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Thermal aspects of the reproductive ecology of the Double-crested Cormorant (Phalacrocorax auritus) in southern Alberta

by

ⓒ William James Van Scheik

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Thermal aspects of the reproductive ecology of the Double-crested Cormorant (Phalacrocorax auritus) in southern Alberta submitted by William James Van Scheik in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Vic Lewin
Supervisor

Fred C. Zwickel

External Examiner

Date Aug. 15, 1985

Dedication

To my wife, Joyce, for her great capacity to tolerate me and my endeavors, for her unfailing encouragement and willingness to help in every way she could; and to my sons, Bill and Rick, who willingly assisted in the field work and put up with my absence, this thesis is gratefully dedicated.

Abstract

The response of the eggs and nestlings of Double-crested Cormorants (Phalacrocorax auritus) to their thermal environment was studied in their natural environment and under laboratory conditions. The colony studied was located at Scope Reservoir 17 km east of Vauxhall, Alberta. Data were gathered in May, June and July of the 1982, 1983 and 1984 nesting seasons. Behavior of nesting adults was recorded by video camera and temperature data were obtained by radio telemetry. Results were interpreted in terms of the viability of embryos and nestlings under varying exposures to ambient and experimental conditions.

Embryos were very cold tolerant with 90% survival after eggs were exposed to 0.5°C. Internal egg temperatures of 41.5°C caused 33% embryo mortality while those of 42.2°C caused 50% mortality. Incubation temperatures varied with the number of eggs present. Incubation begins gradually during laying and does not reach its maximum intensity until the clutch is completed. The hatch spans fewer days than does the laying period.

A video camera was used to determine how cormorants incubate their eggs. Eggs were loaded onto the warm totipalmate feet with the abdomen and breast then lowered onto the eggs. Measurements of feet and egg area indicate that the feet are able to accommodate the average clutch (3.53 eggs) with ease.

Nestlings less than 10 days old cooled rapidly and became comatose at 12 to 19°C, but quickly revived with passive warming with no apparent harm. Deep body cooling below 11.5°C resulted in death. Nestlings exposed to direct solar insolation heated rapidly. Attempts to thermoregulate by gular fluttering did not prevent hyperthermia and death occurred if the deep body temperature exeeded 45.7°C. Temperature correlated behaviors are defined and described.

Adult cormorants utilize a variety of behaviors to stabilize the thermal environment of eggs and nestlings and minimize thermal stress on themselves. Gular flutter may occur at any time during incubation or brooding even though there is no evidence of thermal stress. Gular flutter rates ranged from 450 to 540/min. Increasing heat loads caused an increase in the amount of flaring of the hyoid apparatus rather than an increased rate of flutter. Adults, while incubating and brooding, favored a tail-to-wind or tail-to-sun position over other positions.

The structure of the Double-crested Cormorant eggshell is different from that of most bird species in that it lacks a cuticle and has a covering layer of calcite 20 to 80 microns thick. This layer obscures the pigmented true shell and causes it to heat faster and cool at a slower rate than shells without such a cover.

Studies of the blue shell pigment by absorbance and excitation spectroscopy disclosed low absorbance at all wavelengths above 300 nanometres. Excitation at 280 nanometres resulted in weak fluorescence at 330 nanometres. The function of the eggshell pigments remains unclear since no thermal or cryptic value can be ascribed to it. Some cryptic coloration is provided by smeared defecation of the Western Hen Flea (*Ceratophyllus niger*). The function of the blue eggshell pigment, largely obscured either by the calcite layer or by flea defecation, may be lost in the evolutionary history of the species.

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Table of Contents

List of Tables

List of Figures

I. Introduction

Background

The "climate space" within which birds must function thermodynamically consists of at least four factors: radiation, humidity, air velocity, and air temperature (Porter and Gates 1969, Gates 1970). Although these environmental conditions may vary widely, adult birds normally can thermoregulate and maintain body temperatures within limits compatible with their modes of existence. While some species can adapt to environmental extremes by brief forays into hypothermia or hyperthermia, homeostasis usually is maintained by an integration of physiological and behavioral adjustments.

Eggs and nestlings are less able to cope with the vagaries of the environment than are adults. Eggs must be incubated for embryonic development to proceed and nestlings of most species, especially those classified as altricial, must be brooded periodically until homeothermy is established. The time between the laying of eggs and the age at which homeothermy is established constitutes a period of thermal vulnerability for the developing embryo or nestling.

Double-crested Cormorants (*Phalacrocorax auritus*), as with other members of the Pelecaniformes, lack brood patches. Clearly, some pelecaniform birds incubate by foot contact with eggs as seen in the Northern Gannet, *Morus* bassanus (Nelson 1966); in others, such as tropic birds (Phaethon rubricauda) and boobies (Sula sula), the feet do not provide the main source of heat (Howell and Bartholomew 1962). The totipalmate foot, however, does increase the area potentially available for incubation, and may, along with behavioral and physiological adaptions, provide the necessary thermal environment that allows Double-crested Cormorants to successfully exploit Alberta at both the northern and western limits of the midcontinental breeding range.

Double-crested Cormorants were declared to be an "endangered" species in 1977 by the Alberta Wildlife Act and, subsequently, a plan for the habitat management and protection of the species was proposed (Brechtel 1981). Initial research, directed toward documenting reproductive success, general reproductive ecology, and response to human disturbance, was conducted on colonies in southern Alberta (Brechtel 1983). Recreational use of nesting areas and active management programs cause disturbances in the nesting colonies with resultant losses in reproductive success. While some loss is probably unavoidable, a more complete understanding of the factors limiting survival are important to successful management of the species. Of the limiting factors, thermal stress must be considered of major potential importance, both in the management of this species and others such as White Pelicans (Pelecanus erythrorhynchus), which have similar general reproductive strategies and limitations.

The physiological, behavioral, and morphological thermal adaptations of the eggs, nestlings and adult Double-crested Cormorants are the subject of this research. Specifically, this research is directed toward answering the following questions:

1. What is the normal thermal environment of Double-crested Cormorant eggs in the nest and to what limits can eggs be stressed and remain viable?

2. What is the normal thermal environment of nestlings and to what limits can they be stressed?

3. How is adult behavior, physiology, and morphology related to the maintenance of an optimal thermal environment for eggs and nestlings?

4. What is the thermal significance of shell pigmentation and structure?

The species

Of the Pelecaniformes, the family Phalacrocoracidae, long-necked, long-billed, diving birds, contains some 30 species worldwide, six of which live along the sea coasts or on inland lakes and rivers in North America. The

Double-crested Cormorant is the most widely distributed of the North American species with a breeding range extending from Alaska to the Baja Peninsula on the west, Newfoundland to Florida on the east, along the Gulf Coast to Mexico, and inland throughout the prairie provinces and Great Lakes region (Palmer 1962). In Alberta, it reaches the northern and western limits of its midcontinent breeding range (Brechtel 1983). P. a. auritus, the only subspecies exploiting the interior of the continent, is migratory and winters primarily along the Gulf Coast.

Breeding Double-crested Cormorants nest in colonies of a few birds to several thousand pairs. Nests are located in trees, on cliff faces or on the ground on islands, usually in association with other colonial nesting species. Nests in southern Alberta are an aggregation of coarse sticks and other available material about 60 cm high and 60 cm in diameter. A clutch of one to five chalky pale blue eggs is laid in late April or early May at a rate of one egg every two days (Robertson 1971, Brechtel 1983). The hatch is asynchronous, spanning six days of an average incubation period of 27.2 days (Brechtel 1983). Nestlings are naked, blind, and have very limited abilities to thermoregulate.

Previous research

The first intensive studies of the Double-crested Cormorant were undertaken by Lewis (1929) and Mendall (1936) and concerned the ecology and distribution of the species, primarily on the Atlantic coast. Later, reproductive parameters of the species on the west coast were studied by van Tets (1959, 1965), Robertson (1971), and van de Veen (1973). Midcontintent populations have been less studied until recently. Mitchell (1977) studied the breeding biology of two colonies in Utah, and Vermeer (1969a, 1969b, 1969c, 1970a, 1970b, 1970c, 1973) established the population status in the prairie provinces of Canada. Population changes in this region have been documented by Weseloh et al. (1977), Markham and Brechtel (1978), and Brechtel (1981). Most recently, Brechtel (1983) described the reproductive ecology of this species in southern Alberta.

In spite of their wide distribution, until recently cormorants have attracted little attention in avian research other than ecologic and demographic. Drent (1975), in his broad review of incubation, notes that birds which incubate without obvious brood patches present a puzzle which defies the generalizations made for other birds. He further notes that some Pelecaniformes use their feet as the primary source of heat for incubation but that in other cases the feet are not used.

The question of energetics, endothermy, and development has received considerable attention. Dunn (1975a, 1975b, 1976) describes the development of thermoregulation and energy requirements in Double-crested Cormorants and other altricial birds, as do Calder and King (1974), primarily under laboratory conditions. Responses to high temperature in nestling Double-crested and Pelagic Cormorants (P. pelagicus) were described by Lasiewski and Snyder (1969). Their study involved nestlings 3.5 or more weeks of age--well beyond the age of established endothermy found by Dunn (1976). The response of nestling Double-crested Cormorants to thermal stress from hatching to the age of endothermy has not been described to date.

A number of studies on other species relevant to the question of thermoregulation and thermotolerances have been done, possibly as a result of the early work of Scholander et al. (1950a, 1950b, 1950c). Bartholomew and Dawson (1952, 1954) described body temperatures and temperature regulation in young pelicans (Pelecanus occidentalis), herons (Ardea herodias), and gulls (Laris occidentalis). Evans (1984) described the development of thermoregulation in young White Pelicans (Pelecanus erythrorhynchos) in Manitoba. Clark and Balda (1981) conducted stress tests on nesting Piñon Jays (Gymnorhinus cyanocophalus) and found that endothermic response was related to brood size; i.e., broods handled stress better than individuals.

Several studies on Larid Gulls concerning the physiological response of embryos to temperature have been conducted, including those on Heermann's Gull, Larus heermannis (Bennett and Dawson 1979) and Western Gulls, Larus occidentalis (Bennett et al. 1981). In these studies, heart rate varied directly with temperature and ceased at temperatures above and below normal incubation ranges. Warming of cooled embryos caused a spontaneous resumption of heart activity, but heat-stressed embryos experiencing heart failure did not respond to cooling. Unbrooded nestling Western Gulls were very cold hardy and became comatose when body temperatures fell to 14 to 16°C, but recovered completely by passive warming (Dawson and Bennett 1981). Cold hardiness of young showed a high correlation with the range of ten species of European ducks (Koskimies and Lahti 1964).

The relation of solar insolation to the thermoregulation of ectothermic vertebrates has been described (Heath 1970) but its relevance and importance to endotherms has been largely overlooked (Hennemann 1983). Solar insolation can act as a source of energy reducing the cost of thermoregulation but at high ambient temperatures can be a source of stress, particularly for exposed eggs and nestlings which have limited abilities to thermoregulate. Nestlings of White Pelicans die from overheating (Bartholomew et al. 1953) as do cormorant nestlings (Brechtel pers com).

While there is no universal incubation temperature, internal egg temperatures of most species range from 34 to 39°C, with lower temperatures slowing development (Drent 1975, Wheelwright and Boersma 1979). Temperatures above this range bring the embryo close to the limits of its ability to survive. Eggs exposed to direct solar insolation may be cooled by incubation (Walsberg and Voss-Roberts 1983, Grant 1982) or may possess shell qualities such as pigments which have high infrared reflectance that contribute to heat unloading (Bakken et al. 1978). Why the eggs of large birds, such as cormorants and herons whose nests are exposed, are blue, or for that matter, pigmented at all, is not clear.

Behavorial thermoregulation as it relates to several species of Charadriiformes has been described by Grant (1982). Although Yamamoto (1967) and Jefford and Urban (1972) describe behavior relevant to cooling of nestling cormorants, no studies describing adult behavior with reference to thermal aspects of nesting ecology per se have been conducted to date.

Literature Cited

Bakken, G. S., V. C. Vanderbilt, W. A. Buttemer and W. R. Dawson. 1978. Avian eggs: thermoregulatory value of very high near-infrared reflectance. Science 200: 321-323.

Bartholomew, G. A., and W. R. Dawson. 1952. Body temperature in nestling Western Gulls. Condor 54: 58-60.

Bartholomew, G. A. and W. R. Dawson. 1954. Temperature regulation in young pelicans, herons and gulls. Ecology 35: 466-472.

Bartholomew, G. A., W. R. Dawson and E. J. O'Neill. 1953. A field study of temperature regulation in young White Pelicans, Pelecanus erythrorhynchos. Ecology 34: 554-560.

Bennett, A. F. and W. R. Dawson. 1979. Physiological responses of embryonic Heermann's Gulls to temperature. Physiol. Zool. 52(4): 413-421.

Bennett, A. F., W. R. Dawson and R. W. Putnam. 1981. Thermal environment and tolerance of embryonic Western Gulls. Physiol. Zool. 54: 146-154.

Brechtel, S. H. 1981. The White Pelican, Double-crested Cormorant and Great Blue Heron in Alberta - 1980 Unpubl. Report. Alberta Dept. of Energy and Natural Resources, Fish and Wildlife Division. Edmonton, Alberta.

Brechtel, S. H. 1983. The reproductive ecology of Double-crested Cormorants in southern Alberta. M.Sc. Thesis, Univ. of Alberta, Edmonton, Alberta. 119 pp.

Calder, W. A. and J. R. King. 1974. Thermal and caloric relations of birds. In Avian Biology, Vol. 4. Farner, D. S., and J. R. King eds. Academic Press, New York, N.Y. pp. 259-413.

Clark, L. and R. P. Balda. 1981. The development of effective endothermy and homeothermy by nestling Piñon Jays. Auk 98(3): 615-619.

Dawson, W. R. and A. F. Bennett. 1981. Field and laboratory studies of the thermal relations of hatchling Western Gulls. Physiol. Zool. 54(1): 155-164.

Drent, R. H. 1975. Incubation. In Avian Biology, Vol. 5. Farner, D. S. and J. R. King eds. Academic Press, New York, N.Y. pp. 333-420.

Dunn, E. H. 1975a. The timing of endothermy in the development of altricial birds. Condor 77: 288-293.

Dunn, E. H. 1975b. Growth, body components and energy content of nestling Double-crested Cormorants. Condor 77: 431-438.

Dunn, E. H. 1976. Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. Condor 78: 350-356.

Evans, R. M. 1984. Development of thermoregulation in young White Pelicans. Can. J. Zool. 62: 808-813.

Gates, D. M. 1970. Animal climates (Where animals must live). Environ. Res. 3: 132-144.

Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30, Amer. Ornithol. Union.

Heath, J. E. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. Condor 72: 50-59.

Hennemann, W. W. 1983. Environmental influences on the energetics and behavior of Anhingas and Double-crested Cormorants. Physiol. Zool. 56(2): 201-216.

Howell, T. R. and G. A. Bartholomew. 1962. Temperature regulation in the Red-tailed Tropic Bird and the Red-footed Booby. Condor 64: 6-18.

Jefford, T. G and E. K. Urban. 1972. Behavioural responses to temperature in cormorants (*Phalacrocorax carbo lucidus*) from Lake Shala, Ethiopia. Proc. 15th Internat. Orn. Congr. 1970: 656-657.

Koskimies, J. and L. Lahti. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81: 281-307.

Lasiewski, R. C. and G. K. Snyder. 1969. Responses to high temperature in nestling Double-crested Cormorants and Pelagic Cormorants. Auk 86: 529-540.

Lewis, H. F. 1929. The natural history of the Double-crested Cormorant (Phalacrocorax auritus auritus [Lesson]). (Cornell University, Ithaca, N.Y., Ph.D. Thesis) Ru-Mi-Lou Books, Ottawa, Ontario.

Markham, B. and S. Brechtel. 1978. Status and management of three colonial waterbird species in Alberta. Proc. 1978 Conf. of the Colonial Waterbird Group, New York, N.Y.: 55-64.

Mendall, H. L. 1936. The home life and economic status of the Double-crested Cormorant. University Press, Orono, Maine.

Mitchell, R. M. 1977. Breeding biology of the Double-crested Cormorant on Utah Lake. The Great Basin Naturalist 37(1): 1-23.

Nelson, J. B. 1966. The breeding biology of the Gannet, Sula bassana on the Bass Rock, Scotland. Ibis 108: 584-626.

Palmer, R. S. 1962. Handbook of North American Birds, Vol. 1. Yale University Press.

Porter, W. P. and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39: 227-244.

Robertson, I. 1971. The influence of brood size on reproductive success in two species of cormorant, Phalacrocorax auritus and P. pelagicus, and its relation to the problem of clutch size. M.Sc. Thesis, Univ. of B.C., Vancouver, B.C.

Scholander, P. F., V. Walters, R. Hock and L. Irving. 1950a. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99: 225-236.

Scholander, P. F., R. Hock, V. Walters, F. Johnson and L. Irving. 1950b. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99: 237-258.

Scholander, P. F., R. Hock, V. Walters and L. Irving. 1950c. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99: 259-271.

van de Veen, H. E. 1973. Breeding biology and demography of the Double-crested Cormorant. Ph.D. Thesis, Univ. Groningen, Holland.

van Tets, G. F. 1959. A comparative study of the reproductive behavior and natural history of three sympatric species of cormorants, (Phalacrocorax auritus, P. penicillatus, and P. pelagicus) at Mandarte Island, B.C. M.A. Thesis, Univ. of B.C., Vancouver, B.C.

van Tets, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithol. Monogr. 2, Amer. Ornithol. Union.

Vermeer, K. 1969a. Colonies of Double-crested Cormorants and White Pelicans in Alberta. Can. Field-Nat. 83: 36-39.

Vermeer, K. 1969b. Some aspects of the breeding chronology of Double-crested Cormorants at Lake Newell, Alberta. Murrelet 50: 19-20.

Vermeer, K. 1969c. The present status of Double-crested Cormorant colonies in Manitoba. Blue Jay 27: 217-220.

Vermeer, K. 1970a. Arrival and clutch initiation of Double-crested Cormorants at Lake Newell, Alberta. Blue Jay 28: 124-125.

Vermeer, K. 1970b. Colonies of Double-crested Cormorants and White Pelicans in Saskatchewan. Can. Field-Nat. 84: 39-42.

Vermeer, K. 1970c. Some aspects of the nesting of Double-crested Cormorants at Cypress Lake, Saskatchewan, in 1969; a plea for protection. Blue Jay 28: 11-13.

Vermeer, K. 1973. Great Blue Heron and Double-crested Cormorant colonies in the prairie provinces. Can. Field-Nat. 87: 427-432.

Walsberg, G. E. and K. A. Voss-Roberts. 1983. Incubation in desert-nesting doves: mechanisms for egg cooling. Physiol. Zool. 56(1): 88-93.

Weseloh, D. V., S. Brechtel and R. D. Burns. 1977. Recent population changes in Double-crested Cormorants and California and Ring-billed Gulls in Alberta, Canada, with a note on White Pelicans. Proceedings 1977 Conf. of the Colonial Waterbird Group, DeKalb, Illinois: 10-18.

Wheelwright, N. T. and P. D. Boersma. 1979. Egg Chilling and the thermal environment of the Fork-tailed Storm Petrel (Oceanodroma furcata) nest. Physiol. Zool.

52(2): 231-239.

Yamamoto, H. 1967. Phalacrocorax capillatus as a breeding bird on Iwate coast, Honshiu. Misc. Rep. Yamashina Inst. Ornithol. 5: 48-60.

II. Egg incubation and thermal tolerance in Double-crested Cormorants in southern Alberta

Introduction

Successful incubation requires that egg temperatures be maintained within the viable limits of the embryo under highly variable and potentially thermally stressful environmental conditions. Adaptive parental behaviors protect embryos from predators and may moderate the effects of other factors such as hatch asynchrony. Integration of data gathered from both the physiological tolerances of the embryo and adaptive behaviors of parents should broaden our understanding of avian incubation and provide a basis for management of particular species.

The concept that once incubation has started egg temperatures remain constant or at least vary within narrow limits is changing. Recent studies indicate that in some species embryos tolerate temperatures well below levels where development occurs. While embryonic development is arrested below "physiological zero" (25 to 27°C), successful hatching eventually occurs if incubation temperatures are held between this temperature and the optimal temperature (Matthews 1954, Spellerberg 1969, Boersma and Wheelwright 1979, Vleck and Kenagy 1980, Zerba and Morton 1983, Roby and Ricklefs 1984). Embryos may remain viable for moderate periods of exposure to temperatures slightly below 0°C, although abnormal development may result if ice crystals form (Drent 1975). Small increases in internal temperature above 42°C bring embryos to the limit of their ability to survive. Where the possibility of overheating exists, thermoregulatory behavior by parents, such as shading (Howell and Bartholomew 1962), incubation (Grant 1982, Walsberg and Voss-Roberts 1983), or wetting of the eggs (Yom-Tov et al. 1978, Grant 1982), is necessary to ensure survival.

Double-crested Cormorants (Phalacrocorax auritus) nesting in southern Alberta, near the northern and western limits of their midcontinental range, initiate clutches in late April or early May when ambient temperatures may fall as low as -11.7°C at night. During the day in late May and early June, ambient temperatures of 25 to 30°C are not uncommon and eggs exposed to direct solar radiation may reach temperatures lethal to embryos. Although a parent is ordinarily in attendance at the nest at all times, disturbance associated with recreation, wildlife management, or predation may expose embryos to thermal stress. Cormorant nests in southern Alberta consist of a loose aggregation of sticks up to 50 cm high, depending on the number of seasons the nest has been used. The shallow cup in the top of the nest offers little or no protection from sun and wind.

In this paper, I examine the normal thermal environment of Double-crested Cormorant eggs and the tolerance to thermal stress by embryos.

Study area and methods

The colonies studied in May and June of 1982, 1983, and 1984 consisted of approximately 250 nests situated on three islands in Scope Reservoir, an irrigation reservoir located 17 km east of Vauxhall, Alberta, 50.6°N, 111.9°W (Figure II-1). Dominant vegetation, as described by Brechtel (1983), included burning bush (Kochia scoparia) and lambs quarters (Chenopodium album), with lower areas containing cocklebur (Xanthium ilalicum), spike rush (Eleocharis palustris), and water smartweed (Polygonum coccineum). Nests here are directly exposed to the effects of sun and wind. Meteorological data were obtained from the Agriculture Research Station, Vauxhall, Alberta.

Incubation and egg temperature

Since ambient temperatures fluctuate over a range of up to 40°C during the time eggs are in the nest, an effort was made to estimate egg temperatures over that time.

Model eggs were prepared by sawing around the small end of freshly laid eggs with a fine hacksaw to the membrane which was then cut with a scalpel. The contents were removed and a transmitter (Mini-Mitter Model V, Mini-Mitter

Co. Inc., Box 3386, Sunriver, Oregon 97702) was suspended in the shell in a 1.5 g/100 ml agar solution. The transmitters (diameter 12 mm, length 19 mm) broadcast pulsed data in the AM band with a transmission range of up to one meter. Transmitters were sealed in their plastic capsules with wax prior to being placed in the eggs. The small end of the eggshell was reattached by quick-setting epoxy after being filled with agar.

A comparison of the thermal response of model eggs and fresh eggs with a YSI (Yellow Springs Instrument Co., Yellow Springs, OH 45387) probe inserted to the center indicated that model eggs took slightly longer (two to four minutes) to equilibrate (Figure II-2). Temperatures of the model eggs and those obtained with the YSI telethermometer agreed within ±.2° at equilibrum.

Model eggs were substituted for an egg in naturally occurring one-, two-, three-, and four-egg nests over the duration of the incubation phase of nesting. Artificially enlarged clutches also were monitored by replacing the egg in one-egg nests with a model egg and adding eggs as necessary to make two-, three-, and four-egg clutches. A loop antenna around each nest containing a model egg detected and carried the transmitted signals to a Realistic Minisette 10 (Radio Shack) radio cassette recorder activated by an electronic timer switch (see Appendix) which turned the system on for 15 seconds every 14 minutes (Figure II-3).

The short broadcast range of the transmitters and the loop antennas around each nest containing a transmitter allowed nests being monitored to be within two meters of one another without interference.

Since Double-crested Cormorants have no brood patches, the means by which eggs are incubated is uncertain. A variety of opinions exist as to when incubation starts (Brechtel 1983, Mitchell 1977, Mendall 1936, Lewis 1929). To answer these questions and to provide behavioral data to correlate with telemetry data, a video camera and cassette recorder (Sears Model 30133D) were positioned in the colony to monitor events at nests containing model eggs for four and one-half hours during the day. A nest with a transparent bottom was substituted for an active nest containing eggs. A mirror allowed video recordings to be taken through the bottom of the nest (Figure II-4).

Cormorants forage in water which at the beginning of incubation may be substantially below body temperature, ranging from 0 to 10°C. The bare legs and totipalmate feet may be a source of heat loss while in water, or they could be a source of heat during incubation. This mechanism, if such exists, which prevents significant heat loss through the feet and legs of adults while in water and also facilitates heat transfer during incubation, has not been investigated.

To determine the potential of the feet as a possible heat source for incubation, an incubating adult was trapped at a nest. Cutaneous temperatures at several locations on the feet and legs (Figure II-5), deep body temperature (12 cm cloacally), and the cutaneous temperature of the abdomen just posterior to the sternum, were measured.

The foot area of the adult was determined by tracing around a foot on graph paper and this was compared to the longitudinal area of an average cormorant egg.

To determine the ability of embryos to tolerate both heat and cold stress, 152 eggs were gathered May 10, 1982, eight days after the first eggs were observed in the colony. Whole clutches of four eggs were taken to provide a sample of embryos at different developmental stages to that date. Groups (12 to 16 eggs) made up of whole clutches were stressed in stress chambers at temperatures ranging from -11 to 55°C. One egg of each group was used to obtain internal temperature by inserting a telethermometer probe. After seven days incubation at 37°C and 60% relative humidity, the eggs were opened to determine if the embryos were alive. Embryos were measured and compared to those of known age. Infertile eggs were excluded from the results.

The rate at which cormorant eggs heat and cool was determined by inserting a YSI probe into the middle of an egg and securing it with epoxy. These eggs were then exposed to ambient conditions in a nest which had been removed from the colony.

Results

Temperature of eggs in nests

Cormorants accepted and incubated model eggs without hesitation and were tolerant of considerable manipulation of the nest itself as long as it was not moved in relation to neighboring nests.

During the incubation period of May 4 through June 9 of the 1982, 1983, and 1984 nesting seasons, air temperatures ranged from -8 to 31.5°C. Model egg temperatures incubated in nests over the same period ranged from 6.4 to 37.4°C. For 27 nests containing one to four eggs, the correlation between the number of eggs in the nest and the average incubation temperature was positive and significant ($r = .712$, $p < .01$). One- and two-egg clutches, though not significantly different from each other, were significantly colder than three- and four-egg clutches ($p < .001$ t-test). Three- and four-egg clutches were not significantly different from one another. Table II-1 compares mean egg temperatures and numbers of eggs in the clutch. These data are taken from 27 nests and represent a total of 577 hours of monitoring time.

Artificially enlarging clutches did not alter the incubation temperatures as compared to one-egg nests. The sudden appearance of eggs in the nest did not stimulate incubation activity but instead egg temperatures declined as the number of eggs increased. Although egg temperatures were negatively correlated with clutch size in the 21 artificially enlarged clutches ($r = -.33$, $p > .05$), there were no significant differences among average temperatures in one-, two-, three-, and four-egg clutches as indicated in Table II-1.

Embryo viability

Exposure to temperatures above or below optimal incubation temperature poses a potential threat to embryo survival. Embryos survived when internal temperatures fell to below freezing if the exposure was not prolonged (Table II-2). Approximately 90% of the embryos survived internal temperatures of 0.5°C, while about 79% survived a 1.5 hour exposure to internal temperatures of -3.5°C. The effects of thermal stress above normal incubation temperatures were more immediately lethal. Internal temperatures of 41.5°C were sufficient to cause embryo mortality of 33%, while a temperature of 48.5°C caused 100% mortality.

Tolerance to thermal stress, according to Drent (1975), decreases with age. The age of dead experimental embryos was determined by comparison to a developmental series of embryonic cormorants (Table II-3). Of the 113 embryos stressed at sublethal temperatures (temperatures at which some embryos survived), 33 were considered to be at less than five days incubation, and of these, 17 (51.5%) died. Only 11.25% of embryos at more than six days incubation died

(Table II-4).

Heating and cooling rates of exposed eggs

Eggs in nests exposed to solar radiation gained a significant amount of heat and internal egg temperatures rose rapidly. Figure II-6 shows a typical heating pattern of an exposed egg. The rate of temperature rise varied with environmental conditions (wind, cloud, humidity) and sun angle. Heating rates ranged in six trials under varying conditions from .36°C/min to .04°C/min.

An egg cooling rate of 0.59°C/1°h^{-1} was calculated for seven eggs exposed in cormorant nests. Eggs used were in early developmental stages, i.e. one week or less since laying. Embryonic heat production can be considered to be insignificant at that stage. The cooling curve shown in Figure II-7 is typical for exposed eggs on a day with scattered cloud cover.

Incubation potential of cormorant feet

Video data obtained through the bottom of nests and by observation of incubating parents reveals that cormorants incubate with various intensities and modes. In the full incubation mode, eggs are loaded on the tops of the feet. The breast and abdomen are then pressed on to the eggs. Less intense modes involve contact with only the breast, abdomen or feet.

The total surface area of the feet of the trapped adult male was 123 cm^2. A cormorant egg of average dimensions (length 61.19 mm, SD 2.77, n = 66; width 38.60 mm, SD 1.12, n = 66) has a longitudinal area through the center of approximately 19.2 cm^2. Clutch size ranges from one to six with an overall mean of 3.53 eggs (Brechtel 1983). Four eggs can, therefore, be positioned on the feet with little trouble. Data obtained with the video system reveals that the eggs are usually in contact with the feet, though not fully resting on them at all times. Active loading of eggs on to the top of the feet increases in frequency as eggs are added to the clutch and corresponds to a rise in egg temperature of 3.5°C by the time the clutch is completed (Table II-1).

Although the deep body temperature of an adult male Double-crested Cormorant was close to 42°C, the temperature of the feet and unfeathered portion of the leg decreased as the distance from the body core increased. The summary presented in Table II-5 suggests that a counter current exchange mechanism prevents excessive heat loss from the feet. Such a mechanism would allow for gradual warming of the feet when the thermal gradient was small, as is the case when the bird is incubating.

Discussion

Double-crested Cormorants in southern Alberta lay their eggs in May and incubate them when ambient temperatures may fluctuate between -11.7 and 34°C (Environment Canada 1981). Cormorant eggs can tolerate exposure to temperatures below freezing but embryo mortality increases sharply if internal temperatures remain below 0°C for extended periods. Although ambient temperatures do fall below the freezing point during the incubation period, internal temperatures of model eggs in actively incubated nests never fell below 6°C. Periods of depressed temperature were brief with minimum temperatures persisting for short periods (15 minutes or less) (Figure II-8). Only in one-egg clutches did egg temperatures fall below the minimum temperature required for development (about 27°C) for several hours.

Brechtel (1983) noted that each successive egg spends less time in the nest and although the first egg laid hatches first, the hatch overall is markedly asynchronous spanning at least six days for a clutch laid over an eight day period. The time between hatching of the first and last eggs in a five-egg clutch is on the average two days less than the time between laying of the first and last eggs. Asynchrony of hatch has generally been regarded as a factor limiting fledging success. Older nestlings tend to outcompete their younger siblings for parental feedings with the result that younger nestlings often starve or are trampled in the nest. The effect on younger nestlings is more pronounced as the age difference increases (Mitchell 1977, Des Granges 1982, Zach 1982).

Normally, one adult cormorant is attendant at the nest at all times, protecting and covering the eggs. As shown in Figure II-8, the constancy of the incubation effort increases with the number of eggs in the nest. For one-egg nests, the average incubation temperature was 30.86°C, however, for much of the time, the egg temperature was well below 27°C, the point at which development stops (Drent 1975). As the number of eggs increased, so did the average incubation temperature (Table II-1). Brechtel (1983) suggested that partial incubation may begin after the first egg was laid. The data presented here confirm that suggestion. The shorter time spread of the hatch as compared to the laying period may be due to a combination of effects. Egg size decreases as laying proceeds, with the fourth and fifth eggs in a clutch of five being significantly smaller than the others (Brechtel 1983). Small eggs generally have shorter incubation periods (Parsons 1975). Since full incubation; i.e., constant incubation temperature, is maintained before the last two eggs are laid, the rate of development of these eggs would be faster (Keen and Parker 1979).

Parental incubation behavior as observed by the video technique suggests that parents respond differently to the presence of one, two, and three or more eggs. When a single egg is present, the incubating bird maintains only casual contact with it. The egg, though covered, is probably not kept in contact with the feet, and since cormorants lack brood patches, internal temperature of the egg is low. Maintaining eggs below the minimum temperature at which development occurs would be one method of delaying development and reducing hatch asynchrony. With two eggs in the nest, internal egg temperatures average 32.59°C (n = 9), possibly due to increased incubation effort by the parent resulting in more egg contact with the feet. After the third egg was laid, incubating birds were observed to actively load eggs on to the tops of their feet more frequently and appeared to press them close to their feathered breasts. The internal temperature of eggs at this stage is maintained at an average temperature of 36.04°C (n = 5).

The shape and size of the totipalmate feet could permit the loading of up to six eggs on the top surface. In practice, however, the problems associated with close packing elliptical solids probably limits effective contact between feet and eggs to four eggs at any given time. Heat exchange can occur between eggs and between breast and belly feathers even if eggs are not in contact with the feet. Whether the feet merely insulate the egg or actually supply heat to it is unclear; however, increased contact between the egg and the feet results in higher egg temperatures. Both Robertson (1971) and Brechtel (1983) report successful hatching of all eggs in six-egg clutches, although hatching success generally declined in clutches of more than four. Incubation capacity does not appear to limit clutch size.

The onset of full incubation as indicated by a rise in average egg temperature is apparently unrelated to the presence of the eggs. Artificially enlarged clutches were treated essentially like one-egg clutches. Intensity of incubation may be related to factors other than the presence of eggs, such as a gradual increase in hormone levels over the laying period or possibly a combination of both tactile stimulation and hormone levels. Brechtel (1983) noted that no clutch of only one egg produced young. This suggests that more than one factor is involved in initiating incubation behavior and maintaining it at a sufficiently intense level to produce young.

Embryo viability drops off sharply at temperatures only slightly above normal incubation temperatures (36 to 37°C). When internal egg temperatures reached 43.5°C only 20% of the embryos survived. These data indicate that 50% of the embryos would be killed at an internal temperature of 42.2°C. Drent (1975) indicates that while no fixed upper lethal internal temperature can be defined, significant embryo mortality occurs in most species at temperatures between 42.2 and 48.3°C. Bennett et al. (1981) noted that the upper thermal limits of gull embryos were species dependent. Cormorant embryos of less than five days incubation were more subject to death by thermal stress than were older embryos, contrary to Drent's (1975) findings. No clear reason for this is evident, although the initial stages of development appear to progress more slowly than might be expected. Eggs [illegible] the early developmental stages may be less hardy because of the slow pace of development.

By collecting whole clutches soon after eggs were first observed in the colony, it was hoped to obtain some uniformity in the age of embryos stressed, but some variability no doubt existed. I assumed that embryos found dead after stressing died during or immediately after stressing. Evidence for the validity of this assumption is found in the fact that most of the embryos found dead were in a state of decay when opened. A few larger embryos found dead showed no signs of decay, possibly indicating recent death. The effects of stress may not be immediately lethal to the embryo; therefore, determining the exact age at the time of stressing is problematic.

Several factors affect the rate of temperature change of an exposed egg. Ambient air temperature, developmental state, wind velocity, solar radiation and angle, and amount of shell staining are all important. At the Scope Reservoir, eggs appear to be in little danger of being stressed by either heat or cold. Eggs are exposed only when the parents are driven from the nests. In May and early June conditions which could produce embryo stress (high ambient temperatures with no wind and intense solar input) are seldom encountered. The air is seldom calm and slight increases in wind velocity can bring about cooling of an egg which was increasing in temperature due to solar input. Egg temperatures can increase at a rate of 0.36°C/min (21.6°C/hr), however, at no time during tests on exposed eggs in nests were temperatures attained that were potentially lethal to embryos.

Egg cooling rates of $0.59^oC/1^oh^{-1}$ were higher than those reported for other avian eggs (Drent 1975, Afton 1979). This is not surprising since the high porosity of the cormorant nest would provide little insulative value. Cormorants do not cover their eggs or insulate them with down as do Northern Shovelers (<u>Anas clypeata</u>) (Afton 1979). High rates of cooling would pose little threat to developing cormorant embryos since they are extremely cold hardy. The wide tolerance to cold stress shown by embryos of Double-crested Cormorants suggests that factors other than temperature control the northern extent of their breeding range in Alberta.

Literature Cited

Afton, A. D. 1979. Incubation temperatures of the Northern Shoveler. Can. J. Zool. 57: 1052-1056.

Bennett, A. F., W. R. Dawson, and R. W. Putnam. 1981. Thermal environment and tolerance of embryonic Western Gulls. Physiol. Zool. 54: 146-154.

Boersma, P. D. and N. T. Wheelwright. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-Petrel. Condor 81: 157-165.

Brechtel, S. H. 1983. The reproductive ecology of Double-crested Cormorants in southern Alberta. M.Sc. Thesis, Univ. of Alberta, Edmonton, Alberta. 119 pp.

Des Granges, J. 1982. Weight growth of young Double-crested Cormorants on the St. Lawrence Estuary, Quebec. Colonial Waterbirds 5: 79-86.

Drent, R. H. 1975. Incubation. In Avian Biology, Vol. 5. Farner, D. S., and J. R. King, eds. Academic Press, New York, N.Y. pp. 333-420.

Environment Canada. 1981. Canadian Climate Normals, T[illegible]rature and Precipitation, Prairie Provinces. A[illegible]spheric Environment Service. 429 pp.

Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30, Amer. Ornithol. Union.

Howell, T. R. and G. A. Bartholomew. 1962. Temperature regulation in the Red-tailed Tropic Bird and the Red-footed Booby. Condor 64: 6-18.

Keen, R., and D. L. Parker. 1979. Determining expected duration of development under conditions of alternating temperatures. J. Theor. Biol. 81: 599-607.

Lewis, H. F. 1929. The natural history of the Double-crested Cormorant (*Phalacrocorax auritus* [Lesson]). Cornell University, Ithaca, N.Y., Ph.D. Thesis. Ru-Mi-Lou Books, Ottawa, Ontario.

Matthews, G. V. T. 1954. Some aspects of incubation in the Manx Shearwater, *Procellaria puffinus*, with particular reference to chilling resistance in the embryo. Ibis 96: 432-440.

Mendall, H. L. 1936. The home life and economic status of the Double-crested Cormorant. University Press, Orono, Maine.

Mitchell, R. M. 1977. Breeding biology of the Double-crested Cormorant on Utah Lake. The Great Basin Naturalist 37(1): 1-23.

Parsons, J. 1975. Seasonal variation in the breeding success of the Herring Gull on experimental approach to prefledging success. J. Anim. Ecol. 44: 553-573.

Robertson, I. 1971. The influence of brood size on reproductive success in two species of cormorant, Phalacrocorax auritus and P. pelagicus and its relation to the problem of clutch size. M.Sc. Thesis, University of B.C., Vancourver B.C.

Roby, D. D. and R. E. Ricklefs. 1984. Observations on the cooling tolerance of embryos of the Diving Petrel Pelecanoides georgicus. Auk 101: 160-161.

Spellerberg, I. F. 1969. Incubation temperatures and thermoregulation in the McCormick Skua. Condor 71: 59-67.

Vleck, C. M. and G. C. Kenagy. 1980. Embryonic metabolism of the Fork-tailed Storm-Petrel: physiological patterns during prolonged and interrupted incubation. Physiol. Zool. 53: 32-42.

Walsberg, G. E. and K. A. Voss-Roberts. 1983. Incubation in desert-nesting doves: mechanisms for egg cooling. Physiol. Zool. 56(1): 88-93.

Yom-Tov, Y., A. Ar., and H. Mendelsohn. 1978. Incubation behavior of the Dead Sea Sparrow. Condor 80: 340-343.

Zach, R. 1982. Hatching asynchrony, egg size, growth and fledging in tree swallows. Auk 99: 695-700.

Zerba, E. and M. L. Morton. 1983. Dynamics of incubation in Mountain White-crowned Sparrows. Condor 85: 1-11.

Table II-1. Mean temperatures of cormorant eggs in naturally occurring clutches of different sizes and in artificially enlarged clutches. Means connected by vertical lines are not significantly different by t test.

Naturally occurring		Artificially enlarged	
No. of eggs	Mean egg temp.	No. of eggs	Mean egg temp.
1	30.86±2.98 n = 7	1	32.77± n = 6
2	32.59±1.15 n = 9	2	32.678± n = 5
3	36.04±0.61 n = 5	3	31.33± n = 5
4	35.60±0.91 n = 6	4	31.74± n = 5

Table II-2. Survival of cormorant embryos following thermal stress.

Time (hrs.)	Stress chamber temp. (^{0}C)	Internal egg temp. (^{0}C)	No. alive	No. dead	Percent survival
4	-11	- 2.2	0	14	0.0
1.5	-11	- 3.5	11	3	78.6
1	-10	.5	10	1	90.9
1	- 5	6.5	12	2	85.7
1	0	11	7	3	70.0
1	5	15.5	10	0	100
1	40	40	8	1	88.9
1	45	41.5	6	3	66.6
1	50	43.5	3	12	20
1	55	48.5	0	11	0.0
Controls	37	37	20	1	95.5

Table II-3. Growth of body components of embryonic Double-crested Cormorants.

Length of incubation (days)	Mean eye diameter (mm.)	Mean crown rump (mm.)	Mean wing* length (mm.)	Mean leg* length (mm.)	Mean beak length (mm.)	No.
7	0.5	9.2				3
8	0.9	10.0				2
9	1.5	11.3				2
10	1.4	14.1				1
11	2.3	17.0	2.2 b	2.4 b		2
12	3.1	17.5	4.2 b	5.3 b	1.3	3
13	3.4	20.0	4.3 b	4.7 b	1.5	2
14	3.9	20.1	5.2 b	6.3 b	1.9	3
15	5.7	25.1	8.1 u	6.9 b	4.5	4
16	5.8	27.0	8.8 u	5.3 t	4.9	2
17	6.3	30.3	10.5 u	7.5 t	6.4	2
18	6.5	30.4	10.7 u	7.0 t	6.6	2
19	6.7	31.9	11.5 u	8.0 t	7.3	2
20	7.0	38.5	11.7 u	7.7 t	7.3	2
21	7.5	34.9	12.1 u	8.0 t	8.3	2
22	7.1	38.0	12.4 u	8.0 t	7.9	3
23	7.0	36.3	14.0 u	9.8 t	8.2	2
24	7.9	40.5	13.6 u	9.5 t	8.9	3
25	7.9	45.9	14.9 u	10.2 t	8.7	2
26	8.9		15.7 u	10.8 t	8.9	2
27	9.0		17.4 u	13.8 t	9.2	2

*b = bud, u = ulna, t = tarsi

Table II-4. Summary of embryonic mortality.

Embryo classification	Total eggs stressed	No. dead	Percent dead
Controls (all stages of incubation)	21	1	4.76
< 5 days incubation at time of stressing	39	23	58.9
6 days incubation or more at time of stressing	99	28	28.3
Stressed at sublethal temperatures*	113	26	23.0
< 5 days incubation stressed at sublethal temperatures	33	17	51.5
6 days incubation or more at time of stressing	80	9	11.25

*Temperatures at which some embryos survived were considered sublethal.

Table II-5. Foot, leg, and body temperatures of an adult male Double-crested Cormorant trapped on a nest containing three eggs, May 7, 1984. Positions refer to locations where temperatures were measured as shown in Figure II-2.

Position	Trial 1	Trial 2	Trial 3	Average °C
1	14.7	18.2	18.5	17.1
2	20.6	24.5	22.8	22.6
3	22.4	23.6	27.1	24.4
4	27.3	28.9	29.6	28.6
Deep body	42.0°	42.0°	41.6°	41.9
Abdomen, among feathers	36.5	36.5	36.5	36.5

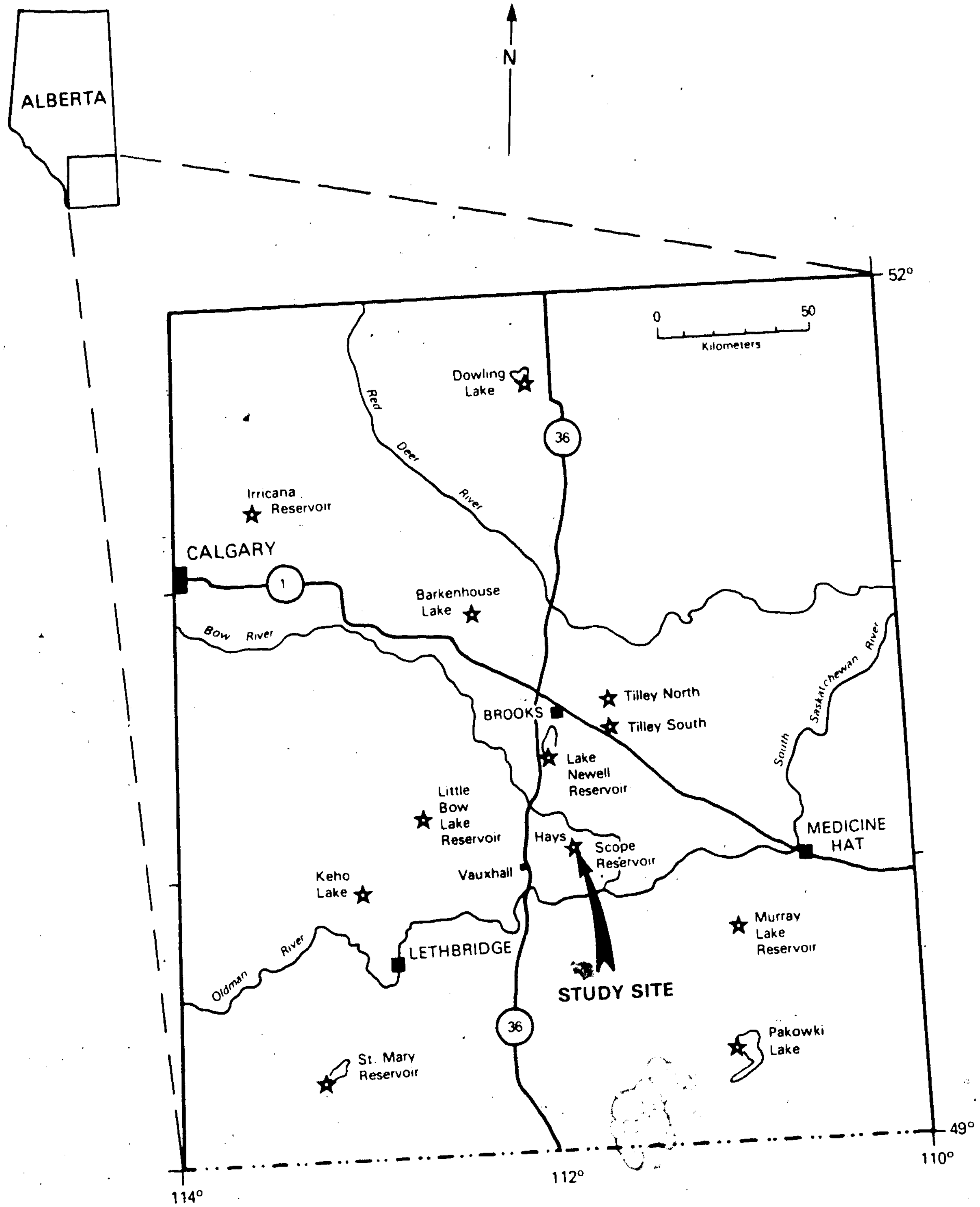

Figure II-1. Location of Scope Reservoir and other Double-crested Cormorant colonies (indicated by stars) in southern Alberta (after Brechtel 1983).

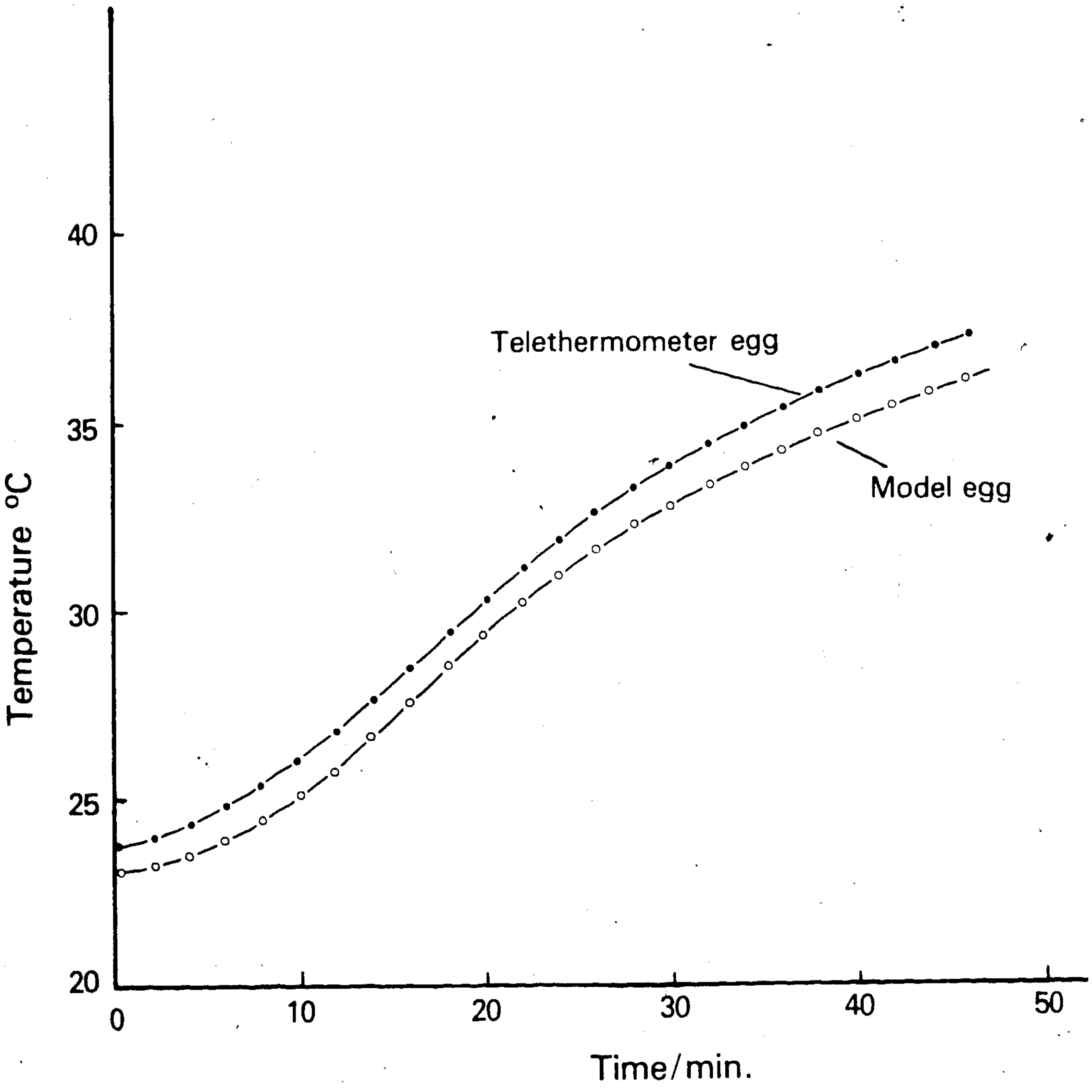

Figure II-2. Comparison of thermal response of a chicken egg with a YSI telethermometer probe and a model chicken egg containing agar and a Mini-Mitter transmitter.

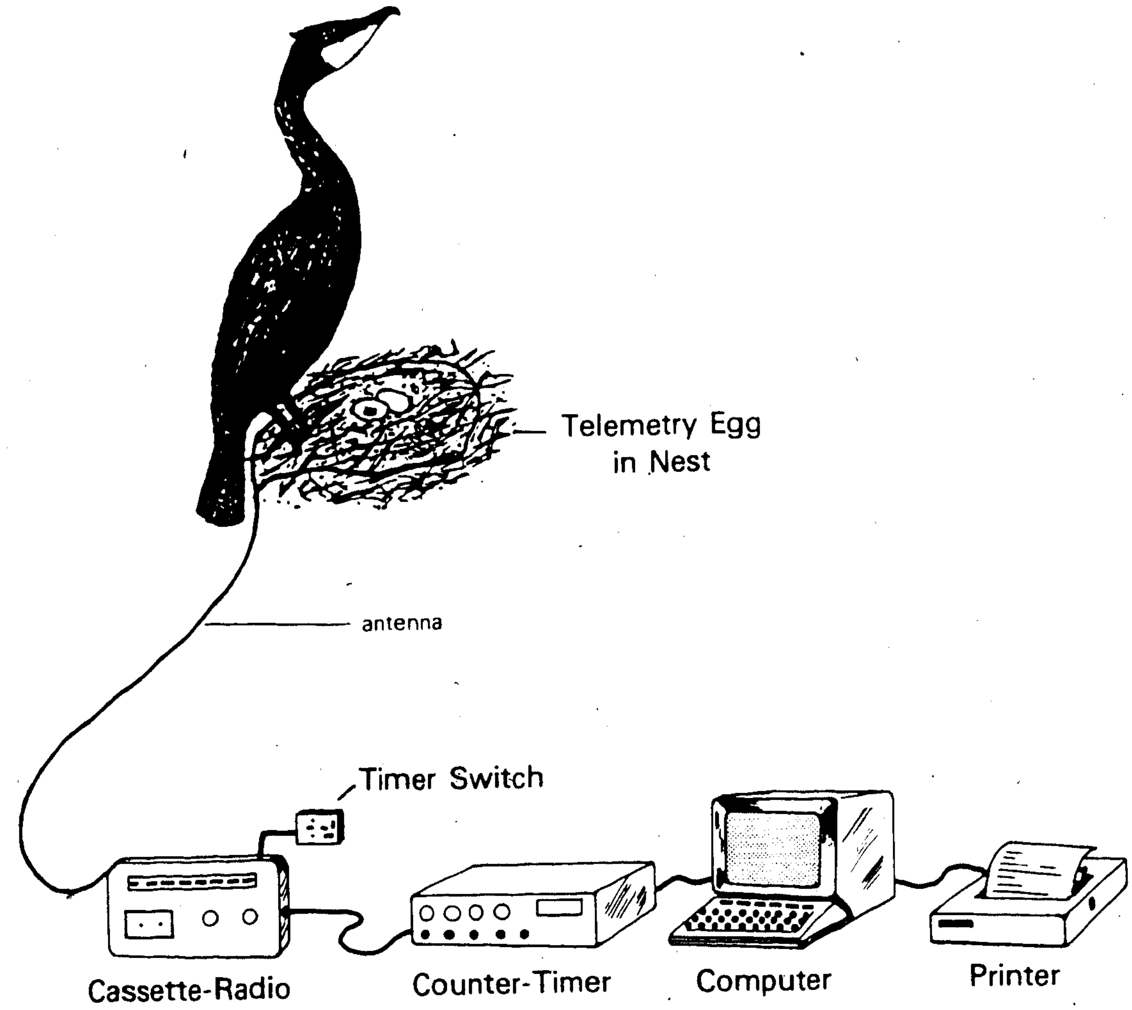

Figure II-3. Data acquisition and analysis system.

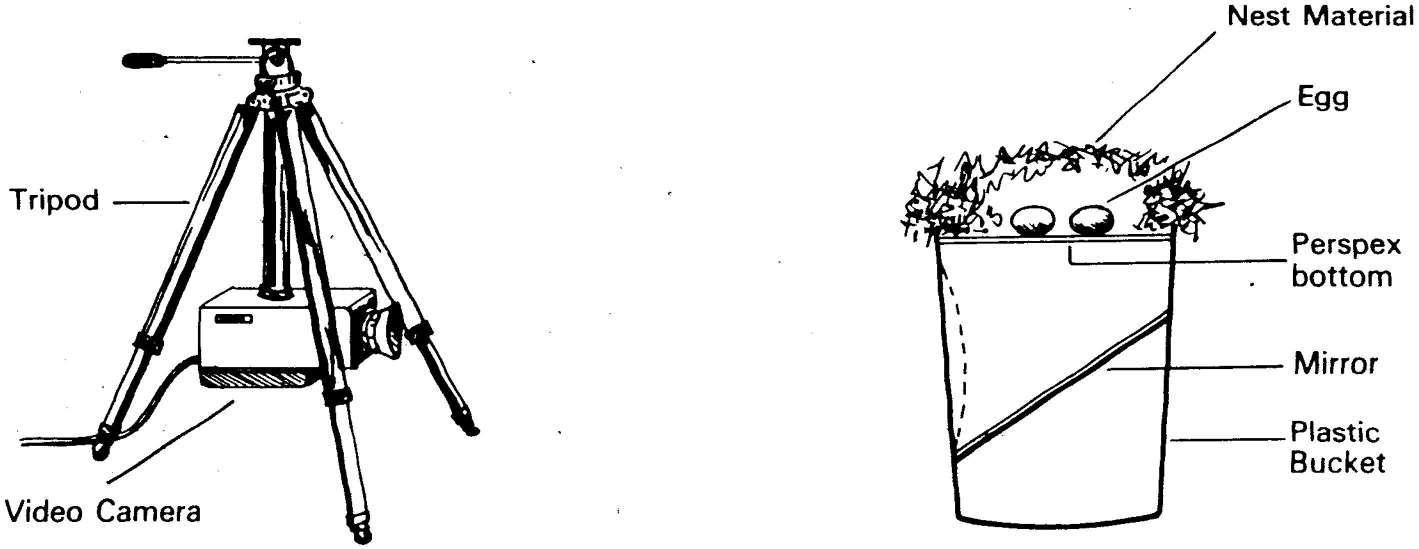

Figure II-4. Arrangement for viewing through the bottom of a cormorant nest.

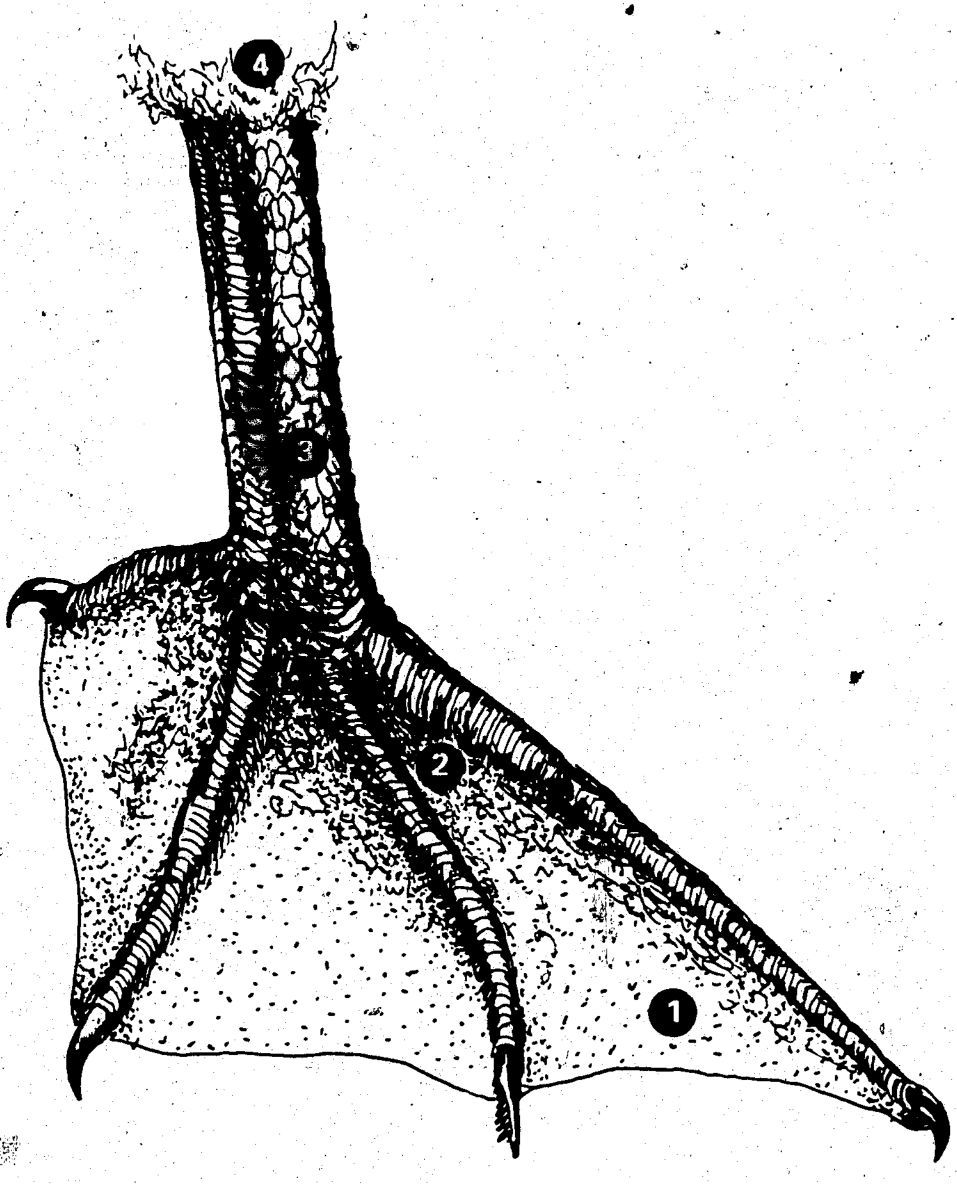

Figure II-5. Leg and foot of Double-crested Cormorant showing location of temperature measurements (life size).

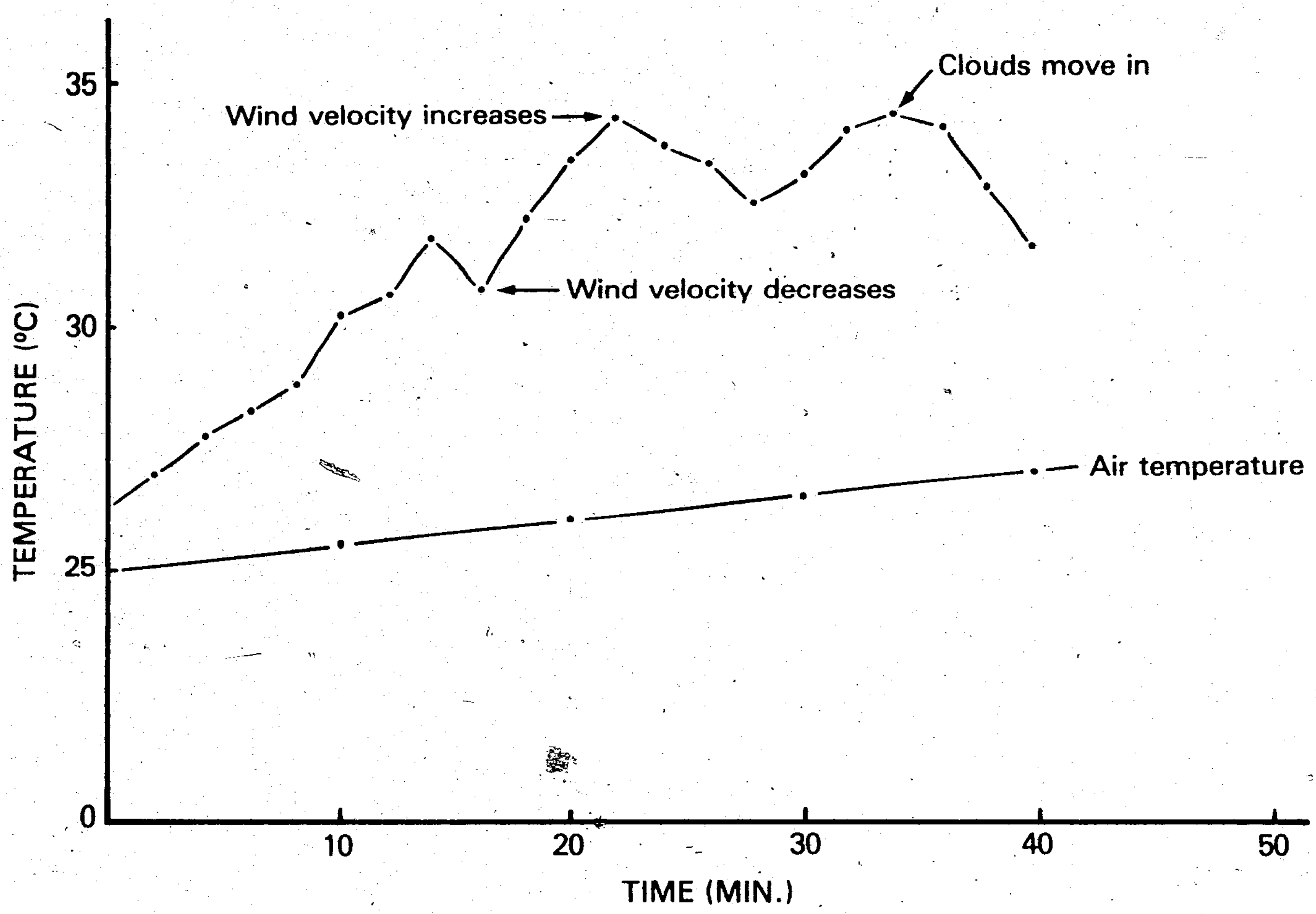

Figure II-6. Heating curve of cormorant egg exposed in a nest at ambient conditions.

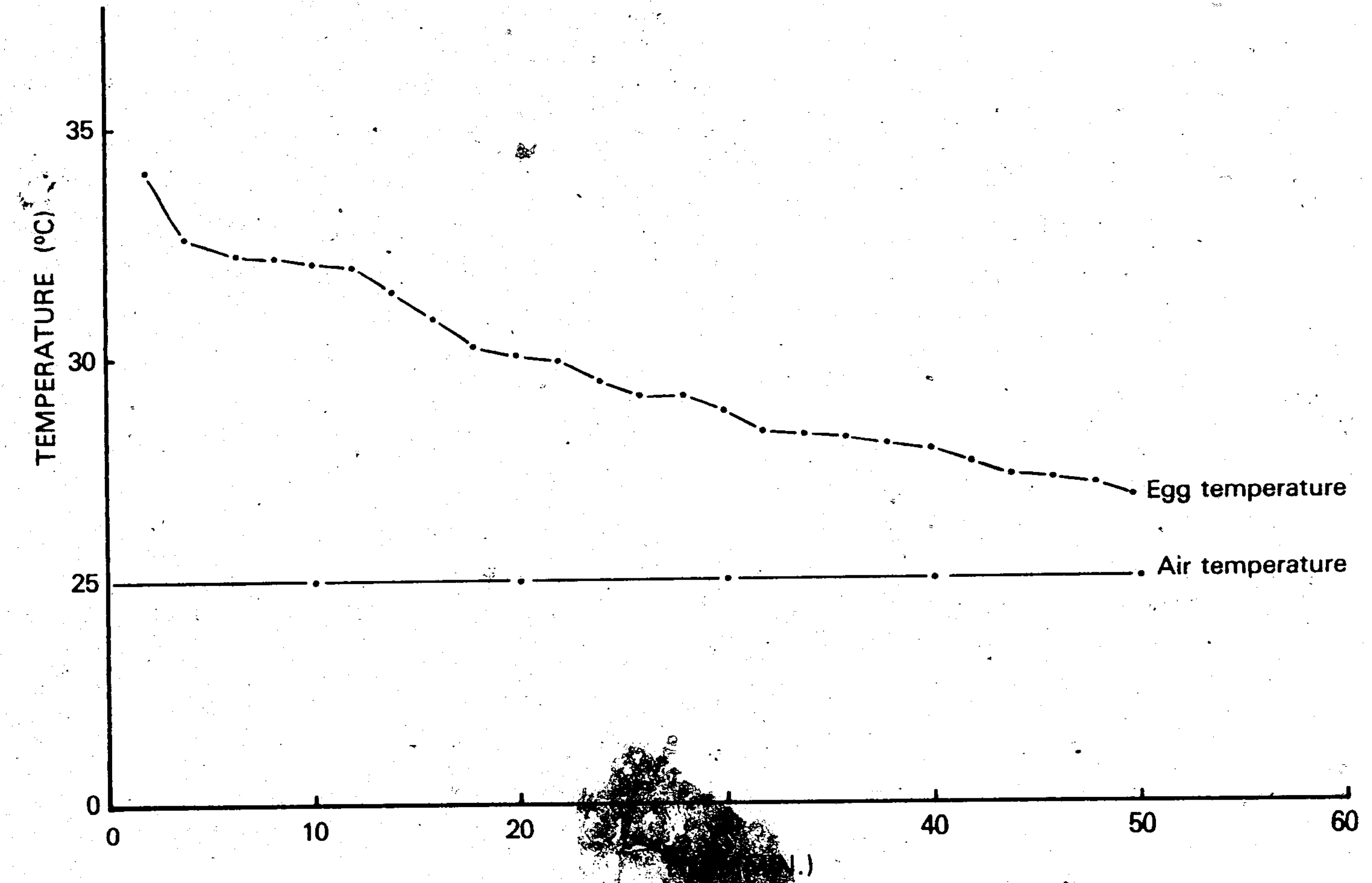

Figure II-7. Cooling curve of cormorant egg exposed in a nest at ambient conditions on an overcast day. Ambient air temperature 25°C.

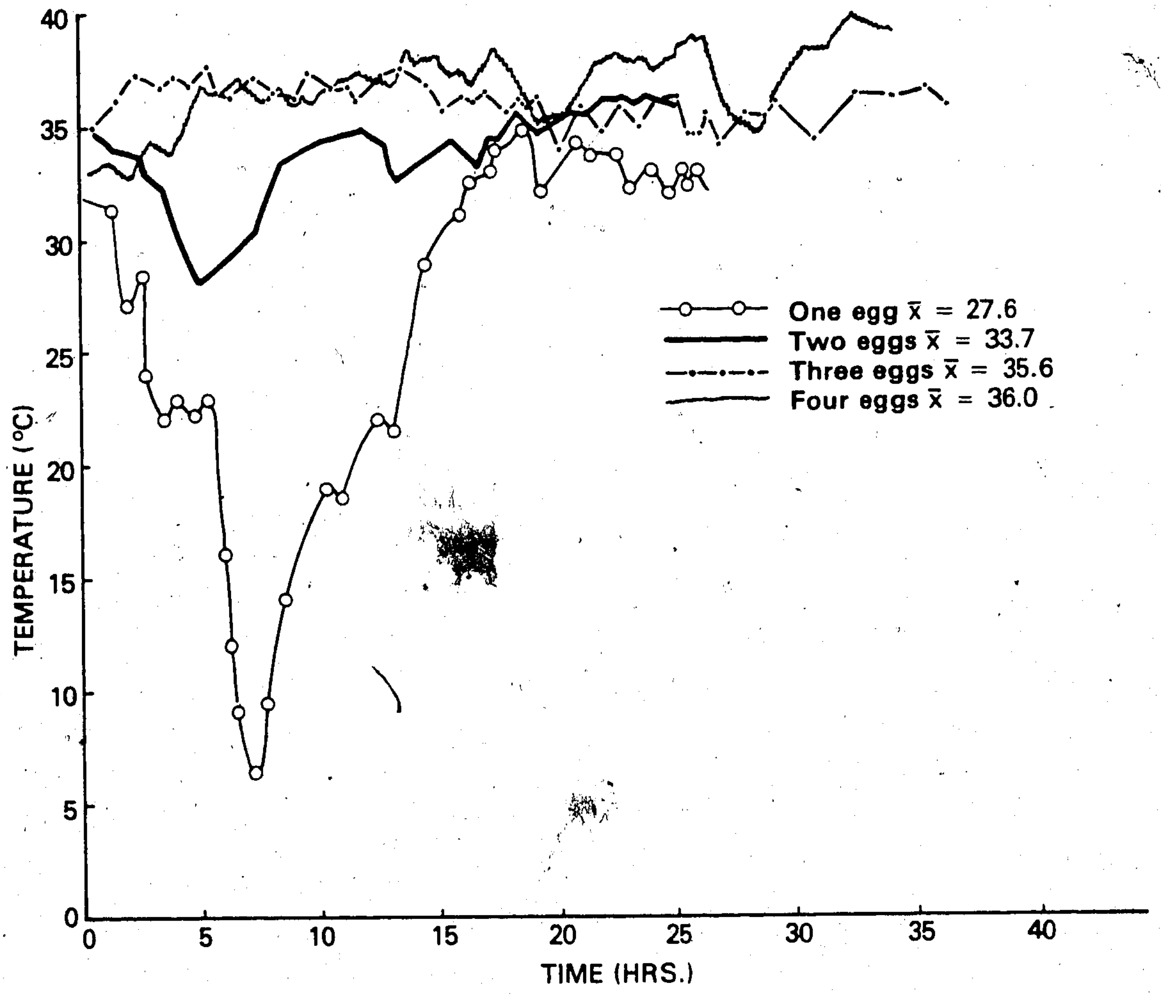

Figure II-8. Temperatures of eggs in single one-, two-, three-, and four-egg clutches of Double-crested Cormorants in southern Alberta during the first week of incubation.

III. Thermal relations in nestling Double-crested Cormorants in southern Alberta

Introduction

Thermoregulatory capabilities of nestling altricial birds develop gradually and vary among and within species (Dunn 1975a). Prior to full homeothermy, a nestling is vulnerable to the effects of exposure. Thermal flexibility may vary geographically (Hudson and Kimzey 1966, Trost 1972, Koskimies and Lahti 1964), and details of the adaptability of a species should enhance understanding of geographical differences and provide data for management specific to local conditions.

Nestlings of Double-crested Cormorants (Phalacrocorax auritus) gradually achieve effective thermoregulatory ability so that by the time a nestling weighs 500 g, it can tolerate considerable thermal stress; it is able to maintain homeothermy at about 14 to 15 days after hatching (Dunn 1976). The relatively long period preceeding homeothermy represents a period of potential vulnerability to thermal stress and unless parental behavior compensates for the inability to thermoregulate, death from hypothermia or hyperthermia can result.

This paper reports on thermal relations of prehomeothermic Double-crested Cormorants in the nest, and on the ability of nestlings to cope with induced thermal stress. From these data, I will assess the effect of short-term disruption of parental attentiveness on the survivability of nestlings under particular sets of conditions and consider the advantages of hatch asynchrony in that regard.

Study area and methods

The colony studied in May, June, and July of 1982, 1983, and 1984, was located on three islands in Scope Reservoir, an irrigation reservoir located 17 km east of Vauxhall, Alberta, 50.6°N, 111.9°W. Details of the colony and the dominant vegetation are given by Van Scheik (1985a).

Field observations

Deep body temperatures of 100 nestlings, ranging in age from 0 to 14 days posthatch, were measured by inserting a YSI 400 series (Yellow Springs Instrument Co., Yellow Springs, OH 45387) probe > 2 cm into the cloaca. Readings were recorded from a Cole-Parmer Model 8523-00 Digi-sense thermister thermometer (Cole-Parmer Instrument Co., Chicago, IL 60684). Temperatures were taken within five minutes of the departure of the parent and all measurements were made between 10:00 a.m. and midday, with ambient temperatures ranging from 19.5 to 21°C. Nestlings were weighed with a Pesola spring balance.

Deep body temperatures were studied by gently forcing Mini-Mitter Model V transmitters (The Mini-Mitter Co. Inc., Box 3386, Sunriver, Oregon 97702) into the alimentary canals, via the esophagi, of 16 nestlings 5 to 10 days old. Data were recorded on Realistic Minisette 10 (Radio Shack) radio cassettes activated by a timer switch (see Appendix) which turned each unit on for 15 seconds every 14 minutes. Thermally relevant behavior of nestlings in the nest was sampled for 4.5 hours during the day with video camera and cassette recorder (Sears Model 30133D). Transmitter positions in the bodies of two nestlings were determined by x-ray and dissection. The nestlings appeared unharmed by the transmitters which were recovered from the guano around the nest a week to 10 days later.

Laboratory studies

Thirty-eight nestlings from 1 to 11 days old were collected at the nesting colony and their thermoregulatory abilities assessed through thermal and behavioral responses to direct solar radiation. Heat stressing was conducted in a cormorant nest which had been removed from the colony to minimize disturbance during testing. Body temperatures were measured either by radio telemetry using the system described above or by a YSI 400 series probe coupled to a ole-Parmer Model 8523-00 Digi-sense thermometer. The probe was inserted > 2 cm cloacally and temperatures were recorded every two minutes. A comparison of the heating rates of a live seven-day-old nestling and a dead nestling the same age and weight was made to determine if early attempts at thermoregulation were effective. Temperatures on the downless back skin of nestlings < one and seven days old were taken and compared to their deep body temperatures taken at the same time. Specific behavioral responses, such as vocalizations, gular flutter, gasping or thrashing movements, were noted.

Cold stressing was done in a styrofoam test chamber cooled with crushed ice. Twenty-three nestlings, varying in age from 1 to 12 days old, were placed in the test chamber on an insulating platform and allowed to cool until they became comatose. Temperatures were recorded every two minutes.

The age of all nestlings was determined by comparision to weights and measurements reported by Dunn (1975b).

Results

Field observations

Body temperatures of nestlings taken within five minutes of the departure of attending parents were significantly correlated with the number of days since hatching (r = .687, P < .01, n = 100, Pearson product moment correlation, Figure III-1). Nestlings older than 11 days had body temperatures within the range reported for adults

(Neumann et al. 1968). Body temperatures of nestlings younger than 11 days declined at a rapid rate and were constantly lower than average body temperatures of nestlings brooded in the nest. The effects of even brief exposure were rapid. Telemetry data indicate that the body temperatures of individual nestlings may vary as much as 13°C even while the parent is in attendance at the nest (Figure III-1).

The location of transmitters was determined by both autopsy and x-ray (Figure III-2). For the two nestlings dissected, the transmitters were found in the stomach among food and gravel. The presence and function of 19 pieces of gravel (.2 to 1.5 cm, 9.5 g) in the stomach of one of the nestlings could not be explained.

Experimental studies

When exposed to the sun, nestlings heated rapidly, with heart failure being abrupt and irreversible. The average deep body temperature at which death occurred was 45.68 ± 1.72°C (n = 38) and took an average of 22.65 ± 11.56 minutes (Figure III-3).

Nestlings less than two weeks old and not subjected to high heat loads rest quietly in the nest with occasional head movements and quiet vocalization. As heat loads begin to build, the following series of temperature correlated behaviors were observed:

1. Quiet

Nestlings with body temperatures below 35°C rested quietly in the nest cup. Occasional head movements and weak vocalizations were noted but typically the mouth was closed and breathing movements were not noticeable.

2. Gular flutter

The description of gular flutter as given by Lasiewski and Snyder (1969) is typical of nestlings at 0 to 14 days. The hyoid, depressed and flared, expanding the buccal and pharyngeal areas, moves rapidly, drawing air over the moist membranes facilitating evaporative cooling. Periodic gular flutter began when body temperatures reached 37 to 39°C.

3. Vocalizing

One of the first indicators of heat stress was the repeated production of a shrill chirp. Unlike the quiet vocalizations given at lower temperatures, this chirp was accompanied by head waving, thrashing movements of wings and legs, and gular fluttering. Repetitive vocalizations every three to five seconds occurred when the body temperature was about 38°C if the nestling was fully exposed to the sun. Skin surface temperatures would be some 2°C higher.

4. Head waving

Moving the head from side to side rapidly and with accompanying vocalization in nestlings up to four or five days old was an early indication of heat stress. Head waving behavior began at about the same temperature as repetitive vocalizing.

5. Thrashing movements

Young nestlings moved wings, head and legs in an uncoordinated manner. More mature birds able to coordinate their movements attempted to escape and would climb out of the nest cup and fall to the ground. When this happened, the nestlings were returned to the nest cup by the observer. This behavior, which usually began at about 39°C and continued to around 42°C, usually marked a sharp increase in internal body temperature.

6. Continuous gular flutter

Rapid continuous movement of the gular region with maximal extension of the hyoid apparatus occurred when internal temperatures reached 40°C.

7. Gasping

As nestlings neared the limit of their ability to cope with heat stress, the rate of gular flutter decreased and eventually stopped. Nestlings stopped moving and with their mouth open took in and exhaled large gulps of air. Gasping began after internal temperatures reached 42°C and signaled imminent death. Birds which were shaded at this point revived as their body temperatures fell.

8. Comatose

Nestlings which continued to be exposed after gasping occurred became comatose within four minutes. No amount [illegible] shading or other cooling could revive the birds at this stage.

Figure III-4 depicts behavioral events of an exposed nestling at various stages of heat stress. Cormorant nests are porous and stand some 50 cm above the ground and are appropriately structured and positioned to catch any wind. The effect of wind on the heating rate of nestlings is immediately evident. At higher wind velocities nestlings were able to withstand longer exposure to direct solar insulation.

The black, naked skin of nestlings heats rapidly, particularly if the air is calm. Very young nestlings, up to three days old, attempt to cool by gular flutter and become more efficient at cooling with increasing age. Figure III-5 compares skin and deep body temperatures of an exposed seven-day-old nestling with the deep body temperatures of a dead seven-day-old nestling of the same weight. Gular flutter was effective in slowing the rate of heating.

Cold stress

Nestling cormorants accepted cold stress passively. Vocalizations, which were loud and frequent when nestlings were first placed in the test chamber, diminished in strength and frequency as stressing continued, ceasing altogether when deep body temperatures reached 21°C (N = 5). Shivering, an early indication of endothermy, was observed first at six days after hatching; however, the effort was not sustained and was ineffective in preventing the body temperature from dropping. Twelve-day old nestlings, though unable to generate enough heat by shivering to maintain constant body temperature, were able to slow the cooling rate. Figure III-6 summarizes the data for cold stressed nestlings and indicates a general trend toward endothermy as age increases. At 12 days cold-stressed nestlings were still active after up to three hours of exposure.

Nestlings subjected to cold stress became hypothermic and comatose between 16 and 19°C. Although comatose nestlings were motionless and unresponsive to external stimuli, they soon recovered their initial state of consciousness when placed in a warm environment. While passive warming revived comatose nestlings if exposure was not prolonged, no nestling whose deep body temperature fell below 11.5°C could be revived. No permanently adverse effects resulted from chilling.

Discussion

Removal of the stable thermal environment provided by attending adults has a profound effect on exposed nestlings. Naked nestling cormorants are heavily pigmented, facilitating absorption of solar radiation, but are deficient in their ability to dissipate heat. Even at ambient temperatures of less than 25°C the dark, naked bodies act like "black bodies" and gain heat rapidly. Although very small nestlings may compensate partially for heat gained through their relatively large surface areas by behavioral responses which help dissipate heat, such efforts are not fully effective until the third week after hatching.

The ability to maintain homeothermy develops gradually and coincides with the appearance of dense, black down at about a week and which completely covers the body by two weeks. Dunn (1975a) lists the age of endothermy for several altricial species. For Double-crested Cormorants she indicates that nestlings 12 days old can maintain body temperatures 75% as high above ambient (15 to 25°C) as can adults. My data are in agreement since 12-day-old nestlings could maintain body temperatures above 20°C indefinitely at ambient temperatures ranging from 8 to 15°C. Younger nestlings became torpid and comatose with the rate at which this occurs inversely proportional to their age.

Unlike the Brown Pelecans (*Pelecanus occidentalis*) studied by Bartholomew and Dawson (1954), nestling Double-crested Cormorants can gular flutter on the day of hatching, and by seven days of age, this behavior was sufficient to slow the rapid rise in body temperature of an exposed nestling compared to that of a dead nestling of the same age (Figure III-5). Evans (1984) notes that White Pelicans (*Pelecanus erythrorhynchos*) could gular flutter on the day of hatching but were not observed to do so in the colony until 11 days of age. Cormorants in the Scope Reservoir colony did gular flutter on the day of hatching. Evaporative cooling by gular flutter is a primary means of temperature control in nestlings older than three weeks (Lasiewski and Snyder 1969). It appears to be equally important in young nestlings, and along with other temperature-related behaviors, can serve not only as an indicator of stress, but can be used to gauge the level of stress. Nestlings less than three days old did gular flutter while being brooded in the nest, with no exposure to direct solar radiation, suggesting that this behavior is controlled by body temperature and is in agreement with the conclusion reached by Evans (1984) for White Pelicans.

Heat-stressed nestlings which are able to move often fall from the nest. The fate of these birds is certain death, either by gull predation or exposure. This type of mortality, induced indirectly by heat stress, may account for a large portion of nestling deaths which would not have occurred by heat stress alone. Therefore, while significant mortality of nestlings less than two weeks old can occur in less than 20 minutes by heat stress alone (Figure III-3), heat stress-related mortality may result from much shorter exposures.

Poor development of air sacs was noted during dissection to determine the location of radio transmitters. This limited air sac development and may be a contributing factor to the rapid increase in the body temperatures of nestlings exposed to heat stress.

Asynchronous hatching has been considered advantageous as a mechanism for brood reduction in habitats with unpredictable resources (Lack 1954), as a counter predation strategy (Hussell 1972), as an insurance against failure of the first egg (Stinson 1979), and as a means of spreading food demand on parents (Hussell 1972). Any or all of these explanations may be valid in a given situation, however, where the interval between hatching is large and the nestlings altricial, as in the case of cormorants, asynchrony may be thermally advantageous.

For instance, nestlings less than a week old have been reported by Dunn (1976) to move into the shade of parents. Similar behavior was observed in southern Alberta involving older siblings. The markedly asynchronous hatch, spanning up to six days, results in nestlings in the same nest varying considerably in size and weight. On several occasions on hot days, younger nestlings, with presumably a low ability to thermoregulate, were observed to move into the shade of older siblings. Considering the rapidity with which hyperthermia can occur, particularly in nestlings less than a week old, this behavior, coupled to hatch asychrony, is highly adaptive and provides a survival option not available in synchronous hatch situations. As age increases, homeothermy develops and the nestling is better able to stabilize its own thermal relationship to its environment. In so doing, it may provide heat for younger, less advanced siblings through passive contact, or it may provide passive cooling in heat stress situations through body contact or by providing shade.

Rapid cooling occurs when nestlings are exposed to ambient temperatures less than 25°C, in shade or overcast conditions. Cold stress poses considerably less risk than does heat stress. Nestlings respond passively to cooling and make virtually no attempt to generate heat metabolically. Shivering was seldom seen and was not sustained when it did occur. Recovery of comatose nestlings with body temperatures as low as 11.5°C was generally rapid and complete. Nestlings which recovered from hypothermia grew normally and eventually fledged, after being returned to their nests.

Cold tolerance is not unique to cormorants. Altricial White Pelican nestlings (Evans 1984), semiprecocious Western Gulls (Larus occidentalis) (Dawson and Bennett 1981), and Ring-billed Gulls (Larus Delewarensis) (Dawson et al. 1976) also recovered normal functioning if warmed after being comatose. Ring-billed Gulls nest on the same islands as Double-crested Cormorants in southern Alberta and occupy much of the same range. The ability to recover from acute hypothermia may be characterisitic of all species having altricial young.

The gradual development of homeothermy is probably the result of a number of age-related factors, including increased mass, development of down, and increased coordination. In the absence of fully developed homeothermy, the ability to withstand thermal stress, particularly cold stress, has permitted cormorants to successfully exploit the northern midcontinental part of their range and perhaps the northern limits of their range in Alaska and Newfoundland as well.

Literature Cited

Bartholomew, G. A. and W. R. Dawson. 1954. Temperature regulation in young pelicans, herons, and gulls. Ecology 35: 466-472.

Dawson, W. R. and A. F. Bennett. 1981. Field and laboratory studies of the thermal relations of hatchling Western Gulls. Physiol. Zool. 54(1): 155-164.

Dawson, W. R., A. F. Bennett and J. W. Hudson. 1976. Metabolism and thermoregulation in hatchling Ring-billed Gulls. Condor 78:49-60.

Dunn, E. H. 1975a. The timing of endothermy in the development of altricial birds. Condor 77: 288-293.

Dunn, E. H. 1975b. Growth, body components and energy content of nestling Double-crested Cormorants. Condor 77: 431-438.

Dunn, E. H. 1976. Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. Condor 78: 350-356.

Evans, R. M. 1984. Development of thermoregulation in young White Pelicans. Can. J. Zool. 62: 808-813.

Hudson, J. W., and S. L. Kimzey. 1966. Temperature regulation and metabolic rhythms in populations of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol. 17: 203-217.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317-324.

Koskimies, J. and L. Lahti. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81: 281-307.

Lack, D. 1954. The natural regulation of animal numbers. London: Oxford Univ. Press.

Lasiewski, R. C. and G. K. Snyder. 1969. Responses to high temperature in nestling Double-crested Cormorants and Pelagic Cormorants. Auk 86: 529-540.

Neumann, R., J. W. Hudson and R. J. Hock. 1968. In P. L. Altman and D. S. Dittmer (eds), Metabolism. Fed. Am. Soc. Exptl. Biol., Bethesda, Maryland, pp. 334-343.

Stinson, C. H. 1979. On the selective advantage of fratricide in raptors. Evolution 33(4): 1219-1225.

Trost, C. H. 1972. Adaptations of Horned Larks (Eremophilia alpestris) to hot environments. Auk 89: 506-527.

Van Scheik, W. J. 1985a. Egg incubation and thermal tolerance in Double-crested Cormorants in southern Alberta. Ph.D. Thesis, Univ. of Alberta, Edmonton, Alberta.

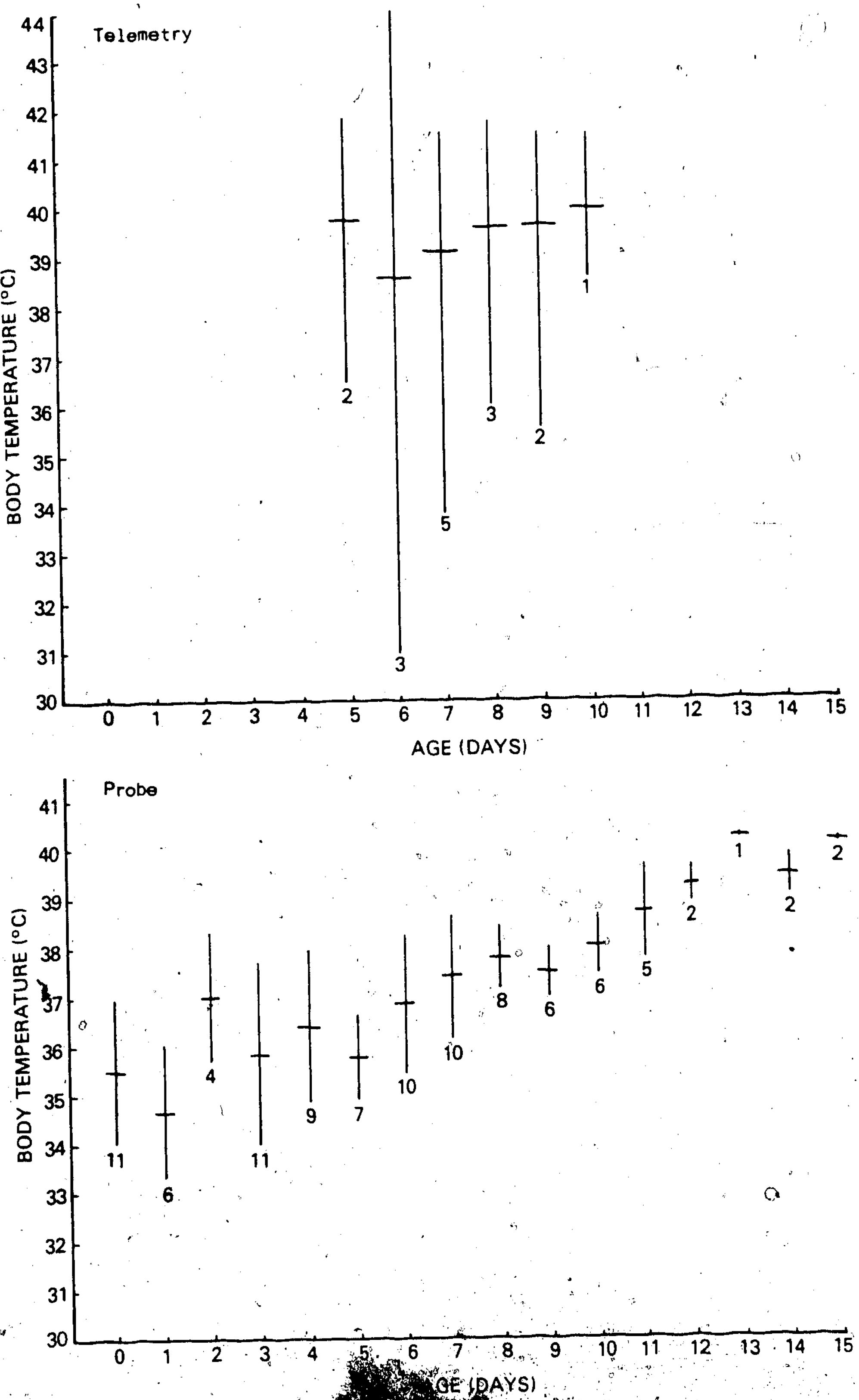

Figure III-1. Mean b[illegible]eratures of Double-crested Cormorant nestl[illegible]ical lines represent range.

Figure III-2. X-ray photograph of nestling with implanted transmitter. Position of transmitter indicated by arrow. Other opaque objects are pieces of gravel.

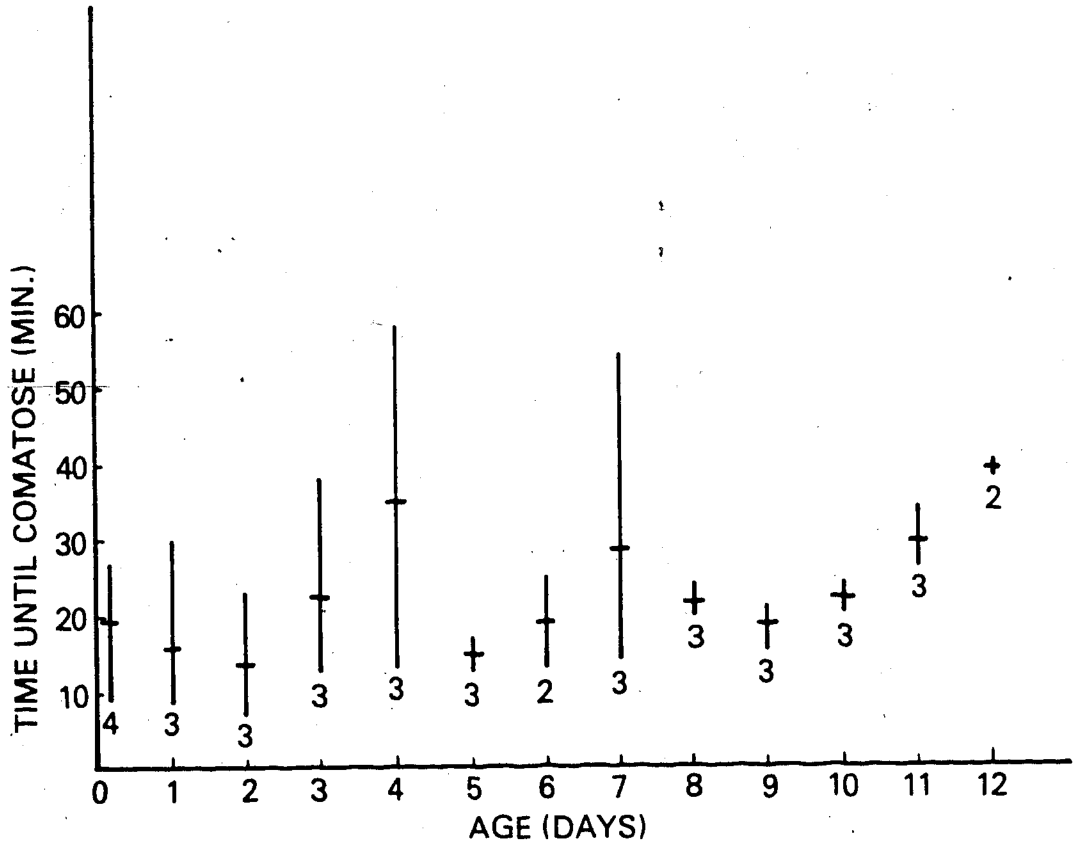

Figure III-3. The time of exposure to the comatose condition for Double-crested Cormorant nestlings of different ages exposed to the sun. Vertical lines = range.

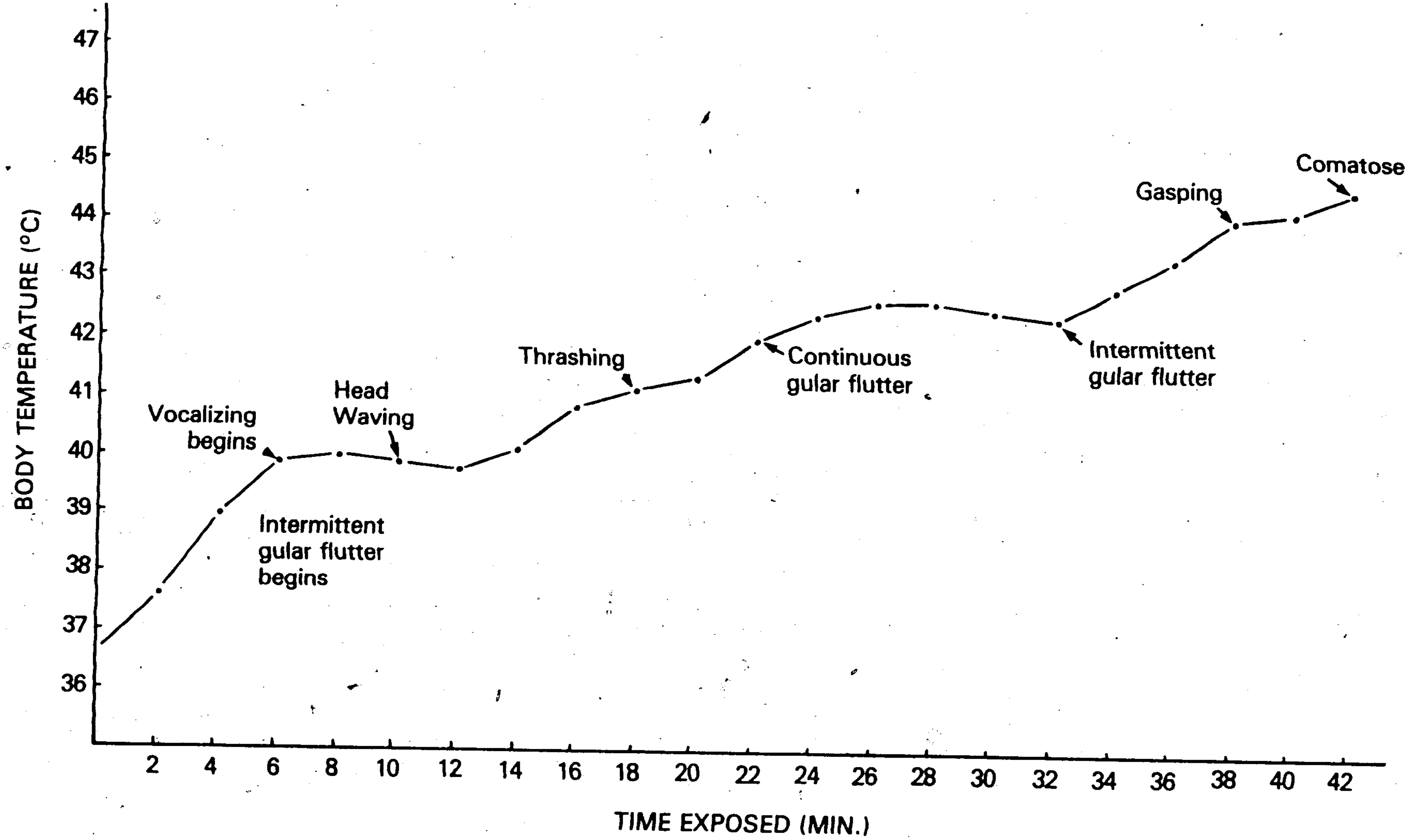

Figure III-4. Behavioral events of exposed Double-crested Cormorant at various stages of heat stress.

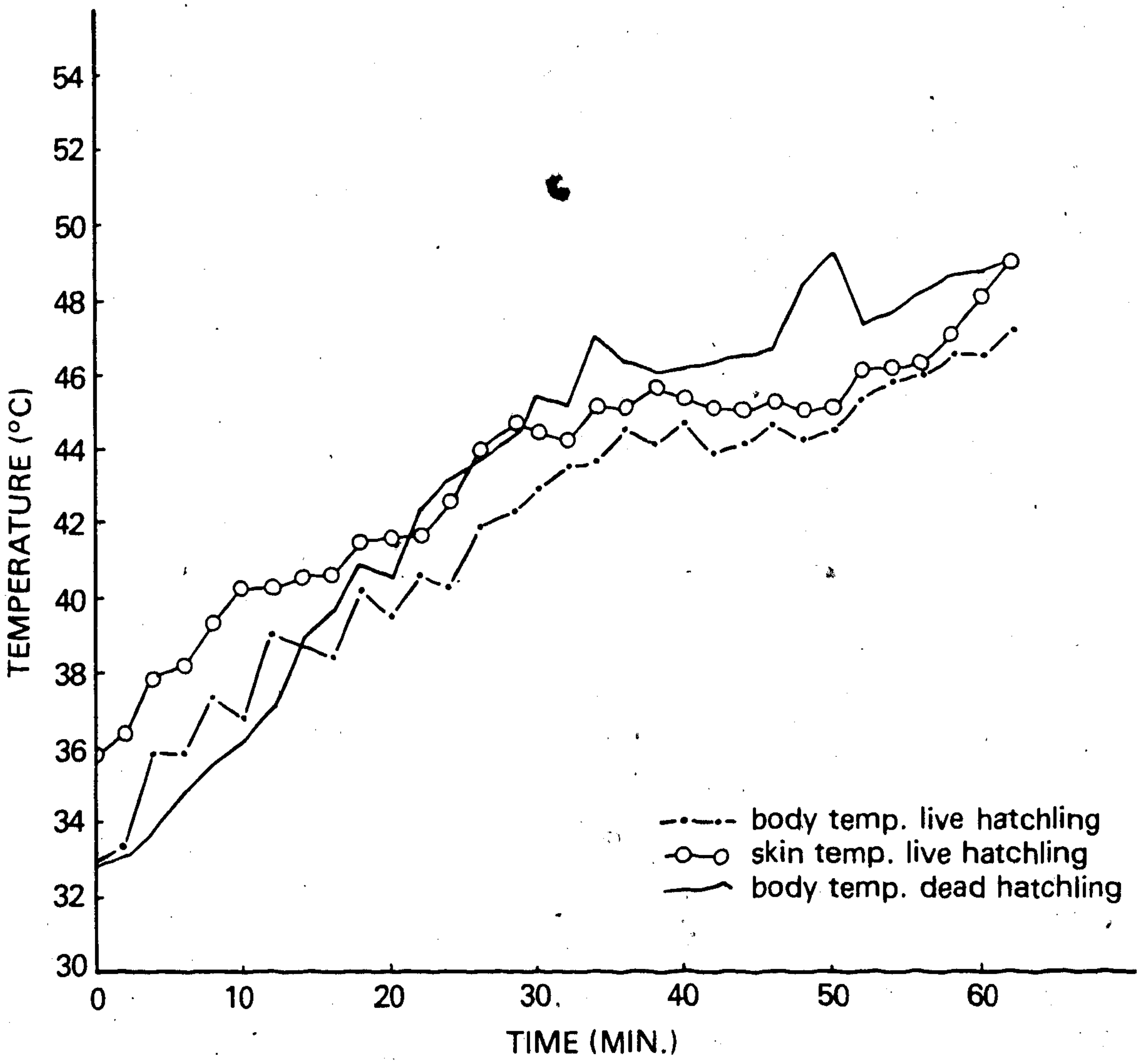

Figure III-5. Comparison of deep body and skin temperatures of a live seven-day-old Double-crested Cormorant nestling with the deep body temperature of a dead nestling the same age.

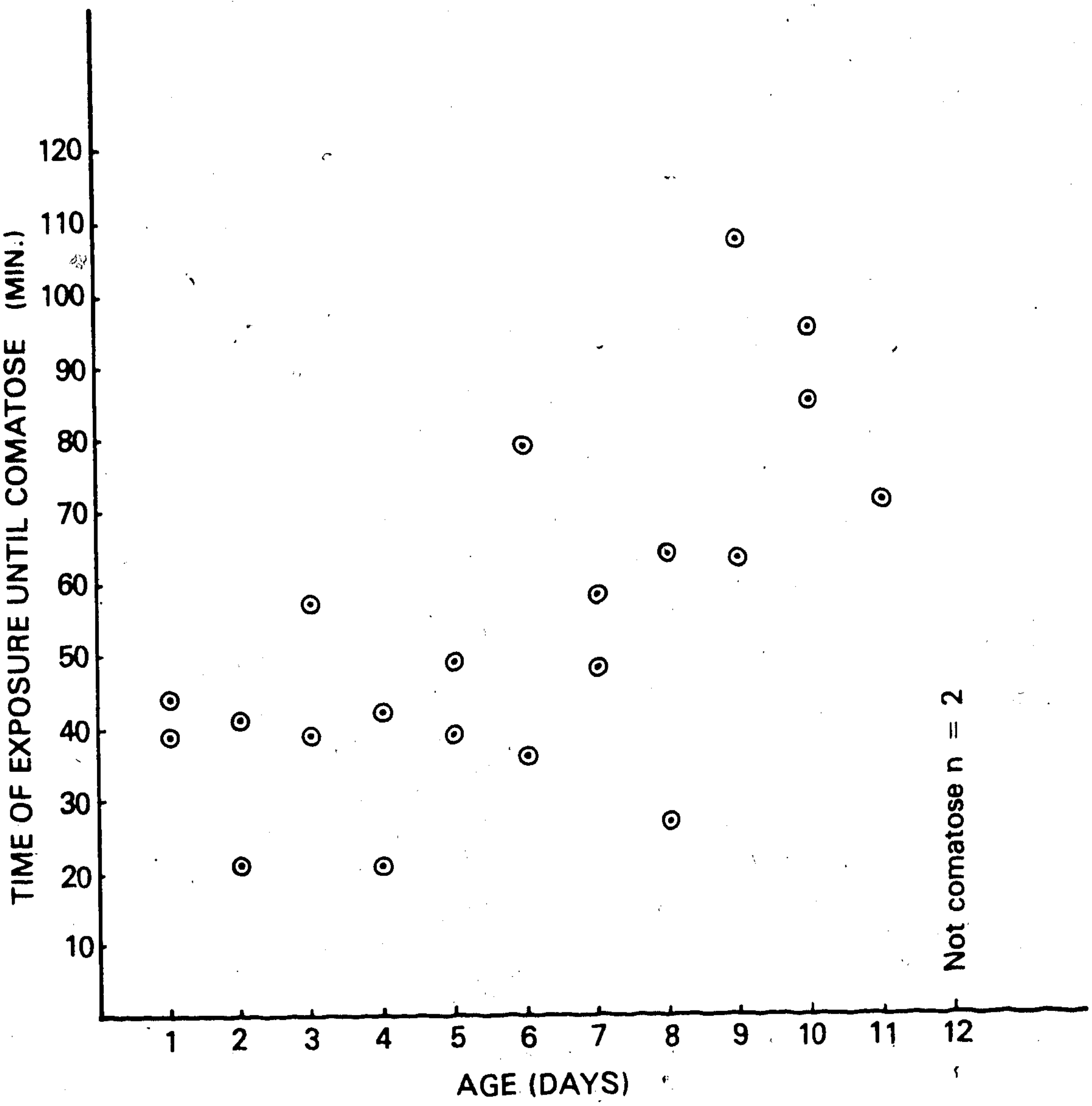

Figure III-6. The effect of exposure to cold ambient temperatures on Double-crested Cormorant nestlings one to twelve days old. Ambient = 8-15°C.

IV. Incubation and brooding behavior of Double-crested Cormorants in southern Alberta

Introduction

Thermoregulation in birds is dependent to a considerable extent on their ability to choose or construct an environment that minimizes thermal stress. Because eggs and nestlings of many species have limited abilities to cope with thermal stress from temperature, wind, or solar radiation, nest site selection and nesting behavior may be extremely important aspects of reproductive success. Responses to thermal stress during the breeding season vary from species to species and geographically. Birds nesting in situations which are thermally stressful may avoid stress by utilizing sheltered areas or by building protective nests (Hensley 1954, Ricklefs and Hainsworth 1969, Orr 1970, Calder 1971). Several species nesting in harsh desert conditions have been studied by Grant (1982) to determine how the effects of high temperature are relieved, allowing successful reproduction in fully-exposed nests.

Those species which choose to nest in northern midcontinental regions may, during the nesting season, have to cope with both high and low temperatures. Double-crested Cormorants (*Phalacrocorax auritus*) are typical examples. Clutches are initiated in late April or early May when night temperatures fall well below freezing. Nestlings may be subject to potentially lethal heat loads in early June. The lack of brood patches in pelecaniform birds presents complications for both thermoregulation and incubation of eggs (Drent 1975).

This report deals with the behavioral adaptations of Double-crested Cormorants for optimizing thermal relationships within the nesting environment.

Study area and methods

All observations were made at the nesting colony on three islands in Scope Reservoir 17 km east of Vauxhall, Alberta (50.6°N, 111.9°W) during May, June, and July of 1983 and 1984. The vegetation and topography of the island have been described by Brechtel (1983).

Data on incubation temperatures and nestling deep body temperatures were obtained by methods described previously (Van Scheik 1985a). Behavior of incubating and brooding adults was recorded on video cassette tapes by a Sears Model 30133D video cassette recorder powered by a car battery. Continuous video recordings, each four and one-half hours long, were made by equipment left in the colony focusing on nests containing telemetry equipment.

Analysis of the video data was done in the laboratory. Behaviors thermally relevant to eggs, nestlings, or adults were categorized into eight categories defined as follows:

1. Orientation of adult

Orientation of adult is the position of the adult with reference to the position of the sun or wind. Birds facing 45° on either side of the sun position or wind direction were considered to be facing the sun or wind. Tail-to-sun or wind orientation was evaluated similarly. When the bird was facing at a right angle to the sun or wind the bird was considered to be oriented laterally.

2. Gular flutter

Gular flutter is the rapid oscillation of the gular region and hyoid apparatus. Gular flutter rates were measured from video recordings using a mechanical stroboscope.

3. Egg movement

Egg movement refers to the turning or rolling of the egg as a result of moving the feet or loading the egg on top of the feet with the bill.

4. Full incubation

Full incubation refers to eggs that are in contact with the top of the feet and the breast.

5. Partial incubation

Partial incubation refers to eggs that are not on top of the feet but in loose contact with the breast.

6. Brooding

Brooding refers to nestlings totally covered or mostly covered by and in contact with the parent.

7. Shading

Shading refers to nestlings in the shade of the parent.

8. Exposed

Nestlings are fully exposed to ambient conditions of wind and temperature, either in the shade or in the sun.

Results

Results are based on 69 hours of video data. Incubation-related data consisted of 43.5 hours of video recordings of nests containing one to five eggs. The remaining 25.5 hours of recordings focused on the brooding of nestlings.

Attentive behavior is related to the time since the laying of the first egg and to the number of eggs present in the nest. A comparison of attentive behavior and average incubation temperatures for nests with one to four eggs is shown in Figure IV-1. The percent of time spent in full incubation increased gradually as eggs were laid. Eggs were continually either partially or fully incubated following the laying of the third egg. Attentiveness is reflected in the fluctuating temperatures of model eggs in nests with varying numbers of eggs (Figure IV-2). As the incubation period progresses and the number of eggs increases, temperature oscillations tend to be smaller. The amount of time spent in full incubation is reflected in the increasing mean egg temperature. While average egg temperatures were variable, there was no difference in the frequency at which eggs were moved in the nests. Eggs were moved once every 12.12 ± 2.66 minutes in the 16 nests observed.

Gular flutter, an indication of rising heat loads, was seldom observed at temperatures below 20°C. Above that temperature, a large percent of the time parents were at the nest involved gular flutter (Table IV-1). Rates of gular flutter ranged from 450 to 540/min. While gular flutter rates were relatively constant, the amplitude; i.e., the amount of flaring of the hyoid, was more variable. At low heat loads, little flaring was observed, but as heat loads increased, flaring of the gular region increased.

Orientation on the nest is an aspect of behavioral thermoregulation which, with wind, gular flutter, and sun angle, can be used to adjust heat loads. During incubation in southern Alberta, the relatively constant light southwest winds and moderate temperatures probably reduced the need for the use of orientation as a means of thermoregulating. However, as summarized in Figure IV-3, orientation during incubation deviated significantly from random. Incubating birds assumed a tail-to-sun orientation most often ($X^2 = 201$, df = 2, $P < .001$). Orientation to the wind also deviated significantly from random with incubating birds either facing the wind or in a tail-to-wind position ($X^2 = 327.5$, df = 2, $P < .001$).

The appearance of nestlings in the nest toward the end of May and the early part of June coincides with long, warm, sunny days in southern Alberta. Young nestlings with naked black skins are vulnerable to hyperthermia and, therefore, must be protected from direct solar insolation. Fully exposed nests subject attending adults to high heat loads and increased thermal stress. Orientation of the parent at the nest is important both for limiting heat load and to ensure that shade is available for nestlings in the nest. Adult orientation while brooding, summarized in Figure IV-4, shows that the tail-to-sun position was assumed significantly more of the time ($X^2 = 108.9$, df = 2, $P < .001$). Orientation with regard to wind direction was highly significant with tail-to-wind position being the favored position ($X^2 = 775.4$, df = 2, $R < .0001$).

Nestlings less than seven days old are seldom fully exposed but are alternately brooded or shaded by the parent. Exposed nestlings, though shaded and subject to the cooling effects of wind, usually rest quietly on the feet of the adult. Brooded nestlings often are covered totally except for the head which may be fully exposed to the sun. Day-old nestlings, observed to gular flutter while being brooded under ambient conditions, did not appear to be stressed. The percent of time spent by nestlings exposed in shade, brooded, or exposed to the sun is summarized in Figure IV-5.

Discussion

Attentive behavior, as exhibited by Double-crested Cormorants, appears to serve three important functions during the incubation period: protecting eggs from predators, maintaining egg temperatures within a range which ensures viability and development, and reducing the degree of asynchrony of the hatch. The presence of adults at the nest is sufficient to protect eggs and young nestlings from attacks by gulls. Unless driven from the nest by disturbance, one or both of the nesting pair are at the nest at all times. Eggs may be shaded, partially incubated or fully incubated, depending on the amount of contact with the feet and/or breast of the attending bird. Egg temperatures are effectively controlled by varying the amount of time in each mode of incubation in a manner similar to that described by Grant (1982) for the various charadriiforms he studied.

Partial incubation alternated with full incubation results in fluctuating egg temperatures (Figure IV-2). As implied by Drent (1975) and others, development gradually s[illegible] temperatures decline to the point of no development (25 to 27°C). Through partial incubation prior to clutch completion, cormorants may reduce hatch asynchrony, thereby enhancing the survivability of nestlings from eggs laid last and at the same time preventing problems of disproportionate heart growth and other anomalies associated with constantly low incubation temperatures in first laid eggs (Drent 1975). Completion of the clutch, usually four eggs, results in a greater amount of time being spent in the full incubation mode and the stabilization of egg temperatures.

While providing a suitably constant environment for optimal embryonic development, incubating adults need to compensate for the effect of environmental stress on themselves. Gular flutter, orientation on the nest, and nest relief are likely the primary methods of relieving thermal stress in incubating adults. At ambient temperatures above 20°C, adult cormorants gular flutter almost constantly. Measured gular flutter rates of incubating birds were constant between 450 to 540/min, slightly lower than the 615 to 677/min reported for juveniles of the same species in Washington by Lasiewski and Snyder (1969) or 645 to 730/min for adults in California (Bartholomew et al. 1968). Gular flutter may function independently of heat loads (Lasiewski and Snyder 1969).

Day-old nestlings were observed to gular flutter while being brooded. In most cases when this occurred, the nestling's head was exposed to direct sunlight. The temperature regulation center is located in the hypothalamus of the brain. Day-old nestlings have featherless heads and very thin skulls. Direct stimulation of the hypothalamus may elicit cooling behavior even though body temperature is not elevated.

Dark coat colors may either increase or decrease the solar heat load, depending on how species specific factors such as plumage insulation and feather microstructure interact with wind velocity. Provided the wind exceeds 3 m/sec (10.8 km/h), a black feathered bird can heat radiatively out of the wind or reduce heat loads in the wind by erecting plumage (Walsberg et al. 1978, Walsberg 1982). Orientation toward the sun, along with postural adjustments, can regulate heat gain from solar insolation by regulating the amount of surface area exposed and by either exposing or protecting those surface areas which are most absorptive to solar radiation (Lustick et al. 1978). As the angle of incidence of incoming radiation increases, the difference in heat transfer between light and dark plumages disappears (Lustick et al. 1980). By postural adjustments, therefore, a dark feathered bird can respond thermally as though it were white.

Bare-skinned areas were found to be important in temperature regulation in black vultures (Coragyps atratus) (Larochelle et al. 1982). Double-crested Cormorants are black and have featherless skin in the gular region. It may be expected, then, that orientation should play an important part in their thermoregulation. Facing toward or away from the sun reduces the surface exposed to the sun to a minimum. The tail-to-sun position has the additional advantage of shading the gular region, thereby permitting gular flutter to proceed with maximum efficiency.

At low wind velocities, birds with large, white-feathered areas may reduce radiative heat gain by facing the sun and exposing the white areas (Grant 1982, Lustick et al. 1978). In the absence of wind, Heermann's Gulls (Larus heermanni) oriented randomly (Bartholomew and Dawson 1979) while Masked Boobies (Sula dactylatra), white birds except for feet and wing primaries, faced away from the sun regardless of wind direction (Bartholomew 1966). Since the winds in southern Alberta are predominantly from the southwest, it is difficult to determine if orientation on the nest is the result of wind or sun. Winds greater than 3 m/sec may be more important than sun in determining orientation on the nest (Dexter 1961). A tail-to-wind position would maximize the effect on cooling when feathers were erect and at the same time coincide with a facing-away-from-the-sun position during the hottest part of the day.

Nestlings and eggs are dependent on adults for thermoregulation. Adult cormorants use wind, orientation, and gular flutter to thermoregulate. In southern Alberta, eggs and nestlings are protected against hypothermia and hyperthermia by the ability of the adults to meet the thermal stress of the environment.

Literature Cited

Bartholomew, G. A. 1966. The role of behavior in the temperature regulation of the Masked Booby. Condor 68: 523-535.

Bartholomew, G. A. and W. R. Dawson. 1979. Thermoregulatory behavior during incubation in Heermann's Gulls. Physiol. Zool. 52: 422-437.

Bartholomew, G. A., R. C. Lasiewski and E. C. Crawford, Jr. 1968. Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. Condor 70: 31-34.

Brechtel, S. H. 1983. The reproductive ecology of Double-crested Cormorants in southern Alberta. M.Sc. Thesis, Univ. of Alberta, Edmonton, Alberta. 119 pp.

Calder, W. A. 1971. Temperature relationships and nesting of the Calliope Hummingbird. Condor 73: 314-321.

Drent, R. H. 1975. Incubation. In Avian Biology, Vol. 5. Farner, D. S. and J. R. King eds. Academic Press, New York, N.Y. pp. 333-420.

Dexter, R. W. 1961. Further studies on nesting of the Common Nighthawk. Bird-Banding 32: 79-85.

Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30, Amer. Ornithol. Union.

Hensley, M. M. 1954. Ecological relations of the breeding bird population of the desert biome in Arizona. Ecological Monogr. 24: 185-207.

Larochelle, J., J. Delson, and K. Schmidt-Nielsen. 1982. Temperature regulation in the Black Vulture. Can. J. Zool. 60: 491-494.

Lasiewski, R. C. and G. K. Snyder. 1969. Responses to high temperature in nestling Double-crested Cormorants and Pelagic Cormorants. Auk 86: 529-540.

Lustick, S., M. Adam and A. Hinko. 1980. Interaction between posture, color, and radiative heat load in birds. Science 208: 1052-1053.

Lustick, S., B. Battersby and M. Kelty. 1978. Behavioral thermoregulation: orientation toward the sun in

Herring Gulls. Science 200: 81-83.

Orr, Y. 1970. Temperature measurements at the nest of the Desert Lark (Ammomanes deserti deserti). Condor 72: 476-478.

Ricklefs, R. W. and F. R. Hainsworth. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71:32-37

Van Scheik, W. J. 1985a. Egg incubation and thermal tolerance in Double-crested Cormorants in southern Alberta. Ph.D. Thesis, Univ. of Alberta, Edmonton, Alberta.

Walsberg, G. E. 1982. Coat color, solar heat gain, and conspicuousness in the Phainopepla. Auk 99: 495-502.

Walsberg, G. E., G. S. Campbell and J. R. King. 1978. Animal coat color and radiative heat gain: a re-evaulation. J. Comp. Physiol. 126: 211-222.

Table IV-1. Percent of time incubating birds spent gular fluttering at various dates and ambient conditions. Each date represents a different incubating pair.

Date	Time	Average air temp. (°C)	Average wind velocity (km/h)	Time gular flutter (%)
May 8	9:30 am - 2:00 pm	17.5	21.5	0
May 12	7:30 am - 11:50 am	13.0	16.7	0
May 15	1:00 pm - 5:00 pm	22.0	16.1	66.1
May 18	5:00 pm 9:30 pm	16.5	12.5	0
May 22	1:00 pm - 5:00 pm	20.5	14.2	91.8
June 3	1:00 pm 5:00 pm	24.0	16.6	88.3

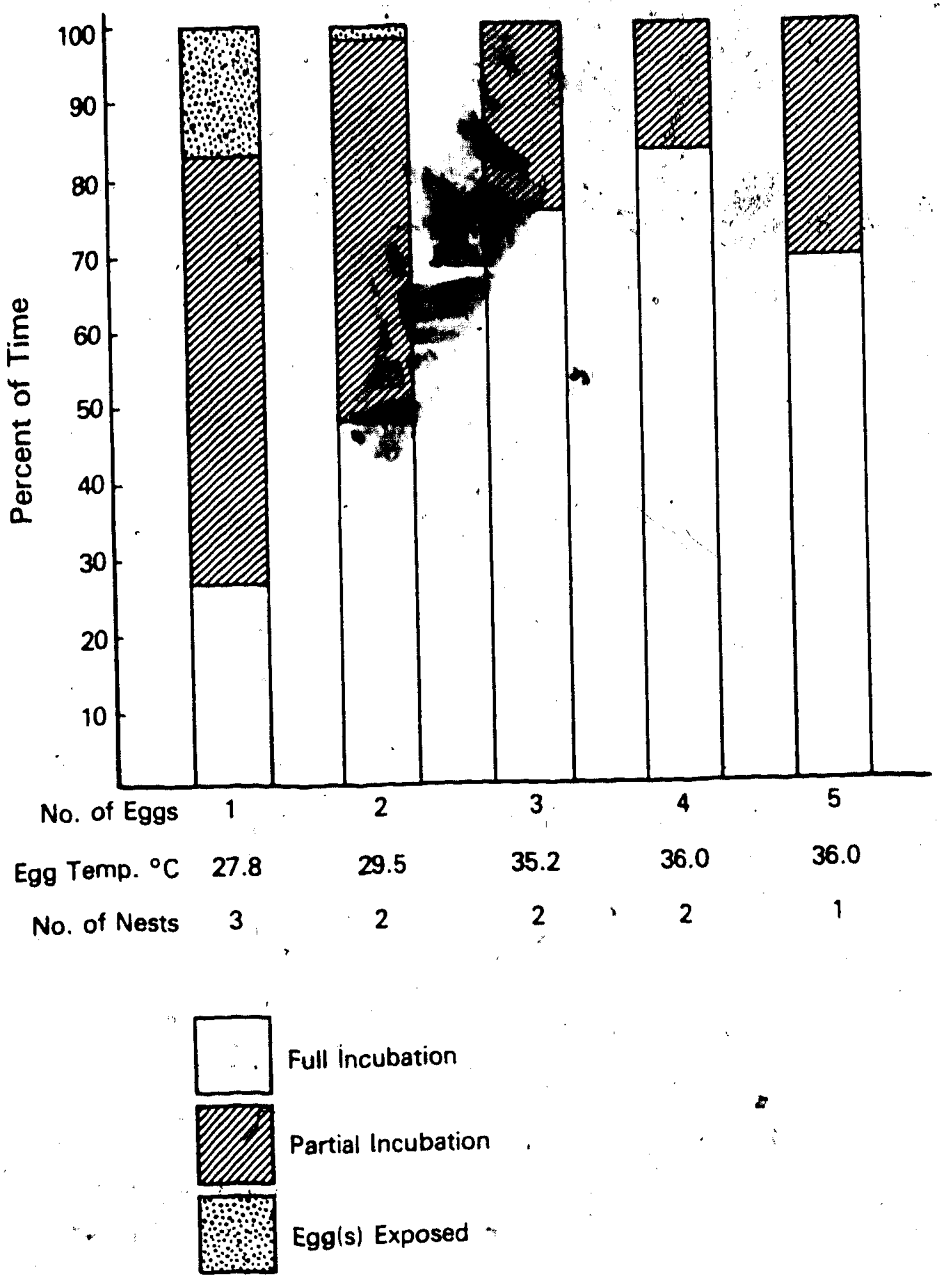

Figure IV-1. Incubation attentiveness of Double-crested Cormorants in relation to the number of eggs in the nest and egg temperature.

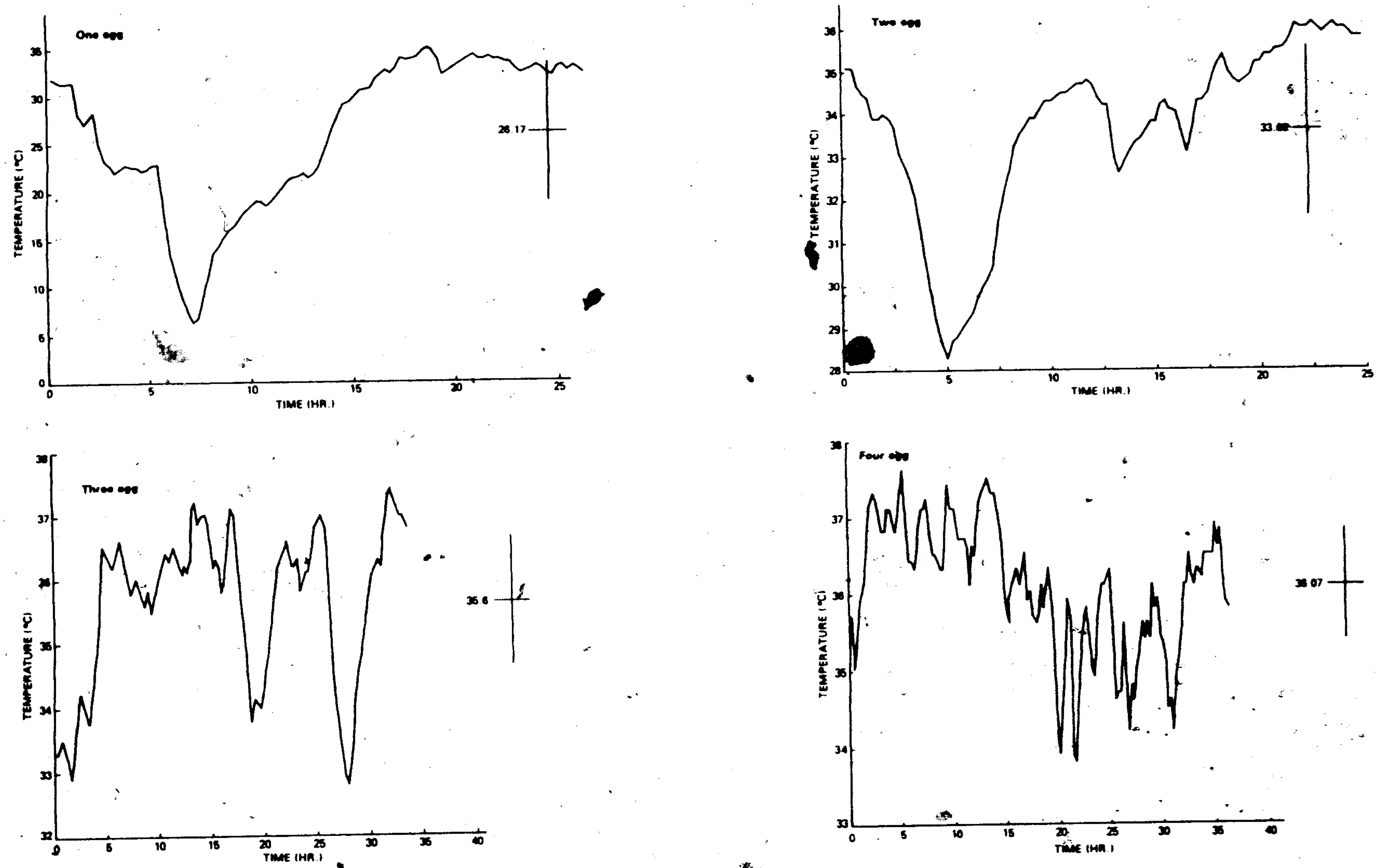

Figure VI-2. Temperatures of model eggs in nests containing one, two, three and four eggs, May 8-12, 1983. Note different temperature scales. Vertical line = standard deviation, horizontal line = mean for that nest.

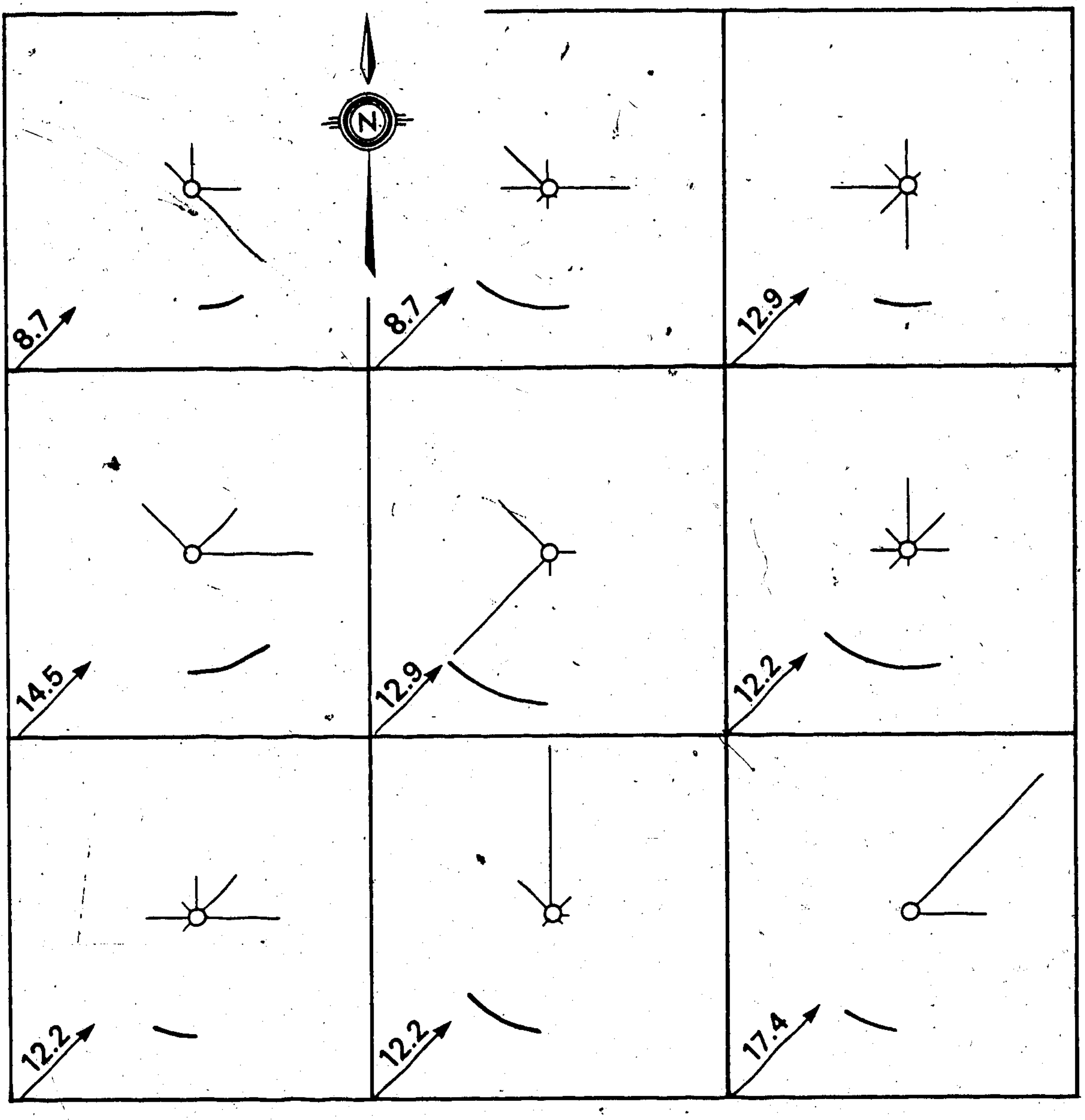

Figure IV-3. Orientation of nine different incubating Double-crested Cormorants with respect to sun and wind. Arrow indicates wind velocity (km/h). The curved line represents the sun arc and the bars radiating from the nest indicate the percent of time facing that direction.

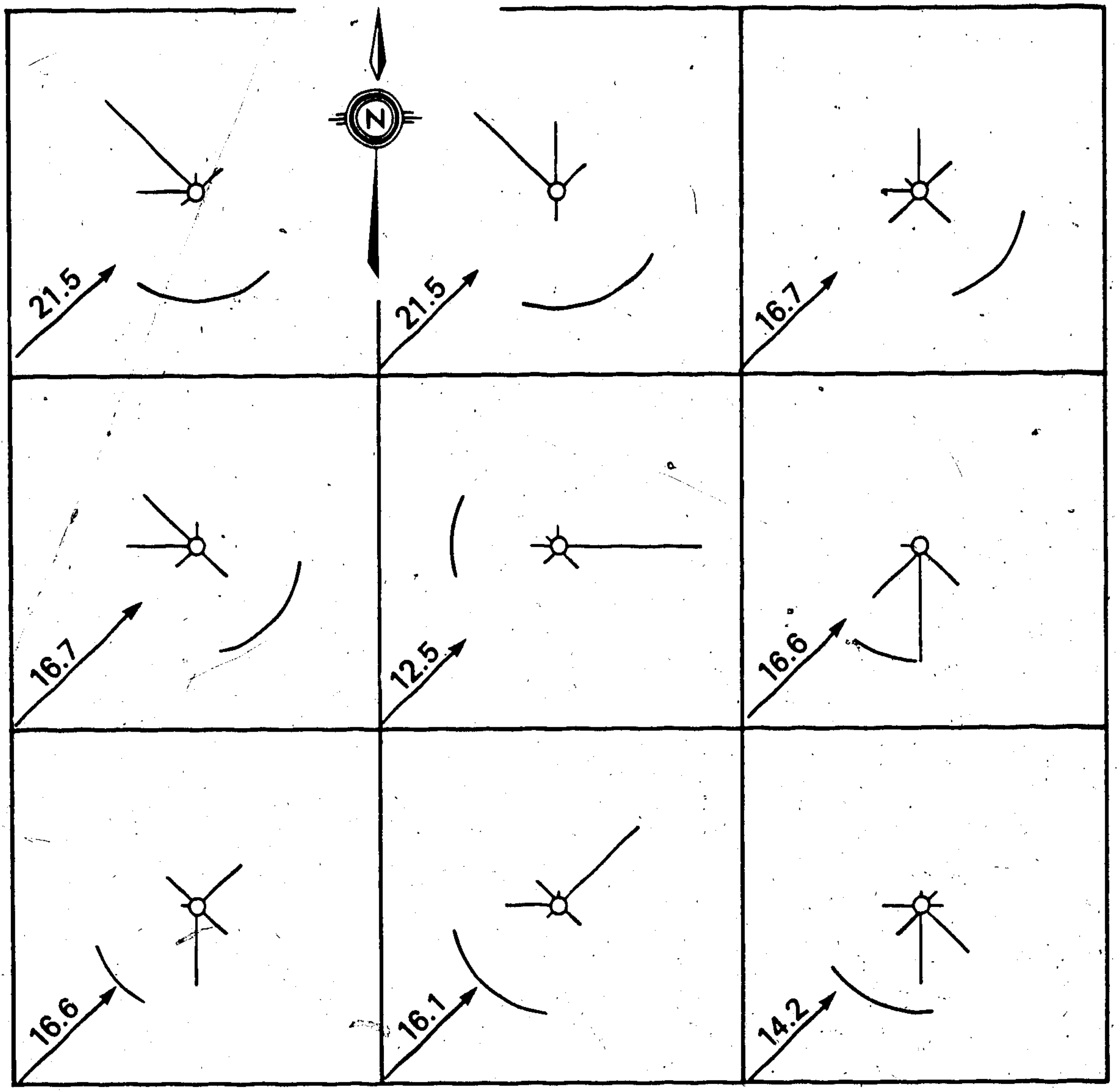

Figure IV-4. Orientation of nine different brooding Double-crested Cormorants with respect to sun and wind. Arrow indicates wind velocity (km/h). The curved line represents the sun arc and the bars radiating from the nest indicate the percent of time facing that direction.

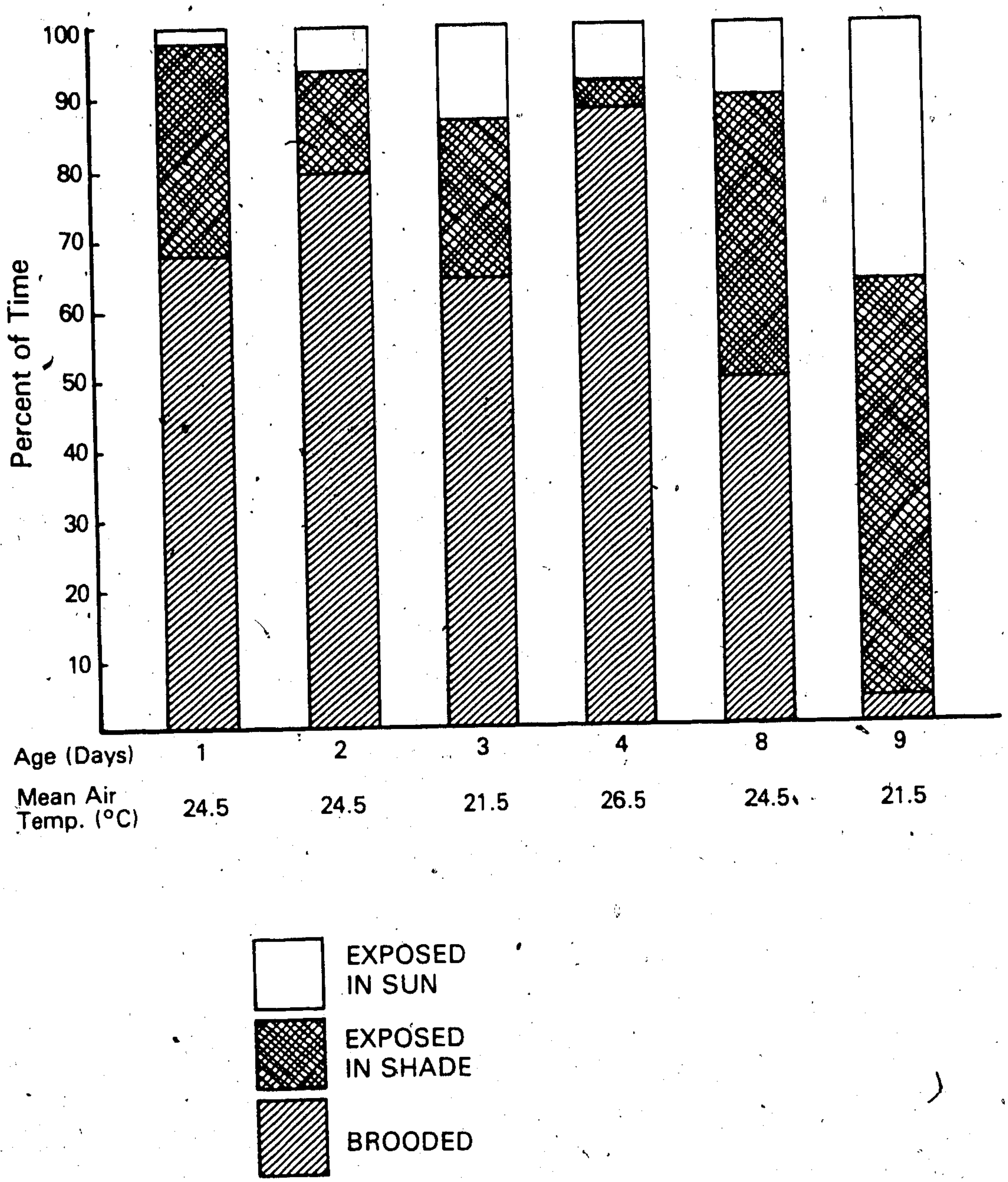

Figure IV-5. Percent of time nestlings were exposed or brooded in relation to age and air temperature. Observations on each nestling were made continuously for four and one-half hours at midday.

V. Thermal significance of Double-crested Cormorant shell structure and pigmentation

Introduction

Factors affecting the thermal properties of avian eggs are known to include pigmentation (Bakken et al. 1978), surface staining and deposits (Grant 1982). Other factors such as shell thickness and the volume of the egg itself would affect the rate of temperature change following exposure. Cavity nesting birds and those which begin to incubate after the first egg is laid usually lay white eggs, while open nesting, particularly ground nesting birds, lay colored eggs which are often cryptic (Lack 1958).

Eggs of many bird species are known to reflect as much as 90% of incident solar radiation in the near infrared part of the spectrum (Bakken et al. 1978). Infrared (wavelengths of 800 nanometres to 50 microns) accounts for slightly less than half of incident solar radiation. The remaining energy in solar radiation is in the ultraviolet-visible portion of the spectrum. Brown protoporphyrins, blue bilivardin IXa and its green zinc chelate are the principal shell pigments which influence the amount of solar radiation absorbed (Kennedy and Vevers 1973). Double-crested Cormorants (Phalacrocorax auritus) lay blue eggs in exposed nests. Blue birds (Sialia sp.) also lay blue eggs but are cavity nesters. If, as Lack (1958) suggests, egg color is associated with the type of nest site, the value of blue pigmentation in both cormorants and blue birds is unclear.

The effect of shell structure, pigments, and soiling as factors in the thermal environment of eggs has received little attention. In this paper, the effect of shell structure, pigmentation, and soiling in relation to heat transfer by fluorescence and infrared emission is reported.

Methods

Shell pigment analysis

Blue shell pigments were extracted by putting the ground up shell into a small volume of 6 mole/litre HCl and stirring at high speed with a magnetic stirrer. The resulting light blue colored froth was removed as it formed and agitated with methanol. After settling, the blue supernatant liquid was centrifuged 10 minutes at 15,000 RPM. The clear pigment solution was decanted and stored in light proof containers. This method was much more efficient than that used by Kennedy and Vevers (1973).

To determine the number of different pigments present in the pigment extract, a sample was concentrated by evaporation. Thin layer chromatography using methanol as the solvent was used to attempt separation of pigments.

Spectral characterization of the pigment was undertaken for both fluorescence and absorptivity. Absorbance was scanned between wave lengths of 200 to 800 nanometres using a Hewlett Packard diode array spectrophotometer. Excitation spectroscopy and fluorescence measurements were made with a Ferrand MK2 spectroflurometer.

Shell structure analysis

Shell fragments (ca 5 mm^2) from eggs which had minimal, light, and heavy calcite deposits and flea defecation on the surface were selected for scanning electron microscopy. Untreated shell fragments were mounted perpendicularly on separate stubs, sputter coated with gold (150 A) in a Nanotec coater and examined using a Cambridge Stercoscan 100 electron microscope. Representative and selected portions of the fragments were photographed. Contact prints of these photographs were prepared for study purposes. The structure and nature of the calcite deposit on the shell surface was examined both qualitatively and quantitatively.

Thermal properties of the shell

A comparison of the heat transmission properties of shell fragments (ca 3.6 cm^2) for clean shell with minimal calcite deposit, heavy soiling, spotted soiling, normal Ring-billed Gull shell, and white chicken eggshell was made by monitoring the temperature change of agar 2 mm below the inner shell surface. The shell fragments were sealed to the top of a glass shield with silicone adhesive after the agar contact between the shell and temperature probe had set (Figure V-1). Temperatures were recorded every 30 seconds for 20 minutes.

The same shell fragments used to compare heat transmission properties were used to compare infrared emission. After being placed on a styrofoam block, the shell fragments were heated in a drying oven to 65°C. The uniformly heated shells were removed from the oven and immediately monitored using an Aga Thermovision 750 (AGAtronics Ltd., Toronto, ON M8Z 4X4) infrared camera system. A permanent record of the video display was made by taking polaroid pictures every 15 seconds as the shells cooled.

Results

Pigment analysis

The light blue pigment extracted from the shell was unstable in light but would keep for several weeks if stored in foil-wrapped vials. Only one pigment could be detected by thin-layer chromatography. The single pigment known to produce blue eggshell coloration is biliverdin (Kennedy and Vevers 1976).

An absorbance spectrum of the pigment revealed absorbance in the region of 280 nanometres with declining absorbance as the wavelength increased (Figure V-2). The low absorbance in the visible and near infrared region of the spectrum would imply high transmission in this region. The pigment samples fluoresce, although the emission is weak with maximum fluorescence occurring at 330 nanometres (Figure V-3). Excitation spectra resemble the ultraviolet-absorption spectra very closely, suggesting a reasonably pure sample. No emission could be detected with excitation at wavelengths longer than 300 nanometres, although this region was examined.

Shell structure

The structure of the Double-crested Cormorant eggshell is typical of most other bird species for structures below the cuticle. Scanning electron microscopy reveals the absence of a true cuticle in this species (Figure V-4). The outermost layer overlaying the true shell is a calcite layer which may completely hide the pigmented shell beneath. Total thickness of various types of shells is summarized in Table V-1. Thickness of the calcite cover of shell fragments examined by electron microscopy varied considerably, ranging from 20 to 80 microns.

Whole shell properties

Thermal absorbance properties of the eggshells were found to be variable depending on the thickness of the calcite cover and the amount of soiling. Clean blue eggshells generally heated more slowly while eggshells with calcite covers heated more quickly than shells spotted or smeared with flea excrement. Soiling due to smearing by flea excrement had variable effects but did not increase the heat absorbing qualities of the shell. Table V-2 summarizes the time taken for various shell types to reach 42.2°C.

Shell fragments cooled at different rates as determined by infrared thermography. The thinner shells cooled fastest as expected, however, eggshells soiled with smeared flea excrement cooled faster than thinner chicken eggshells or those spotted with flea excrement. The cooling order--gull, blue cormorant, smear-soiled cormorant, chicken, spot-soiled cormorant, heavy calcite-covered cormorant--was consistent over the 20 observations. Thermographs taken at 15-second intervals over the cooling period are shown in Figure V-5.

Discussion

The presence of pigments in the eggshells of birds has long been a subject of discussion. Two questions have persisted: How does the pigment reach the shell? What is its function?

The first question is beyond the scope of this study. Answers to the second revolve around the function of the pigment in the shell calcification process (Kennedy and Vevers 1973) or in terms of the cryptic value a combination of pigments may afford the egg (Tinbergen et al. 1962, Lack

1958). Recently Bakken et al. (1978) suggest that eggshells containing protoporphyrins and bilin may, in addition to giving cryptic protection, provide high reflectivity in the near infrared while absorbing only visible radiation.

During incubation, cormorant nests are heavily infested with the Western Hen Flea (<u>Ceratophyllus niger</u>). These blood-sucking parasites breed in guano and congregate in large numbers under the warm eggs in the nest. Following blood meals on adult birds, the fleas deposit excrement on the eggs and nest material. These spots smear, causing the eggs to stain a brown color. The amount of staining increases directly as the length of time the egg is in the nest so that the order of laying can be determined by noting the amount of egg discoloration. While the blue pigment in cormorant eggshells has no apparent cryptic value, heavily soiled eggs are far more cryptic than clean blue or chalk white freshly laid eggs. Soiling has little or no effect thermally but is probably advantageous to the bird because of the protection afforded the egg by making it less obvious in the nest.

The purified, extracted pigment absorbs energy in the ultraviolet region of the spectrum (280 nanometres) but at wavelengths greater than 300 nanometres absorbance is very low. It is noteworthy, however, that excitation at 280 nanometres results in fluorescence at 330 nanometres. The pigment is effectively unresponsive to all wavelengths examined above 330 nanometres. High transparency would reemphasize the question of the function of this pigment. Clearly the response of the isolated pigment is inadequate to explain the response of the eggshell and pigment to solar radiation. Cormorant eggs heat rapidly when exposed to direct solar insolation. Reflectance of incident solar radiation in conjunction with shell structural properties is the most probable function of pigment, yet a pigment obscured by a layer of calcite can hardly be expected to contribute to the reflective properties of the surface. All Double-crested Cormorant eggs have a detectable calcite cover which, in most eggs, totally or partially obliterates the pigmented true shell. It is tempting to speculate that the pigment's function is buried in the evolutionary history of the species.

Tyler (1969) notes that shells of the Podicipediformes and Pelecaniformes (except for the Phaethontidae) have a calcereous cover over the shell. The thickness is variable within and among species in these families. Among the Phalacrocoracidae, cover thickness varied from as little as 4 microns in Phalacrocorax carbo novaehollandae to 80 microns in P. auritus (Tyler 1969).

This cover completely hides the true shell surface and the pore mouths. As seen in Figure V-4, this covering layer is very porous. This type of structure would be expected to minimize heating by conduction and facilitate cooling by interstitial convection, yet eggs having calcite covers heated more quickly than those with little or no cover. The same shells also cooled more slowly. This seems at first to be inconsistent with the needs and properties of the eggs, but further consideration suggests it is not. Under normal circumstances, cormorant eggs are not exposed to direct solar insolation likely to result in overheating; therefore, having a highly heat absorbing cover is no disadvantage. Since incubation depends on warming the egg without contact to a brood patch, as in most bird species, having a heat absorbing cover may be distinctly advantageous. Shells which heat quickly and retain heat well would allow more efficient energy utilization, both reducing the energy cost of incubation to the parent and stabilizing the thermal environment of the egg, thus facilitiating continuous and uniform development of the embryo.

Literature cited

Bakken, G. S., V. C. Vanderbilt, W. A. Buttemer and W. R. Dawson. 1978. Avian eggs: thermoregulatory value of very high near-infrared reflectance. Science 200: 321-323.

Grant, G. S. 1982. Avian incubation: egg temperature, nest humidity and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30, Amer. Ornithol. Union.

Kennedy, G. Y. and H. G. Vevers. 1973. Eggshell pigments of the Araucano Fowl. Comp. Biochem. Physiol. 44B: 11-25.

Kennedy, G. Y. and H. G. Vevers. 1976. A survey of avian eggshell pigments. Comp. Bioehcm. Physiol. 55B: 117-123.

Lack, D. 1958. The significance of color in Tudine eggs. Ibis 100: 145-166.

Tinbergen. N., G. J., Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk and E. Szulc. 1962. Eggshell removal by the Black-headed Gull. *Larus ridibundus*, L.: a behavior component of camouflage. Behaviour 19: 74-117.

Tyler, C. 1969. A study of the eggshells of Gaviiformes, Procellariiformes, Podicipitiformes and Pelecaniformes. J. Zool. Lond. 158: 395-412.

Table V-1. Thickness of Double-crested Cormorant, Ring-billed Gull and chicken eggshells.

Shell type	Thickness (mm)	n
Cormorant		
clean blue	.358 ± .031	10
spot soiled	.402 ± .020	10
smear soiled	.414 ± .017	10
heavy calcite cover	.468 ± .047	10
Chicken	.343 ± .029	3
Gull	.298 ± .032	3

Table V-2. Summary of the time for various shell types to reach 42.2°C.

Shell type	n	Average time to reach 42.2°C (min)	Average shell thickness (mm)
Cormorant			
clean blue	7	11.0	.358 ± .031
spot soiled	4	10.6	.402 ± .020
smear soiled	4	9.6	.414 ± .017
heavy calcite cover	7	9.1	.468 ± .047
Chicken	3	8.5	.343 ± .029
Gull	3	7.85	.298 ± .032

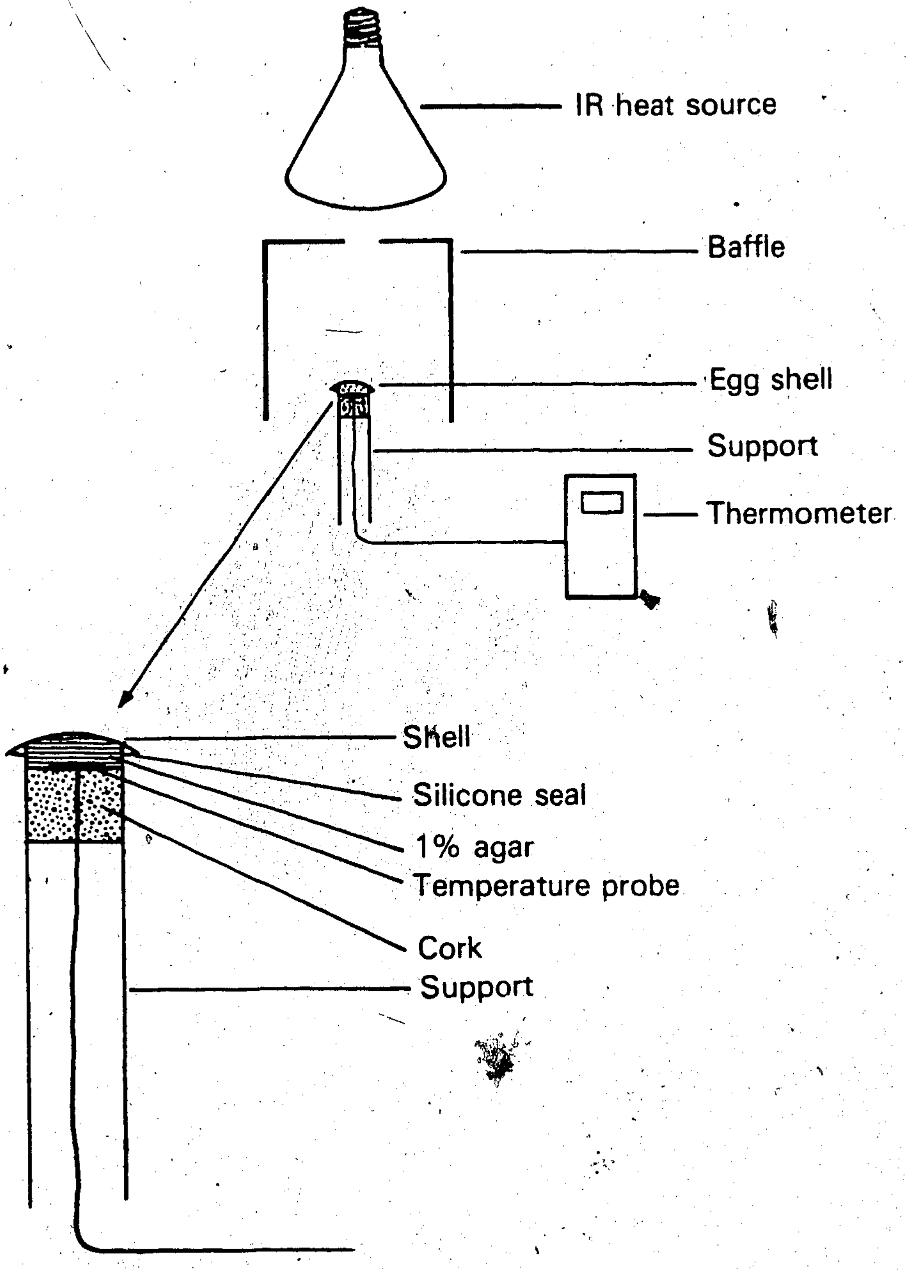

Figure V-1. Apparatus used to test thermal conductance of eggshell.

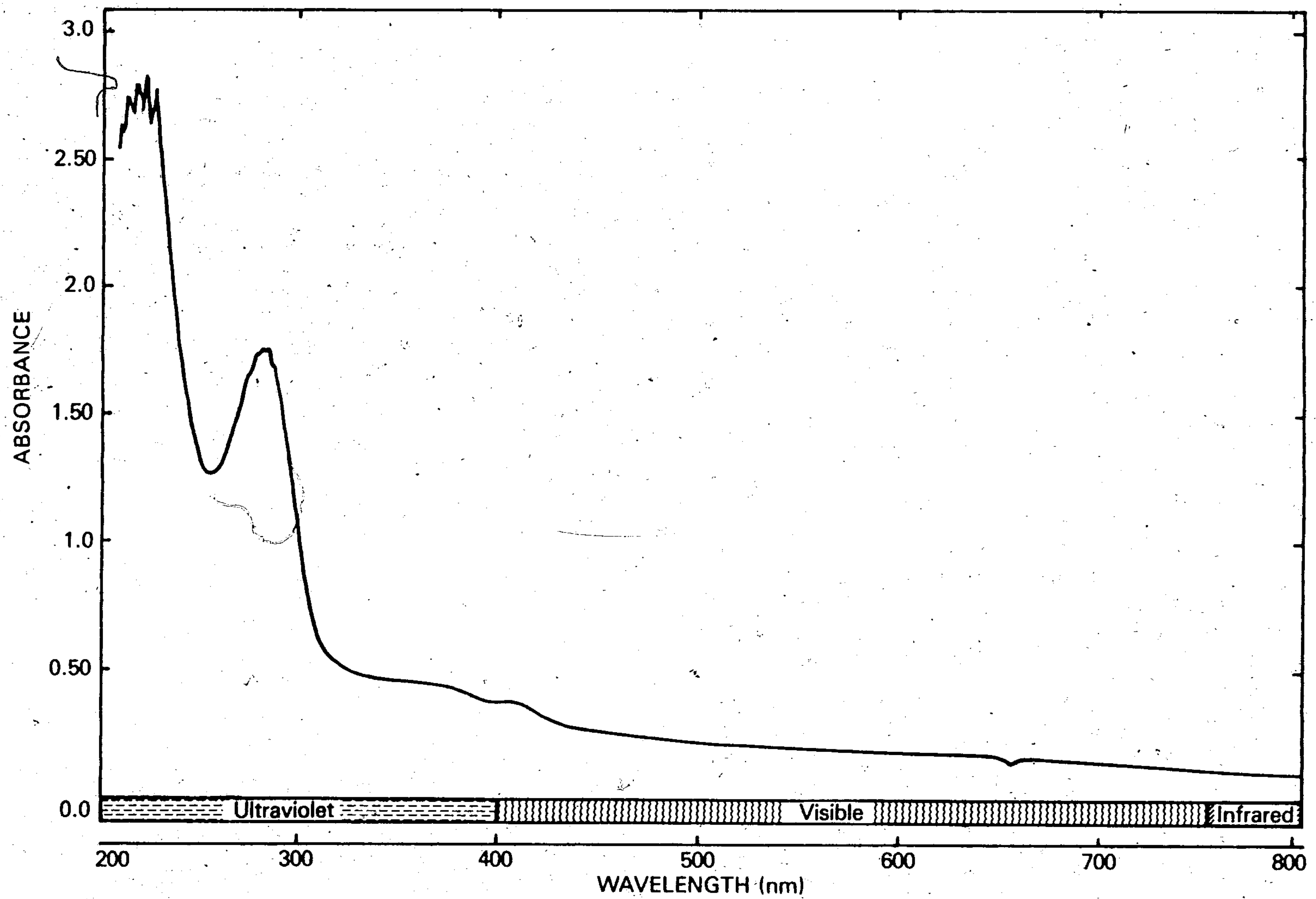

Figure V-2. Absorbance spectrum of the light blue cormorant eggshell pigment.

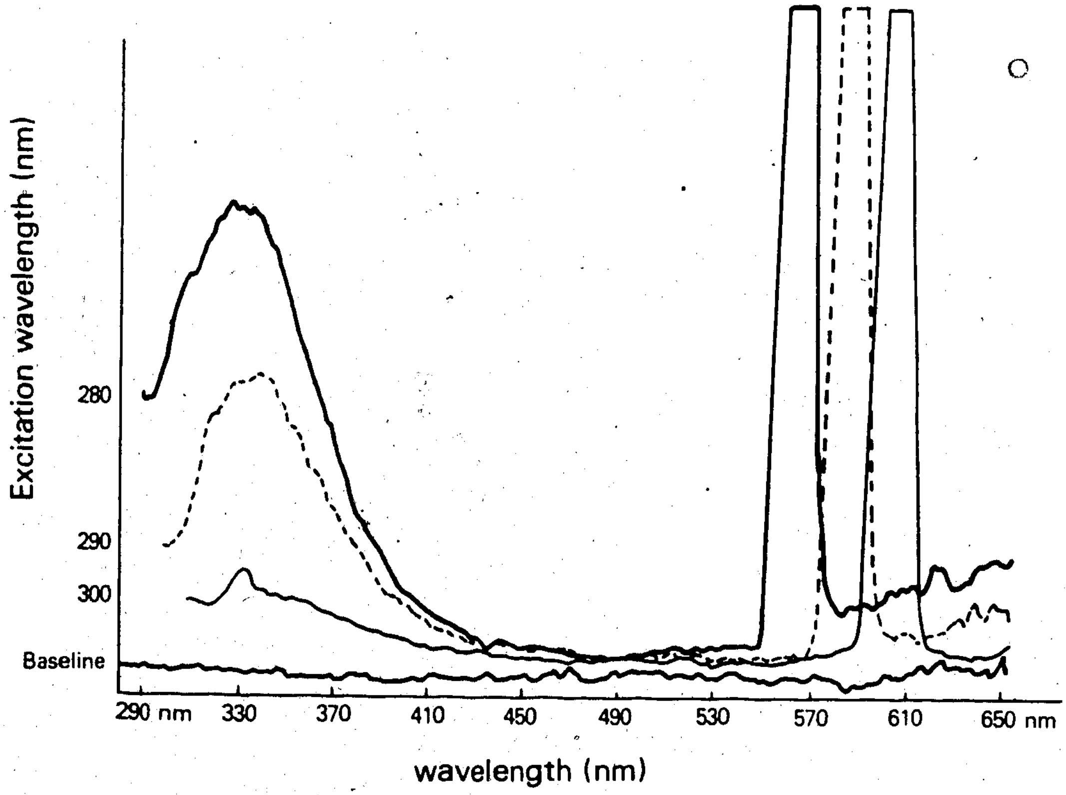

Figure V-3. Excitation spectrum of Double-crested Cormorant eggshell pigment. Note that the peaks in the 560-610 nm region are 2X harmonics of the excitation frequency.

Figure V-4. Structure of Double-crested Cormorant eggshells collected one week after laying. A. Radially fractured eggshell 158X including (a) outer eggshell membrane, (b) mammillary layer, (c) palisade layer, and (d) cover (scale bar = 200 um). The calcified cover B. is seen to be placed directly on top of the palisade layer (1000X) and is about 58 um thick (scale bar = 50 um). In C. the cover is magnified 5040X. Note random arrangement of calcite spherites and high porosity (scale bar = 10 um). In D. the calcite cover is overlaid by a spot of flea defecant before smearing (317X, scale bar = 100 um).

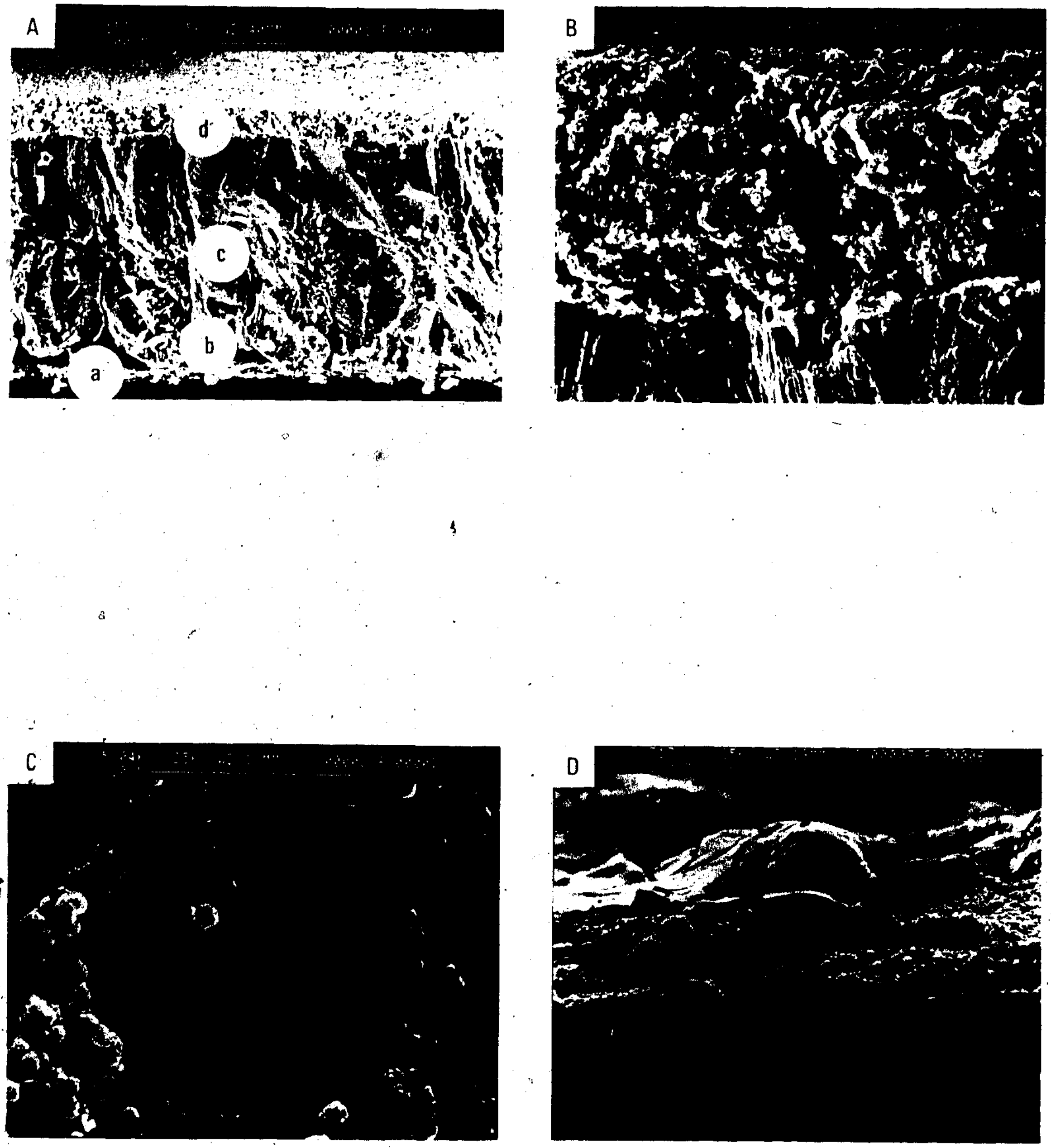
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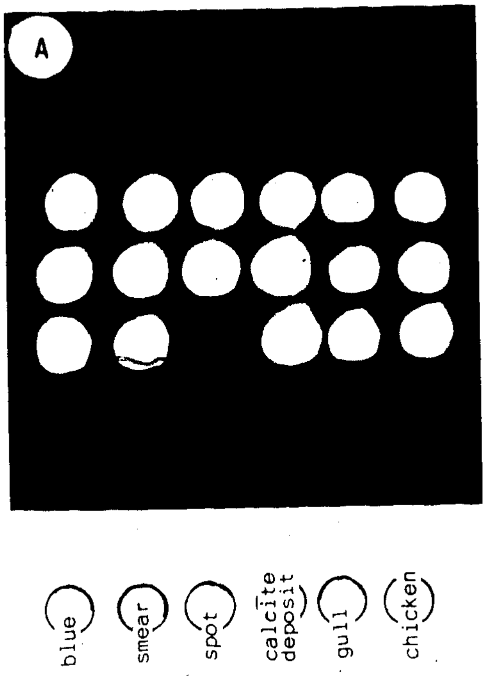
Figure V-5. Thermographs showing differential cooling rates of eggshells heated to 65°C and observed with infrared thermography at 15 sec intervals. Circles under the thermographs identify the shell type in that column. Note that in A. 15 sec after removal, infrared emission is uniform. In B. 30 sec after removal, both the gull eggshells and the blue cormorant shells show definite signs of cooling. Thermography C. 45 sec after removal indicates cooling is detectable in all shell types but shells with heavy deposit are warmest. In D. one minute after removal, only shells with heavy deposit are emitting detectable amounts of infrared.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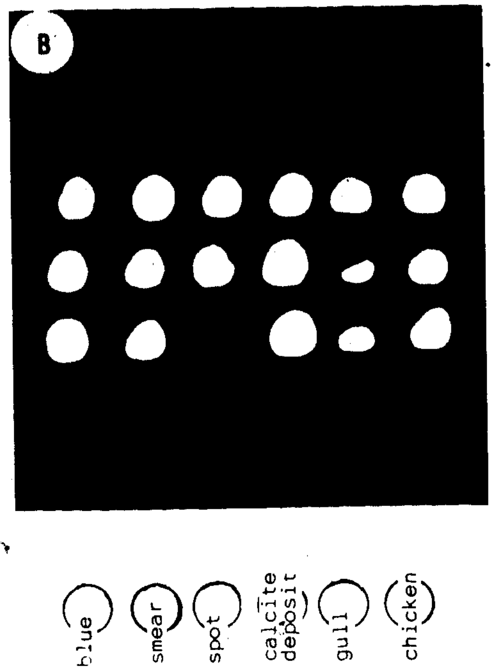
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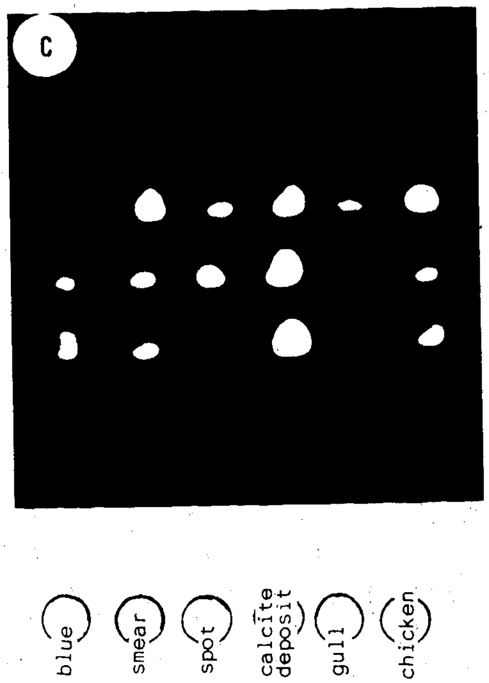
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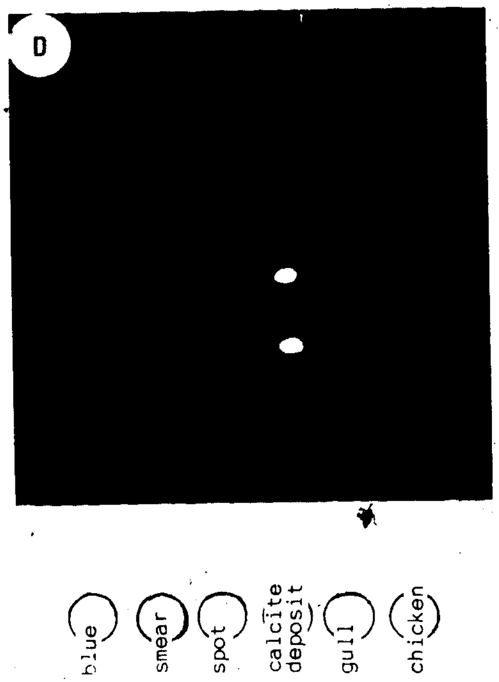
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VI. Concluding Discussion

Bird distribution, according to Welty (1979), is a result of the interplay of two great dynamic agents: the perpetually changing environment and the continually evolving bird. Ecological fitness; i.e., those abilities and characteristics which make survival and reproduction possible at the local level, provides clues as to the problems of geographic distribution. Large-scale distribution patterns require the consideration of greater and more persistent forces, such as those of geology, climatology, and adaptive radiation. Energy exchange in living organisms embraces a variety of subjects and is central to consideration of such topics as geographic distribution, productivity, and thermoregulation. Thermoregulation and heat transfer, fundamentally important considerations for all homeotherms, become overriding considerations in the reproductive ecology of birds. While maintaining a steady state between heat income and loss in an adult bird may not be difficult given the high degree of mobility of birds, thermal balance becomes exceedingly complex with the presence of eggs and young which are both immobile and thermally dependent. The heterogeneity of the environment with constantly fluctuating thermal parameters, such as the constantly changing temperatures of air, nest and surrounding substrate, variable wind speed, humidity, and solar insolation, requires high levels of adaptability on the part of the adult and considerable thermal plasticity on the part of the embryo or nestling.

Thermal aspects of the reproductive ecology of Double-crested Cormorants can be considered in four distinct categories: embryonic hardiness, nestling hardiness, parental adaptive behaviors, and structural adaptations. The normal thermal environment of eggs in the nest and the ability of embryos to withstand fluctuations in that environment is of primary importance.

In this study the high mortality of embryos at temperatures above 42.2^{o}C is consistent with data on other species (Drent 1975, Bennett et al. 1981). Eggs exposed to direct solar insolation can heat rapidly; in reality, however, the risks of overheating are minimal as eggs would only be exposed during disturbance. No disturbance, other than that caused by my presence in the colony or as a result of management procedures, was ever observed during the three nesting seasons studied. During the time eggs are present in the nest, solar insolation is weak and is accompanied by a constant light breeze. To be harmful to the embryos, exposures would have to be prolonged. Although internal egg temperatures were shown to increase at a maximum of 0.36^{o}C/min when exposed in no-wind situations, internal temperatures reaching lethal limits in the field were never observed. In all cases, wind or cloud prevented excessive temperature increases. Cold hardiness of embryos, coupled with the low probability of heat stress, suggests that factors other than temperature control the breeding range of this species in Alberta.

Embryonic cold tolerance allows truncation of the hatch. Maintaining the first-laid eggs at lower temperatures slows embryonic development and thus reduces asynchrony. Egg temperatures increase as more eggs are laid. Maximum egg temperatures are not attained until after the third egg is laid, at which time an internal temperature of about 36°C is maintained. The absence of a brood patch may facilitate the control of egg temperature by permitting a number of differing modes of incubation. Contact with the totipalmate feet and feathers of the breast may be present or absent, tight or loose, thus allowing the fine tuning of internal egg temperature to suit short-term developmental requirements and long-term considerations of asynchrony.

Lack (1954) suggested that hatch asynchrony, as seen in a few species such as owls and hawks, is the exception to the general rule of synchronized hatch of most birds. He considered hatch asynchrony to be an adaptation to widely fluctuating food supplies for hawks and owls, particularly in the arctic. When food supplies are low, adjustment of brood size allows parents to cut their losses by eliminating those chicks in which their investment is smallest.

Synchronous hatching would be particularly advantageous in situations of abundant food, low predation threat, and high thermal stability. It optimizes the effects of environmental stability and equilibium. Asynchrony would be advantageous where the parameters contributing to nesting success are less predictable.

Asynchronous hatching is widespread among bird species. Clark and Wilson (1981) summarize data on 87 altricial species and indicate hatch spreads varied from seven hours to eight days. In Double-crested Cormorants hatch spreads of six days are not uncommon for a clutch of five eggs (Brechtel 1983).

Where the egg laying spread is great, mechanisms which reduce overall hatch asynchrony may be present. Double-crested Cormorants with interegg intervals of up to two days (Robertson 1971) and subject to egg predation before clutch completion have mechanisms to reduce but not eliminate asynchrony. Egg size decreases with each successive egg and the last two eggs in a clutch of five are significantly smaller than the others (Brechtel 1983). Small eggs have shorter incubation periods than large ones (Bryant 1975, Parsons 1970, 1975). Egg size differences in cormorants thus tend to reduce hatch asynchrony. Holding egg temperatures at low levels until the clutch is nearly complete results in further truncation of the hatch.

Hatching asynchrony as a mechanism primarily to facilitate nestling loss (Lack 1954, Ricklefs 1965) seems simplistic. As an insurance against nest failure, asynchrony may contribute directly to both individual and brood survival. Broods handle thermal stress better than individuals (Clark and Balda 1981). Clutches of one egg never fledged nestlings in Brechtel's (1983) study, possibly because of the inability of the nestlings to handle thermal stress alone. Nestlings are known to move into the shade of adult birds (Dunn 1976). In southern Alberta colonies, small nestlings moved into shade provided by older siblings. Clearly hatch asynchrony in this instance is a mechanism for preventing brood reduction.

Hatch asynchrony in Double-crested Cormorants may serve several functions and provide options which ensure maximum productivity. In situations of limited food resources, Lack's (1954) brood reduction hypothesis could be functional. Where food is not limiting, however, hatch asynchrony may function to facilitate survival by spreading the food demand, as suggested by Hussell (1972), or by providing thermal stability for younger nestlings by older ones. The adaptive significance of hatch asynchrony in a functional sense needs further investigation.

Double-crested Cormorant nestlings are more susceptible to thermal stress than are embryos, particularly during the first two weeks after hatching. Their naked, black bodies absorb heat rapidly and must be shaded. Death from hyperthermia can occur in as little as 11 minutes in day-old nestlings. Heat tolerance and thermoregulatory capabilities increase with age during the first 12 to 14 days; however, this is the period of greatest vulnerability for the nestling. Parents are most attentive during this part of nesting (Brechtel 1983) and provide both warmth and shade, as needed.

The nestling stage up to the age of thermal independence represents a period of considerable risk, probably greater than at any other time from egg to fledging. Western Gulls (Larus occidentalis wymani) produce semiprecocial nestlings and are considered to be thermally at greater risk than exposed eggs of the same species (Bennett et al. 1981). This also is true of the Double-crested Cormorants I studied. The risk of death due to thermal stress is greatest in the first two weeks after hatching. The risk is compounded by the inability of the nestlings to escape exposure. Efforts by nestlings to escape solar induced heat stress often result in nestlings falling from the nest. Even though direct mortality from heat stress may not occur, nestlings less than two weeks old which fall out of the nest are certain to be taken by gulls.

Gular fluttering is generally considered to be indicative of thermal stress. Evans (1984) suggests that control of this behavior in White Pelicans resides in the body temperature. In Double-crested Cormorants, gular flutter was observed in day-old nestlings. Nestlings being brooded would gular flutter when their head was exposed to the sun. It is doubtful that these nestlings were heat stressed, although this behavior suggests that exposure of the head alone may be sufficient to trigger gular flutter, perhaps in anticipation of heat stress.

The cold hardiness of nestlings, the thermal stability provided by parental behavior, and to some extent by hatch asynchrony, are without doubt features of definite survival value. The reason Double-crested Cormorants are not at present exploiting the abundantly available resources farther north is unclear. Both eggs and nestlings are sufficiently cold hardy to permit utilization of suitable habitat north of their present range. Cold hardiness and low heat tolerance is highly correlated to the distribution of other waterfowl (Koskimies and Lahti 1964). If true for cormorants, range expansion may be anticipated as population pressures build in the present locations in south central Alberta. Cormorants breed over a wide range of latitude and do not demonstrate a distinct preference to cooler northern parts of their range as did the ducks studied by Koskimies and Lahti (1964). Perhaps the range of altricial species, such as Double-crested Cormorants and White Pelicans, are limited by factors other than thermal or metabolic considerations. Large altricial birds need sufficient time to develop physically for migration. The short but intense nesting season in latitudes farther north may not allow sufficient development to make exploitation of the midcontinental part of this region viable.

Attentiveness of the parents at the nest during incubation and brooding provides thermal stability for eggs and nestlings. At the same time, the parents must maintain their own thermal balance; therefore, adult behavior at the nest is often a tradeoff between the thermal requirements of the eggs or nestlings and the thermal tolerances of the adult.

Drent (1975) contends that during incubation parental behavior is adjusted in response to external clues, such as embryo vocalization, air temperature, radiation, and egg temperature. Double-crested Cormorants do respond to air temperature and radiation by adjusting the amount of flaring of the gular region, thus regulating their own body temperatures. Regarding egg temperatures, however, external clues appear to be factors resulting in coarse adjustment of incubation temperatures. Artifically enlarging clutches did not result in increased incubation temperatures. I therefore conclude that the mechanism for fine tuning of incubation temperatures resides within the parents, and is possibly the result of a gradual increase in hormone levels. This remains to be tested by the appropriate blood chemistry. It seems safe to say, however, that tactile feedback from the eggs plays little if any role in adjusting incubation intensity in cormorants.

Nestling behavior in response to thermal stress is predictable and stereotyped. Because of the predictable nature of this behavior under thermal stress, it is possible to gauge the stress level. Unlike the Western Gull chicks studied by Bennett et al. (1981), comatose hyperthermic cormorant nestlings do not recover.

Considering the ubiquity of pigmented eggshells, there is a paucity of information available on their nature and function. Evidence that pigments are functional in the shell calcification process are at best circumstantial (Kennedy and Vevers 1973). Indeed, Laskey (1943) reports that 9.1% of the Bluebird (Sialia sialia) population he studied laid white eggs instead of the typical blue ones of this species. Evidently, lack of pigment did not inhibit the shell calcification process in this instance. While the cryptic value of heavily pigmented shells of birds nesting in open exposed nests cannot be disputed, the function of pigment in the shells of cavity-nesting species or species whose eggs are continuously covered is undetermined. No thermally significant function could be determined for the pigment in Double-crested Cormorant shells. Thermal properties of the shell are more directly influenced by the calcite cover, shell thickness, and to a limited extent, nest soiling.

Management Implications

Increased human populations and the concomitant demand for greater access to and wider use of the environment often result in habitat destruction, interruption of the natural processes of reproduction, and ultimately in decreased species diversity. The tension between human utilization of the environment and the preservation of habitat suitable for the reproduction and maintenance of wild species will continue and increase. Management of wildlife resources is a tradeoff between the economic, recreational, and political demands of people on one hand and the needs of habitat and wildlife on the other. Managerial decisions demand information, explanations, and predictions for guidance. With this in mind, I have included this section.

As pointed out by Brechtel (1983), Double-crested Cormorants never actively defend their nests from human disturbance. While the eggs are in the nest from early May through mid-June, the likelihood of human disturbance is small. During that period, recreational use of reservoirs in southern Alberta is minimal and usually limited to a few weekend sportsmen fishing from shore well beyond the range at which the colony is disturbed. As human population pressures increase, more intense recreational use is probable, with a corresponding increase in the disturbance factor. Eggs are much less vulnerable to problems caused by disturbance than are nestlings. Embryos are very cold tolerant and can normally withstand prolonged periods during which internal temperatures are well below the minimum temperature required for development (27°C).

Cormorant embryos and nestlings are not at risk as long as parental attendance is not interrupted by disturbance. If eggs or nestlings are deprived of parental care, mortality from gull predation and thermal stress increases sharply. In southern Alberta, disturbance related mortality of embryos would generally be the result of gull predation. Only rarely would conditions be suitable to bring about thermally related mortality at the egg stage, although nestlings less than 12 to 14 days old are extremely sensitive to heat stress. Consequently, nesting colonies should be protected from disturbance during nesting, especially when young nestlings are present (June 1 to July 15). Although the risk of nestling mortality decreases as nestlings achieve thermal independence, the spread of hatching (Brechtel 1983) would imply that up to half of the nestlings would be vulnerable from the middle of June to the middle of July. Colonies should not be visited during that time, or if visited, the duration and time of the visit are critically important. In general, overcast days present low risk. However, on bright, sunny days mortality will be significant if colony disturbance lasts longer than about 20 minutes or occurs after 10:00 a.m. Care must be exercised during banding operations of other waterfowl. Air boat activity can seriously disrupt cormorant colonies for considerable periods, inadvertently causing significant nestling mortality.

Because of the threat of predation by gulls whenever the adults leave the nest, it is essential that colony inspections include enough personnel to protect the eggs and nestlings. Adult cormorants do not return to the colony during inspections. Effective protection would require one person for approximately 200 nests.

Although Double-crested Cormorants are sensitive to human disturbance, they tolerate considerable disturbance provided the events are separated in time and do not result in nest failure. Abandonment resulted when a colony was visited twice in one day with one hour between visits. This occurred early in June shortly after the hatch began at the time of greatest sensitivity to disturbance.

Manipulation of nests, eggs, and hatchlings during nesting are tolerated well. Prior to the initiation of nesting, nests relocated within the colony are accepted readily. These observations suggest that moving a colony or development of new colonies may be feasible.

The development of a reliable system for sampling short-range telemetry data in the field, along with field portable video recording equipment, should be useful in obtaining data on behavior and body parameters of other difficult-to-observe species.

Literature Cited

Bennett, A. F., W. R. Dawson and R. W. Putnam. 1981. Thermal environment and tolerance of embryonic Western Gulls. Physiol. Zool. 54: 146-154.

Brechtel, S. H. 1983. The reproductive ecology of Double-crested Cormorants in southern Alberta. M.Sc. Thesis, Univ. of Alberta, Edmonton, Alberta. 119 pp.

Bryant, D. M. 1975. Breeding biology of House Martins _Delichon urbica_. Ibis 120: 16-26.

Clark, A. B. and D. Wilson. 1981. Avian breeding adaptations, hatching asynchrony, brood reduction, and nest failure. Quart. Review of Biol. 56: 253-277.

Clark, L. and R. P. Balda. 1981. The development of effective endothermy by Piñon Jays. Auk 98: 615-619.

Drent, R. H. 1975. Incubation. In Avian Biology, Vol. 5. Farner, D. S. and J. R. King, eds. Academic Press, New York, N.Y. pp. 333-420.

Dunn, E. H. 1976. Development of endothermy and existence energy expenditure of nestling Double-crested Cormorants. Condor 78: 350-356.

Evans, R. M. 1984. Development of thermoregulation in young White Pelicans. Can. J. Zool. 62: 808-813.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317-324.

Kennedy, G. Y. and H. G. Vevers. 1973. Eggshell pigments of the Araucano Fowl. Comp. Biochem. Physiol. 44B: 11-25.

Koskimies, J. and L. Lahti. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81: 281-307.

Lack, D. 1954. The natural regulation of animal numbers. London: Oxford Univ. Press.

Laskey, A. R. 1943. The nesting of bluebirds banded as nestlings. Bird Banding 14: 39-43.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (_Larus argentatus_). Nature 228: 1221-1222.

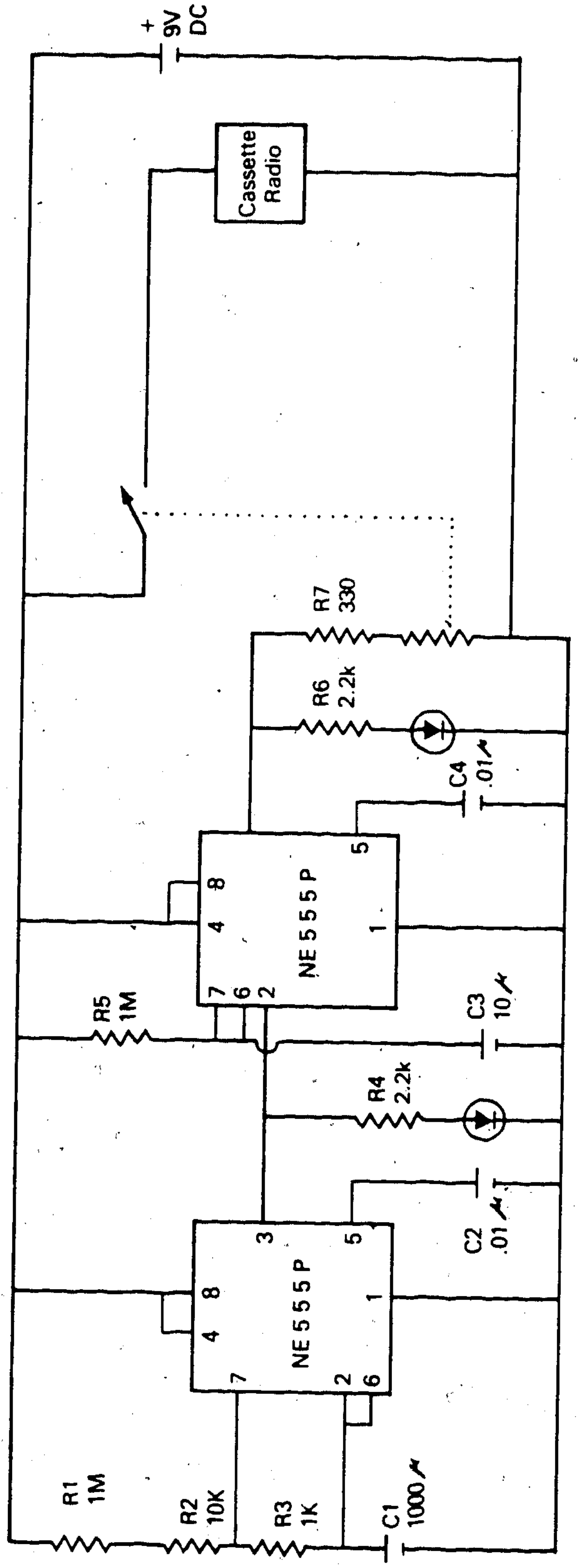
Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull (*Larus argentatus*). Ibis 117: 517-510.

Ricklefs, R. E. 1965. Brood reduction in the Curved-billed Thrasher. Condor 67: 505-510.

Robertson, I. 1971. The influence of brood size on reproductive success in two species of cormorant, *Phalacrocorax auritus* and *P. pelagicus*, and its relation to the problem of clutch size. M.Sc. Thesis, Univ. of B.C., Vancouver, B.C.

Welty, J. C. 1979. The life of birds. Philadelphia: Saunders College Publishing, 623 pp.

APPENDIX



Schematic diagram of the timer-switch circuit used to control the radio cassette.