Hypothermic tolerance in an embryonic American kestrel (*Falco sparverius*)

Keith W. Sockman and Hubert Schwabl

Abstract: Embryos of several bird species tolerate acute hypothermia. However, the extent to which it can be tolerated by wild species living under natural conditions is poorly documented. At a single American kestrel (*Falco sparverius*) nest 15 days into incubation, we observed a 21-h bout of egg neglect by the parents during which nest (egg) temperature averaged 12.7°C. Normal incubation patterns resumed thereafter, and one of three viable eggs hatched 32 days after incubation onset, an incubation period 2.5 days longer than the mean in this study. The nestling appeared to develop and fledge normally. Although embryonic tolerance of extended hypothermia is known to occur in some seabirds, its presence in Falconiformes has not heretofore been recorded. Embryonic hypothermic tolerance may be adaptive in species with extended periods of parental absence during incubation.

Résumé : Les embryons de plusieurs espèces d'oiseaux sont capables de tolérer une forte hyperthermie. Cependant, l'ampleur de cette tolérance chez des espèces sauvages vivant dans des conditions naturelles a été peu étudiée. Nous avons observé un nid de Crécerelles d'Amérique (*Falco sparverius*) négligé par les parents pendant une période de 21 h, 15 jours après le début de l'incubation; la température des oeufs a été en moyenne de 12,7°C au cours de cette période. Les parents se sont remis à couver les oeufs normalement après ce temps et l'un des trois oeufs viables a éclos après 32 jours d'incubation, une période de 2,5 jours de plus que l'incubation moyenne évaluée au cours de cette étude. L'oisillon semble s'être développé normalement jusqu'à l'envol. Bien que la tolérance embryonnaire à l'hypothermie soit un phénomène courant chez certains oiseaux marins, ce phénomène n'avait jamais été observé auparavant chez un Falconiforme. La tolérance des embryons à l'hyporthermie peut être interprétée comme une adaptation chez les espèces qui doivent subir de longues absences des parents au cours de l'incubation.

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Introduction

In birds, incubation temperature regulates the rate of embryonic growth and the duration of the incubation period. Within species, there is little variation in the mean incubation temperature under which normal embryonic development can proceed (Deeming and Ferguson 1991). For example, in the domestic fowl (*Gallus gallus*), a 1–2 C° reduction can increase the incubation period by 1–2 days, and a further reduction or an increase of 1 C° causes mortality of the embryo (Romanoff et al. 1938). Nonetheless, temporary suspension of development is natural and adaptive for some species (Ewert 1991) and occurs when the egg temperature becomes too low. In fact, some embryonic seabirds can withstand hypothermic exposures of 1 to several days (Pefaur 1974; Boersma and Wheelwright 1979; Vleck and Kenagy 1980; Roby and Ricklefs 1984). The degree to which embryonic hypothermia can be tolerated in other species is poorly known, particularly for wild species living under natural conditions.

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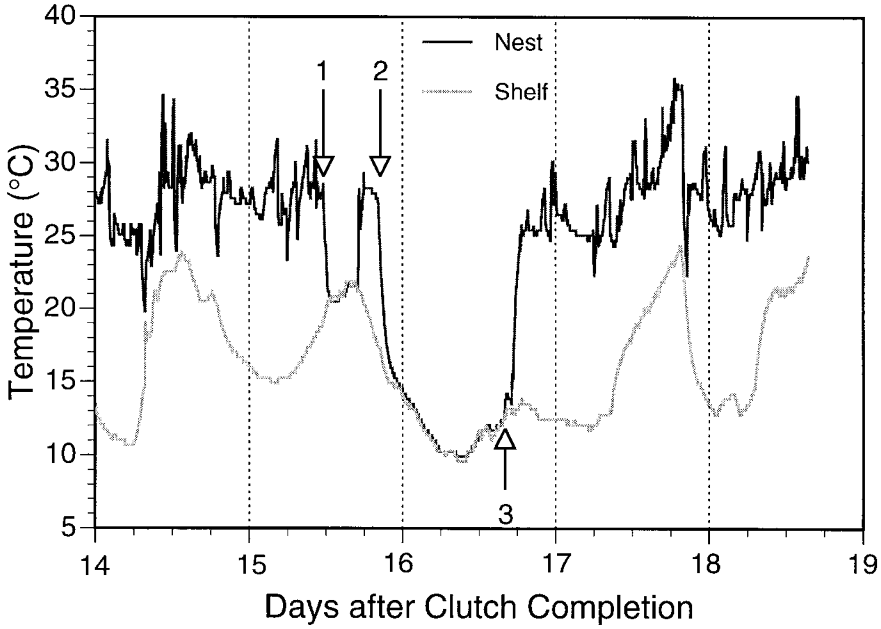
As part of a study on incubation behaviour, we observed hypothermic tolerance over an extended period in an embryonic American kestrel (*Falco sparverius*). Such observations raise questions regarding the physiological basis underlying cold-tolerance and the adaptive significance of cold-tolerance under conditions embryos might normally experience, such as those when parents leave the nest to forage. Some embryos may also experience overnight cooling if parents are flushed from nests by predators.

Materials and methods

Nest boxes for American kestrels were hung in spring 1997 in primarily agricultural areas of eastern Washington State. Boxes were typically checked every 3–4 days for signs of occupancy. Once the first or second egg appeared, a thermistor was taped among the eggs to the inside of the nest-box floor and connected through a small hole in the floor to a temperature logger (Onset Computer Corp., Pocasset, Massachusetts) positioned on a shelf 4 cm below the floor of the box. A second thermistor and temperature logger were placed on the shelf to record the temperature of the nest's immediate surroundings. Temperature was logged at approximately 3-min intervals. By comparing the nest and shelf temperatures, we were able to determine when a bird was incubating.

During laying, boxes were checked every 2 days, and new eggs were numbered (if the laying order was known). Towards the end of incubation, nest boxes were visited once or twice daily to identify various stages of hatching and to determine hatching order. Beginning on the day of emergence, we measured nestling body mass at least every 5 days. From 25 days after eggs hatched, we visited nest boxes daily to determine when fledging occurred. We did not

Fig. 1. Temperatures of *Falco sparverius* nest 22 and its immediate surroundings (shelf). Arrows indicate when the female was captured in and returned to the nest box (1), the nest was abandoned (2), and incubation resumed (3). Vertical lines indicate midnights.



handle nestlings older than 26 days so as to minimize the risk of causing premature fledging.

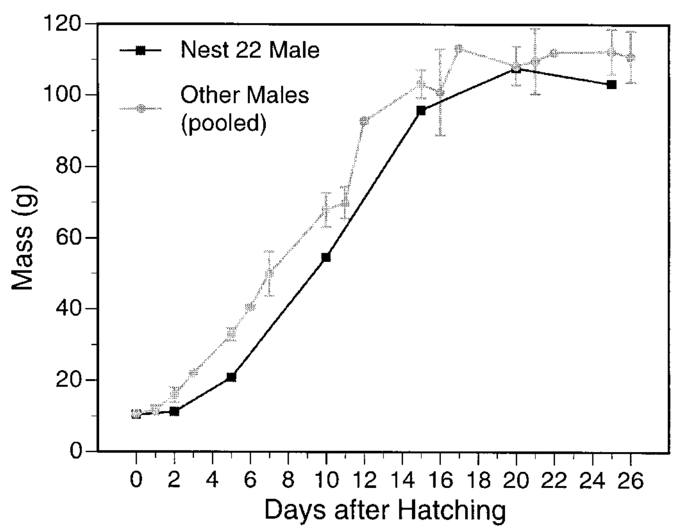
Results

Temperature loggers for nest 22 indicated that shortly after we had captured the female 15 days after clutch completion, both members of the pair temporarily abandoned the nest for nearly 21 h (Fig. 1). Incubation had been progressing normally to this point, as revealed by nest temperatures consistently well above those of the immediate surroundings. However, a few seconds after we returned the female to the nest box following her capture, she left the box and remained off the eggs for at least 5 h, as indicated by the sudden drop in nest temperature to ambient from 12:07 to 17:03. At 17:03, the nest temperature rose well above the surrounding temperature, indicating the presence of an incubating adult. From 20:12 to 17:06 on the following day, the nest remained unattended. During this time, the nest temperature dropped to a minimum of 9.9°C and averaged 12.7°C. Nest attendance resumed at 17:06 (16 days after clutch completion) and continued normally for at least another 2 days, after which the temperature loggers were removed.

Nest 22 had 4 eggs, which we examined daily from 24 days after clutch completion to hatching. We candled the eggs 26 days after clutch completion and all were opaque, indicating the presence of embryos. By 29 days, egg 4 was pipped. By 30 days, peeping and tapping were coming from within the egg, and by 32 days, egg 4 hatched. No other eggs ever showed signs of hatching, and we did not inspect their contents. Egg 1 was cracked, leaking, and therefore inviable. In 3 other nests in which hatching occurred, mean hatching success was 89%.

On hatching day, the nestling weighed 10.4 g, and by 15 days after hatching, a white and bluish tint of flight-feather shafts indicated that he was male. Figure 2 shows his gain in mass and, for comparison, the mean masses during the nestling period for 3 other males, each from 3 different nests.

Fig. 2. Change in body mass of the *Falco sparverius* nestling in nest 22 and mean body masses during the same stages of development for 3 other male nestlings from 3 separate nests. Vertical bars show ±1 SE. Points without bars represent data from only 1 nestling.



Discussion

Both male and female kestrels incubate, although the female is primarily responsible for incubation (Bortolotti and Wiebe 1993; personal observation). It seems probable that our capturing the female at nest 22 caused her to immediately abandon the nest and that incubation by the male caused the subsequent 3-h increase in nest temperature during the afternoon. That only 1 of 3 viable eggs hatched suggests that the temperature conditions during the period of abandonment may have approached the limit of hypothermic tolerance in kestrel embryos.

We recorded nest, not egg, temperature. Chicken embryos of any age are limited in their ability to generate their own heat (Tazawa et al. 1988), and their temperature is probably not more than 1.5 C° above that of their immediate surroundings (Sotherland et al. 1987). Therefore, during the period of neglect, the embryo temperature in this nest was probably very near the recorded nest temperature.

Growth of this nestling resembled that which has been documented previously for this species (Wiebe and Bortolotti 1992), suggesting that an extended period of hypothermia did not alter nestling development. However, this egg required the longest incubation period (32 days) of any in this study (mean = 29.5 days), underscoring the importance of constant temperature throughout the incubation period (Deeming and Ferguson 1991).

Webb (1987) and Ewert (1991) have reviewed avian embryonic tolerance to hypothermia. They point out that in addition to temperature, both the stage of embryonic development during exposure and the duration of exposure are important factors in determining the fate of embryos. Unfortunately, most published assessments of embryonic hypothermic tolerance fail to account for each of these three variables. Those that do often involve temperatures, stages of development, or durations of exposure very different from what we observed, making it difficult to compare our results with others'. Although very brief exposure to hypothermia probably occurs frequently in many bird species (i.e., during periods when both parents are off the nest), it seems unlikely for most species that embryos well into development could endure periods of neglect as long as those we observed. However, some exceptional examples of embryonic hypothermic tolerance occur in the Procellariiformes (Pefaur 1974; Boersma and Wheelwright 1979; Vleck and Kenagy 1980; Roby and Ricklefs 1984), which routinely forage for 1 to several days, leaving eggs unattended, and in pheasants, wrens, and domestic fowl (see below).

Prior to the onset of incubation, eggs have a relatively high tolerance to hypothermia (Weinrich and Baker 1978). Once embryonic development starts, however, that tolerance declines (but see Matthews 1954). Exposure of ring-necked pheasants (*Phasianus colchicus*) to 13°C for 24 h caused relatively low mortality in 2-day-old embryos and moderate mortality in 10-day-old embryos, but nearly complete mortality in the oldest (22-day-old) embryos (MacMullan and Eberhardt 1953). Similar changes in cold-tolerance were observed in house wrens (*Troglodytes aedon*; Baldwin and Kendeigh 1932) and domestic fowl (Moreng and Bryant 1956). It is tempting to conclude from our study that only egg 4 survived because it was the youngest and therefore least susceptible to hypothermia-induced mortality. However, our temperature records indicate that full incubation did not begin until completion of the clutch, suggesting that embryos probably began developing fairly synchronously. It therefore seems unlikely that the embryos differed enough in development prior to hypothermia to affect the probability of their survival.

Maternal steroids are deposited in yolks in concentrations that vary in some species with laying order and environmental conditions (Schwabl 1996). Thyroid hormones have been found in yolks as well (Sechman and Bobek 1988; Prati et al. 1992). Although we know of no supporting studies, it is intriguing to speculate that such hormones may influence embryonic survivorship by enhancing development and possibly cold-hardiness. Future experiments should address how hypothermic conditions of variable duration affect embryos of different ages and how the attributes of specific eggs, such as laying sequence, hormone concentration, size, and sex, might affect cold-hardiness.

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