

DEVELOPMENT OF THERMOREGULATORY ABILITY DURING ONTOGENY IN THE WHITE STORK *CICONIA CICONIA*

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SUMMARY.— *Development of thermoregulatory ability during ontogeny in the White Stork Ciconia ciconia.* The development of thermoregulation abilities in White Stork *Ciconia ciconia* nestlings was examined. Our results showed that body mass, and not age, was the best predictor for thermoregulatory ability despite what was found in passerines. White Stork nestlings did not develop their thermoregulatory abilities abruptly since their capacity to keep their body temperature developed gradually. When nestlings reached 1700 g they have just finished to growth at their maximum rate (inflexion point in the growth curve) and they were able to keep their body temperature above 39.5 °C either in the nest or individually isolated at ambient temperature. The homeothermy index (HI) showed a negative correlation with growth rate (GR). Results suggests that White Stork nestlings invest little in thermoregulation before finishing their faster growth period, which is in accordance with the energy allocation hypothesis.

Key words: *Ciconia ciconia*, nestling growth, ontogeny, thermoregulation.

RESUMEN.— *Ontogenia de la capacidad de termorregulación en la Cigüeña Blanca Ciconia ciconia.* Este trabajo examina el desarrollo de la capacidad de termorregular que muestran los pollos de Cigüeña Blanca *Ciconia ciconia*. Los resultados indican que la masa, y no la edad, es la variable que mejor explica la capacidad de termorregulación, en contra de los resultados obtenidos en aves paseriformes. La maduración de la capacidad de termorregulación se produjo gradualmente y no de forma brusca. El punto de inflexión de la curva de crecimiento, momento en el que los pollos tienen la máxima tasa de crecimiento, se alcanzó a los 1700 g, tras el cual los pollos mostraron pocas diferencias de temperatura corporal ya estuvieran dentro o aislados fuera del nido. La tasa de crecimiento (GR) de los pollos a lo largo de su desarrollo estuvo negativa y significativamente correlacionada con el índice de termorregulación (HI). Estos resultados son compatibles con la hipótesis de reparto de la energía según la cual los pollos desarrollan su plena capacidad de termorregular cuando han terminado la fase de crecimiento rápido, dada la dificultad de compatibilizar el gasto energético de ambas funciones.

Palabras clave: crecimiento de pollos, *Ciconia ciconia*, ontogenia, termorregulación.

INTRODUCTION

Newly hatched birds show a great variation in their thermoregulatory abilities, from an ectothermic state in altricial birds to different degrees of endothermy in precocial species (Whitow & Tazawa, 1991; Konarzewski, 1995). There is also important difference in growth rates between precocial and altricial nestlings of similar size (Ricklefs, 1979, 1984), the latter growing much faster. To explain these differences in growth rate, Dawson & Evans (1960) introduced the energy allocation hypothesis, by that the young altricial nestlings can allocate

more energy to growth and development, owing to a complex of attributes that reduces the diversion of energy to activity and thermoregulation. The hypothesis of Dawson & Evans (1960) predicts a negative relationship between growth rate and the capacity for maintaining body temperature due to the high cost of thermoregulation.

Konarzewski (1995) proposed two alternatives to the energy allocation hypothesis to explain the relationships between the allocation of energy to growth and respiration in chicks. Based on results of Dunn (1980), Konarzewski proposed the energy independence hypothesis.

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Dunn (1980) compared energy budgets of five bird species, concluding that, under particular selective pressure, an energetic extravagance could be selected for. According to this hypothesis, the amount of energy allocated to growth and to other processes such as basal metabolism, thermoregulatory or activity costs, is independent of each other. The third hypothesis proposed by the author is the functional relation hypothesis. Evolutionary changes in growth rate may affect operating costs of the metabolic processes that maintain growth, which could result in a positive functional relationship between the energy allocated to growth and to respiration, hence producing a functional relationship between them. To test the energy allocation, energy independence and the functional relation hypothesis, the author predicted a negative relation, no relation and a positive relation, respectively, between growth and respiration, although this author found generally inconclusive results, noting especially that prediction from the different hypotheses are difficult to distinguish.

The energy allocation hypothesis has been supported by several laboratory studies in passerines testing that the period of highest growth rate precedes the development of endothermy (Dunn, 1975; Olson, 1992). Within altricial birds a wide range of temperature regulation ability is also found due to factors such as body size and brood size, based on the effects of a more favourable ratio of heat production to heat loss in bigger chicks and broods (Visser & Ricklefs, 1993; Thomas *et al.*, 1993).

Here, we examine the postnatal development under natural conditions in nestlings of the White Stork (*Ciconia ciconia*), an altricial bird with an adult body mass of 3000-3700 g and 1.2 m in height. Breeding pairs typically raise 2-3 nestlings that hatch naked and helpless and take 50-65 days to reach asymptotic body mass (Tortosa, 1992) following the general growth pattern described for altricial birds. Previous studies in some groups of birds such as seabirds (Konarzewski & Taylor, 1989) or aerial insectivores (McCarty, 2001) have found that nestlings subject to short-term shortages of food can delay their growth although they can attain full body mass, as also found in the nestlings of White Storks (Tortosa & Redondo, 1992). Therefore, interspecific variation in growth rate among White Stork nestlings can

produce a large variation in mass at a given age. This study investigated the effect of growth rate, mass and age on the thermoregulatory competence from 24 h after hatching until fledgling.

METHODS

The study was conducted during April-June 1991 in a breeding colony of White Storks located in Jerez de la Frontera, Southern Spain. Twenty-two nestlings from eight broods, with ages between 0 and 70 days, were monitored weekly from hatching to fledgling. Only 15 out of the 22 chicks survived until the fledging stage, so analyses include only those 15 successful nestlings. Body mass was measured to the nearest 2 g with an electronic balance until nestlings reached 2 kg and to the nearest 25 g with a Pesola® spring balance until fledging. Body temperature (Tb) was recorded by means of an electronic thermometer (Nist traceable digital thermometer, VWR Scint. Inc.) to the nearest 0.1 °C, inserting the thermistor probe at a depth of 1-2 cm into the rectum. Initial body temperature (Tbi) of each chick was measured in the nest between 10.00 and 11.00 a.m. Each chick was then kept into an open wooden box (50 cm × 50 cm × 50 cm) protected from the wind. Temperature inside the box was recorded at its bottom and chicks were exposed to ambient temperature within the box (21 ± 1 °C) for 45 min, after which the final body temperature (Tbf) was measured. Finally, the nestlings were returned to their original nests.

We used the homeothermy index (HI) as an indicative of thermoregulatory ability (Ricklefs, 1987):

$$HI = \frac{T_{bf} - T_a}{T_{bi} - T_a}$$

where Tbi and Tbf are the initial and final body temperature and Ta the ambient temperature.

The body mass data were fitted to the logistic curve according to Ricklefs' (1967) equation to estimate the inflection point and the asymptotic body mass. Instantaneous growth rates were calculated according to the equation of Brody (1945):

$$GR = \frac{\ln X2 - \ln X1}{t2 - t1}$$

where X1 and X2 are the body mass at age t1 and t2 respectively.

The correlation between HI and the GR was analyzed in order to test whether White Stork nestlings reach endothermy after they finished their maximum rate of growth, as predicted by the energy allocation hypothesis.

Statistical analyses were performed according to Zar (1984). Since the same individuals were measured throughout their growing phase, a repeated-measures ANOVA design (SAS Institute 1987) was used to ensure statistical independence between data points. All probabilities are two-tailed.

RESULTS

Nestling growth

White Stork nestlings took 55-60 days to reach their asymptotic body mass, an average of 3,326 g. The inflection point in the growth curve was reached at day 23 when nestlings weighed 1,664 g (derived by extrapolating the growth curve), which is about half their asymptotic body mass. This body mass was reached when nestlings had completed 38% of the nestling period (Fig. 1).

Body temperature of nestlings

Nestlings in the nest always showed a T_{bi} above 36°C. A logarithmic relationship between T_{bi} and body mass was found ($r = 0.81$, $df = 90$, $P < 0.001$; Fig. 2). The younger hatchlings (1 week old) were able to keep their body temperature at least 15°C above ambient temperature (21°C), a value which was at least 90% of the adult value when exposed to the ambient temperature.

T_{bf} also showed a strong logarithmic correlation with age ($r = 0.89$, $df = 90$, $P < 0.001$) and body mass ($r = 0.95$, $df = 90$, $P < 0.001$; Fig.2). T_{bf} decreased with body mass and the younger hatchlings always showed a T_{bf} lower than 31°C (Fig. 2). However, when the effect of body mass and age on each other was

controlled their relationships with T_{bf} changed significantly. Partial correlation between body mass and T_{bf} still remained significant after controlling for the effect of age (partial correlation: $r = 0.56$, $df = 90$, $P < 0.001$), whereas no relation was found between age and T_{bf} when the effect of body mass was controlled for (partial correlation: $r = -0.11$, $df = 90$, $P > 0.05$).

To test the prediction of a negative relationship between growth rate and thermoregulatory ability, the correlation coefficient between HI and GR was calculated. Both variables were weekly estimated from hatchling until the 9th week of age, when all nestlings reached their asymptotic body mass. GR showed a negative relationship with body mass ($r = 0.46$, $df = 52$, $P = 0.001$; Fig.3), while HI experienced a logarithmic increase with body mass ($r = 0.90$, $df = 90$, $P < 0.001$; Fig. 3). Both variables, HI and GR, showed a strong and negative exponential relationship between them ($r = -0.47$, $df = 52$, $P < 0.001$; Fig. 4).

DISCUSSION

Results showed that White Stork nestlings grew at their maximum rates until they reached about 1700 g, after which their growth rate decreased. During the fast growth period a great variability in the GR was observed, since it is greatly influenced, at least in White Storks, by factors such as brood size and the hatching order which determine a variable period between hatching and independence in this species (Tortosa, 1992; Redondo *et al.*, 1995). It is known that the younger White Stork nestlings in the brood can delay their growth to continue growing later in the normal way, when they are properly fed (Tortosa & Redondo, 1992).

After nestlings have reached 1700 g, their growth rate declines, this coinciding with a homeothermy index close to 1 ($T_b = T_{bf}$), indicating that chicks maintained their body temperature when exposed at 21°C. This could be due to the intervention of thermogenic mechanisms with a heat production rate sufficiently elevated to compensate for the heat loss and which allows them support a T_b above ambient temperature. This finding suggests that, as proposed by the energy allocation hypothesis, nestlings only develop their thermoregulatory

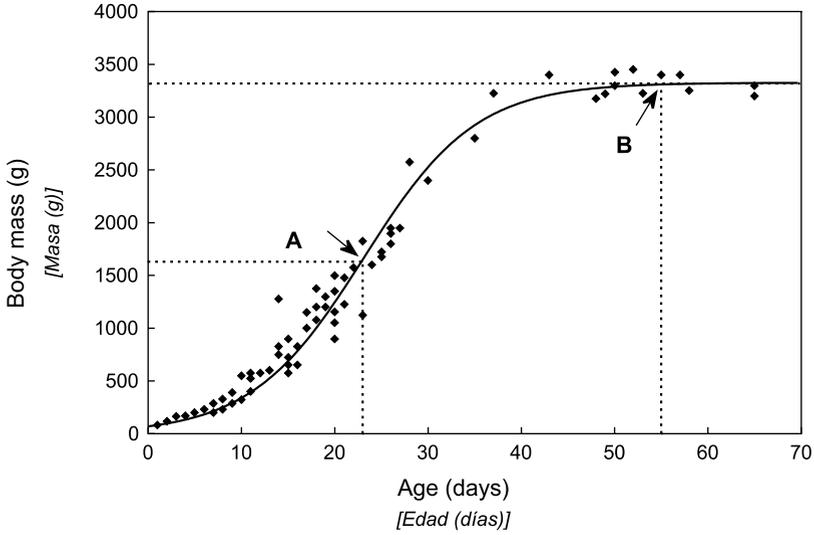


FIG. 1.— Body mass of White Stork nestlings in relation to age and its fit to a logistic curve. A and B points coincide with the inflection point curve (23 days old and 50% of asymptotic body mass) and the age at which estimated asymptotic body mass was reached, respectively.
 [Masa de pollos de Cigüeña Blanca en función de la edad y su ajuste a una curva logística. Los puntos A y B coinciden con el punto de inflexión de la curva (23 días de edad y 50% de la masa asintótica) y la edad a la que se alcanza la masa asintótica estimada, respectivamente.]

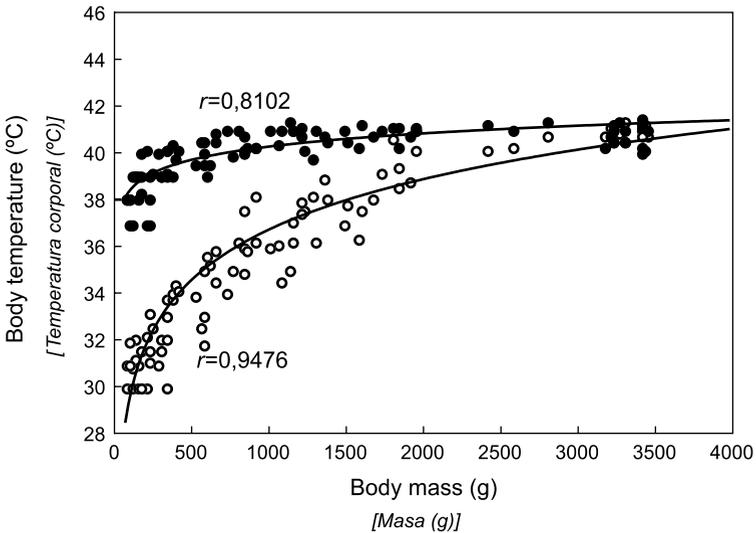


FIG. 2.—Relationship of body mass to body temperature of White Stork nestlings before removing from the nest (Tbi, closed symbols) and after being isolated for 45 min at an ambient temperature of 21°C (Tbf, open symbols). The lines represent the logarithmic regression equations fitted to data.
 [Relación entre la masa y la temperatura corporal de pollos de Cigüeña Blanca antes de sacarlos del nido (Tbi, símbolos cerrados) y después de 45 minutos con una temperatura ambiental de 21°C (Tbf, símbolos abiertos). Las líneas representan el ajuste de los datos a ecuaciones de regresión logística.]

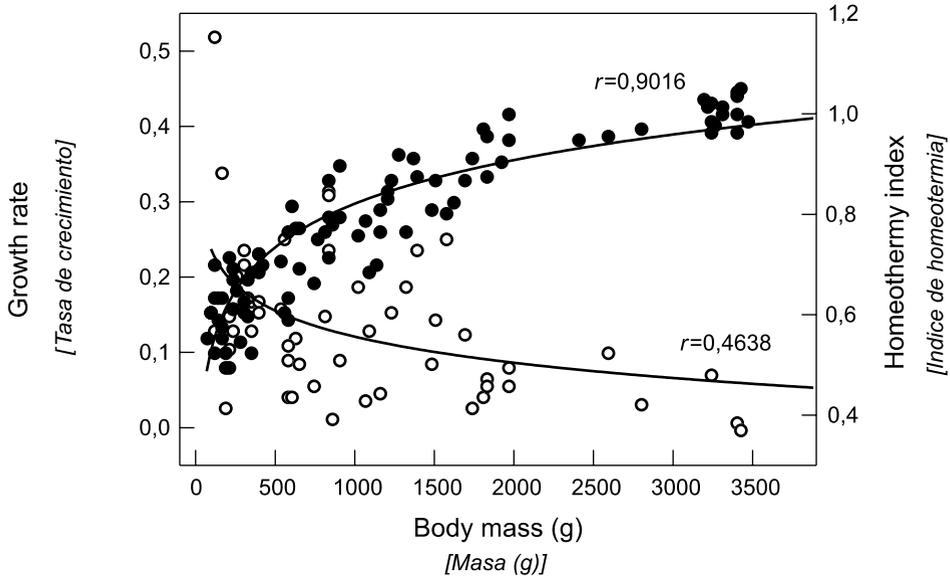


FIG. 3.—Relationship of body mass to growth rate (GR) and homeothermy index (HI). The lines represent logarithmic regression equations fitted to data.
 [Relación entre la masa corporal y la tasa de crecimiento (GR) con el índice de homeotermia (HI). Las líneas representan el ajuste de los datos a ecuaciones de regresión logarítmica.]

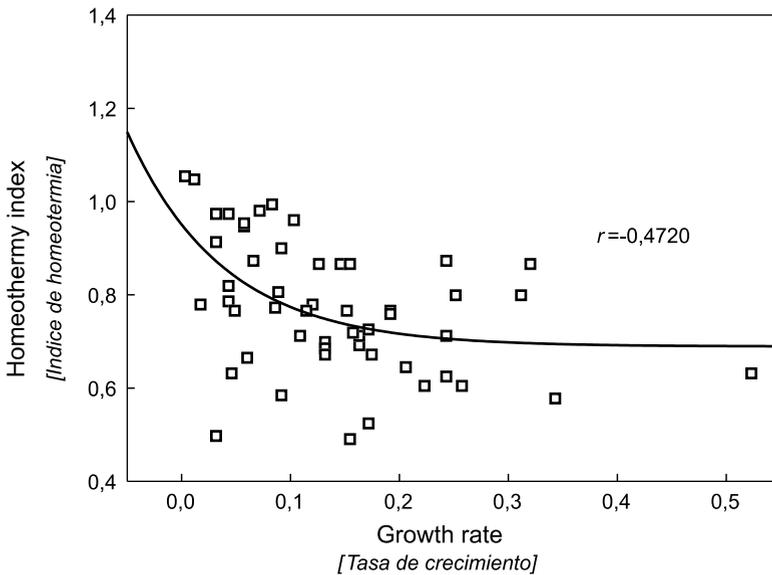


FIG. 4.—Relationship of homeothermy index to instantaneous growth rate. Data are fitted to an exponential regression curve.
 [Relación entre el índice de homeotermia y la tasa de crecimiento instantáneo. Los datos se han ajustado a una curva de regresión exponencial.]

abilities fully when they have finished growing at their maximum rate.

Contrary to results found in small birds such as the Red-Winged Blackbird *Agelaius phoeniceus* (Olson, 1992) or in the Arctic Tern *Sterna paradisaea* (Klaassen & Bech, 1992), we found that nestling body mass and not nestling age was the better predictor of thermoregulatory ability. This fact could have important ecological implications for White Storks nestlings. The relationship between thermoregulation and body mass independent of age provides a useful way to ensure that the cost of thermoregulation only will occur when body mass is above a given threshold. This result suggests that White Stork nestlings have a great capacity to control their energetic budgets, and to adjust them to prevailing food conditions, which is in accordance with the great variability in the growth rate and the nest period observed in this species (Tortosa & Redondo, 1992).

Results from studies on thermoregulatory abilities of altricial nestlings showed that the most common pattern is an abrupt development of endothermy (Dawson & Evans, 1957, 1960). However, further studies in passerines as the Red-Winged Blackbird (Olson, 1992) found that the development of endothermy occurs in stages. White Stork nestlings did not develop their thermoregulatory abilities abruptly and instead their capacity to keep their body temperature was gradually attained. During the first weeks of life parental care, microclimate in the nest (Tortosa & Villafuerte, 1999), brood size and basal metabolism of chicks are factors that probably contribute to the existence of an effective endothermy in White Stork nestlings, allowing young to keep a body temperature at least 90% of adult's Tb at the nest. After the exposure of chicks to cold ambient temperature, the heat loss rate is greater than heat production, as indicated by the low Tbf (only between 45 and 75% as high as adult's Tb). The high GR values and low HI values indicate that the disposable energy is mainly allocated to nestling growth during the first weeks of life.

Dunn (1975) defined that the age of physiological endothermy was the age at which individual nestlings can keep their body temperature to at least 75% of adult Tb when exposed to ambient temperature. According to Dunn (1975), White Stork nestlings develop their physiological endothermy after their first week

of life. The progressive increasing of Tbf could be caused by a greater development of feathers (Snow, 1961; Verbeek, 1995) that insulate the chick and by the increase of body mass that provides a more favourable surface-to-volume ratio for retaining body heat (Visser & Ricklefs, 1993). These factors would reduce energetic costs for nestlings and would allow rapid growth and thermogenesis to overlap for a short period. In contrast, maximum growth in passerines, with a smaller body mass, clearly precedes the greatest improvements in thermoregulatory capabilities (Dunn, 1975; Olson, 1992).

When nestlings reached 1700 g, which represents half the asymptotic body mass, they are in the inflection point at the growth curve. After this point HI reached a value of 1 or nearly 1, and the growth rate declined. In addition to feather development, the more favourable ratio of surface to volume and metabolic maturation would allow nestlings to regulate their body temperature to reach a Tbf as high as adults. According to the results exposed in this work, we conclude that our data are consistent with predictions derived from the energy allocation hypothesis (Dawson & Evans, 1957, 1960).

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