BRAIN, EYE, AND SKULL GROWTH IN EMBRYONIC GEESE[1]

UWE GILLE, FRANK ZACHEN AND FRANZ-VIKTOR SALOMON
*Institute of Veterinary Anatomy, University Leipzig, An den Tierkliniken 43, D-04103 Leipzig, Germany,
e-mail: gille@vetmed.uni-leipzig.de*

Abstract. We tested the hypothesis that bill proportions at hatching are a byproduct of overall skull proportions which are a result of constraints of brain growth. We measured brain and eye weights, eye diameter, and some skull dimensions in domestic geese (*Anser anser* f. domestica) varying in age between embryonic day 7.5 and 29.5 (hatching), and in five adult geese. With respect to age, weights show divergent growth patterns resulting in complex allometry for eye but simple allometry for brain weight. This differs from the situation in Galliforms and probably reflects the high cerebralization of Anseriforms. Length measurements show similar growth patterns. Cranial length realizes a larger part of overall growth during incubation when compared to facial length. Cranial width is similar to eye diameter and brain weight. Bill width exhibits a unique growth pattern. Bill proportions are similar to the whole head but differ from those of the bony brain capsule. Therefore, although all craniometric measurements strongly correlate to brain size, brain growth probably influences growth of the cranial but not of the facial part of the skull.

Key words: allometry, Anser anser, bill, brain, craniometry, goose, growth curve.

In hatchlings, bill width has a higher proportion of its adult value than does bill length. In a previous paper (Gille and Salomon 1999), we added support to the hypothesis of Caccamise (1980) that this phenomenon is a result of a close relationship between bill and skull dimensions in ducks. Moreover, Caccamise (1980) suggested that skull dimensions result from constraints of brain growth. However, little is known about the principal growth relationships of brain and skull during embryonic development.

In chickens (*Gallus gallus*), relative brain growth rate falls below that of overall growth in the middle of incubation (Schmalhausen 1926, Sutter 1943), which results in allometric exponents decreasing with embryonic age (Sutter 1943, Neff 1973). In other birds, there is constant negative allometric growth throughout incubation (Neff 1973, Nol and Boire 1996).

The eye of the chicken shows a growth pattern similar to the brain (Schmalhausen 1927). In Mallards (*Anas platyrhynchos*) and altricial birds, there is complex allometry with decreasing allometric exponents (Neff 1973).

For skull growth, Schumacher and Wolff (1966) found negative allometry for measurements of the cranium (the bony brain capsule) with respect to overall skull length, whereas measurements of the facies (the facial part of the skull) showed an inverse pattern in chickens and Black-headed Gulls (*Larus ridibundus*). When related to a sum of several skeletal measurements, skull length shows negatively allometric scaling in Galliformes (Maschlanka 1972). Comparisons between embryonic growth of brain and skull have not been performed yet.

The aim of the present study was to analyze brain, eye, and skull growth in embryonic geese (*Anser anser* f. domestica) in order to test the hypothesis that bill proportions at hatching are a byproduct of overall skull proportions. Secondly, we test the assumption that skull proportions are a result of constraints of brain growth.

METHODS

Incubated geese eggs were obtained from a commercial breeder. Incubation temperatures were 37.6°C within the first week and 37.4°C thereafter. Humidity varied between 70 and 80%. Seven eggs were opened every second day at 11 different ages between embryonic day (ED) 5.5 and 29.5 (hatching). Furthermore, we measured five adult female geese in order to obtain values relative to adults. The brain and the left eyeball were dissected and weights were obtained to the nearest milligram with an electronic balance. The equatorial diameter of the eyeball was measured with a caliper. Five measurements of the skull were taken with a caliper between ED 9.5 and hatching. Bill length was measured between its tip and the transition from horn to skin. Bill width was measured at the caudal end of the nostrils. Cranial length was measured between the base of bill and occiput. Cranial width was measured in the region of the Os squamosum. Head length was obtained between bill tip and occiput. All measurements were in mm.

With respect to age, the Janoschek growth curve (Janoschek 1957), $W = A - A \cdot \exp(-kt^p)$, was fitted to the age group means. W is the corresponding length or weight at time t (embryonic days, ED), A is the asymptotic value, k is a time-scale parameter, and p a shape parameter adjusting the point of inflection. With respect to body weight, the allometric formula, $y = ax^b$ was fitted to the individual measurement pairs. In this function, y represents the respective linear or weight measurement, x the body weight, the allometric exponent b a measure of the proportion of both relative growth rates, and a is the integration constant. Allo-

TABLE 1. Parameters of the Janoschek curve (k, p, A) and some growth curve characteristics.[a]

Parameter	k	p	A [g or mm]	CD	t_i [ED]	t_{50} [ED]	u_0 [%]
Body weight (g)	2.41E-7	4.656	143.8	0.997	25	23	2.3
Brain weight (g)	1.32E-6	4.321	2.6	0.999	22	21	24.5
Eye weight (g)	1.20E-4	3.084	0.7	0.994	16	16	19.5
Brain weight$^{1/3}$ (g)	1.10E-2	1.401	1.9	0.995	10	14	64.2
Eye diameter (mm)	1.02E-2	1.776	12.1	0.996	8	11	58.1
Bill length (mm)	1.75E-3	2.161	18.2	0.967	14	15	24.3
Head length (mm)	3.81E-3	1.818	59.8	0.998	14	15	37.6
Cranial length (mm)	5.73E-3	1.606	44.8	0.973	14	15	52.2
Bill width (mm)	2.00E-3	1.701	21.2	0.987	23	18	36.1
Cranial width (mm)	1.98E-2	1.348	22.6	0.988	7	12	46.7

[a] CD = nonlinear coefficient of determination, t_i = age at point of infection, t_{50} = age at which 50% of the hatching value is attained, u_0 = hatching value in percent of the adult value, ED = embryonic day.

metric relationships were analyzed between brain weight (x) and skull dimensions (y) in the same way.

RESULTS

With respect to age, the three weight measurements showed divergent growth patterns. Eye weight exhibited a very early point of inflection. Its growth rate peaked as early as ED 10 (t_1, Table 1) and 50% of the weight at hatching was attained at ED 14 (t_{50}, Table 1). Body-weight growth rate peaked at ED 25. Brain weight showed characteristics between these extremes. Although body weight had the highest percentage growth rate (PGR, absolute growth rate divided by the weight at hatching), the PGR for eye and brain were higher than for body-weight until ED 19 and 22, respectively (Fig. 1). Both eye and brain weights had a much higher hatching/adult ratio (u_0) than the whole body (Table 1).

All length measurements showed a similar growth pattern. This becomes more clear when viewing the PGR (Fig. 2). Their points of inflection were in the middle of incubation and close to t_{50}. However, lengths differed markedly with respect to u_0 for which cranial length had twice the value as bill length (Table 1). Because growth curves are not independent of dimension, we introduced the cubic root of brain weight as an arbitrary measurement for comparison with skull growth. Cubic root of brain weight, eye diameter, and cranial width grew similarly. Their growth rates peaked earlier than those of length measurements (Fig. 2). Bill width exhibited a unique growth pattern. It showed a more constant increment throughout incubation, with a late point of inflection and minimal decrease in growth rate until hatching.

All measurements except bill width showed negative allometric growth during the second half of incubation (Table 2). For eye measurements and bill length, a period of strong positive allometry preceded this negative allometry. Bill width had an inverse allometric pattern. It showed negative allometry until ED 15.5, and strong positive allometry thereafter. With respect to brain weight, length measurements showed isometry. Cranial width scaled biphasic with isometry until ED 15.5 and negative allometry thereafter. Bill
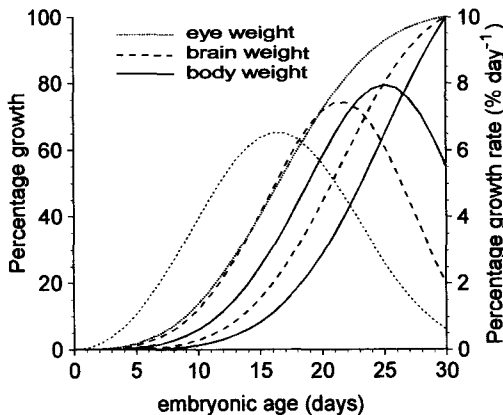

FIGURE 1. Percentage growth and growth rate curves for body, brain, and eye weight of geese (Anser anser f. domestica). Percentage curves were obtained by dividing each absolute curve by the corresponding weight at hatching.
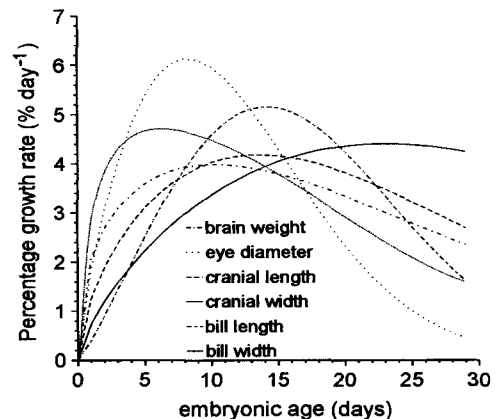

FIGURE 2. Percentage growth rate curves for craniometric measurements of geese (Anser anser f. domestica).

TABLE 2. Allometric coefficients (a, b) and coefficients of determination (CD).

Parameter	Body weight				Brain weight			
	Age interval [ED]	b ± SD	a	CD	Age interval [ED]	b ± SD	a	CD
Brain weight (g)	5.5–29.5	0.75 ± 0.01	0.07	0.99				
Eye weight (g)	5.5–11.5	1.28 ± 0.36	0.05	0.98				
	13.5–29.5	0.36 ± 0.01	0.13	0.96				
Eye diameter (mm)	5.5–11.5	0.40 ± 0.01	4.76	0.98				
	13.5–29.5	0.13 ± 0.01	6.45	0.94				
Head length (mm)	9.5–29.5	0.29 ± 0.01	12.46	0.99	9.5–29.5	0.36 ± 0.01	34.33	0.99
Cranial length (mm)	9.5–29.5	0.29 ± 0.60	8.07	0.97	9.5–29.5	0.29 ± 0.01[a]	8.07	0.97
Bill length (mm)	9.5–13.5	1.43 ± 0.10	1.42	0.94	9.5–13.5	1.20 ± 0.11	45.52	0.87
	13.5–29.5	0.24 ± 0.01	5.35	0.94	13.5–29.5	0.32 ± 0.01[a]	12.27	0.92
Cranial width (mm)	9.5–29.5	0.19 ± 0.01	7.69	0.96	9.5–13.5	0.32 ± 0.04[a]	17.22	0.78
					13.5–29.5	0.25 ± 0.01	15.08	0.96
Bill width (mm)	9.5–18.5	0.25 ± 0.03	2.08	0.76	9.5–18.5	0.26 ± 0.03[a]	4.43	0.72
	18.5–29.5	0.43 ± 0.01	1.26	0.97	18.5–29.5	0.56 ± 0.01	5.72	0.98

[a] b-value not statistically different from isometry (1 for weights, 0.33 for linear measurements), t-test, $P = 0.05$.

width changed from negative to positive allometry at ED 18.5 (Table 2). Correlation of craniometric measurements with brain weight was high (Table 2) as were correlations among linear measurements (data not shown).

DISCUSSION

The Janoschek growth curve provides an excellent fit to the most diverse growth data (Gille and Salomon 1995). Its flexibility is similar to that of the Richards model and allows application to most sigmoid and exponential growth courses. Contrary to three-parameter models as the Gompertz, logistic, or Bertalanffy growth curves, the ratio of inflection ordinate and asymptote are flexible for both the Janoschek and the Richards growth curve. Because initial parameter estimates are easily obtainable and procedural problems rarely occur, we prefer the Janoschek growth curve.

Body, brain, and eye weight show divergent growth patterns. Eye weight grows rapidly in early incubation. The divergence between brain and body weight is less pronounced. This explains the differing allometric patterns. Whereas allometric growth in eye weight is biphasic, brain weight shows simple negative allometry throughout incubation as reported in Mallards and altricial birds (Neff 1973). The higher growth rate of brain when compared to eye weight in late incubation combined with prolonged incubation time probably enables the high cerebralization in Anseriform species where the nucleus basalis and the complexus paleostriatus are well developed (Starck 1989, 1993). The growth pattern in geese is close to altricial birds, where brain growth rate hardly declines (Sutter 1943) and simple allometry is present (Neff 1973).

Length measurements of the skull show similar embryonic growth patterns. However, the peak of PGR is lower and its decline less pronounced for cranial length when compared to bill length. This is reflected by negative allometry for cranial length and positive allometry for bill length as in chickens and gulls (Schumacher and Wolff 1966). The bony brain capsule re-

alizes a larger part of overall growth than the facial part during embryonic ontogeny. On the other hand, cranial width grows similarly to eye diameter and (cubic root of) brain weight as suggested by Caccamise (1980). The biphasic allometric growth for eye diameter can be explained by the much higher PGR (Fig. 2) when compared to brain weight and skull width.

Although all skull measurements closely correlate to each other and to brain weight, bill width exhibits a strikingly different mode of growth. It shows a late point of inflection, a minimal decrease in embryonic growth rate, and a strong positive allometry in late incubation. This is in sharp contrast to posthatching growth, where bill width and length exhibit similar patterns (Gille and Salomon 1999). When considering the part of overall growth realized until hatching (u_0), the length-width-ratios of head and bill are similar but differ from those of the brain capsule. Therefore, there must be other factors responsible for facial proportions. Bill proportions at hatching presumably reflect the general trend in skeletal proportioning. Bone width is more developed than length in young. This agrees with the hypothesis of Caccamise (1980) and our previous study (Gille and Salomon 1999). However, the unique growth pattern of bill width as well as differences between facial and cranial parts do not support the extension of this hypothesis that brain growth is responsible for facial proportions. On the contrary, the length of the cranial part of the head has a higher u_0 than does width. This inverse length-width relationship for the bony brain capsule indicates constraints of brain development.

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CLOACAL MICROBES IN HOUSE SPARROWS[1]

REUVEN STEWART[2]

Department of Zoology, University of Leicester, University Road, Leicester, LE1 7RH, U.K.

T. BIRCH RAMBO

T. H. Morgan School of Biological Sciences, 101 Morgan Building, University of Kentucky, Lexington, KY 40506-0225

Abstract. We examined the communities of bacteria and fungi associated with the cloaca of adult House Sparrows (*Passer domesticus*) to investigate whether microbes could be transferred during copulation and thus represent a cost to mating. The levels of microbes in the cloacae of the male and female of eight breeding pairs were significantly correlated. The levels of microbes on the rim of the cloacal protuberance, which comes into direct contact with another bird during copulation, were similar to those inside the cloaca. These findings are consistent with microbes being transferred during copulation. Females could also receive non-cloacal pathogens during copulation, given that two of five males sacrificed had microbes within their testes, which could be incorporated into the ejaculate. Undeveloped eggs were screened for the presence of microbes, although only a low proportion (18%) was contaminated. It seems unlikely that microbial contamination is a general cause of egg failure in this species.

Key words: cloaca, copulation, egg failure, House Sparrow, microbes, Passer domesticus.

In many avian species, a proportion of individuals seek copulations outside of their social bond (Birkhead and Møller 1992). Males which can achieve successful extra-pair copulations (EPCs) benefit by siring more offspring without incurring additional rearing costs. Females which can achieve successful EPCs might benefit in several ways, such as increasing the genetic diversity or quality of their offspring (Petrie and Kempenaers 1998).

Extra-pair copulations might not always be beneficial, however. A frequently cited cost of EPCs, which could be incurred by both sexes, is the risk of acquiring a sexually transmitted disease (STD) (Birkhead and Møller 1992). Unfortunately, despite the burgeoning theoretical interest which STDs have attracted (Hamilton 1990, Graves and Duvall 1995, Thrall et al. 1997), there are few empirical data regarding their prevalence and transmission in wild birds (Sheldon 1993, Petrie and Kempenaers 1998).