (mins.)
E	43	1550 (mins.)

Table 8

Incubation Session Length of Successful Nest*

Nest	N	Mean	Minimum	Maximum
B	95	6.45	.33	42.83
C	29	17.46	.97	45.55
E	28	16.76	.82	93.73

* all values in hours.

over the course of the incubation period, while for female

C this figure was 17.46 hours. Female E averaged 16.76 hours

between recess periods. The shorter session length for

female B is related to the 96 recess periods this goose took

during her incubation period.

A multiple regression analysis was conducted on the in-

cubation session lengths (total = 138) for the successful

nests. Initially, all the weather variables, time of day,

day of incubation, nest, and all possible two way interactions

were included in the regression equation. Then the non sig-

nificant variables and interactions were removed from the

regression equation. Those removed from the equation in-

cluded (a) time of day F = .40, (b) wind speed F = .17, and

(c) day of incubation F = .05. These three variables were

not significantly related to session length.

The results of the multiple regression analysis using

the "new" regression equation are presented in Table 9. Five

of the variables showed a positive significant relationship

to session length. These were (a) temperature - accounting

for 3.9% of session length variability, (b) humidity - 2.5%

of the observed variance, (c) solar radiation - 2.2% of the

observed variance, (d) temperature X humidity interaction -

3.8% of the observed variance, and (e) temperature X solar

radiation interaction - 4.9% of the observed variance. Those

variables which were significantly related to session length

accounted, individually, for at most 4.9% of the variance of

session length. Combined, however, they account for 33.4%

Table 9

Multiple Regression Analysis of Session Length

Dependant Variable : Session Length

Source	df	F value	sr^2
Nest	2	1.38	--
Temperature	1	7.43**	.039
Humidity	1	4.66*	.025
Solar radiation	1	4.15*	.022
Temperature X nest	2	2.36	--
Humidity X nest	2	1.97	--
Solar radiation X nest	2	1.14	--
Temperature X humidity	1	7.08**	.038
Temperature X solar radiation	1	9.22**	.049
Humidity X solar radiation	1	2.04	--

* $p < .05$ ** $p < .01$

N = 138 F ratio = 4.44 $p < .0001$ at 14/138=df

r = .578 r^2 = .334

of the variance of session lengths. Obviously other factors must be affecting the length of the sessions.

Egg Temperatures

The average egg air cell temperature and egg core temperature, over the course of the study period for the successful nests, are presented in Table 10. Figure 15 shows the egg air cell temperatures over the course of the incubation period for nest C. The data from the other successful nests are very similar to those presented in Figure 15. During the egg laying period the air cell temperature is lower than during later incubation. Further, it should be noted that this temperature increases steadily during the egg laying period. The mean air cell temperatures and daily attentiveness figures for the successful nests, during the egg laying period are presented in Table 11.

Table 12 shows that the highest mean shell temperature is reached when the shell is directly against the incubating female's breast (side = 1). When the shell is against the bottom of the nest cup (side = 2) the mean shell temperature was 30.49^{o}C, averaging 5.71^{o}C lower than when against the female's brood patch. When the side of the egg monitored was in between the top and bottom positions the shell temperatures did not vary greatly ; side 3 = 34.34^{o}C and side 4 = 34.06^{o}C. The mean shell temperature difference between sides 3 and 4 and side 1 was 2.02^{o}C lower, and 3.69^{o}C higher between sides 3 and 4 and side 2.

These egg temperature gradients are affected by a number

Table 10

Average Study Egg Temperatures for Successful Nests*

	Mean	Minimum	Maximum	s^2
Air cell temperature	34.4°	18.0°	39.69°	3.63°
Egg core temperature	34.8°	19.0°	39.00°	2.06°

* All values in $^{\circ}$C. From 8,352 observations.

Figure 15. Egg air cell temperatures during egg laying and incubation for Nest C
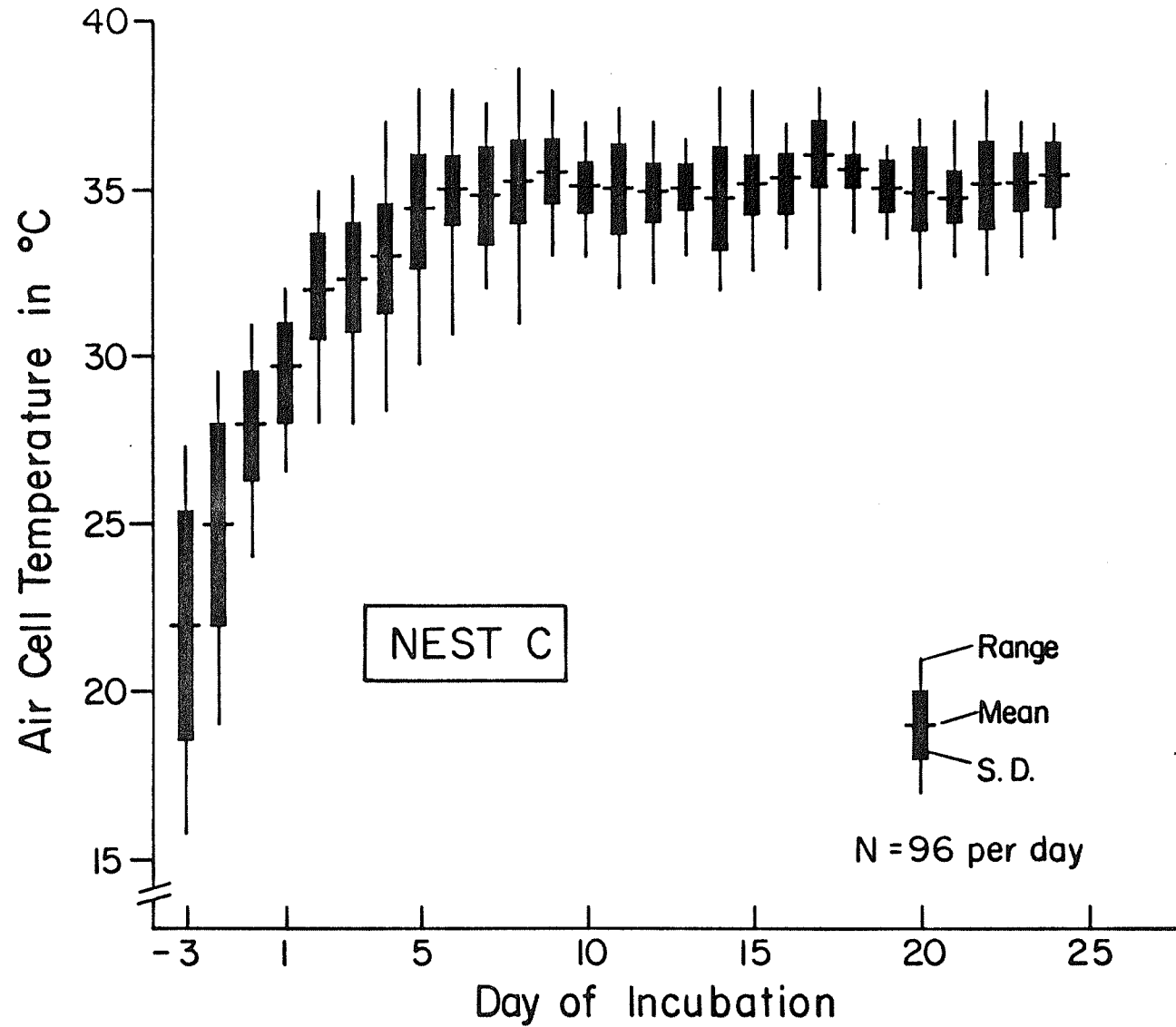
Table 11

Daily Egg Air Cell Temperatures and Attentiveness during the

Egg Laying Period*

Incubation Day	Air cell temperature	Attentiveness
- 4	18.5^{O}C	85.3%
- 3	22.7^{O}C	90.5%
- 2	27.4^{O}C	92.4%
- 1	31.8^{O}C	93.1%

* for successful nests.

Table 12

Egg Shell Temperatures for the Successful Nests*

	Side of Egg	$\overline{X}$ temp	Minimum	Maximum	s^2
1=	facing female's breast	36.21	32.4	41.1	2.0
2=	facing bottom of nest	30.49	21.0	34.6	2.4
3=	facing right side	34.32	30.1	40.9	3.0
4=	facing left side	34.06	29.2	39.7	2.9

* All values in ^{O}C.

of factors. These factors range from the amount of direct physical contact between the female's incubation patch and the egg shell, the thermal qualities of the nest structure, and whether or not the egg being monitored is in contact with the other eggs in the clutch, as well as the egg shell temperature of the eggs that the monitored egg comes into contact with.

From Table 13 it can be seen that the egg air cell temperature dropped an average of $3.59^{\circ}C$ during a recess period, while the egg core temperature dropped an average of $2.49^{\circ}C$ during the female's absence (Table 13). This data indicates that the air cells cooled quicker than did the core of the eggs and that both air cell and core temperatures are relatively stable during recess periods. This relationship is probably related to the short length of the recess periods and the female covering her eggs with down and nest material before departing on a recess period.

The incubation periods of the successful nests were arbitrarily divided into four stages. Incubation day 1 to day 6 was specified as stage 1, day 6 to 12 stage 2, day 12 to 18 stage 3, and incubation day 18 to 24 was labelled stage 4. A multiple regression analysis was conducted using these four stages to analyze their effects on the three egg temperatures during incubation (Table 14). The stage of incubation appears to affect air cell, core, and egg shell temperatures. All of these egg temperatures increased over the course of the incubation period. It is important to point out, however, that the stage of incubation accounts for 3.7%

Table 13

Egg Temperatures before and after Recess Periods for Successful Nests*

Egg Temperature	BEFORE RECESS					AFTER RECESS			
	$\overline{X}$	Min.	Max.	s^2		$\overline{X}$	Min.	Max.	s^2
Air cell temperature	35.39	32.13	38.23	2.48		31.8	27.65	35.5	3.26
Egg core temperature	35.47	32.9	37.66	2.04		32.98	30.35	36.2	1.9

* All values in ^{O}C.

Table 14

Regression Analysis of Stage of Incubation on Egg

Temperatures

Dependent Variable : Air Cell Temperature

Independent Variable	df	F value	r	r^2
Stage of incubation	3	88.98***	.192	.037

Dependent Variable : Egg Core Temperature

Stage of Incubation	3	218.37***	.294	.087

Dependent Variable : Egg Shell Temperature

Stage of Incubation	3	195.79***	.281	.079

***$p < .0001$ N = 6824

Correlation Coefficents*

	Air Cell Temp.	Egg Core Temp.	Egg Shell Temp.
Air Cell Temp.	1.0	.8166	.5434
Egg Core Temp.	.8166	1.0	.7020
Egg Shell Temp.	.5434	.7020	1.0

* all correlations $p < .0001$

of the observed variance in egg air cell temperature, 8.7%
of the variance of egg core temperature, and 7.9% of the egg
shell temperature variance. The three F values reported in
Table 14 are indeed significant ($p < .0001$), however the re-
gression equations used account for a small amount of the
observed variance. Other factors apparently influence egg
cell, core, and egg shell temperatures during the incubation
period.

Another regression analysis was conducted on the three
egg temperatures using time of day as the independent var-
iable. The results of this analysis are presented in Table
15. It seems, due to the significant F values, that the time
of day does affect the three egg temperatures. Again, it is
important to note that time of day accounts for less than 1%
of the three egg temperatures variance. Hence, the signi-
ficant F values are a function of the large number of ob-
servations and not a meaningful indicator of the relationship
between the three egg temperatures, and the time of day.

Finally, a multiple regression analysis was conducted to
determine if there were any effects of weather variables,
nest attendance, and day of incubation on air cell, core, or
egg shell temperatures (Table 16).

The regression equation for air cell temperature accounted
for 48.5% of the observed variability. The nest variable's
unique contribution to this total was the largest at 20.6%,
approximately one-fifth of the observed variability of air
cell temperature. Nest attendance's unique contribution was

Table 15

Regression Analysis of Time of Day on Egg Temperatures

Dependent Variable : Air Cell Temperature

Independent Variable	df	F value	r	r^2
Time of Day	1	5.33*	.026	.0007

Dependent Variable : Egg Core Temperature

Time of Day	1	19.22***	.052	.0028

Dependent Variable : Egg Shell Temperature

Time of Day	1	23.58***	.058	.0034

*$p < .05$ *** $p < .0001$

Table 16

Multiple Regression Analysis of Effects of Weather Factors on
Egg Temperatures [1]

Dependent Variable : Air cell temperature

Source	df	F value	sr	sr^2
Day of incubation	1	39.48***	.058	.003
Nest	2	2408.49***	.454	.206
Attendance	1	206.01***	.132	.017
Temperature	1	74.16***	.079	.006
Humidity	1	2.39	--	--
Wind speed	1	54.48***	.068	.004
Solar radiation	1	.02	--	--
Attendance x temperature	1	10.15**	.029	.0008
Attendance x wind speed	1	4.42*	.0003	.0000

N=6025   F ratio = 708.16   p<.0001   10/6015 = df

r = .6963 r^2 = .4849

Table 16 (continued)

Dependent Variable : Egg core temperature

Source	df	F value	sr	sr^2
Day of incubation	1	542.45***	.188	.035
Nest	2	3749.47***	.494	.244
Attendance	1	102.82***	.082	.007
Temperature	1	195.69***	.113	.013
Humidity	1	1.02	--	--
Wind speed	1	77.47***	.071	.005
Solar radiation	1	19.35***	.035	.001
Temperature x solar radiation	1	12.84**	.028	.0008
Temperature x humidity	1	21.78***	.038	.0014

N=6025   F ratio = 1169.27   p<.0001   10/6015 = df

r = .78   r^2 = .6085

Table 16 (continued)

Dependent Variable : Egg shell temperature

Source	df	F value	sr	sr^2
Day of incubation	1	517.16***	.210	.044
Nest	2	1994.54***	.414	.171
Attendance	1	545.61***	.216	.046
Temperature	1	179.84***	.124	.015
Humidity	1	16.60***	.037	.0014
Wind speed	1	28.69***	.049	.0024
Solar radiation	1	20.85***	.042	.0017
Temperature x wind speed	1	16.63***	.037	.0014
Temperature x solar radiation	1	8.37**	.026	.0007

N = 6025   F ratio = 704.88 $p < .0001$ 10/6015 = df

r = .6954 r^2 = .4837

[1] Main effects and significant two-way interactions presented for successful nests.

* $p < .05$

** $p < .01$

*** $p < .0001$

1.7%. Whether the female was on or off the nest only ac-
counted for less than 2% of the observed variance in egg air
cell temperature. Humidity and solar radiation had no sig-
nificant effect on air cell temperature. No single weather
variable or interaction accounted for more than 1% of the
observed variance. Clearly, these weather variables, al-
though statistically significant, do not directly exert a
large influence on air cell temperatures.

The regression equation for egg core temperature ac-
counted for 60.8% of the observed variability in egg core
temperatures (Table 16). Again the nest variable's unique
contribution was the largest at 24.4%. In this equation the
nest variable accounted for almost one-quarter of the observed
variability in core temperature. Day of incubation accounted
for 3.5% of the variance in egg core temperature, while ambient
temperature accounted for 1.3% of the observed variance. The
only non-significant variable in this regression equation
was relative humidity. Again, the other statistically signi-
ficant variables accounted uniquely for less than 1% of the
observed variance of egg core temperature.

The regression equation for egg shell temperature ac-
counted for 48.3% of the observed variability in egg shell
temperatures (Table 16). The nest variable once again made
the largest unique contribution at 17.1%. The variable nest
attendance's unique contribution was 4.6% of the observed
variance. It is not surprising that nest attendance would
have a greater effect on egg shell temperature than on air

cell temperature or egg core temperature, since the egg shell temperature is expected to be more readily affected by female absences. Day of incubation accounted for 4.4% of the variance in shell temperatures. Ambient temperature accounted for 1.5% of the observed variability in egg shell temperatures. Again the other statistically significant variable's unique contribution, in this equation, was less than 1% of the observed variance.

Overall it can be seen that the regression equations used for egg air cell temperature and egg shell temperature accounted for approximately one half of the observed variability. The regression equation for egg core temperature, on the other hand, account for 3/5's of the observed variability. Clearly important variables have been included in these three regression equations, however other factors remain that influence egg temperatures. Some of these other possible factors are identified in the discussion section.

Egg Turning

The percentage of time each side of the five study eggs was facing up during the incubation period is presented in Table 17. The study eggs that were prepared with two "heavy sides" (Eggs A, B, and E) were expected to show an almost equal split between sides 1 and 2 facing the top of the nest during incubation. The data collected, however, does not support this expectation. Instead side 1 of eggs A and B was facing the top of the nest more than 50% of the incubation period. Eggs A and B have a very similar pattern of

Table 17

Percentage of total incubation period that each side of
the study eggs faced the top of the nest

Eggs with two heavy sides

Eggs	Side 1*	Side 2*	Side 3	Side 4
A[1]	52.82	6.02	15.34	25.83
B	58.46	5.53	14.86	21.16
E	3.23	19.79	72.54	4.39

Eggs with one heavy side

Eggs	Side 1	Side 2*	Side 3	Side 4
C	45.52	4.00	33.67	16.81
D[1]	46.67	10.59	26.08	16.67

[1] unsuccessful nest

*heavy side of egg

which side of the egg is facing up during incubation, while egg E does not follow a pattern similar to any of the other study eggs. It was assumed that eggs A, B, and E would show a similar pattern in regards to the percentage of time each side of the egg was facing the top of the nest. The reason for the discrepancy of egg E is unknown.

The study eggs which were prepared to have one "heavy side" (Eggs C and D) were expected, from the water dish trials, to have side 1 of the egg facing the top of the nest almost 100% of the time. Again, however, the data does not support this expectation. Instead sides 1 and 3 were facing the top of the nest for the largest percentage of the incubation period in both eggs C and D. Eggs C and D also show a very similar pattern of which side of the egg is facing up over the course of the incubation period.

The number of turns over the course of the incubation period, for each study egg, are presented in Table 18. A turn was classed as any time the egg rotation counter changed channels (ie. from 1 to 3, 1 to 2, 1 to 4, 2 to 4, etc.). It is possible that this data is not fully representative of true egg turning, since the egg may be turned 360°, multiples of 360°, or less than 90°, and yet the egg rotation device in these study eggs would not be able to detect this rotation. In this situation the channel closed would be the same before and after the egg had been turned.

The data in Table 18 does show a great deal of variation in the number of turns each egg received during the study

Table 18

Egg Turning Data for Each Study Egg over the Study Period

Nest	# of Turns	$\overline{X}$ time between Turns (mins.)	Range (mins.)
A*	50	142.2	(15.0-675.0)
B	367	110.96	(15.0-1515.0)
C	242	135.86	(15.0-1830.0)
D**	33	268.63	(15.0-1500.0)
E	107	286.54	(15.0-4650.0)

* 139 hrs. of data collected from Nest A. (unsuccessful nest)

** 168 hrs. of data collected from Nest D. (unsuccessful nest)

period. When we look at the successful nests with the same incubation periods (24 days for nest C and E) there is also a great deal of variation in the number of turns each egg received during this time period. It is also evident that the turning variation cannot be accounted for by simply the two different weight types of the study eggs. Study eggs B and E, although of the same weight type, do show a large difference in the number of turns they received during the incubation period.

The mean time between turns ranged from 110.96 minutes (1.8 hrs.) to 286.54 minutes (4.76 hrs.) with a mean of 188.83 minutes or 3.14 hours. The females under study turned their eggs 96.84% of the time after returning from a recess period. Although the reasons for this behavior are unclear, it may be a result of the below normal egg shell temperature coming into contact with the female's brood patch on her return. Egg turning was carried out often without the female rising from her eggs. When the behavioral observation data was compared with the egg turning data for the same time period, it was found that the study egg had been rotated without the observer being aware of it. This behavior would certainly be adaptive for the incubating female in terms of not drawing unnecessary attention through unneeded movement to her and her nest site with such a large number of avian predators in the nesting area.

Egg turning was carried out by incubating females at all hours of the day (Table 19). Of the five study nests only

Table 19

Effects of Time of Day and Stage of Incubation on Egg Turning

Nest	Time of Day x Turn (df=23)	Stage of Incubation x Turn (df = 4)	Time of Day and Stage of Incubation x Turn (df=119)
A[1]	x^2=11.3	x^2=2.21 (df=1)	x^2=27.54 (df=47)
B	x^2=27.47	x^2=2.07	x^2=61.86
C	x^2=47.56**	x^2=93.99***	x^2=72.05
D[1]	x^2=5.94	x^2=2.63 (df=1)	x^2=14.85 (df=47)
E	x^2=14.30	x^2=79.64***	x^2=59.67

** $p < .01$ *** $p < .001$

[1] Data collected for the first two stages of incubation only. (unsuccessful nests).

nest C showed a significant effect of time of day on the
number of times the study egg was turned. Nest C had two
peak time periods when the egg was turned. Turning between
06:00 and 07:00 accounted for 7.0% of the total turns and
turning between 21:00 and 23:00 accounted for 9.92% of the
total turns. No other nests showed peak times of egg turning.
Egg turning was studied further by dividing the study period
into five stages of incubation. These were : if day of in-
cubation was less than 1 (egg laying period) then stage = 1,
if day of incubation was between incubation day 1 and 7 then
stage = 2, if day of incubation was between 7 and 13 then
stage = 3, if it was between day 13 and 18 then stage = 4,
and if it was between day 18 and 24 then stage = 5. Of the
three successful nests, both nest C and E showed a significant
effect of stage of incubation on egg turning (Table 19).
Specifically, during the last stage of incubation (preceding
hatching) the amount of egg turning fell off sharply. Through-
out the four other stages of incubation the amount of egg
turning, for all the focal females, did not differ signifi-
cantly. It is not known whether stage of incubation, past
stage 2, would have affected nests A and D. Table 19 also
shows that there were no significant interactions between
time of day, stage of incubation and egg turning for any of
the five nests.

A multiple regression analysis was conducted to study
the relationships between the time between egg turns and the
following variables: egg air cell temperature, egg core

temperature, egg shell temperature, day of incubation, nest
(A - E), ambient temperature, relative humidity,wind speed,
solar radiation and all possible two way interactions of
these variables (Table 20). There were only two significant
main effects, namely, egg air cell temperature and nest. The
egg air cell temperature accounts for .6% of the observed
variance of time between egg turns, while the nest variable
accounts for 1.8% of the total variance accounted for by this
regression equation. Clearly, this suggests that individual
females turned their eggs at different rates. There were
also three significant two way interactions found. They were ;
egg air cell temperature by humidity, egg core temperature
by humidity, and an egg core temperature by solar radiation
interaction. These accounted for 1.1%, .6%, and .6%, respect-
ively of the variance accounted for in the regression equation
of time between egg turning. The equation used for this
multiple regression analysis accounted for 17.2% of the ob-
served variance in time between egg turning. Again, there
must be other factors influencing the time between egg turn-
ing.

Table 20

Multiple Regression Analysis on Time Between Egg Turns[1]

Dependent Variable : Time Between Turns

Source	df	F value	sr^2
Egg air cell temperature	1	5.05*	.006
Egg core temperature	1	2.94	--
Egg shell temperature	1	.86	--
Day of incubation	1	.18	--
Nest	4	14.16***	.018
Air temperature	1	.02	--
Humidity	1	.22	--
Wind speed	1	.18	--
Solar radiation	1	.01	--
Egg air cell temperature x humidity	1	8.63**	.011
Egg core temperature x humidity	1	5.03*	.006
Egg core temperature x solar radiation	1	4.75*	.006

*$p < .05$ **$p < .01$ ***$p < .001$

N=679; F ratio = 3.95*** at 34/645 df; r= .415, r^2 = .1724.

[1] only main effects and significant interactions are presented.

Discussion

Nest Attendance

The successful nests monitored during this study showed an average attentiveness (% of incubation period on the eggs) of 95.03% from the time the female began sitting on the eggs until they hatched. Cooper (1978), working with giant Canada geese (B. c. maxima), reported an incubation constancy of 98.5% from fifteen females. While Cooper's figure is somewhat higher than the attentiveness associated with the present study, this discrepancy could be attributable to methodological differences in data collection techniques. Cooper's (1978) data on incubation constancy was taken from fifteen females whose first nests were monitored for five days or longer. His data was not collected for the entire study period and did not include the egg laying period as did the present study. This fact alone could account for the 3% difference between these two sets of data.

The high degree of nest attentiveness found in the Canada goose and the limited time spent feeding are most likely associated with the fasting by the female during incubation. Since the arctic nesting grounds are still covered with snow when the geese arrive, they must have sufficient nutrient reserves prior to nest initiation if they are to successfully complete the incubation period. Many studies have found that arctic nesting geese are relatively heavy, have large fat reserves on arrival at the breeding grounds, and show reduced feeding during the egg laying and incubation periods (Ankney,

1977; Barry, 1962; Cooch, 1958; Hanson, 1962; Ryder, 1970).

The physiological stress of the egg laying and incubation

periods, coupled with a decreased food intake, have a detri-

mental effect on the nutrient reserves of the nesting female

goose. These effects have been found by data showing weight

loss of nesting females during the breeding season in several

species of arctic nesting geese (Ankney & MacInnes, 1978;

Barry, 1962; Cooch, 1958; Hanson, 1962; Harvey, 1971;

Ryder, 1970). Both Cooch (1958) and Harvey (1971) found that

lesser snow goose females had lost 25% of their spring weight

by the time hatching occurred. Ankney and MacInnes (1978)

showed that weight loss in nesting female lesser snow geese

resulted from use of nutrient reserves (mainly fat and pro-

tein) for egg production and incubation. The rate at which

weight loss occurs in nesting geese is related to environ-

mental conditions during the incubation period (Harvey, 1971).

Harvey (1971) stated that, "the metabolism of stored nutrients

results in weight loss, the rate being proportional to the

metabolic rate required to replace body heat lost to the en-

vironment" (p. 232). Severe weather during the nesting season

could result in a considerable weight loss to an incubating

goose and may cause the female to alter her rhythm of nest

attentiveness. Extreme weight loss during incubation can

result in the death of the incubating goose (Ankney & MacInnes,

1978; Harvey, 1971). Harvey (1971) also reported that female

lesser snow geese were accompanied by their mates if they

left their nests and were then apt to lose their nests to

parasitic jaegers and herring gulls. Since egg loss only
occurred in the absence of both geese, the jaegers and gulls
acted as scavengers rather than predators. This fact sug-
gests that there would be selective pressure favoring those
females who had sufficient nutrient reserves to maintain a
high level of nest attentiveness. It is possible that in-
sufficient nutrient reserves or periods of severe weather
could affect behavior patterns and, subsequently nesting suc-
cess of incubating geese.

The amount of nutrient reserves carried to the breeding
grounds by female geese not only plays an important role in
determining nest attentiveness during incubation, but may
also affect clutch size. Ryder (1970) hypothesized that
clutch size in arctic nesting geese has evolved in relation
to the size of the energy reserves that females carry to the
breeding grounds. In fact, Ankney and MacInnes (1978)
found that heavier female lesser snow geese laid larger
clutches than did lighter females. This result suggests that
the size of a female's clutch was determined by the size of
her nutritional reserves. The implication is that once the
female arrives on the breeding grounds a certain amount of
her nutritional reserves are required for the incubation pro-
cess. The amount of reserves remaining after this "withdrawal"
can be used for egg production and, thus, determines the
clutch size.

The observed constancy of incubation found in this study
is probably only possible in species whose young are precocial.

Once the eggs have hatched the female goose does not have to
invest large amounts of energy obtaining food for her young,
as is the case in species whose young are altricial. Instead,
the goslings follow the parents and pick up food where it is
found. Hence, the female goose can devote a large amount of
her energy to the incubation process since she need not be
in top physical condition when her goslings hatch. In addit-
ion, her mate, who is in better physical condition than she
is (Ankney & MacInnes, 1978), can defend both her and her
goslings after they hatch.

Lazarus and Inglis (1978) found that the pink-footed goose
gander had a greater parental investment (fed less and was
more vigilant) during fledging than did his mate. Presumably,
this behavior allowed the female to recover from her own
greater investment during incubation.

In the present study the individual nest attentiveness
figures ranged from 93% to 97%. While this variation does
not appear large, it should be noted that in a species where
a single parent incubates the eggs, the nest attentiveness
for the species can fluctuate widely (Breckenridge, 1956;
McCourt, Boag & Keppie, 1973; Norton, 1972; Skutch, 1962).
There is a possible explanation for this variation. In the
present study, for example, the female who took more recess
periods could have had fewer nutritional reserves. The lower
limits of incubation constancy may be set by the heat require-
ments of the developing embryo, and the upper limits of in-
cubation constancy are probably related to the internal food

reserves of the incubating female. Female B had the smallest clutch (2 eggs) as well as the lowest nest attendance (93%). Possibly the nutrient reserves of this female allowed her to lay only 2 eggs and her remaining reserves imposed the incubation schedule which was recorded.

The progressive increase in nest attentiveness during the egg laying period in this study is similar to that found by Cooper (1978) in the Canada goose as well as by Caldwell and Cornwell (1975) in the mallard and Cooper (1979) in the trumpeter swan. The data collected in the present study, however, indicated a relatively high degree of nest attendance on the day the first egg was laid. Cooper (1978) found that the Canada goose does not begin incubation at a specific time, but becomes progressively more attentive during the egg laying period. Nest attentiveness during the egg laying period may be an adaptation to protect the eggs from predators and also to protect the eggs from low temperatures which occur on arctic nesting grounds. A pattern of increased nest attentiveness during the egg laying period and a high level of attentiveness during incubation may be typical of most waterfowl (Cooper, 1979).

Recess periods were taken at all hours of the day, with an average of 2.15 recesses taken each day. Each recess averaged 20.9 minutes in length. These findings agree with those of Balham (1954), Brakhage (1965), Collias and Jahn (1959) as well as Cooper (1978). Cooper (1978) found a change in the frequency and duration of recesses in his study

while the present study found no change in the frequency and duration of recess periods. The reason for this difference in behavior may be related to climatic and photoperiod differences between northern Manitoba (present study site), and central Manitoba (Cooper's 1978 study site). Life in the almost continuous daylight of high latitudes, especially on the open tundra, exposes a bird to diurnal predators more than in lower latitudes (Armstrong, 1954). Therefore, it seems that the behavior of taking recess periods at all hours of the day by arctic nesting Canada geese has survival value.

The data from the current study showed no significant linear effects of weather, day of incubation, or hour of the day on the length of the recess periods. Cooper (1979) reported similar findings for the trumpeter swan. Both these sets of data indicate that recess length is influenced by other factors. One of these factors may be the nutritional requirements of the incubating female. As Gibb (1954) discovered in titmice, the time devoted to feeding varies inversely with body weight. It may be the case that a lighter (fewer nutritional reserves) female may have to take longer recess periods to obtain sufficient food to maintain her metabolism than would a heavier female. As Skutch (1962) stated, "these and a number of other records of incubation I have analyzed suggest some correlation between size or weight and the constancy of sitting in birds in the same family. The larger birds tend to take longer sessions and to keep their eggs covered a greater proportion of the day" (p. 132).

In the literature, one finds statements indicating no relationship between attentiveness and temperature (Davis, 1960; David, Fisler and Davis, 1963; Weeden, 1966) or an inverse relationship such that attendance decreases with increased temperature (Hann, 1937; Kendeigh, 1952; Kluijver, 1950; Lawrence, 1953; Prescott, 1964; Verner, 1965; Whitehouse & Armstrong, 1953; White & Kinney, 1974). As White and Kinney (1974) state, "the precise relationship between attentiveness and environmental temperature has remained unclear" (p. 186). The results of the present study showed that temperature, humidity, solar radiation, temperature by humidity interaction and temperature by solar radiation interaction all had a significant effect on the length of incubation sessions (time on the eggs). Incubating females seemed to respond to these factors when sitting on the eggs. The exact reasons for attending to these factors are unknown. Cooper (1979) also found that session length, in the trumpeter swan, was not significantly related to ambient temperature, solar radiation, or rainfall.

Several reports have suggested that at air temperatures near the mean egg temperatures reported by Huggins (1941), attending birds cease to incubate (Howell & Bartholomew, 1962; Ward, 1965). For some birds, attentiveness at high temperatures may take on the form of postural shading of the eggs to prevent overheating (Balham, 1954; Howell & Bartholomew, 1962). White and Kinney (1974), on the other hand, found no relationship between nest attendance and en-

vironmental temperature except at high ambient temperatures.
In the present study the ambient temperature never approached
the mean egg temperatures and yet nest attentiveness was
still affected by ambient temperature as well as by the other
weather variables mentioned previously.

It must be remembered that, when combined, the weather
variables accounted for 33.4% of the variance in incubation
session lengths. Obviously, other factors must be affecting
the length of the sessions. None of the weather factors
that had a significant influence on incubation session length
had a significant effect on recess period length.

Egg Temperatures

The mean egg air cell temperature found during this study
($\bar{x}$ = 34.45^{o}C) falls within the range reported by Huggins
(1941). Huggins (1941) found that the average incubation
temperature in nests of 37 species of 11 orders was 34.0^{o} $\pm$
2.38^{o}C. Cooper (1978) reported an average air cell tempera-
ture of 34.3^{o}C for the giant Canada geese he studied at
Marshy Point, Manitoba. In the Canada goose nest that
Huggins (1941) monitored, the average air cell temperature
was 34.8^{o}C. Kossack (1947), on the other hand, reported an
average air cell temperature of 38.5^{o}C in the Canada geese
he studied. The average air cell temperature reported by
Kossack (1947) is higher than that found in the present study
or by Cooper (1978) and Huggins (1941). Kossack's (1947)
data are not representative of an entire incubation period
since his measurements were taken in the last two weeks of

incubation. The data obtained in the present study represents the entire incubation period. The egg temperature data presented in the present study represents the temperatures of the study eggs which were shifted in the nest bowl throughout the incubation period. Since the study eggs were treated in this manner, it can be assumed that they were exposed to the different egg temperatures that have been reported between central and peripheral eggs in a nest. For example, Huggins (1941) reported an average difference of $5.6^{\circ}C$ in a clutch of mallards (Anas platyrhynchos), while Mertens (1970) found a similar gradient in a clutch of Blue Tit (Parus caeruleus). The temperature data gathered by the study eggs in this research cannot, however, take into account embryo thermogenesis in a viable egg. Drent (1970) showed that in the herring gull egg the embryonic heat production surpasses the evaporative heat loss of the egg after approximately ten days of development. Although the study eggs used in the present research could not take into account the heat produced by embryo thermogenesis, the egg temperature data gathered by the study eggs compares favorably with results obtained from viable eggs (Cooper, 1978; Huggins 1941).

The shell temperature readings taken when the egg shell thermistor was at the bottom of the nest showed a mean temperature difference of $5.71^{\circ}C$ when compared to the temperature reading taken when the egg shell thermistor was facing the incubation patch of the female. The only other documented reading of this nature on Canada goose eggs was

a reported temperature gradient of 5.6°C (Kossack, 1947).

The incubating female compensates for this thermal gradient
on the egg by turning the eggs at regular intervals. As
Chattock (1925) stated, "when an egg is turned over the
warmer upper surface goes below and the cooler under surface
comes up. The temperature of the egg is consequently more
uniform" (p. 409).

Brakhage (1965), Collias and Jahn (1959), and Kossack
(1950) all stated that in Canada geese incubation begins with
completion of the clutch. My data, however, does not fully
support this notion. This data agrees with Cooper's (1978)
data that the Canada goose does not begin incubation at a
specific time. Successful females became attentive 85.3% of
the day as soon as the first egg was laid. The second day of
egg laying the mean attentiveness represented 90.5% of the
day, while the third and fourth days of egg laying had a mean
attentiveness of 92.4% and 93.1% respectively. Cooper (1978)
also reported some females spending as much as 90% of the day
on the nest two or three days before laying the last egg.
This phenomenon makes one wonder what day incubation really
does begin? Swanberg (1950) aptly commented on this problem
when he stated, "even when the adult bird is observed sitting
on the eggs frequently, or for long periods of time, in the
egg laying period, this does not necessarily mean that the
eggs are being subjected to full incubation heat" (p. 68).
To try to solve this puzzle one must look at the records of
egg temperatures during the egg laying periods and the early

stages of incubation.

The data presented on air cell temperatures during the laying period showed a definite temperature increase as the clutch was completed (Figure 15). This phenomenon could be a result of the brood-patch defeatherization not being complete until the time the clutch is complete, as has been reported by Baldwin and Kendeigh (1932), Drent (1970) and Kossack (1947). Hanson (1959), working with Canada geese, stated that "the female goose plucks her breast chiefly as the clutch nears completion" (p. 143). Or perhaps the phenomenon is a result of increasing vascularity of the brook patch over the course of the egg laying and incubation period as has been suggested by Jones (1971)? It seems reasonable to conclude, since the nest attentiveness is realtively stable during the laying period, that the progressive increase in air cell temperature is a function of the heat source (the female's brood-patch). The data shows a substantial range in air cell temperatures during the laying period, when compared to the air cell temperature range during the incubation period. This data from nest C is representative of egg air cell temperatures from the successful nests during the entire study period. The question now arises as to whether or not the observed air cell temperatures during the laying period were high enough to allow embryonic development. Kendeigh (1963) stated, "the rate of embryonic development is proportional to the rate of energy metabolism of the embryo and this can be determined from the rate of oxygen absorption" (p. 455).

Unfortunately, no figures on oxygen absorption in Canada goose eggs were found in the literature. A great deal of work has been conducted on the domestic fowl's egg temperatures during incubation (Lundy, 1969). Lundy (1969) discovered that the optimal temperature for this species was 37-38°C and that 25-27°C was the "physiological zero temperature" at which no development occurred. This physiological zero temperature (25-27°C) cannot be applied to eggs of all species, however, since Kendeigh (1963) found the physiological zero temperature in the house wren egg to be 17.2°C. Research should be undertaken to establish the physiological zero temperature for arctic nesting geese.

There were times during the egg laying period when egg air cell temperatures surpassed the 25-27°C temperature range, and hence development probably occurred. Caldwell and Cornwell (1975) also found that in mallards periodic heating of eggs by the female during clutch formation resulted in embryos varying in stages of development. Afton (1979) also found that periodic heating of eggs by laying female northern shovellors (Anas clypeata) resulted in significant embryonic development. The present research showed that each egg in a clutch received a different amount of thermal input (above the physiological zero temperature), during the egg laying period and yet each clutch hatched within a 12 hour period.

This synchronization may be related to the factors found by Vince (1969). Hatch synchronization has an adaptive significance in species such as the Canada goose in which

the female leads the young from the nest together. She does

not return for late-hatchers which would therefore be left

behind. The fact that in this study Nest B had an incubation

period four days longer than either of the other successful

nests (28 days for Nest B vs. 24 days for Nests C and E), may

be a result of lack of inter egg communication that Vince

(1969) has shown as an important factor in the hatch synchro-

nization process. Since Nest B had only two eggs, and one

was a telemetering study egg, the viable egg would not have

received any inter egg stimulation. In fact, the single egg

in Nest B may have been ready to hatch after 24 days of in-

cubation, but the lack of normal egg stimulation may have

extended the incubation period.

The weather variables (ambient temperature, humidity,

solar radiation, wind speed and their interactions) accounted

for a very small percent of the variation in air cell, core

and egg shell temperatures. This result is not surprising

when one remembers the high degree of nest attendance during

the incubation period. Although the obtained F values for the

weather variables were statistically significant due to the

large sample size, the small amount of egg temperature var-

iance they account for questions whether these results are of

biological significance. The overall regression equations

for air cell temperature, core temperature, and shell tempera-

ture accounted for 48.4%, 60.8%, and 48.3% of the respective

observed variance. This finding indicates that there were

factors used in the regression equation that, when combined,

had a significant effect on the three egg temperatures. One
other factor that would definitely affect egg temperatures
during incubation, and was not quantified in this study, was
the insulative qualities of the nest structure. It seems
reasonable to conclude that the body temperature of the in-
cubating female, plus the nest environment, produces the re-
sulting egg temperatures needed for embryonic development.

Egg Turning

It has been found that in early incubation the yolk mass
in the egg is free to revolve within the shell. As incuba-
tion progresses, however, the extra-embryonic membranes and
shell membranes fuse. Approximately midway into incubation
embryo position is fixed in relation to the shell and the
egg becomes asymmetrical in weight (Drent, 1970; New, 1957).
Caldwell and Cornwell (1975), Drent (1970), and Lind (1961)
all found that eggs assumed a stable position in the nest as
incubation progressed. All of these researchers felt that
this stable (or mean) egg position was related to the weight
asymmetry of the egg as incubation proceeded. They also felt
that egg shifting by the incubating bird simply reduced the
friction between the eggs of a clutch and allowed each egg
to assume its characteristic position according to the location
of the centre of gravity. This approach to the study of egg
turning has been labelled the "gravitational theory" of egg
turning. The study eggs built for the present research were
constructed so that two eggs had one side of the egg weighted
heavier than the other three sides, and the three eggs had

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two sides weighted (see Figure 9). According to the gravita-
tional theory" of egg turning these heavy sides should have
been spent the majority of the incubation period facing the
bottom of the nest. The results of this study (presented in
Table 17) differ greatly from what the "gravitational theory"
would predict. The heaviest side of eggs A and C spent the
largest percentage of the incubation period facing the top of
the nest. The data collected on the gravitational influence
of egg turning in this study contradicts the data collected
by Caldwell and Cornwell (1975), Drent (1970) and Lind (1961).
The reason for these contradictory findings are unclear. It
is possible however, that the study eggs did not receive the
same egg turning "treatment" as a natural egg would have dur-
ing the incubation period.

Drent (1970) modified three herring gull eggs by cement-
ing a lead strip to one side on these eggs so that they had
a weight symmetry similar to eggs C and D of this study. He
found that at no time over his 194 observations did the lead
weighted side face the top of the nest. My data for eggs C
and D showed that the heavy sides of these two eggs faced
the top of the nest 4% and 10.6% respectively. These per-
centages were indeed the lowest of the four sides, suggesting
that there was some negative influence of weight symmetry of
the egg on egg position during incubation, but there are ob-
viously other factors involved. The shape of the nest bowl,
number of eggs in the clutch, and size of the female's brood
patch may all have an effect on the egg position over the

course of the incubation period.

It must be pointed out that the study eggs used in this research monitored only those egg turns of 90° or more. The data on the number of turns each egg received during this study (previously presented in Table 18) showed a great deal of individual variation. This variability could not be accounted for by the weight type of the study egg or the length of the incubation period. It seems that some other unknown factors must be influencing the number of times the female turns her eggs. Perhaps this egg turning behavior is a behavioral characteristic specific to individual female geese.

It was found that female geese turned their eggs 96.85% of the time after returning from a recess period. Beer (1961) working with Black-headed Gulls (Larus ridibundus) and Drent (1970) studying Herring Gulls (Larus argentatus), found that waggling was associated with every resettling on the nest. Waggling is involved when the parent drops its chest onto its eggs and moves its legs up and down and its tail from side to side (Beer, 1961, p. 68). This waggling behavior was also found to have a major effect on egg movements. Balham (1954), Collias and Jahn (1959), as well as Cooper (1978) have all reported seeing this same type of behavior pattern in female Canada geese when they resettle on their nests. It seems reasonable to assume that the resettling that took place by the female geese in this study accounted for the high rate of egg turning after a recess period.

Egg turning occurred at all hours of the day, but fell off sharply during the last stage of incubation in this study. Drent (1970) found no evidence for a change in the egg shifting behavior of the herring gull from clutch completion until the beginning of hatching. Drent (1970) felt that egg shifting ceased once the egg had begun to pip. It may be assumed that under these circumstances some stimulus from the egg (possibly the cracked egg shell) signals the female to stop egg shifting. The data on egg turning collected during this study showed that egg turning decreased in frequency before hatching started. This finding leads to the suggestion that some stimulus produced by the egg (perhaps the pipping of the gosling in the air cell) inhibits egg turning by the incubating female prior to hatching. It should also be pointed out that this speculative stimulus must function to alter the females behavior towards all the eggs in the clutch, not just the egg producing the stimulus. In other words, since the study egg could not provide a stimulus (as could a viable egg) yet received a decrease in egg turning it seems reasonable to conclude that the female was responding to some other stimulus; perhaps from the other eggs in the clutch.

It is clear from the results of the egg turning data obtained in this study that more research needs to be undertaken to gain a clearer insight into egg turning behavior.

Future Research

The results of this study revealed the scope of the incubation process in arctic nesting Canada geese. These data raise some important issues concerning the incubation process in this species.

The high degree of nest attentiveness, coupled with the adverse environmental factors that were contended with during this study, indicate that the incubation period is physically demanding on incubating female geese. It is not surprising to find reports of arctic nesting geese losing from 25 to 44% of their pre-laying body weight over the course of the incubation period (Ankney & MacInnes, 1978; Cooch, Stirrett, & Boyer, 1960; Harvey, 197; Ryder, 1970). Further research into the relationship between nest attendance and the amount of the females' nutrient reserves is needed. This information would be useful in estimating nesting capabilities and production of young.

The data indicating a high degree of nest attentiveness during the egg laying period raises another important issue in avian breeding biology. Although each egg in a clutch received a different amount of thermal input, all the eggs of a clutch hatched within 12 hours. To gain a better understanding of this process the physiological zero temperature of Canada goose eggs must be determined. Once this is known, experiments where eggs are switched from nest to nest (see Vince, 1969) in the field may provide further insight into the hatch synchronization process.

Although Drent (1973) cautioned against the use of dummy eggs for measuring temperatures, the present data compares favorably with Cooper's (1978) data which used viable eggs for the egg temperature measurements.

The egg turning data gathered in this study contradicts the results of other field studies which have looked at egg turning. A more extensive study on egg turning is certainly warranted and may help to explain and clarify the phenomenon of egg turning.

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APPENDICES

APPENDIX A: DATA SHEET USED FOR BEHAVIORAL OBSERVATIONS

ON NEST   OFF NEST

Sit.	alert	hide	rest.	nest maint.	dir. face	in H_2O	bath.	stand.	sit.	preen.	aggres.	feed

Date: _____

Nest #: _____

Time in: _____

Time out: _____

Notes:

APPENDIX B: LIGHT CONDITIONS DURING STUDY PERIOD

APPENDIX B: Light Conditions during Study Period *

Month	Day	Sunrise	Sunset	Twilight (hrs.)
May	21	0335	2051	2.1
May	22	0333	2053	2.1
May	23	0331	2055	2.2
May	24	0330	2057	2.2
May	25	0328	2059	2.2
May	26	0326	2101	2.3
May	27	0325	2102	2.3
May	28	0323	2104	2.3
May	29	0322	2106	2.3
May	30	0321	2108	2.4
May	31	0319	2110	2.4
June	1	0318	2111	2.4
June	2	0316	2113	2.5
June	3	0315	2115	2.5
June	4	0314	2116	2.5
June	5	0313	2118	2.6
June	6	0312	2119	2.6
June	7	0311	2120	2.7
June	8	0309	2123	2.7
June	9	0308	2123	2.7
June	10	0307	2125	2.8
June	11	0306	2125	2.9
June	12	0305	2126	2.9

APPENDIX B CONTINUED

Month	Day	Sunrise	Sunset	Twilight (hrs.)
June	13	0305	2127	2.9
June	14	0304	2128	2.9
June	15	0304	2128	2.9
June	16	0304	2129	2.9
June	17	0304	2130	2.9
June	18	0304	2130	2.9
June	19	0304	2131	2.9
June	20	0304	2131	2.9
June	21	0304	2131	2.9
June	22	0304	2131	2.9
June	23	0305	2131	2.9
June	24	0305	2131	2.9
June	25	0305	2131	2.9
June	26	0306	2131	2.9
June	27	0306	2131	2.9
June	28	0307	2131	2.9

* This data from Churchill Meteoroligical Station, Churchill, Manitoba.