mentation in the Hoatzin, a Neotropical leaf-eating bird. Science 245:1236–1238.
KARASOV, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. Stud. Avian Biol. 13:391–415.
KARASOV, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology, p. 61–84. *In* C. Carey [ed.], Avian energetics and nutritional ecology. Chapman and Hall, New York.
MAUSETH, J. D. 1995. Botany, an introduction to plant biology. 2nd. ed. Saunders, Philadelphia.
MORTON, E. S. 1978. Avian arboreal folivores: why not?, p. 123–130. *In* G. G. Montgomery [ed.], The ecology of arboreal folivores. Smithson. Inst. Press, Washington, DC.
NAGY, K. A. 1987. Field metabolic rate and food requirements scaling in mammals and birds. Ecol. Monogr. 57:111–128.
RALPH, C. P., S. E. NAGATA, AND C. J. RALPH. 1985. Analysis of dropping to describe diets of small birds. J. Field. Ornithol. 56:111–128.
RICKLEFS, R. E. 1996. Morphometry of the digestive tract of some passerine birds. Condor 98:279–292.
ROSENBERG, B. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. Stud. Avian Biol. 13:80–90.
SIEGEL, S., AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. 2nd ed. McGraw-Hill, New York.
STEEL, R. G. D., AND J. H. TORRIE 1985. Bioestadística: principios y procedimientos. McGraw-Hill, Bogotá.
WARNER, A. C. Y. 1981. Rate of pasage of digesta through the gut of mammals and birds. Nutrit. Abst. Rev. 51B:789–820.
ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Englewood Cliffs, NJ.
ZISWILER, V., AND D. S. FARNER. 1972. Digestion and the digestive system, p. 313–405. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 2. Academic Press, New York.

The Condor 101:710–713
© The Cooper Ornithological Society 1999

GROWTH OF DUCK BILLS[1]

UWE GILLE AND FRANZ-VIKTOR SALOMON
Institute of Veterinary Anatomy, University of Leipzig, Semmelweisstr. 4, D-04103 Leipzig, Germany, e-mail: vethisto@rz.uni-leipzig.de

Abstract. We analyzed growth in length and width of bill in Mallards (*Anas platyrhynchos*), Pekin (*Anas platyrhynchos* f. domestica) and Muscovy (*Cairina moschata* f. domestica) Ducks with growth curve analysis. Bill growth is characterized by a relatively high proportion of growth realized prehatching and early posthatching points of inflection. Individual variability of bill measurements limits its value for estimating age. Bill width is already further developed at hatching than length, a difference that is maintained throughout the posthatching period. Consequently, bill width has a lower allometric exponent than length. This delay in development of length vs. width probably reflects overall development of the skull. Skull development is in turn closely related to brain growth, thus bill dimensions correlated with brain mass with coefficients of determination of ca. 0.9.

Key words: allometry, Anas, *bill, brain, duck, growth curve,* Mallard.

In birds, bill width has a higher proportion of its adult value at hatching than does bill length. This phenomenon has been explained by two hypotheses. O'Connor (1977) considered faster growth of width a mechanism for increasing gape width to allow for intake of larger food items in altricial birds. This differential growth, however, is present in self-feeding precocial birds (e.g., ducks) as well (Bruggers and Jackson 1977, Siegfried 1977). In precocial birds, bill length may have greater significance for food intake. Conversely, Caccamise (1980) suggested that this phenomenon is a result of close relationship between bill and skull dimensions. Because the brain is one of the most advanced developed organs in the newly hatched chick, the osseous brain capsule must be of a corresponding size, and skull width is thought to be of more importance than skull length (Caccamise 1980). In the Barnacle Goose (*Branta leucopsis*), both bill and skull length had similar proportions of the adult value at hatching (Würdinger 1975). If bill size correlates to skull size and this in turn is related to brain size, then bill measurements and brain mass must correlate. Our study has two main objectives. First, we describe dynamics of bill growth with growth curve analysis and examine its usefulness for estimating age. Second, we perform regression analyses of brain mass with respect to both bill width and length.

METHODS

Captive-reared Mallard (*A. platyrhynchos*), domesticated White Pekin (*A. platyrhynchos* f. domestica; line

[1] Received 14 October 1998. Accepted 12 March 1999.

TABLE 1. Growth characteristics of culmen length (CL) and bill width (BW) for 11 species of ducks.[a]

Species	Variable	W_0 (mm)	A (mm)	t_{50} (days)	p	CD	u_0 (%)	t_{90} (days)	t_i (days)	W'_i (mm day^{-1})
Mallard	CL	17.2	61.52	11.2	1.138	0.98	28.0	50	4	1.27
(*Anas platyrhynchos*)	BW	9.8	25.56	5.1	1.188	0.98	38.2	31	4	0.63
Pekin	CL	17.5	70.62	12.8	1.702	0.98	24.7	33	12	1.92
(*Anas platyrhynchos*)	BW	10.8	30.71	7.5	1.178	0.98	35.2	40	5	0.64
Muscovy Duck	CL	14.1	64.14	17.2	1.586	0.98	22.0	45	15	1.32
(*Cairina moschata*)	BW	8.9	27.68	10.6	1.092	0.97	32.2	57	3	0.48
Greenland Mallard[b]	CL	17.0	61.00	10.2	1.120	0.99	27.7	46	3	1.39
(*Anas platyrhynchos*)	BW	10.0	23.60	2.3	0.962	0.99	42.3	32	—	—
Green-winged Teal	CL	12.0	36.57	6.9	1.538	0.99	32.8	23	8	1.20
(*Anas crecca*)	BW	7.0	13.18	14.1*	1.438	0.98	53.1	19	6	0.32
Shoveler	CL	18.0	64.52	9.6	1.450	0.99	27.9	31	8	1.79
(*Anas clypeata*)	BW	9.0	20.53	3.9	1.452	0.99	43.8	25	8	0.50
Ferruinous Duck	CL	12.0	42.19	14.1	1.305	0.99	28.4	52	10	0.72
(*Aythya nyroca*)	BW	7.0	18.31	8.0	1.470	0.99	38.2	35	11	0.36
Gadwall	CL	12.0	43.79	7.2	1.032	0.99	27.4	36	1	1.52
(*Anas strepera*)	BW	7.0	19.90	3.5	0.788	0.99	35.2	44	—	—
Pochard	CL	16.0	49.00	7.7	1.157	0.99	32.7	38	4	1.15
(*Aythya ferina*)	BW	9.0	20.16	2.3	1.213	0.99	44.6	24	4	0.54
Lesser Scaup	CL	13.3	41.52	8.7	1.273	0.99	32.0	37	7	0.94
(*Aythya affinis*)	BW	9.2	23.53	5.9	1.257	0.99	39.1	35	6	0.49
Canvasback	CL	16.2	62.93	14.0	1.292	0.99	25.7	50	9	1.19
(*Aythya valisineria*)	BW	8.6	21.50	5.8	1.215	0.99	40.0	38	6	0.41

[a] W_0 = value at hatching, A = adult value, t_{50} = time to grow to half of the adult value (* c, because $t_{50} < 0$), p = shape parameter, CD = coefficient of determination, u_0 = percentage of adult value at hatching, t_{90} = time to grow to 90% of the adult value, t_i = age at point of inflection, W'_i = growth rate at point of inflection.
[b] Additional data for Greenland Mallard by Greenwood (1974); Green-winged Teal, Shoveler, Ferruinous Duck, Gadwall, and Pochard by Veselovsky (1952); Lesser Scaup and Canvasback by Lightbody and Ankney (1984).

20), and domesticated Muscovy Ducks (*Cairina moschata* f. domestica) were used in this study. Food and water were supplied ad libitum. Four males of each species were killed by ether inhalation at 12 different ages between 0 (hatching) and 154 days. Culmen length and bill width (at base of bill) were measured with a caliper to the nearest mm. The brain was carefully excised and immediately weighed to the nearest 0.001 g with an electronic balance. Body mass was measured to the nearest gram.

A re-parameterized JANOSCHEK growth curve (Janoschek 1957, Gille and Salomon 1995):

$$W = A - (A - W_0)\exp([-t/c]^p)$$

was fitted to age group means by nonlinear regression. W is the corresponding bill dimension (in mm) at time (age) t (in days). This equation contains four parameters: A, the asymptotic value (adult size), W_0, the size at hatching, and c and p, parameters adjusting slope and shape of the curve, respectively. Value p is a shape parameter that adjusts the percentage value (value at time t divided by the asymptotic value) at the point of inflection, i.e., where the growth curve turns from concave to convex. If p is ≤ 1, the growth course is simply exponential; for $p > 1$, a sigmoid pattern is present. In contrast to the Gompertz and Logistic growth curves, the Janoschek growth curve has a flexible relative inflection ordinate. Its flexibility is close to that of the Richards curve. However, the Janoschek curve causes less procedural problems in nonlinear regression than does the Richards curve (Gille and Salomon, 1995). Value c can be replaced by t_{50}, the time to grow to 50% of the asymptote, by $c = t_{50}/(\ln[2 - 2W_0/A])^{1/p}$ (for details see Gille and Salomon 1995). Therefore, if t_{50} is larger than zero, t_{50} is given instead of c. In addition to our measurements, we analyzed data available from literature for bill measurements. We also analyzed the individual pairs of bill measurements with the allometric relation $y = ax^b$ with respect to data for body and brain mass. In this relation, y is the corresponding bill measurement (length, width) and x is the corresponding body or brain mass. Parameter b is the allometric exponent and a is the integration constant.

RESULTS

The parameters of the Janoschek growth curve are given in Table 1. The coefficients of determination were ≥ 0.97, indicating a good representation of measurement values. Both measurements grew sigmoidally with early points of inflection. At hatching, culmen length was 28% of its adult value in mallards, 25% in pekins, and 22% in muscovies. The corresponding values for bill width were 10% higher. This higher percentage of the adult value of bill width remained throughout the growing period (Fig. 1). Whereas in mallards both growth curves had their point of inflection at the same time, it was earlier for bill width in domesticated pekins and muscovies (t_i, Table 1). The age at point of inflection corresponds to age when growth rate peaks. Contrary to Mallards, for domesticated ducks both percentage growth curves (absolute growth curve divided by the respective final value)

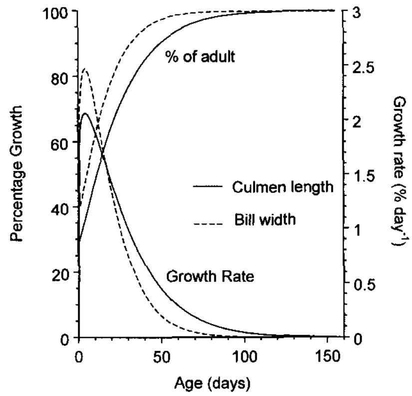

FIGURE 1. Percentage growth and growth rate curves (absolute curves divided by asymptote) for bill measurements in Mallards.

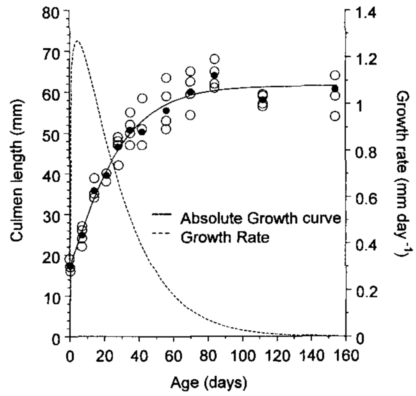

FIGURE 2. Absolute growth and growth rate curves for culmen length in Mallards (open circles = individual measurements, closed circles = means of measurements).

intersected each other. Therefore, the age at which 90% of the adult value is attained (t_{90}, Table 1) was higher for bill width than length. The amplitude of the absolute growth rate peak was higher for culmen length than for bill width in all stocks (W'_i, Table 1). The growth in culmen length in Mallards is depicted in Figure 2, including individual measurements. Although the means were well represented, variability between individuals allowed only a coarse estimate of age until day 35. During this period, no overlap existed between subsequent age groups. However, measurements were taken only weekly.

The approximation to data for Greenland Mallards (Greenwood 1974) yielded nearly the same growth curve characteristics as our data for Mallards reared in captivity. The only exception is that no point of inflection was found for bill width. Beside differences in absolute dimensions, the relations between growth patterns of bill length and width were essentially the same as described above in both dabbling and diving ducks (Table 1).

With respect to body mass, both bill length and width followed simple allometry. The allometric exponents indicated isometry for culmen length (b around ⅓) and negative allometry for bill width (Table 2). With respect to brain mass, both bill length and width showed simple allometry as well. The coefficients of determination were ca. 0.9 (Table 2). The allometric exponents were ca. 1.

DISCUSSION

The bill, one of the earliest used structures in birds, is well developed at hatching (O'Connor 1984). Growth of bill length and width exhibit early points of inflection. Bill width is further developed at hatching than is length, a difference that is maintained throughout the period of posthatching growth. This relationship also was described for Monk Parakeet (*Myiopsitta monachus*, Caccamise 1980). The delay in growth of bill width relative to length in the upper asymptotic area and the shift in the point of inflection in domesticated ducks is presumably because of stochastic errors. For wild ducks, the maximum growth rate for bill width is always close to that of length (Table 1). Greenland Mallards are virtually devoid of a point of inflection for bill width. Because p is only slightly smaller at 1, this point of inflection is presumably shortly before hatching, but stochastic errors might obscure its presence as well. Bill width has a slower relative growth than length as indicated by the allometric exponents. Grant (1981) reported a similar pattern in Darwin's finches.

We suggest that delay in growth of length vs. width

TABLE 2. Allometric coefficients (a, b) and coefficients of determination (CD) for culmen length (CL) and bill width (BW) with respect to body mass and brain mass.

Species	Variable	Body mass			Brain mass		
		a	b	CD	a	b	CD
Mallard	CL	4.46	0.37 ± 0.01	0.94	0.096	0.958 ± 0.05	0.90
	BW	3.66	0.28 ± 0.01	0.95	0.080	1.255 ± 0.07	0.87
Pekin	CL	4.59	0.35 ± 0.01	0.95	0.182	0.807 ± 0.05	0.83
	BW	4.03	0.26 ± 0.01	0.97	0.113	1.154 ± 0.06	0.90
Muscovy	CL	4.48	0.34 ± 0.01	0.94	0.137	0.927 ± 0.06	0.84
	BW	3.97	0.24 ± 0.01	0.98	0.719	1.383 ± 0.06	0.91

is a developmental constraint. Head length and width have a similar relationship to each other in ducks (Salomon et al. 1987a) and geese (Salomon et al. 1987b). Skull development in turn must be consistent with brain development which is also fast in pre- and early posthatching ontogeny (Gille and Salomon 1998). This explains the close relationship between bill measurements and brain size we have shown. The allometric exponents, when relating bill size to brain size, were around 1, indicating a nearly linear relationship, and providing indirect support for Caccamise's (1980) hypothesis.

The distribution of individual measurements around the growth curve of culmen length indicates that an estimation of age from bill measurements is possible only during the first 4 to 5 weeks, with an accuracy of about ± 3 days. Age estimation on the basis of external measurements seems to be more valid with characters that have a larger absolute net growth increment posthatching. Culmen length grows only 33 mm between hatching and day 35 in Mallards. Therefore, individual variability as well as inaccuracy in measurements are of great influence. Wing or ulna length (Gard and Bird 1992) or multivariate measures with these measurements (Gilliland and Ankney 1992) may be more useful because they have larger absolute growth increments.

In conclusion, bill measurements can serve only as a poor estimate of age in ducks. Field ornithologists therefore should obtain external measurements on limbs of ducks instead. Our data support the suggestion of Caccamise (1980) that bill growth is closely related to overall skull growth, which is, in turn, mainly influenced by brain growth.

LITERATURE CITED

BRUGGERS, R. L., AND W. B. JACKSON. 1977. Morphological and behavioral development in the Mandarin Duck. Auk 94:608–612.

CACCAMISE, D. F. 1980. Growth and development of major body components in the Monk Parakeet. Wilson Bull. 92:376–381.

GARD, N. W., AND D. M. BIRD. 1992. Nestling growth and fledging success in manipulated American Kestrel broods. Can. J. Zool. 70:2421–2425.

GILLE, U., AND F.-V. SALOMON. 1995. Bone growth in ducks with special reference to the Janoschek growth curve. Growth Devel. Aging 59:207–215.

GILLE, U., AND F.-V. SALOMON. 1998. Posthatching changes in brain size in ducks. Proc. Congr. Europ. Assoc. Vet. Anat. 22:89.

GILLILAND, S. G., AND C. D. ANKNEY. 1992. Estimating age of young birds with a multivariate measure of body size. Auk 109:444–450.

GRANT, P. R. 1981. Patterns of growth in Darwin's finches. Proc. Roy. Soc. Lond. B 212:403–432.

GREENWOOD, R. J. 1974. Reproductive aspects, growth, and development of Greenland Mallards. Condor 76:223–225.

JANOSCHEK, A. 1957. Das reaktionskinetische Grundgesetz und seine Beziehungen zum Wachstums- und Ertragsgesetz. Stat. Vjschr. 10:25–37.

LIGHTBODY, J. P., AND C. D. ANKNEY. 1984. Seasonal influence on the strategies of growth and development of Canvasback and Lesser Scaup ducklings. Auk 101:121–133.

O'CONNOR, R. J. 1977. Differential growth and body composition in altricial passerines. Ibis 119:147–166.

O'CONNOR, R. J. 1984: The growth and development of birds. John Wiley and Sons, Chichester, UK.

SALOMON, F.-V., G. SAGER, M. AL HALLAK, AND H. PINGEL. 1987a. Wachstumsspezifische Approximationen von 11 Körperdimensionen beim Geflügel. 3. Mitt.: Analyse der Wachstumsreihen bei Enten. Arch. Geflügelk. 51:136–141.

SALOMON, F.-V., G. SAGER, M. AL HALLAK, AND H. PINGEL. 1987b. Wachstumsspezifische Approximationen von 11 Körperdimensionen beim Geflügel. 4. Mitt.: Analyse der Wachstumsreihen bei Gänsen. Arch. Geflügelk. 51:205–209.

SIEGFRIED, W. R. 1977. Post-embryonic development of the Ruddy Duck *Oxyura jamaicensis* and some other diving ducks. Int. Zoo Yrbk. 17:77–87.

VESELOVSKY, Z. 1952. Postembryonale Entwicklung unserer Wildenten. Sylvia 14:36–79.

WÜRDINGER, J. 1975. Vergleichende morphologische Untersuchungen zur Jugendentwicklung von Anser und Branta-Arten. J. Ornithol. 116:65–86.