

THERMAL TOLERANCE OF AVIAN EMBRYOS: A REVIEW¹

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Abstract. Avian eggs usually experience temperatures of 30 to 40°C during the incubation period, but eggs often cool to much lower temperatures. Hyperthermia is less common. Passerines do not show higher incubation temperatures than other orders that have been studied extensively. Field measurements of incubation temperatures are usually lower than the optimal temperatures for development found in laboratory studies. Some species regulate egg temperatures closely throughout incubation; but in at least one penguin species, mean egg temperature increases and ranges of egg temperature decrease through the incubation period.

Both the optimal temperature for continuous exposure and the range of temperatures producing high survivorship differ among species. Species also differ in their responses to temperature exposures of limited duration. Thus, the use of a "physiological zero" applicable to all species is not warranted. Penguins have both a lower optimum and a broader range of acceptable incubation temperatures than do other species studied. Age, duration, and temperature of exposure significantly affect survivorship. Hyperthermia is evidently more injurious to the developing embryo than is hypothermia. Resistance to cold exposure is a heritable trait, but the genetics and physiology of the response(s) are not known. For older embryos, the physiological effects of hyperthermia are similar to those of adult birds in terms of the organ systems that are first to fail. An estimate of thermal tolerance for short exposures in most species studied is 16 to 41°C and, for exposures lasting several hours, 36 to 39°C.

Key words: Thermal tolerance; eggs; embryos; nests; incubation.

INTRODUCTION

Overall hatching success of avian eggs averages about 90% and is influenced by latitude, social organization, diet, and nest type (Koenig 1982). More proximately, the failure of an egg to hatch may result from infertility, from genetically determined developmental defects, from improper exchange rates of respiratory gases and water vapor, from failures of the parental incubation regime that lead to lethal chilling or heating of the eggs, or from mechanical destruction. This review examines both the actual temperatures experienced by eggs and the tolerance of the embryos to those temperatures. Ornithologists have focused considerable effort on determining the temperatures of eggs during natural incubation. Such data are of greatest utility when viewed from the perspectives of what, if any, deleterious effects result from exposure to extremes of temperature. Moreover, determination of the effects of temperature on embryonic survival, growth,

and development is a necessary precedent to an understanding of the consequences of variation in incubation behavior on fitness.

It is a reasonable guess that failures of parental attentiveness typically result from unusual thermal or trophic stresses, but less obvious compromises between self-maintenance of the parent and its incubation program may occur when food supplies are low, spatially scattered, or distant from the nest. In such cases, the survival of unattended eggs will depend on their rates of cooling or heating and on embryonic resistance to extreme temperatures that may kill them outright or induce developmental defects. Although the death of embryos as a result of inadequate parental care does not often seem to be a major demographic variable, there is currently too little knowledge about the ways in which the thermal properties of eggs and parental behavior interact to forecast when or why incubation may fail in either mild or extreme environments. Parental attentiveness may produce close regulation of egg temperature even though it imposes stresses on the adults. Furthermore, the lack of any effect on mortality at the present time does not imply that such factors have been unimportant in the past or will remain unimportant in the future. For

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example, fluctuating environments may impose selective episodes only occasionally (Wiens 1977).

Previous work on the thermal tolerance of avian embryos, cited herein, has established a number of generalizations about the effects of exposure of eggs to various thermal regimes. These include (1) the application of an estimate of the physiological zero (the temperature at which development stops) to embryos of any age or species, (2) that optimum incubation temperatures (those producing highest survivorship) are broadly similar across species, (3) that parental regulation produces egg temperatures that are roughly similar over all species, (4) that embryos of different ages are similarly affected by thermal exposures, and (5) the well-established belief that hyperthermia is more injurious to the embryo than is hypothermia. This "conventional wisdom" is sometimes stated explicitly in published reports; more often, it forms the implicit context in which research methodologies are determined. Although the work done to date cannot provide answers to all questions of interest in embryonic tolerance, the data presented here are sufficient to contravene most of the points above.

I begin this account with an update of earlier compilations of egg temperatures during incubation (Huggins 1941, Shilov 1968, Drent 1975) and then turn to these questions: (1) Are there clusters of means and extremes of incubation temperatures that are correlated with taxa, nest location, habitat, or mating system? (2) Are there taxonomic differences in average egg temperatures or in the amount of variation in egg temperatures? (3) What incubation temperatures are optimal for various species and what reductions in survivorship occur at nonoptimal temperatures? Throughout this review I use the term optimal to mean that range of temperatures producing the highest survivorship of embryos. (4) What are the effects (if any) of duration of exposure, age of the embryo, temperature, and interactions among these variables on embryonic survivorship? (5) Is thermal tolerance heritable and amenable to selection? (6) What is the physiological basis of thermal tolerance (i.e., which physiological systems are first to fail at extreme temperatures)? (7) Are there significant sublethal effects, either positive (such as developmental canalization leading to increased resistance, tolerance, or behavioral flexibility) or negative (such as slowing of development), that attend exposure to extreme temperatures? (8) How do hypo- and

hyperthermia differ in their effects on the embryo?

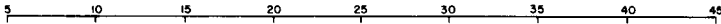
Data on the thermal tolerance of chickens in this report are limited to the physiology and genetics of thermal tolerance. However, some less strongly domesticated species are included in the analysis of the effects of temperature on survivorship vs. temperature. The literature on all aspects of chicken embryonic survivorship has been ably reviewed previously (Landauer 1967, Lundy 1969, Romanoff 1972). Chickens have been exposed for many generations to selective regimes that differ widely from those of other birds (to say nothing of the differences in mating systems and influence of genetic drift). The hybrid advantage in embryonic survival reported by Romanoff (1972, p. 37) indicates inbreeding depression, although wild birds may not be completely free from this problem.

INCUBATION TEMPERATURES IN NATURE

Even when not coupled with measures of survivorship, records of egg temperatures during incubation serve as a useful antecedent to laboratory studies of thermal tolerance. Knowledge of natural incubation temperatures can serve as a guide to the temperature regimes for laboratory exposure, as well as for comparison of realized incubation temperatures with those producing maximum hatching success. Also, sufficient data over a broad taxonomic spectrum can demonstrate interspecific differences in incubation temperature, if they exist. If species differ in their incubation temperatures, then evolutionary differentiation of thermal tolerance in different phyletic lines may have occurred. But without analysis of weather, nest microclimates, attentiveness, and other components responsible for the maintenance of egg temperatures (Webb and King 1983), one cannot determine whether interspecific differences in measured egg temperatures are due to different environmental factors or to differences in preferred egg temperatures. I begin with an analysis of recorded egg temperatures for which the authors make no distinctions with respect to embryonic age (Fig. 1). I next turn to the few studies that examine changes in egg temperatures with age (Fig. 2).

METHODS

Certain data are excluded from this analysis of the temperatures of natural incubation because



Struthioniformes

• • Male incubating } Ostrich
Female incubating

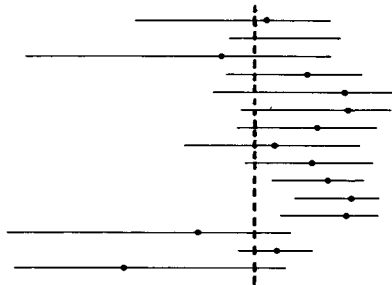
Siegfried and Frost 1974

Rheiformes

Rhea

Shilov 1988 ?

Sphenisciformes



Emperor Penguin
King Penguin
Adelle Penguin
Adelle Penguin

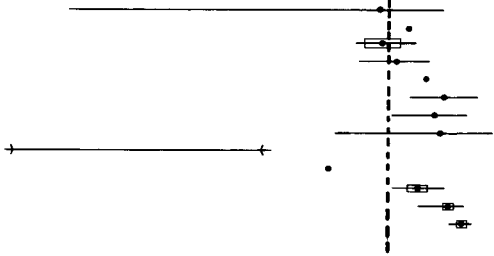
Drent 1970 &
Eklund and Chariton 1959

Jackass Penguin

Burger and Williams 1979 ?

Gentoo Penguin
Macaroni Penguin

Procellariiformes



Diving Petrel
Bonin Petrel

Thoresen 1969 &
Grant, et al. 1982

Leach's Storm-petrel
Leach's Storm-petrel

Ricklefs and Rahn 1979
Drent 1975

Leach's Storm Petrel
Southern Giant Fulmar

Williams and Ricklefs 1984

Wilson's Storm Petrel
Fork-tailed Storm-petrel

Wheelwright and Boersma 1979

Fork-tailed Storm Petrel
Wedge-tailed Shearwater

Boersma 1982

Laysan Albatross
Black-footed Albatross

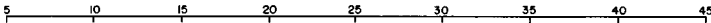
Howell and Bartholomew 1961b
Howell and Bartholomew 1961a

Pelecaniformes

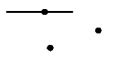


Red-tailed Tropic Bird
Red-footed Booby
Brown Noddy

Howell and Bartholomew 1962b
Brown 1977



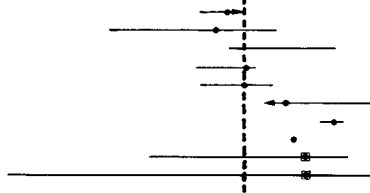
Ciconiiformes



Great Blue Heron
Cattle Egret
Great Egret

Huggins 1941
Vleck et al. 1983

Anseriformes



Whistling Swan
Snow Goose
Canada Goose
Mallard
Mallard
Mallard
Eider Duck
Green-winged Teal
Pintail

Huggins 1941
Krechmar and Syroechkovsky 1978 #
Kossack 1947 &
Huggins 1941
Caldwell and Cornwell 1975 &
Shilov 1968 ?
Atton 1979 &

Falconiformes



Marsh Hawk
Golden Eagle

Huggins 1941
Ellis and Varney 1973 #

Galliformes



Ring-necked Pheasant
Capercaillie

Huggins 1941
Lennerstedt 1966 #

Gruiformes



Virginia Rail

Huggins 1941

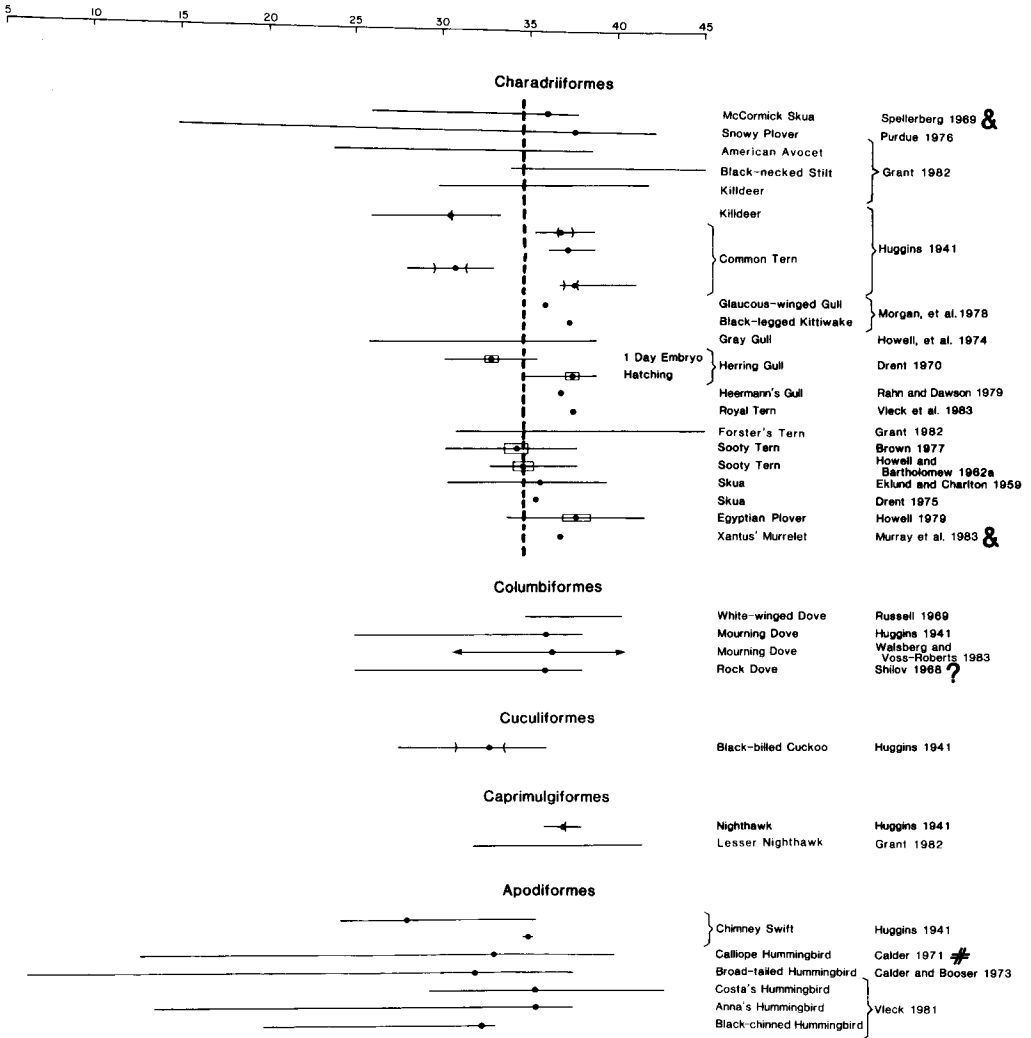
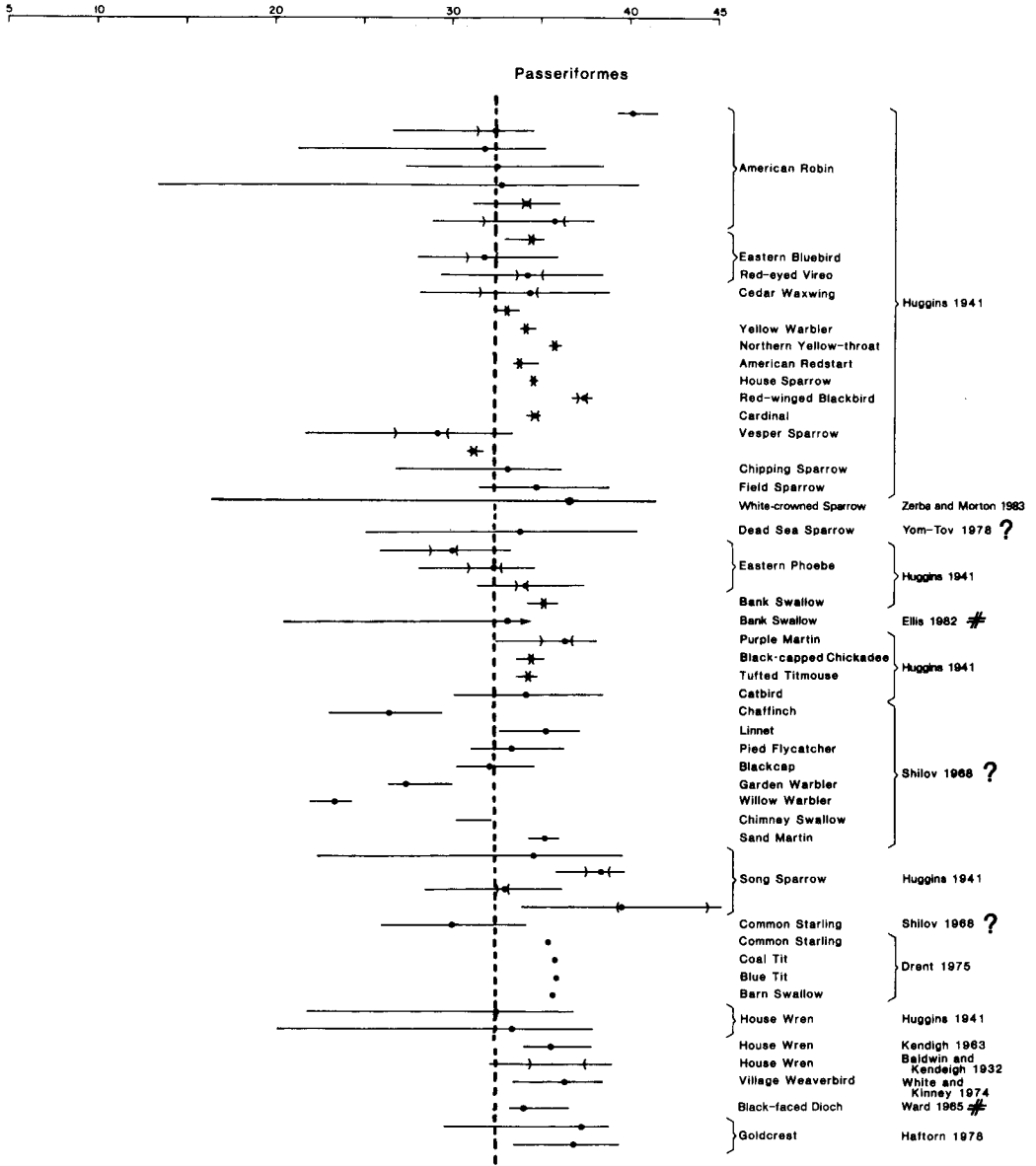


FIGURE 1. Natural egg temperatures (°C) during the incubation period. The line delimits the range of temperatures measured. Overall mean is shown by a solid dot; (= attentive mean; box shows ±2 SE or 95% confidence limits (if reported). Arrow indicates an unknown extreme temperature in the direction indicated. A “#” after the source indicates that artificial eggs were used; a “?” indicates that I could not clearly determine whether or not artificial eggs were used. “&” indicates that measurements were made of the air cell temperature. Vertical dashed lines are mean incubation temperatures for the order. Egg temperatures reported as a function of embryonic age are given in Figure 2.

of methodological problems. For example, Norton's (1972) otherwise comprehensive data have an imprecision of 3°C due to temperature-dependent errors of the chart recorder used. Data which represent only the air temperature of the nest cup or those in which the measuring technique is likely to have changed the temperature of the egg are also excluded; for example, the use of a large thermistor probe in a small egg. A

partial list of these excluded references may nonetheless be of interest to some readers (e.g., for data on nest attentiveness: Howell and Dawson 1954, Irving and Krog 1956, Westerskov 1956, Farner 1958, Kessler 1960, Valanne 1966, Orr 1970, Maclean 1976, Cain and McCuiston 1977, Derksen 1977).

Also excluded from this report are brief data on egg temperatures gathered incidentally to oth-



er goals, for example: the comprehensive water loss investigations of Carey et al. (1983). In some reports the original papers were not available. These values are included but the reviewing authors are cited (usually Shilov 1968 or Drent 1973). Artificial eggs are not excluded from this analysis; however, eggs filled with silicone, wax, or some other compound that may not approximate the heat transfer characteristics of avian

eggs (Webb and King 1983) are marked (#) in Figure 1. Several authors recorded air cell temperatures. Unless the sensor is touching the embryo, measurement of air cell temperature may record a temperature somewhat different from that of the embryo, especially in large eggs. These studies are marked (&) in Figure 1.

I estimated the means for the data of Calder (1971) and Purdue (1976). As with other graph-

ical data, I interpolated the values in Howell (1979), but also used equidistant sampling on his data points to normalize the data vs. time. For graphical data, I used a computer-driven digitizer, accurate to 0.03°C at the scale used in the graphs. Authors sometimes reported sample sizes as the number of spot readings taken of the temperature probe, sometimes as the hours of continuous recording by a chart recorder, sometimes as the number of eggs or nests monitored, and sometimes not at all. Thus, greater (statistical) ranges in Figure 1 may not be so much a result of the exigencies of the environment interacting with the physiology and behavioral repertoire of the species as of inequality of sample sizes.

Another potential problem is the timing of data collection during the incubation period. The most obvious bias here is unequal sampling between day and night. Less obvious, perhaps, are unequal distributions of sampling with regard to embryonic age and to potential changes in parental behavior. As the data reviewed below indicate, these can alter results substantially. Nonetheless, this compilation represents the broadest set of data yet presented. Although the present focus is on egg temperature, not whether it is regulated physiologically or behaviorally, both inattentive “)” and attentive “(” mean egg temperatures are denoted in Figure 1.

RESULTS AND DISCUSSION

The most general conclusion to be drawn from Figure 1 is that most egg temperatures are usually in the low to mid-30s. Hummingbird eggs often experience low temperatures, although mean temperatures differ only slightly from those of other birds (Fig. 1; Vleck 1981). It also appears that the incubation temperatures of penguins are lower than those of most other birds. This accords with the results of both the intensive incubation temperature measurements of Burger and Williams (1979) and the survivorship of embryos during continuous temperature exposure (see below). Many penguins, of course, breed in very cold areas, and hummingbirds are known to sometimes enter torpor while incubating (Calder and Booser 1973). American Robins (*Turdus migratorius*) occasionally also have low minimum egg temperatures (Fig. 1).

I also computed average egg temperatures for those orders in which more than three species had been studied. Sphenisciformes have the lowest egg temperatures (30.7°C), followed by the 55

studies done on 36 species of passerines (32.2°C), then Procellariiformes (32.5°C), Anseriformes (33.8°C), and Charadriiformes (34.3°C). Perhaps surprisingly, the Passeriformes do not have higher egg temperatures than the other orders, and, in fact, average egg temperature for passerines is lower than for all other orders except penguins. There is also no evident trend for the range of egg temperatures to be smaller in passerines than in other orders. Again, this may reveal more about the difficulties small birds encounter in regulating the temperature of their eggs than it does about the best temperatures for embryonic growth and development. Empirical measures of egg temperature from several White-crowned Sparrow (*Zonotrichia leucophrys*) nests showed minima near 17°C (Zerba and Morton 1983). Heat exchange models coupled with simultaneous behavioral observations (Webb and King 1983) showed that birds in two other populations of White-crowned Sparrows prevented eggs from chilling below 16.7°C, and that birds in the different populations adjusted both the timing and the length of trips off the nest to regulate egg temperature. Few studies have examined extremes of egg temperature in a comprehensive way, but regulation of egg temperatures at some mean value may be less important than preventing extreme values.

Measured temperatures across all species are often below 35°C; however, optimal temperatures for incubation in those species that have been studied are usually (except penguins) above 35°C (Figs. 3, 4, 5). This suggests that the exigencies of the thermal environment or the needs of the female for feeding produce mean incubation temperatures that are lower than the optimum. Alternatively, periodic chilling of the eggs may improve hatch, as has been suggested by some Russian researchers (cited in Landauer 1967, p. 57). If so, then to achieve a mean temperature that coincides with the optimum during continuous exposure in the presence of periodic chilling, an incubating parent must regulate egg temperatures at higher levels during other periods. However, this does not answer the question of whether it is better to raise the egg temperature above the optimum during incubation after such a chilling episode or merely allow the mean to be lowered by the chilling periods and to accept the presumed slowing of development thereby entailed. Oppenheim and Levin (1975) suggest that periodic chilling of the embryo could

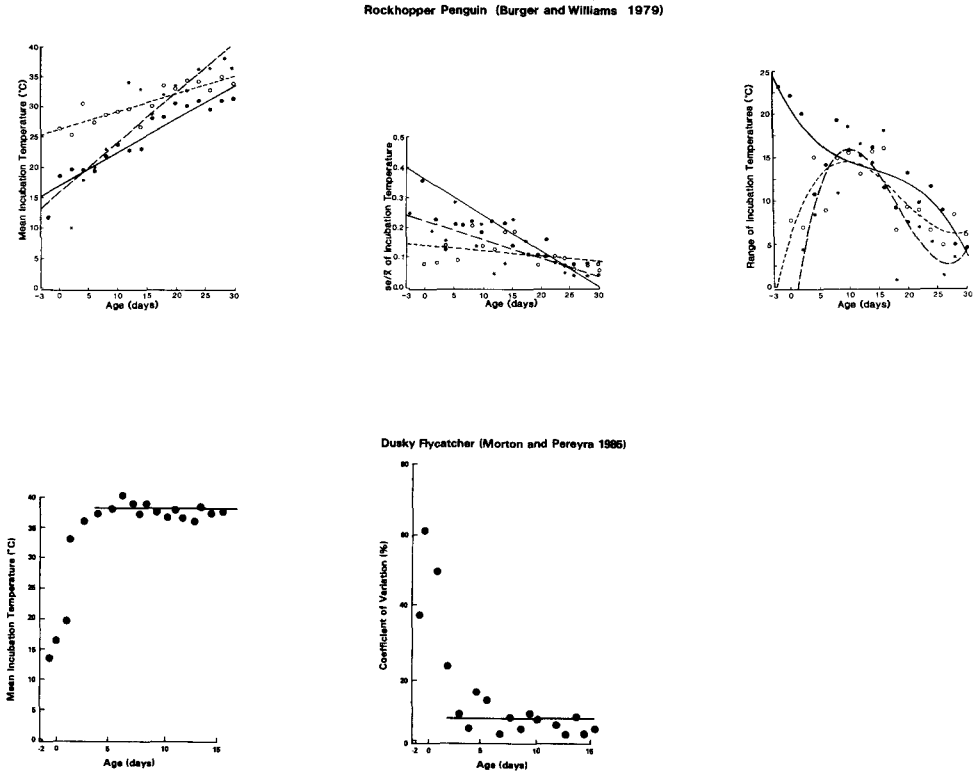


FIGURE 2. Incubation temperatures for four species by embryonic age. The graphs are horizontally aligned at the completion of the clutch (age 0), and the horizontal axes are of equal lengths from that time to the date of hatching. Vertical axes are scaled identically for each variable, except that the range of incubation temperatures has been extended 10°C for the Northern Shovelers and Great Tits. Standard error of the mean is designated as SE. Range is the difference between the maximum and minimum egg temperatures reported per day. Top row: Rockhopper Penguin incubation data—means, SE/ \bar{x} , and range vs. age. Solid line (dots) = first-laid egg, dotted line (circles) = second-laid egg, dashed line (stars) = single egg. Linear regressions of incubation data—

be advantageous by enhancing the development of thermoregulation.

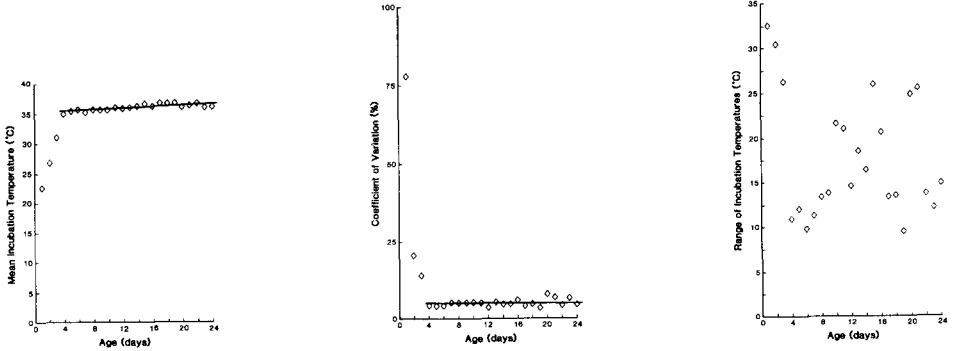
Eggs of some procellariiforms do have very low incubation temperatures, but most others studied do not (average egg temperature for Procellariiformes = 32.5°C). The causes underlying the patterns of incubation reported by Matthews (1954), Pefaur (1974), Wheelwright and Boersma (1979), Boersma et al. (1980), and Vleck and Kenagy (1980) are controversial (Ricklefs 1984). Probably the most extreme examples of birds breeding in hot environments are the Gray Gull, *Larus modestus* (Howell et al. 1974), Dead Sea Sparrow, *Passer moabiticus* (Yom-Tov 1978), White-winged Dove, *Zenaida asiatica* (Russell 1969), and Killdeer, *Charadrius vociferus* (Grant 1982); but the maximum temperatures of the eggs are reported as 39, 41, 40.5, and 42°C, respectively, less than those of many other species

studied. Huggins (1941) reports a high of 45.8°C in the eggs of the Song Sparrow (*Melospiza melodia*), but the effect on the embryo is not noted. Malleefowl (Megapodiidae) incubation mound temperatures range from 31 to 34°C (Frith 1956). Egg temperatures probably approximate those values if strong fluctuations in egg temperature do not exist.

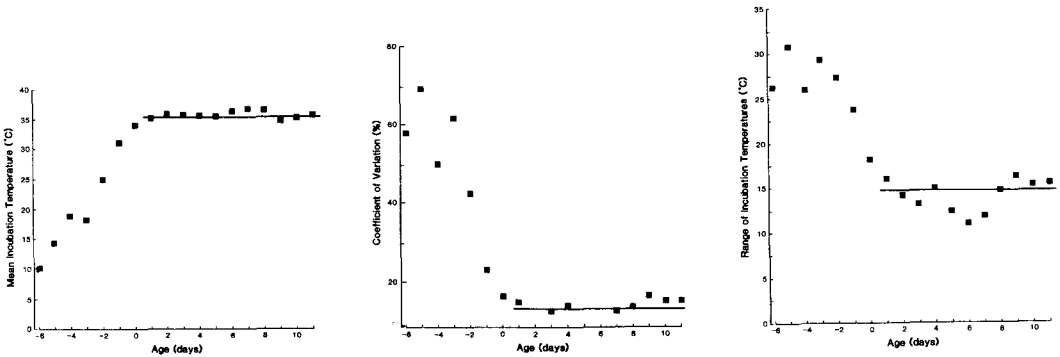
EFFECT OF EMBRYONIC AGE

Only a few studies report nearly continuous recordings over most of the incubation period for several nests of the same species (Fig. 2). These studies include Rockhopper Penguins, *Eudyptes chrysocome* (Burger and Williams 1979), Great Tits, *Parus major* (Haftorn 1983), a montane population of Dusky Flycatchers, *Empidonax oberholseri* (Morton and Pereyra 1985), and an anatid, the Northern Shoveler, *Anas clypeata*

Northern Shoveler (Afton 1979a)



Great Tit (Haftorn 1983)



mean and SE/mean. Slopes of linear regressions are significantly different from zero (5% level). Second row: Linear regressions of Dusky Flycatcher incubation data. Data for ranges of incubation temperatures were unavailable. Third row: Linear regressions of Northern Shoveler incubation data. Slopes of the regressions are not significantly different from zero (5% level). Bottom row: Linear regressions of Great Tit incubation data—mean, coefficient of variation, and range vs. age. Slopes of all three regressions are not significantly different from zero (5% level) after the first day of incubation.

(Afton 1979a). Air cell temperatures (touching the inner membrane) were recorded for Rockhopper Penguins and Northern Shovelers. Rockhopper Penguins have nearly 100% attentiveness after completion of the clutch (Burger and Williams 1979), and the data for the other three species in Figure 2 are based on both attentive and inattentive periods. Zerba and Morton (1983) present data on egg temperatures with respect to embryonic age for a southerly montane population of White-crowned Sparrows. However, only data on egg temperatures during attentive periods vs. age were available for this analysis. To ensure comparability with the four other studies noted above, these data are not considered in the following analysis. However, the White-crowned Sparrow data for egg temperatures during attentiveness appear generally sim-

ilar to the data for Dusky Flycatchers and Great Tits in Figure 2.

The daily mean temperatures for Rockhopper Penguin eggs increase with age of the embryo (Fig. 2). In contrast, the other three species appear to regulate egg temperature more closely, and at a higher temperature throughout the period of incubation, after completion of the clutch. Daily mean temperatures are nearly constant in Dusky Flycatchers, Great Tits, and in Northern Shovelers after the first 3 days of incubation. In these three species, mean egg temperatures are always at about the same level as that attained by the penguins only just before hatching.

Inspection of Figure 2 suggests that a cubic regression is the simplest model that provides for possible asymmetries in the data on ranges of egg temperatures; additionally, such a model

can show the degree of linearity as in the ranges of first-laid Rockhopper Penguin eggs (Fig. 2). Cubic regressions (not shown) on the standard errors reported for the studies in Figure 2 were concave downward ("humped"). This probably results from the very low egg temperatures early in the incubation period; therefore, what should be examined is a variance measure that is corrected for the mean, such as the coefficient of variation (CV). I am not able to retrospectively construct coefficients of variation for Rockhopper Penguins, and thus analyze variation in egg temperatures by dividing the standard errors by the means (Fig. 2). I also constructed plots of SE/mean for the three other species; the trend in those constructs is similar to the trend in the coefficients of variation described below. For Rockhopper Penguins the SE/mean decreases with age, in single or first eggs laid, but not in the second egg laid, suggesting tighter regulation of egg temperature at old embryo ages. This decrease is significant at the 5% level even if temperatures taken before the beginning of "full-time" incubation are excluded. No significant changes (5% level) in the coefficients of variation in incubation temperature occur for Great Tits after clutch completion, or after the second day of incubation for Northern Shovelers or Dusky Flycatchers. Ranges of egg temperature are greater in Northern Shovelers and Great Tits than in Rockhopper Penguins, especially during the first 2 days of incubation. Nonetheless, coefficients of variation in egg temperature are low in these two species, suggesting that extremes of temperature are short-lived.

AGE-SPECIFIC REGULATION OF EGG TEMPERATURE

Although data for only four species were available for this analysis, there are apparently at least two different patterns of regulation used by incubating birds. Dusky Flycatchers, Great Tits, and Northern Shovelers seem to maintain a high egg temperature throughout the incubation period, while egg temperatures of Rockhopper Penguins increase during the incubation period. This relatively low incubation temperature accords with what is known about embryonic tolerance for other penguins. The Adélie Penguin (*Pygoscelis adélie*), a related species, has an optimal temperature for development during exposure to continuous temperatures that is lower than at

least several other species of birds (Weinrich and Baker 1978).

Measures of variation in egg temperature decrease or remain constant during the incubation period in all four species. Regulation of egg temperature is less precise for the penguin. After completion of the clutch, the Great Tit shows a considerably reduced range of egg temperatures. The range of egg temperatures in the Northern Shoveler decreases only slightly with embryonic age and is much larger than the other three species. Nonetheless, Northern Shovelers maintain high mean egg temperatures and the coefficient of variation is low.

These data indicate that the penguins differ from the other three species in terms of the average egg temperature maintained and the level of regulation. There may also be a third pattern of regulation shown by the Northern Shoveler: allowing frequent but brief fluctuations in egg temperature.

EGG TEMPERATURES IN NATURE

Because of the large number of studies depicting natural egg temperatures (Fig. 1), it is probably most useful to focus future studies on (1) changes in egg temperatures related to embryonic age (Fig. 2), (2) the extremes of egg temperature encountered and the duration of exposure to each temperature (e.g., the frequency tables given by Zerbe and Morton [1983] and Morton and Pereyra [1985]), and (3) the relative importance of nest location, nest morphology, and female attentiveness in moderating egg temperatures.

Understanding the reasons for these interspecific differences in egg temperature requires knowledge in several areas. (1) To determine the degree to which egg temperatures result from parental incubation, field studies of egg temperatures must include simultaneous monitoring of the thermal environment. Suppose, for example, that the thermal environment was constant during the Northern Shoveler study in Figure 2 but warmed during the incubation period of the penguins. The changes in egg temperatures through developmental time would then most likely be due to "regulation" by the parental choice of microclimate for the nest or by timing of nesting rather than to direct regulation by parental brooding. (2) In some species, embryos may be able to partially regulate their own temperature. Such regulation could include the ability to maintain an egg temperature higher than that of

the environment and the ability to slow cooling during periods of parental inattentiveness. For the eggs of small altricial species, embryonic thermogenesis is thermally unimportant in real-world conditions (Webb and King 1983), but penguin eggs are much larger and embryonic heat production late in incubation could maintain egg temperatures above the environmental temperature so that less regulation by the parent would be needed in the same environment. (3) Another explanation for differences in egg temperatures among species could be that the temperatures for optimum hatching differ among species and/or change with age. In the remainder of this report I review the evidence for this possibility by examining the data on the thermal tolerance of avian embryos.

SHIFTS IN PARENTAL INVESTMENT OR EMBRYONIC TOLERANCE?

It is tempting to conclude that age-related increases in the precision of regulation and the magnitude of egg temperature by the incubating parent are the result of more stringent requirements by older embryos compared to younger ones. In reality, the problem is more complex. If more precise regulation of embryo temperature at higher levels increases fitness regardless of embryonic age, then parental investment will increase during the incubation period. This could arise because energy stores, defense against predation, the ability to renest, or any other component affecting future reproductive value changes through the incubation period. If so, then the parent(s) should regulate egg temperature at higher and more precise levels as incubation progresses. Thus, regulation at higher temperatures and with greater precision is predicted by both parental investment theory and by possible age-related changes in the tolerance of the embryo. The only feasible tests are laboratory studies of the effects of age on thermal tolerance. Although some studies have shown decreased tolerance with age (see below), such studies cannot rule out parental investment.

The term "regulation" occurs repeatedly in the literature reviewed here and a nonzero cost associated with this regulation is implicit in the parental investment hypothesis presented above. Changes in metabolic rate or panting by the adult clearly entail energetic and water balance trade-offs. But requirements of the embryo resulting in higher attentiveness may also result in a cost

to the parent by constraining the timing and length of foraging trips off the nest. Walsberg and King (1978) have shown that the nest constitutes a protected microclimate for incubating White-crowned Sparrows. Thus, it may be cost-effective to occupy the nest during periods of inclement weather. If the nest is placed in a moderate environment, little or no regulation by the female may be needed. An understanding of the requisite amount of regulation also requires prediction of the temperature that the egg would have without incubation by the female (Webb and King 1983). Such studies can serve as "null models" in determining the role of parental attentiveness. For penguins, montane sparrows, and ducks, the environment is probably sufficiently stringent to require that a significant amount of the parents' time budget be devoted to incubation, but this may not be the case in all species or areas. Embryonic metabolism might also dampen temperature excursions, but this is not likely to occur in small eggs (Webb and King 1983).

SLOWING OF DEVELOPMENT

It is convenient to partition the consequences of thermal extremes into three levels. The simplest and most severe result is (1) the immediate death of the embryo, which generally occurs at the widest extremes of temperature (e.g., Baldwin and Kendeigh 1932). (2) Sublethal teratogenic effects may also ensue and presumably could be so subtle as to affect reproductive success only later (e.g., Thompson et al. 1976). (3) Exposure to cold, and perhaps heat, may also result in a slowing of development.

On a phylogenetic basis, embryonic chilling may be correlated with prolonged incubation and apparent tolerance of low temperatures (Matthews 1954, Pefaur 1974, Boersma and Wheelwright 1979, Wheelwright and Boersma 1979, Vleck and Kenagy 1980). However, the proximate effects of slower development are problematic for most other species. An extended period in the egg stage certainly prolongs the period of potential nest predation and could reduce the time available to fledge, molt, or accumulate fat stores before migration or the onset of inclement conditions. However, the recorded increases of incubation period with low temperature are only a few days for chickens (Romanoff 1972, p. 68). For White-crowned Sparrows, the increased length of the incubation in colder, snowier years was only 1 day in a Colorado population (Hub-

TABLE 1. Sources of data for thermal tolerance.

Continuous exposure			Assessment of survival ¹		
Species	Temperature °C	Source	Assessment of survival ¹	Species	Assessment of survival ¹
Adélie Penguin	26-42	Weinrich and Baker 1978	?	Manx Shearwater	D
Fork-tailed Storm-Petrel	10-34	Vleck and Kenagy 1980	*	Fork-tailed Storm-Petrel	*
Mallard	37-38	Batt and Cormwell 1972	E, W	Mallard	W
Mallard	35.6-39.4	Prince et al. 1969	E, W	White-runner Duck	W
White-runner Duck	35-40.6	Romanoff 1943	W	American Kestrel	D
American Kestrel	36-40	Snelling 1972	D	Northern Bobwhite	D
Northern Bobwhite	37-40.6	Romanoff 1934	D	Northern Bobwhite	E
Northern Bobwhite	37.5-38.1	Wilson et al. 1979	E	Ring-necked Pheasant	D
Ring-necked Pheasant	37-40.6	Romanoff 1934	D		
Limited duration exposure					
Species	Temperature °C	Exposure duration (hr)	Age (days)	Source	Assessment of survival ¹
<i>Puffinus puffinus</i>	13.3-17.8	240-336	—	Matthews 1954	D
<i>Oceanodroma furcata</i>	10-34	1-continuous	varies	Vleck and Kenagy 1980	*
<i>Anas platyrhynchos</i>	0-8	10-240	0-24	Batt and Cormwell 1972	W
<i>Anas platyrhynchos</i>	40-44	3-6	0-24	Snart 1970	D
<i>Anas domestica</i>	35-40.6	144	21-27	Romanoff 1943	W
<i>Meleagris gallopavo</i>	30.5-41.5	72	21-24	Romanoff 1935	D
<i>Colinus virginianus</i>	37.5-40.6	1-480	varies	Wilson et al. 1979	E
<i>Phasianus colchicus</i>	0-22	1-60	2-22	MacMullan and Eberhardt 1953	E
<i>Phasianus colchicus</i>	-12.2-29.4	1-9	2-9	English 1941	E
<i>Larus occidentalis</i>	10-50	—	5-9	Bennett et al. 1981	D
<i>Larus heermanni</i>	5-45	—	2-9	Bennett and Dawson 1979	D
<i>Archilochus colubris</i>	14	5.5	7	Southwick 1977	E
<i>Selasphorus platycercus</i>	6.5	3	—	Calder and Booser 1973	E
<i>Troglodytes aedon</i>	10-47	1-10	—	Baldwin and Kendeigh 1932	E

¹ D = daily, W = weekly, E = at end of hatching period, * = died during embryonic development, ? = not reported.

TABLE 2. Optima for continuous exposure.

	Anatids	Adélie Penguin	Galliforms, kestrel, gull
Temperature for peak survivorship (°C)	37.0	34.7	38.6
Width of temperature range for 90% of peak survivorship (°C)	0.9	8.3	1.4

bard 1978). Morton (1974) found no difference in incubation periods at different altitudes and latitudes throughout the species range; King and Hubbard (1981) found no geographic variation in incubation period, and Morton et al. (1972) could find no correlation between incubation period and mean daily air temperature (albeit a very crude measure of the egg's thermal environment). Thus, proximate slowing of development is evidently not frequently experienced by this montane sparrow. Even fewer data are available for most other species and slowing of development by exposure to low temperatures cannot yet be directly related to survivorship.

CONTINUOUS EXPOSURE TO EXTREME TEMPERATURES

Continuous exposure to any particular temperature is unlikely in nature but represents the first step in the experimental assessment of embryonic thermal tolerance. Some general information on the hatching of 83 species of bird eggs during artificial incubation is given by Wetherbee and Wetherbee (1961), and for three species of finches by Ziswiler (1959). The data presented here represent laboratory determinations of survivorship at different temperatures from a variety of sources (Table 1, Continuous Exposure). Some authors assessed mortality daily or weekly, whereas others determined mortality by failure to hatch. If significant mortality occurred after additional time lags, then the differing methods for determining mortality could constitute an additional source of variation in the subsequent analyses.

METHODS

To express stage of development as a percentage of age, I divided the age of the embryo by the length of the incubation period given in the paper. When no incubation period was given, I used data from Nice (1954) if available for that species; otherwise I used data from Harrison (1978). To determine if the temperature at which peak sur-

vivorship occurs differs between groups, I fit cubic polynomial regressions through each group (Fig. 3), then examined the temperature range over which 90% or greater survivorship resulted. The choice of 90% is arbitrary. To test whether these temperature ranges were significantly different, I used Bartlett's test for homogeneity of variances (Steel and Torrie 1980). Because the variances were not homogeneous, I next employed an approximate *t*-test for unequal variances (adjusting the degrees of freedom to account for the inequality of the variances), and used Bonferonni's technique (Miller 1981) to hold the experiment-wise (i.e., group-wise) error rate to the 5% level.

To determine if these species differ in their response to temperature, I calculated 95% confidence intervals (not shown) for each species in Table 1 (Continuous Exposure). Some caution is necessary in the interpretation of these confidence intervals because of the small number of points represented for any one species. However, the confidence intervals are based on mean values of survivorship, not individual variates. This probably reduces the variation and narrows the confidence intervals.

RESULTS AND DISCUSSION

For all species considered together, survivorship was uncorrelated with temperature. The maximum r^2 for linear, quadratic, or cubic regressions with temperature was only 18%. This indicates either that temperature is unimportant or, more likely, that some other effect, such as taxonomic affinity, is more important. Because the data for the kestrel fall within the 95% confidence intervals for the galliforms and gulls, I included them in a single group. Removal of the kestrel data from the group reduces the peak survivorship by only 4% and shifts that peak by 0.2°C toward lower temperatures.

Each pair-wise comparison of the temperature at which peak survivorship occurred in Figure 3 was significantly different, and the mean for the

anatids differs from that for the galliform/gull/kestrel group by 1.6°C (Table 2). Because the measures are averages, the 1.6°C difference could reflect a much larger population variance and thus be more important biologically. The finding of statistical significance could also be the result of such small sample sizes that only low variances could be expressed. The mean for the penguins differs significantly from that for either the anatids or the other species and is separated from them by 2.3°C and 3.9°C, respectively (Table 2). Furthermore, Adélie Penguins apparently have much greater tolerance to temperature than do either of the other two groups. Adélie penguins show a remarkable range of thermal tolerance as some groups of embryos had 100% survival at temperatures as low as 26°C and as high as 42°C (Weinrich and Baker 1978). To create a scalar for comparing temperature tolerance, I again took 90% of the peak value for survivorship in each side of the cubic regression curve fit through the means. This range of tolerance to temperature extends over 0.9°C for anatids and is slightly greater (1.4°C) for the galliform/gull/kestrel group ("others," Fig. 3) but is much greater (8.3°C) for the penguin (Table 2).

This analysis of the effect of constant temperatures on embryonic survival shows that species differ in both the optimum temperature for development and the breadth of tolerated temperatures. Furthermore, Adélie Penguin eggs, which are apparently exposed to lower temperatures during incubation, have the greatest tolerance to

temperatures deviating from the optimum as well as the lowest optimal temperature for incubation, based on gross survivorship. The optimum temperature for the Fork-tailed Storm Petrel, *Oceanodroma furcata*, is about 34°C, as low as that of the Adélie Penguin (Vleck and Kenagy 1980). Anatid eggs also appear to have greater tolerance to extreme temperatures than other species for which there are data, and Romanoff (1943) has concluded that their thermal tolerance exceeds that of chickens.

EXPOSURES OF LIMITED DURATION

Several species have been studied by exposing eggs differing in age to temperature conditions of variable duration (Table 1). Such experiments mimic changes in egg temperature due to parental inattentiveness.

METHODS

To determine the effects of temperature, duration of exposure, and age at exposure, I first performed multiple-linear regression using these variables and, additionally, a temperature \times temperature variable to account for the humped response of survivorship on temperature found in the analysis of eggs exposed to continuous temperatures. I also included interaction effects of duration with the temperature variables. I initially included all species together to test the hypothesis of no interspecific differences. This regression was not significant and the model explained only about 18% of the variance in survivorship.

RESULTS AND DISCUSSION

Because combining the data without regard to species produced a substantial reduction in r^2 ; and because every version of this model explained substantially more of the variance when partitioned by species, interspecific differences in embryo tolerance to temperature regimes of variable exposure apparently do exist, reinforcing the similar conclusion reached with the continuous exposure data. I next applied the above multiple regression model to each species in turn. Table 3 shows that most variables have a significant effect on survivorship. Furthermore, the model explains a fairly large amount of the variation in survivorship, given the intrinsic variability of these developing systems.

There are anecdotal data available in the literature that bear on the effects of limited dura-

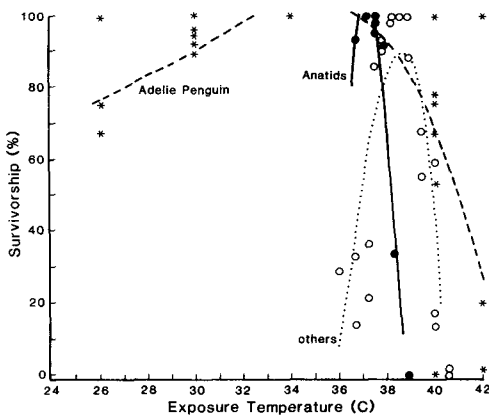


FIGURE 3. Cubic polynomial regressions of survivorship vs. temperature during continuous exposure. Sources of data are given in Table 1 (Continuous exposure). Stars: Adélie Penguin; Dots: Anatids; Open circles: Others (galliforms, kestrel, and gull).

TABLE 3. Multiple regression for limited duration exposures.

Species	Temperature	(Temperature) ²	Duration	(Temperature × duration)	Age	r ² (%) ¹
Manx Shearwater	*2	*	ns	**	*	60
Ring-necked Pheasant	ns	**	**	**	ns	53
Mallard	**	**	*	**	**	41
House Wren	**	**	**	ns	**	95

¹ Combining the data without regard to species reduced the model r² to 18%.

² * = significant at P < 0.05, ** = significant at P < 0.01, ns = not significant.

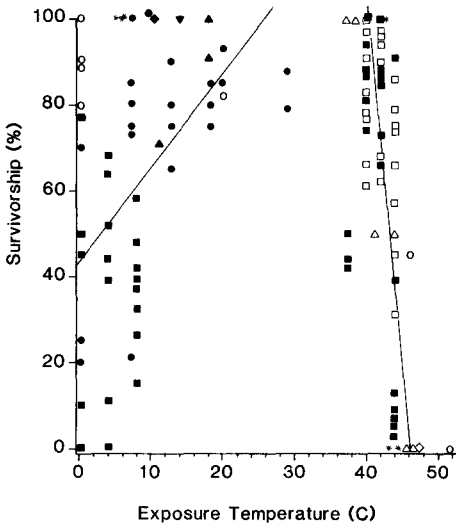
tions of exposure to immoderate temperatures. Southwick (1977) reported that two Ruby-throated Hummingbirds (*Archilochus colubris*) hatched after cooling to about the 14°C for several hours. (His methods did not reveal exact times or temperatures.) Diving Petrel (*Pelecanoides georgicus*) embryos survived chilling to less than 10°C, in some cases for 80 to 104 hr (Roby and Ricklefs 1984). The slowly developing embryos of the Antarctic Giant-Petrel (*Macronectes giganteus*), a continuously incubating procellariiform, are not especially tolerant to cooling, suggesting that hypothermic tolerance is probably unrelated to prolonged incubation periods (Williams and Ricklefs 1984) or that some other constraints operate on this particular species. Calder and Booser (1973) recorded egg temperatures of a Broad-tailed Hummingbird (*Selasphorus platycercus*) and found that one fertile egg hatched even after cooling to 6.5°C overnight, which is also the low temperature record for Figure 1. Two sandpiper eggs survived chilling to near freezing for 16 hr (Norton 1972) and Dusky Flycatcher eggs that cooled to 2.8°C during a period of cold, windy weather also hatched (Morton and Pereyra 1985).

The study of thermal tolerances at differing durations of exposure is inherently multivariate, involving not only the temperature and duration of exposure, but also age at exposure and species as independent variables, plus interaction effects among these. The available data are insufficient to permit predictions of survivorship based on the embryonic age of a particular species and the duration of exposure to a particular temperature. However, the multiple-regression analysis presented above indicates that all of the above factors should be considered and that a single model for all avian species is inappropriate.

EFFECTS OF EMBRYONIC AGE

To determine the importance of embryonic age, I plotted survivorship vs. age, parameterized by

duration of exposure, temperature, and interaction variables for each species in Table 1 (Limited Duration Exposure), both separately and for all species together. In only one case was a trend of survivorship with age apparent, and it was minor. However, there is substantial evidence that the effects of temperature with age differ among species, and this may have obscured the above results. Highest hatchability for Northern Bobwhite (*Colinus virginianus*) occurs at a constant incubation temperature (Romanoff 1934, Wilson et al. 1979); but for pheasant (Romanoff 1934) and for chickens (review in Landauer 1967) highest hatchability was produced by lowering the incubation temperature just before hatching. Romanoff (1972) noted that older chicken embryos were more susceptible to high temperatures, but younger embryos were affected more by low temperatures. Hatchability of Mallard (*Anas platyrhynchos*) embryos exposed to 44°C for 6 hr showed a strong age dependency (Snart 1970), but a 3-hr exposure failed to produce a statistically significant decrease in survivorship. Both early and late critical periods were reported for turkeys (Martin and Insko 1935), similar to those of chickens (reviewed by Romanoff 1972). But older chicken embryos were more susceptible to cold exposure (Moreng and Bryant 1956, Lundy 1969) contra Romanoff (1972). Older Manx Shearwater (*Puffinus puffinus*) embryos were significantly (5% level) more resistant to chilling (Matthews 1954), but Matthews also pointed out that complicating factors in the field study may be involved, such as differential incubation behavior by the parents. His laboratory experiments showed no obvious change in embryo susceptibility with age. Several authors have noted much greater tolerance to temperature extremes by embryos of different species before the beginning of incubation: Batt and Cornwell (1972) and Snart (1970) for Mallards, and Romanoff (1972) for chickens. Weinrich and Baker (1978) stated that 5 days of storage of Adélie Penguin



Duration of Exposure		Species
<5hr	5-10hr	
○	●	Ring-necked Pheasant
□	■	Mallard
△	▲	House Wren
◇	◆	Western Gull
·		Heerman's Gull
*		Broad-tailed Hummingbird
	▼	Ruby-throated Hummingbird
	●	Fork-tailed Storm-petrel

FIGURE 4. Effect of exposures of 10 hr or less duration on survivorship for eight species at various temperatures. The two points near 30°C were excluded from the regressions. Sources of data are given in Table 1 (Limited duration exposure).

eggs less than 3 hr old at 15°C did not affect developmental rate, mortality, or incidence of abnormality. Enhanced thermal tolerance prior to the onset of incubation accords well with the increased temperature fluctuations of eggs prior to the onset of incubation in the Northern Shoveler and Great Tit (Fig. 2).

There are a number of reports (summarized by Landauer 1967) that periodic chilling can increase hatchability. Hatchability of chicken eggs increased when they were allowed to cool to 30°C just after laying (El Jack and Kaltofen 1969). However, the laying hens were kept at air temperatures of 38.3°C as were the control eggs, possibly a slightly hyperthermic temperature. Brief changes in egg temperature, caused by the departure of the incubating adult, have also been hypothesized to serve as an important sensory stimulus during development, leading to in-

creased behavioral abilities after hatching (Oppenheim and Levin 1975). It is also possible that developmental canalization for increased physiological abilities (e.g., vasomotor control or thermogenesis) could occur in embryos exposed to temperature extremes.

Figure 4 shows the effect of temperature on survivorship for eight species at relatively brief exposure durations of 0 to 5 hr (inclusive) and 5 to 10 hr. Unlike data previously presented, not every point on this graph represents a mean of several to hundreds of separate observations. In particular, the sample size is equal to 1 for the House Wren (*Troglodytes aedon*), both gulls, and both hummingbirds. The data are presented here without regard for embryonic age, but I previously analyzed similar plots with four age classes as a parameter. I determined the age classes by dividing the age at exposure by the age at hatching for each species. This treatment assumes that all species undergo similar developmental schedules although linearity is not assumed. A brief summary of these data by age class is as follows: for embryos 0 to 25% of age at hatching, survivorship of Mallards varied markedly at both hyperthermic temperatures (see also Fig. 4). The pheasants exposed for 8 hr were at a lower temperature than those exposed for 4 hr, thus complicating analysis. However, cubic regression fits through these two sets of data joined smoothly, suggesting that the effects of those two durations differ only slightly. Survivorship was sharply reduced above 43°C. For the 25 to 50% age class, survivorship was slightly greater with 3-hr exposures than with 6-hr exposures for Mallards at hyperthermic temperatures. Hypothermic exposures in this age class produced slightly higher survivorship in pheasants than in the other species. Also, some effect of duration for this species is suggested by the slightly higher survivorship for 3-hr exposures at nearly 10°C than for 8-hr exposures at 12 to 25°C. At 50 to 75% of age at hatching Mallards show a very narrow response to temperature, with the peak survivorship at 40 to 42°C (see also Fig. 4), as opposed to peak survivorship at 37°C for continuous exposure. Whether this actually results from a change in the optimal incubation temperature with age (or duration of exposure) or is merely an artifact of lack of sampling at lower temperatures cannot be ascertained from the data. For the 75 to 100% age class, Mallards show a rapid decline in survivorship above 43°C. Ring-necked Pheasant (*Phasianus colchicus*) survivorship is

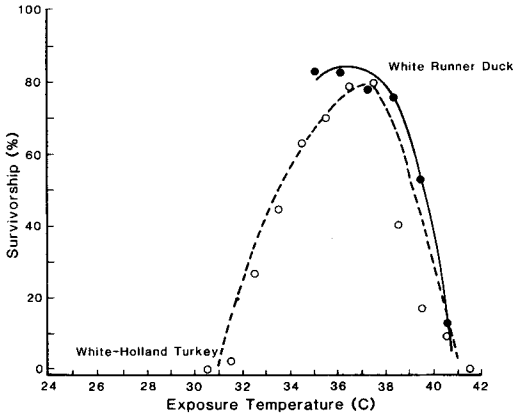


FIGURE 5. Effects of exposures of 72 to 144 hr duration on survivorship at various temperatures: ages for both species are 75 to 100% of the age at hatching. Solid dots = duck; circles = turkey. Curves fit by polynomial regression. Sources of data are given in Table 1 (Limited duration exposure).

greater than 85% at 20°C, declining below that temperature. At nearly 0°C, pheasant survivorship progressively declined with exposure durations from 3 to 7 hr. A duration of 2 hr resulted in higher survivorship than a 1-hr exposure.

Considered in totality, no consistent effects of age on survivorship emerge from the analysis of exposures of less than 10 hr duration. Figure 4 also shows that less scatter and a steeper decrease

of survivorship attends hyperthermic exposures than hypothermic exposures. In fact, great spread in survivorship is evident at low temperatures, and some embryos survive at all temperatures from near 0 to 44°C. The paucity of data moderate temperature makes it impossible to specify an optimal temperature, except to estimate that it should be somewhere in the mid-30s.

Some data are also available for exposures longer than 10 hr. Figure 5 presents survivorship data for ducks exposed for 144 hr and turkeys exposed for 72 hr (Table 1). Here, peak survivorship occurred at 35 to 38°C, similar to that of the continuous exposure data (Fig. 3). The cubic regression curve for the longer duration of exposure (ducks) is slightly higher than for the shorter duration (turkeys); however, the differences in exposure temperatures (Table 1) prevents the assertion that duck embryos are more resistant to thermal extremes than are turkey embryos.

Figure 6 shows plots of survivorship vs. exposure duration and age for two temperature regimes. The plots are primarily based on data from Ring-necked Pheasants, but also include data on the Western Gull (*Larus occidentalis*) and Broad-tailed Hummingbird (Table 1). Typically, higher mortality resulted from the 5 to 10°C exposures than from the 10 to 15°C exposures, at any combination of age or duration of exposure. High mortality occurs at much youn-

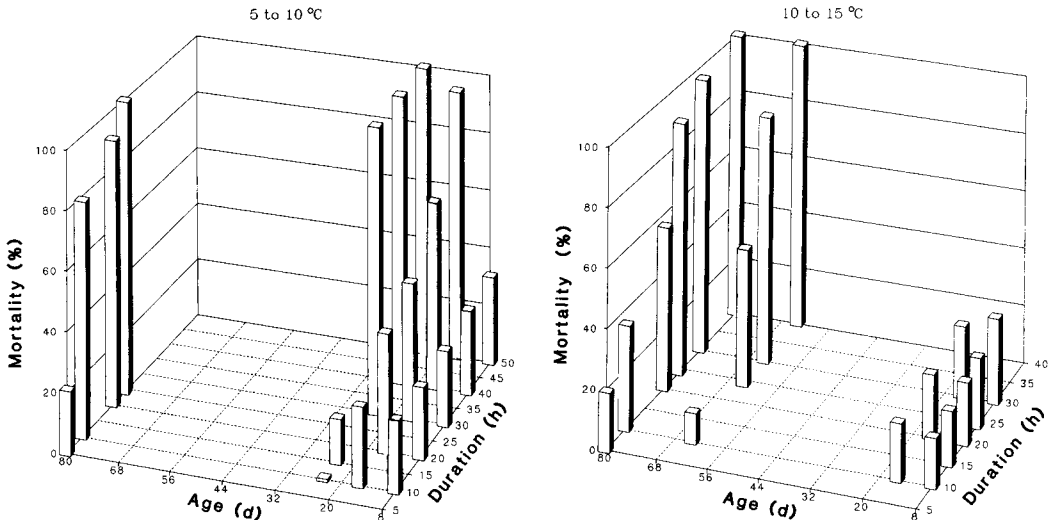


FIGURE 6. Effects of age at hatching and exposure duration on mortality for exposure temperatures between 5 and 10°C, and for exposure temperatures between 10 and 15°C. Data presented are for Ring-necked Pheasants, Western Gulls, and Broad-tailed Hummingbirds. Sources of data are given in Table 1 (Limited duration exposure).

TABLE 4. Responses to selection.

Fitness component	% Change	Significance ¹
Early embryonic viability	0.8	*
Intermediate embryonic viability		
Stressed	17.5	*
Not stressed	5.2	*
Hatchability		
Stressed	14.2	*
Not stressed	4.1	ns

¹ * = significant at $P < 0.05$, ns = not significant.

ger ages for the lower temperatures. In fact, relatively low mortality occurred at the 10 to 15°C exposures except for the oldest embryos. A pronounced effect of age is also shown for the 5 to 10°C exposures. For embryos less than 10 days old even sustained exposures of 40 hr kill less than 40% of the embryos at exposure temperatures of 5 to 15°C. However, exposures lasting only 10 to 20 hr (depending on exposure temperature) can result in nearly complete mortality of the oldest embryos. These data show that age exerts an important effect on mortality and interacts strongly with exposure duration and temperature.

For some other species, the effects of age and duration are less obvious. In the Manx Shearwater (75% of age at hatching), exposures at 15 to 18°C did not lower survivorship appreciably ($n = 10$), but exposure to 19 to 21.1°C for more than 200 hr reduced survivorship to 50% or less ($n = 12$). Plots of survivorship vs. age (not presented here) showed lower survivorships at intermediate ages, but a relatively large degree of scatter was present (see also Matthews 1954). In Northern Bobwhite, exposure to 23°C for 24 hr or 40.6°C for 24 to 48 hr produced survivorships of about 65%.

In sum, the relative age of the embryo can exert strong effects on survivorship for some species, especially at low temperature and for durations of several hours or longer. Furthermore, species differ in age-specific resistance to chilling or heating, and heat and cold stresses apparently do not show similar patterns of mortality with age.

GENETICS

Earlier researchers noted that the eggs of some lines of chickens differed in cold susceptibility (Phillips 1945, Olsen 1951). More recent studies have demonstrated at least slightly increased thermal tolerance in adults based on single loci

(Merat et al. 1974), as well as the efficacy of selection in adaptation to cold stress. Early (0 to 9 days) embryonic viability in chickens was increased by five generations of artificial selection in which fertile eggs were exposed to 2°C for 1 hr 9 days after hatching (Shawer and Moreng 1975a). The lack of significant change in one generation was claimed to show that the increased viability was not due only to developmental effects. The authors interpret reduction in total and additive genetic variance as implying stabilizing selection for heterozygotes on epistatic polygenic systems. Response to selection was slow, suggesting low additive genetic variability for the traits. The importance of maternal effects was reduced as selection progressed. Table 4 shows that relatively large increases in fitness components under cold stress were achieved; only hatchability under nonstressful conditions was nonsignificant. Shawer and Moreng (1975b) also noted that stressed embryos weighed less than nonstressed, and that population differences in mass became significant after the 18th day of development. No treatment effect on adrenal or testes mass was found (Shawer and Moreng 1975c). Lines selected for cold-stress resistance had higher metabolic rates than nonselected lines at both normal and cold incubation temperatures (Shawer and Moreng 1975d).

Garwood et al. (1973) subjected 14-day-old chicken embryos to cold stress of 15.5°C and to heat stress of 42.7°C for 24 hr. The selective regime was sufficient to produce about 75% mortality. One to four generations of selection failed to produce significant changes in hatchability, age at sexual maturity, egg production, body mass, or later mortality. It is unclear as to why these results differed from those of Shawer and Moreng. Possible explanations include differences in experimental procedure (including the number of generations of selection), differences in genetic variability of the lines used, and, for heat stress, functional constraints of enzyme structure. Nonetheless, it appears that exposure to extreme cold can produce a rapid selective response, although less extreme temperatures may be ineffective. Unfortunately, there are apparently no data on altricial or wild species.

PHYSIOLOGY OF THERMAL SUSCEPTIBILITY

Knowledge of the physiological basis of thermally induced teratology and mortality is a prerequisite for a thorough understanding of the

TABLE 5. Physiological effects of thermal exposure.

Species	Temperature	Exposure duration (hr)	Age (days)	Effect	Source
Hyperthermia					
Adélie Penguin	40–42	24–168	—	degeneration of area pelucida and area opaca	Weinrich and Baker (1978)
Chicken	46.5	1	pipped	cardiac failure, respiratory failure	Dawes (1979)
Chicken	40.6–42.8	240–408	10–17	cysts on amniotic membrane	Thin et al. (1977)
Chicken	40	24–72	3–6	liver hypertrophy	Delphia et al. (1967)
Chicken	40	continuous	—	liver hypertrophy, depletion of glycogen stores	Delphia et al. (1967)
Chicken	40	—	18	hepatocyte ultrastructure	Preda et al. (1969)
Heermann's Gull	41	acute	—	cardiac, respiratory failure	Bennett and Dawson (1979)
Western Gull	47	acute	—	blood coagulation	Bennett et al. (1981)
Hypothermia					
Adélie Penguin	26–30	72–240	—	abnormal brain, blood islands, primitive streak, differential growth	Weinrich and Baker (1978)
Mallard	0–8	120–240	0	twinning	Batt et al. (1975)
Canada Goose	–6.1–13.3	—	4	twinning	Batt et al. (1975)
Ringed Turtle-Dove	3–38	3–14	—	twinning	Riddle (1923)
Turkey	32	72	21–24	crippling	Romanoff (1935)
Chicken	37	continuous	—	body mass halved, no change in immunological capability, thyroid, adenohypophysis, or adrenal glands	Preda et al. (1971), Mihail and Preda (1971)
Chicken	35.5	continuous	—	no change in metabolic rate, blood gas composition, or chorioallantoic capillary plexus; slowed development	Tazawa (1973)
Chicken	30	2	10–18	no change in metabolic rate, blood gas composition, or chorioallantoic capillary plexus	Tazawa (1973)
Chicken	25–27	48	1–2	cerebral damage, somite fusion	Azoubel (1974)
Chicken	21	24	17	no effect on body mass	Buckland (1969, 1971)
Chicken	20	2	pipped	respiratory failure; rate reduced	Dawes (1981)
Chicken	10	4	1	reduced growth rate in females, depletion of muscular and hepatic glycogen stores	Davison and Lickiss (1979)
Chicken	5	8	17	increased body mass	Buckland (1969, 1971)
Chicken	4	48	1–2	caudal cephalization	Azoubel (1974)
Heermann's Gull	11	acute	2–9	cardiac failure, respiratory failure	Bennett and Dawson (1979)
Western Gull	8–13	acute	5–9	low heart rate	Bennett et al. (1981)

evolution of thermal tolerance. Unfortunately, our knowledge in this area is largely anecdotal. Hyperthermia and hypothermia apparently have differing effects on survivorship; furthermore, the physiological mechanisms affected by exposure to high or low temperatures differ in several respects (Table 5). The diversity of developmental defects is not surprising given the differing effects of temperature on various physiological and developmental processes (table 1 in Dawson 1984). Hypothermia seems to result in a wide variety of developmental abnormalities, but these generally occur only after prolonged exposure (Table 5). Hypothermia has also been shown to induce twinning in Mallards, Canada Geese, *Branta canadensis*, and Ringed Turtle-Doves, *Streptopelia risoria* (Table 5). Maternal temperature also has some effect, as Sturkie (1946) produced twinning in chicken eggs by inducing hypothermia in the hens prior to laying. It would be interesting to assess this effect in hummingbirds, even given the tolerance of their eggs to cold (Calder and Booser 1973).

Few data exist on the long-term physiological effects resulting from sublethal exposure of embryos to thermal stresses. But perhaps some observations by Davison and Lickiss (1979) on 1-day-old chicken hatchlings are pertinent. These researchers found a reduction of growth rate in females for 2 weeks following the exposure, and the depletion of both muscular and hepatic glycogen stores. Similar effects apparently obtain for embryos. Hypothermic exposure of chicken embryos resulted in hypertrophy of the liver and increased depletion of glycogen stores (Delphia et al. 1967).

Embryos old enough to have differentiated organ systems seem to suffer first from heart and respiratory failure when exposed to extreme temperatures. Heartbeat persisted from embryo temperatures of 10 to 41°C in Heermann's Gulls, *Larus heermanni* (Table 5), but temperatures of 45°C killed the embryos. In Western Gulls, heartbeat persisted from 11 to 46°C (Table 5). Higher temperatures due to solar heating (with an embryonic temperature of 47°C) caused coagulation of blood. These interspecific differences appear unrelated to differences in the thermal environment of the two species (Dawson 1984). Heating pipped chicken eggs to 46.5°C stopped the heart and cooling them to 20°C stopped pulmonary ventilation (Table 5). Metabolic rates and blood gas composition of chicken embryos subjected to both continuous exposure at 35.5°C and acute

exposure at 30°C for 2 hr were similar to those of unexposed embryos, incubated at 38°C, of the same developmental stage.

The temperature range below which embryonic development ceases is commonly known as the physiological zero but might better be termed the developmental zero, especially as all physiological processes do not come to a halt. Whatever the exact term, Edwards (1902) originally indicated a value of 20°C; later, Funk and Bieller (1944) corrected the range to 24 to 26°C, the range usually cited today (e.g., White and Kinney 1974, Carey 1980). This value is based solely on research on chickens; but recently, Miller and Wilson (1975) found that the temperature at which blastoderm development began in another galliform, the Northern Bobwhite, ranged from 24.4 to 25.6°C. Lundy (1969) has suggested that cooling below the physiological zero is less deleterious to the embryo than is cooling to a higher temperature at which development proceeds aberrantly. But lower hatchability of chicken eggs resulted from storage at 15°C for 3 days than from storage at 29.5 or 32°C for 3 days (El Jack and Kaltofen 1969). Furthermore, penguins do not seem to conform to this generalization (Fig. 2).

SKEWNESS OF TEMPERATURE EFFECTS

Both anecdotal evidence and our understanding of the temperature dependence of enzyme systems indicate that high temperatures are more deleterious to the embryo than are low temperatures. That is, a plot of survivorship on temperature should be skewed toward higher temperature with a more gentle decrease of survivorship as the exposure temperature is lowered. Several authors have claimed greater effects at high temperatures (Hamilton 1952, Landauer 1967, p. 57). The data for Adélie Penguins in Figure 3 are skewed but the data for the other groups are not. Skewness is also apparent for brief exposures (Fig. 4). Statistical tests specifically designed to detect skewness in such data are apparently unavailable. I therefore chose a break-point near the maximal survivorship and fit linear regressions for each side of the curve and then tested the slopes of these regressions for equality of their absolute values. As Table 6 shows, significant differences in the slopes are demonstrable for only some groups of data. However, it is those groups for which most data exist that show significant differences between hypothermia and hyperthermia; perhaps the lack

TABLE 6. Survivorship effects of hypo- and hyperthermia.

Exposure group	Slopes in temperature range		Slopes significantly ¹ different
	Low	High	
Short duration			
8 species combined	2.29	-8.10	***
Long duration			
2 species combined	14.61	-20.34	ns
Continuous duration			
Galliforms/Kestrel/ Gull	42.76	-52.39	ns
Anatids	—	-73.70	—
Adélie Penguin	0.86	-23.88	*

¹ — insufficient data, * $P < 0.05$, *** $P < 0.005$; F -test; data for hypothermia transformed by change of sign.

of significance for the other groupings is the result only of inadequate sample size.

THERMAL TOLERANCE

Given a significant effect of duration of exposure on survivorship (Fig. 6, Table 3), a three-dimensional plot of survivorship on temperature and exposure duration should show a ridge spanning the temperature axis, broader at the shortest exposure durations and narrowing as the duration increases to continuous exposures. Currently, insufficient data exist to produce such a multivariate view of thermal tolerance. However, Figures 3, 4, and 5 do give a series of univariate slices through this ridge of survivorship. Examination of these three plots (note the different scale of Fig. 4) shows that increasing exposure duration results in lower survivorship at any suboptimal temperature. The strong effect of the duration of exposure is shown even more clearly in Figure 6. However, only sustained exposure to low temperatures produced low survivorship. At present there is no evidence that the optimal incubation temperature changes with duration of exposure, although age exerts a confounding effect.

Although the available data do not permit a high degree of precision or of confidence in estimates of thermal tolerance, some estimates of those temperatures producing a significant decrease in survivorship are possible for most species. Table 7 presents such estimates based on a 20% reduction in the peak survivorship on the regression curves presented above. For hypothermic temperatures, 35 to 37°C produces significant mortality at exposures of several days'

TABLE 7. Thermal tolerance estimates.

Group	Temperature limits (°C) for 80% of peak survivorship	
	Hypothermia	Hyperthermia
Continuous exposure		
Adélie Penguin	27	39
Anatids	36	—
Galliforms/Kestrel/Gull	37	39
Long duration exposure (24 to 480 hr)		
Duck	—	39
Turkey	35	38
Short duration exposure (<10 hr)		
8 species in Figure 4	16	41

duration (but see Wheelwright and Boersma 1979). Adélie Penguins also show high survivorship when exposed to low temperatures, with no significant decrease until 26°C. Relatively low temperatures (16°C) are required to produce significant mortality when the exposure lasts less than 10 hr. This is the approximate lowest temperature to which the eggs of White-crowned Sparrows are allowed to fall (Webb and King 1983, Zerba and Morton 1983). Significant hyperthermic mortality occurs at 38 to 39°C for durations of a day or more, but the eggs of most species can withstand 41°C for several hours.

CONCLUSIONS

(1) Much of the published information is too fragmentary to support comparative analyses of incubation temperatures in relation to taxon, habitat, nest site, or other characteristics. Nonetheless, several generalities emerge from studies of natural incubation temperatures. Many penguins and some procellariiforms often experience low (<20°C) egg temperatures. However, almost every other avian order studied contains species whose eggs also occasionally experience low egg temperatures. Average temperatures for eggs of the Procellariiformes are not different from those for other orders studied. Passerine eggs are slightly cooler, not warmer than are those of most other orders. (2) A few intensive studies indicate that both mean incubation temperatures and the variability of those temperatures with embryonic age differ at least between Rockhopper Penguins and three other species (Fig. 2). Most studies of natural incubation have been handicapped by an inability to predict egg temperatures in the absence of parental regulation. Recent biophysical models may provide this information. (3) The

optimum incubation temperature during continuous exposure evidently differs among taxa. Adélie Penguins have a lower optimal temperature for continuous incubation and a wider tolerance range than the other species in Table 1. Comparisons of optimal temperatures for incubation with those to which embryos are exposed in the breeding environment have only rarely been examined. (4) During short exposures, the duration of exposure, temperature, and age of the embryo all exert significant effects on egg survivorship, as do interactive effects among these variables. Unfortunately, available data are not suitable for precise prediction of thermal tolerances. Furthermore, species differ in their thermal tolerance and the use of a single "physiological zero" for all species or even for all ages of any one species is inappropriate.

Perhaps the most noteworthy finding to emerge from this analysis is that egg temperatures during natural incubation are often lower than optimal incubation temperatures determined by experiments involving either continuous exposure or short exposures. This finding suggests that embryonic survival and development may often be limited by the parental incubation schedule, by heat transfer to the eggs, by the choice of a thermally appropriate nest site, by a "safety margin" for incubation temperature to preclude excursions into hyperthermia, or by some combination of the above factors. (5) Thermal tolerance is a complexly inherited trait, apparently amenable to selection, and (6) is expressed phenotypically in even more complex fashion. (7) Proximate slowing of development by cold temperatures appears to be infrequent in White-crowned Sparrows, the only wild species for which data are readily available. Other potentially sublethal effects have been little studied. (8) Hyperthermia reduces egg survivorship more strongly than does hypothermia in those species for which adequate data are available.

PROGNOSIS

Despite the amount of data presented in Figure 1, the lack of continuous sampling with age and paucity of analysis with respect to nest site, thermal environment, female age and experience, and possibility of renesting leaves much to be done in the study of incubation temperatures in nature. Most of the work done to date is perhaps best regarded as setting a context for more detailed and thorough investigations. The standard for such studies has been set by the comprehen-

sive investigations by Weinrich and Baker (1978), Afton (1979a), Grant et al. (1982), Haftorn (1983), Zerba and Morton (1983), and Morton and Peryra (1985). Full understanding of incubation temperatures actually represents a problem in subsampling with effects due to the age, experience, future reproductive value, genetic constitution, and exposure history of the mother, as well as the nest site, weather, and thermal tolerance of the embryos.

Studies of egg thermal tolerance are also patchily distributed in a phylogenetic sense. We need a basis from which to compare the thermal tolerances of common birds, nesting in areas of little thermal stress, with the tolerances of those species which may have special adaptations to extreme environmental conditions. Yet such studies of "typical" birds are seriously lacking, though a beginning has been made for birds whose eggs are subject to long periods of neglect or that breed in extremely cold areas. The American Robin is an obvious candidate for such study. It lives under a wide range of environments and its commonness near laboratories makes egg collection easy and obviates the risks of overzealous collecting. Other birds, because of their habits, are of notable interest. Hummingbirds often enter torpor and have been found to do so while incubating. Has there been adaptation in the thermal tolerance of their eggs? Do caprimulgiforms enter torpor during incubation, and if so, what temperatures do their eggs reach? Gulls breed nearly everywhere. It would be of interest to compare the thermal tolerance of eggs of the Gray Gull which nests in hot, arid environments, with those of other larids nesting in the Arctic. Many ducks are notorious egg dumpers—is there any relation between egg thermal tolerance, nest parasitism, and the thermal environment (Friedmann 1932)?

Laboratory studies of thermal tolerance are predicated on knowledge of egg temperatures experienced in nature. But even if eggs are never continuously exposed to extreme temperatures, laboratory experiments using continuous exposures offer a simple and powerful preliminary test of interspecific differences in thermal tolerance. However, if early stress could effect compensatory acclimation in the embryo as suggested by Oppenheim and Levin (1975), extreme caution would be required in the interpretation of these experiments, and this possibility has apparently never been fully studied. The simulation of natural incubation by exposures of limited duration

is at once the most important and least well studied area of research.

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