GROWTH RATES OF CRANES REARED IN CAPTIVITY

ROBERT E. RICKLEFS,[1] DONALD F. BRUNING,[2] AND GEORGE W. ARCHIBALD[3]

[1]*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA,*
[2]*New York Zoological Park, 185th Street and Southern Boulevard, Bronx, New York 10460 USA, and*
[3]*International Crane Foundation, City View Road, Baraboo, Wisconsin 53913 USA*

ABSTRACT.—We measured eggs, incubation periods, growth of chicks, and masses of adults of 10 species of cranes at the Bronx Zoo and the International Crane Foundation. Growth rate constants of Gompertz equations fitted to the data varied between 0.034 and 0.057/day. These values were 50–90% of those for altricial birds of comparable adult mass, and were considerably greater than those of other precocial species, such as galliforms. Rates of growth intermediate between altricial and precocial species are consistent with the fact that crane chicks, although precocial, are brooded and fed by their parents during much of the early development period.

Within species, asymptote (A) and growth-rate constant (K) of the Gompertz equations were negatively correlated, owing to their inherent relationship in the curve-fitting process. Masses of chicks during the first month after hatch were unrelated to the mass asymptote, but correlated strongly with the estimated growth-rate constant.

The mass of the neonate was about 60% of the fresh mass of the egg. Egg mass was unrelated to subsequent chick mass during the first month, but correlated with the mass asymptote in two species when the relationship between A and K was accounted for statistically. Egg mass also was correlated with incubation period, fledging period, and the growth-rate constant in isolated instances.

Growth rate and asymptote among species were inversely related, as found among large samples of diverse bird species. The size of the egg relative to the mass of the adult was related inversely to adult mass, again consistent with patterns in other groups of birds. Fledging period was related strongly to the length of the incubation period and weakly to the asymptote to the growth curve, and it was unrelated to the growth-rate constant of the Gompertz equation. *Received 26 November 1984, accepted 16 August 1985.*

THE cranes (Gruiformes: Gruidae) include three of the rarest and most endangered species in the world: the Whooping (*Grus americana*), Siberian (*G. leucogeranus*), and Japanese cranes (*G. japonensis*) (Archibald et al. 1981). Understanding of breeding is important to the design of recovery programs, but the reproductive biology of cranes has proven difficult to study in the wild. For many species, published information is lacking for such attributes as fledging periods and chick development (Walkinshaw 1973, Johnsgard 1983). Although the breeding of cranes in captivity has become fairly routine, little of the resulting information on reproduction and growth has been published, except where it has bearing on the development of suitable diets and rearing techniques (e.g. Archibald and Viess 1978, Serafin 1982). One purpose of this paper is to present data on eggs, incubation, and chick development of cranes to serve as a basis of comparison for propagation programs at other facilities.

Cranes are of general comparative interest because they exhibit a mode of chick development between the precocial extreme of the galliforms, whose chicks are relatively mobile and feed themselves from an early age, and the altricial extreme of raptors and herons, in which parents brood their nest-bound chicks for considerable periods after hatching and feed them throughout the development period. Nice (1962) classified the cranes, along with the rails and grebes, as precocial 4, a grouping characterized by downy chicks that leave the nest at an early age but follow the parents and are brooded, and are at least initially fed by them. The hatchling crane appears wobbly on its legs and exhibits poor temperature regulation compared with more precocial large galliforms.

According to hypotheses about growth rates

The Auk 103: 125–134. January 1986

TABLE 1. Average masses (g) of crane chicks between 1 and 30 days after hatching.[a]

	Species[b]									
Age	1	2	3	4	5	6	7	8	9	10
1	108	—	129	104	117	125	122	119	73	102
2	96	125	116	100	109	119	115	114	69	98
3	92	125	116	106	106	122	119	114	66	99
4	95	118	118	87	110	128	113	113	72	107
5	97	131	126	101	119	132	122	119	84	116
6	112	145	135	121	122	146	132	129	96	127
7	126	140	148	122	134	166	145	142	106	138
8	133	174	157	140	148	180	152	168	122	141
10	175	209	189	156	173	217	183	219	160	131
15	312	315	306	261	296	357	264	378	324	202
20	508	457	465	454	468	541	386	591	506	291
25	709	709	675	—	712	780	610	1,158	800	—
30	1,069	894	962	1,304	1,023	1,081	964	1,521	1,171	—

[a] Coefficients of variation were on the order of 10–15% during the first 10 days, increasing to about 30% by 30 days.

[b] Species (sample sizes) are 1 = *Grus monacha* (7 individuals), 2 = *G. canadensis* (2), 3 = *G. japonensis* (29), 4 = *G. americana* (1), 5 = *G. vipio* (29), 6 = *G. antigone* (14), 7 = *G. rubicundus* (1), 8 = *G. leucogeranus* (3), 9 = *Anthropoides virgo* (3), and 10 = *A. paradisea* (1).

based on the allocation of either energy, nutrients, or tissues between growth and maintenance (Ricklefs 1969, 1979b), the less-developed state of hatchling cranes should permit more rapid growth than does the more precocious development of galliform chicks. Presumably, rapid growth confers several advantages, including a shorter period of vulnerability to predators and other sources of chick mortality, and, for migratory species, the ability of fledglings to leave the breeding area well ahead of the onset of winter.

To test the generality of the inverse relationship between precocity of development and growth rate, we determined the rate constants of Gompertz equations fitted to growth curves of chicks of 11 species of cranes. In addition, we present data on egg size, incubation period, fledging period, and adult mass. We also analyze relationships among these variables in a few species for which large samples of chicks were available.

METHODS

Our observations involved the following species: Japanese Crane (*G. japonensis*), Hooded Crane (*G. monacha*), Whooping Crane (*G. americana*), Florida Sandhill Crane (*G. canadensis pratensis*), White-naped Crane (*G. vipio*), Sarus Crane (*G. antigone*), Brolga (*G. rubicundus*), Siberian Crane (*G. leucogeranus*), Demoiselle Crane (*Anthropoides virgo*), and Stanley (Blue) Crane (*A. paradisea*). We obtained information on the growth of a Greater Sandhill Crane (*G. c. tabida*) from Walkinshaw (1949) and Common Cranes (*G. grus*) from Heinroth and Heinroth (1926).

At the International Crane Foundation (LaRue 1981), eggs were artificially incubated at 37.5°C (30.0°C wet bulb), turned automatically every hour, and transferred to a hatcher (36.9°C, 33.3°C wet bulb) about two days before hatching. Neonates were transferred to brooder boxes and fed starter diet until they ate without assistance. Chicks were moved to larger pens and switched to a grower diet by two weeks of age. They were exercised every day to prevent leg deformities. Rearing procedures at the Bronx Zoo were similar except for use of specifically developed diets low in sulphur-containing amino acids during the early rearing period to prevent excessive mass gain. Before 1981, diets were restricted to keep daily mass gains below 10%.

We fitted data on growth of individual chicks by Gompertz equations using the Nonlinear Least Squares Procedure of the Statistical Analysis System (SAS; Helwig and Council 1979). The Gompertz equation (a sigmoid equation with a lower asymptote of zero and an upper asymptote that is the mass plateau of the growth curve; Ricklefs 1967, 1983) may be expressed as

$$\mathrm{M}(x) = A \exp\{-\exp[-K(x - I)]\}.$$

$\mathrm{M}(x)$ is the mass at age x, A the asymptote or mass plateau, K the growth-rate constant, and I the age at the inflection, or point of maximum absolute rate of increase, of the growth curve. We expressed age in days and mass in grams. The fitted constants of the Gompertz equations therefore are expressed in grams (A), 1/days (K), and days (I).

TABLE 2. Reproductive parameters of cranes averaged within species. Values are $\bar{x}$ ± SD (n).

	Egg length (cm)	Egg breadth (cm)	Egg volume[a] (cm^3)	Egg mass (g)	Incubation period (days)
Grus japonensis	9.84 ± 0.44 (28)	6.26 ± 0.38 (28)	387.9 ± 60.9 (28)	211.1 ± 14.5 (28)	32.7 ± 0.7 (21)
G. monacha	10.24 ± 0.89 (5)	6.16 ± 0.63 (5)	397.3 ± 115.0 (5)	159.4 ± 16.9 (5)	30.0 ± 0.9 (8)
G. vipio	9.45 ± 0.43 (25)	5.93 ± 0.24 (25)	333.4 ± 33.3 (25)	188.2 ± 11.6 (25)	30.6 ± 1.1 (28)
G. leucogeranus (n = 1)	—	6.30	—	215.3	29.0
G. antigone	9.81 ± 0.35 (13)	6.24 ± 0.19 (13)	382.9 ± 32.2 (13)	214.3 ± 15.8 (13)	31.8 ± 0.4 (11)
G. canadensis	9.42 ± 0.51 (2)	6.05 ± 0.14 (2)	345.1 ± 35.0 (2)	196.4 ± 22.4 (3)	26.7 ± 4.5 (3)
G. rubicunda (n = 1)	9.14	6.30	362.8	198.6	31.0
G. americana (n = 1)	10.84	6.02	392.5	207.1	29.0
G. grus (n = 1)	9.40	6.20	361.3	200	30
Anthropoides virgo	8.14 ± 0.40 (3)	5.01 ± 0.10 (3)	204.7 ± 17.4 (3)	118.8 ± 8.8 (6)	29.3 ± 1.3 (4)
A. paradisea (n = 1)	—	—	—	195.2	31.0

[a] Egg-volume index (cm^3) = length × breadth^2; egg dimensions measured only at International Crane Foundation.

Statistical analyses followed procedures in Sokal and Rohlf (1981) and were carried out using SAS procedures.

RESULTS

Fitted equations.—The Gompertz equation reasonably approximated the growth data for most individual chicks. Data also were fitted by logistic equations (Ricklefs 1983), but the Gompertz equation gave a closer fit to the data in most cases and will be considered exclusively here. Standard deviations of data for each individual about its fitted curve averaged 40–100 g, depending upon the species (i.e. 1–2% of adult mass). But in spite of the general agreement between the fitted equations and the growth curves of the chicks, systematic deviations occurred in all the species during the first two weeks after hatching. Because most chicks lost mass during this period (Table 1), the fitted equations fell below the observed growth curves, giving rise to positive deviations.

A more serious problem arose when chicks were not weighed through the period of attaining asymptotic mass. In such cases, the nonlinear curve-fitting technique may overestimate the asymptote of the growth curve and, as a result, underestimate the growth-rate constant. For a given data set, the two parameters were inversely correlated. That is, errors involved in estimating one of the parameters cause inverse errors in estimating the other. In this study, failure to estimate a reasonable asymptote was a problem with chicks of *G. monacha* not weighed beyond about 50 days, *G. japonensis* (80–90 days), and *G. antigone* (60 days). This caused us to delete data for 1 (of 7), 8 (of 37), and 5 (of 19) chicks, respectively, from our growth-curve analysis.

Breeding parameters.—Measurements of egg size and incubation period, averaged within each species, are presented in Table 2. Postnatal growth and adult mass are presented in Table 3. Both the ICF and the Bronx Zoo have reared enough of 3 species to allow statistical comparison of the fitted growth parameters (Table 4). In no case did the asymptote differ between institutions, but, for all three species, growth rates were lower at the Bronx Zoo than at the ICF, statistically so in two cases. This suggests differences were due to rearing techniques,

TABLE 3. Adult mass and growth parameters of crane chicks averaged within species. Values are $\bar{x}$ ± SD (n).

	Adult mass (g)	Asymptote (g)	Growth rate (1/days)	Age at inflection (days)	SD of mass[a] (g)	Fledging age (days)
Grus japonensis (ICF)[b]	8,786 ± 1,200 (14)	7,506 ± 1,140 (21)	0.0337 ± 0.0043 (21)	50.9 ± 6.9 (21)	95.6 ± 32.9 (29)	102.2 ± 7.2 (13)
G. monacha (6 ICF, 5 BZ)	3,428 ± 677 (11)	3,602 ± 677 (11)	0.0448 ± 0.0098 (11)	38.3 ± 6.8 (11)	43.0 ± 35.2 (12)	—
G. vipio (25 ICF, 7 BZ)	4,663 ± 1,931 (3)	5,276 ± 688 (32)	0.0387 ± 0.0059 (32)	44.1 ± 7.0 (32)	90.4 ± 52.8 (32)	86.0 ± 8.5 (23)
G. leucogeranus (ICF)	5,905 ± 318 (2)	5,325 ± 1,380 (3)	0.0504 ± 0.0064 (3)	34.4 ± 6.8 (3)	75.3 ± 6.6 (3)	76.0 (1)
G. antigone (8 ICF, 1 BZ)	8,863 ± 1,180 (4)	7,096 ± 1,242 (9)	0.0351 ± 0.0049 (9)	48.1 ± 5.4 (9)	70.2 ± 30.6 (14)	109.0 ± 17.4 (4)
G. canadensis tabida (1 BZ, 1 Walkinshaw 1949)	—	3,573 ± 307	0.0385 ± 0.0034	38.6 ± 0.8	61.6 ± 78.4	—
G. canadensis pratensis (2 ICF)	—	5,118 ± 604	0.0317 ± 0.0016	47.0 ± 2.2	46.0 ± 7.4	73.5 ± 0.71
G. rubicundus (1 ICF)	—	4,842	0.0520	39.3	105.3	90.0
G. americana (1 ICF)	—	6,320	0.0491	38.6	61.4	78.0
G. grus (Heinroth and Heinroth 1926)	5,530 ± 705 (5)	4,735	0.0375	32.5	121.1	68.0
Anthropoides virgo (3 ICF, 3 BZ)	—	2,338 ± 469 (6)	0.0574 ± 0.0147 (6)	30.7 ± 7.9 (6)	41.2 ± 53.8 (6)	—
A. paradisea (1 ICF)	—	4,175	0.0403	44.9	150.2	90.2

[a] SD of observations about the fitted growth curve of each individual.

[b] Locality and sample size for data on chick growth.

TABLE 4. Comparison of fitted growth parameters of cranes reared at the International Crane Foundation (ICF) and the Bronx Zoo [$\bar{x}$ (SE)].

Species	n	Egg mass (g)	Asymptote (g)	Growth rate (1/days)
Grus monacha				
Bronx Zoo	6	—	3,682 (353)	0.0399 (0.0039)
ICF	5	—	3,505 (196)	0.0507 (0.0030)
			NS	$0.05 < P < 0.10$
Grus vipio				
Bronx Zoo	7	196.2 (1.5)	5,200 (306)	0.0321 (0.0014)
ICF	25	186.1 (2.3)	5,297 (133)	0.0405 (0.0010)
		NS	NS	$P < 0.001$
Anthropoides virgo				
Bronx Zoo	3	—	2,255 (408)	0.0461 (0.0069)
ICF	3	—	2,421 (97)	0.0687 (0.0023)
			NS	$P < 0.05$

particularly feed restrictions at the Bronx Zoo. But any conclusions must be tempered by the fact that many of the chicks at each institution were siblings, and statistical comparisons may reflect between-parent genotype and maternal differences as much as differences between growth at the two institutions. In addition, the geographical origins of the breeding birds at each institution may have differed, throwing any interpretation of the observed differences further into doubt. In Table 3, all the individuals contributed to the species averages with equal weight, regardless of institution.

Correlations among ages.—Growth equations

TABLE 5. Correlations ($\times 10^2$) among egg mass, A, K, and masses (M) of chicks between 1 and 30 days after hatching.[a]

	Egg	*A*	*K*	M1	M5	M10	M15	M20	M25	M30
Grus vipio[b]/*Grus japonensis*[c]										
Egg	—	12	−30	44*	68***	−26	−46*	−44*	−45*	−38
A	7	—	−56**	3	25	−6	−9	−24	−19	−22
K	−27	−54**	—	−18	−37*	−4	32	57***	59***	67***
M1	64**	−7	6	—	25	−14	−20	−39	−25	−42*
M5	37	−43*	39*	10	—	25	−1	−11	−9	−7
M10	20	−28	39*	−17	73***	—	58***	47**	44*	39*
M15	18	−28	43	−23	67***	90***	—	83***	86***	79***
M20	20	−25	47*	−20	63***	79***	95***	—	90***	87***
M25	25	−31	48***	−4	65***	75***	90***	93***	—	95***
M30	17	−22	50***	−33	61**	80***	88***	91***	88***	—
Grus antigone[d]/*Grus monacha*[e]										
Egg	—	2	27	73	−11	17	24	40	8	−3
A	−26	—	−68*	−31	27	−26	−13	11	5	−5
K	46	−85***	—	22	−32	5	−15	−25	−10	−8
M1	97***	−45	57	—	31	71	73	67	69	71
M5	46	18	−7	38	—	76*	73	83*	78*	78*
M10	29	16	−3	15	90***	—	92**	83*	78*	88**
M15	33	31	−11	11	80**	92***	—	96**	92**	99***
M20	51	−7	−9	47	72*	69*	60	—	99***	98***
M25	24	47	−44	12	76**	74**	80**	82**	—	97***
M30	40	20	−15	44	73**	67*	67*	77**	88***	—

[a] * = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $P < 0.001$.

[b] Lower left triangle (n = 23–29).

[c] Upper right triangle (n = 18–32).

[d] Lower left triangle (n = 7–14).

[e] Upper right triangle (n = 4–12).

TABLE 6. Regression of neonate mass on egg mass for three crane species.[a]

Species	n	R^2	F	P	Intercept	b	s_b
Grus vipio	22	0.407	13.73	0.0014	−30.16	0.781	0.211
G. japonensis	23	0.190	4.91	0.0378	25.67	0.491	0.222
G. antigone	9	0.947	126.14	<0.0001	−19.61	0.667	0.059

[a] n = sample size, R^2 = coefficient of determination, F = ratio of regression to error mean squares, P = probability that $F \leq 1$, intercept (g) = a in the regression equation $y = a + bx$, b = the slope of the regression (g/g), s_b = standard error of the estimate of b.

describe the increase in the mass of chicks in terms of three parameters, *A*, *K*, and *I*. An adjustment in any one of these produces a predictable change in the mass of the chick at each age. If growth of the chick were controlled in the same manner, i.e. by a small number of factors whose influence was expressed evenly at all ages, then variation among individuals in mass at one age would be highly correlated with variation in mass at a different age and with variation in the parameters *A* and *K*. To test this hypothesis, we calculated correlation coefficients between masses (M) at ages 1, 5, 10, 15, 20, 25, and 30 days, egg mass, asymptote (*A*), and growth rate (*K*). We did not include masses at older ages in these calculations because chicks were weighed infrequently after one month of age and sample sizes became too small for useful comparison.

Several patterns of correlation emerged for the four species with large samples of chicks (Table 5). Egg mass correlated strongly with the mass of the neonate (M1) but generally not with that of older chicks. Egg mass was unrelated to either *A* or *K*.

Asymptote was strongly inversely related to *K* within all four species, reflecting a negative correlation inherent to the curve-fitting procedure. *A* generally was not significantly related to mass during the first month of the growth period. Growth rate correlated positively with mass from day 5 onward in *G. vipio* and from day 20 onward in *G. japonensis*, but not in the other two species. Masses of chicks were highly intercorrelated from day 10 onward in *G. japonensis* and from day 5 onward in the other three species. In none of these species, however, was neonate mass (M1) correlated with mass on subsequent days, or with *A* or *K*.

Neonate mass vs. egg mass.—Egg mass bore little relationship to fitted growth constants or to masses of chicks during weeks 2–4 of development. One would, however, expect egg mass to greatly influence the mass of the neonate. In three species, for which samples were 9 or more, neonate mass was significantly correlated with egg mass (Table 6). The slopes of the linear regressions varied between 0.49 and 0.78 g/g, but only that for *G. antigone* (0.67) provided a reliable estimate (0.06 SE). The ratio between the average masses of neonates and eggs in each of the species varied between 0.581 and 0.619, indicating that cranes hatch at about 60% of the mass of the fresh egg.

Relationships among egg measurements.—Egg length correlated weakly with egg breadth in

TABLE 7. Regressions of egg mass on egg-volume index[a] and egg length on egg breadth in several species of cranes.[b]

	df	F	P	R^2	a	b	s_b
Egg mass (g) vs. egg-volume index (cm^3)							
Grus vipio	22	16.05	0.0006	0.42	107.6	0.236	0.059
Grus antigone	11	135.62	0.0001	0.92	34.0	0.471	0.040
Egg length (cm) vs. egg breadth (cm)							
Grus japonensis	26	8.65	0.0068	0.25	61.52	0.590	0.201
Grus vipio	23	6.99	0.0145	0.23	43.52	0.859	0.325

[a] Egg-volume index (cm^3) = length (cm) × breadth^2 (cm^2).

[b] df = error degrees of freedom, F = ratio of regression to error mean squares, P = probability that $F \leq 1$, R^2 = coefficient of determination, a = intercept (g) in the regression equation $y = a + bx$, b = slope of the regression, s_b = standard error of the estimate of b.

TABLE 8. Regressions of incubation period, fledging age, and asymptote vs. growth rate and egg mass.[a]

	df	F	P	R^2	a	b	s_b
(1) Incubation period (days) vs. egg mass (g)							
Grus monacha	5	3.72	0.1116	0.43	32.45	−0.0173	0.0090
(2) Fledging age (days) vs. A (g), K (1/day), and egg mass (g)							
Grus vipio							
Egg mass	19	4.33	0.0511	0.19	132.66	−0.262	0.126
(3) Asymptote (kg) vs. growth rate K (1/day)							
Grus monacha	9	4.16	0.0718	0.32	5.34	−38.72	18.97
Grus japonensis	19	4.08	0.0578	0.18	11.25	−111.1	54.99
Grus vipio	30	12.48	0.0014	0.29	7.706	−62.86	17.80
Grus antigone	7	4.38	0.0747	0.38	12.58	−156.3	74.68
(4) Asymptote (kg) vs. K (1/day) and egg mass (g)							
Grus japonensis							
Total model	17	5.81	0.0120	0.41	2.392		
Egg mass		7.81	0.0124			0.0410	0.0147
K		4.26	0.0547			−101.9	49.38
Grus antigone							
Total model	5	7.80	0.0291	0.757	4.554		
K		11.75	0.0187			−247.8	72.29
Egg mass		8.65	0.0322			0.0511	0.0174
(5) K (1/day) vs. A (kg), egg mass (g), and incubation period (days)							
Grus japonensis							
Total model	11	2.63	0.1162	0.32	−0.0105		
A		2.51	0.1411			−0.00175	0.001
Egg mass		4.60	0.0551			0.000264	0.000123
Grus vipio							
Total model	24	20.99	0.0001	0.47	−0.0050		
A		21.53	0.0001			−0.00542	0.001
Incubation period		14.41	0.0009			0.00239	0.0006
(6) K (1/day) vs. incubation period (days)							
Grus vipio	25	13.48	0.0012	0.35	−0.0540	0.00304	0.0008

[a] df = error degrees of freedom, F = ratio of regression to error mean squares, P = probability that $F \leq 1$, R^2 = coefficient of determination, a = intercept (g) in the regression equation $y = a + bx$, b = slope of the regression, s_b = standard error of the estimate of b.

two of three species (Table 7). Egg mass also was predicted reasonably ($R^2 = 0.42, 0.92$) from the egg-volume index in *G. vipio* and *G. antigone*, but not in *G. japonensis*. The ratios of average egg mass to average egg-volume index were 0.544 in *G. japonensis*, 0.565 in *G. vipio*, and 0.560 in *G. antigone*, and agreed well with the average value (0.548) calculated for 26 bird species (Hoyt 1979).

Relationships among development variables.—Sample sizes for four of the species were sufficient to test certain hypotheses concerning the relationships among egg mass, incubation period, growth rate, fledging age, and asymptote of the growth curve (Table 8). (1) The length of the incubation period was unrelated to egg mass in all four species ($P > 0.10$). (2) We tested the relationship of fledging age to A, K, and egg mass in a multiple regression. In *G. vipio* only, fledging age was negatively related to the mass of the egg. Variation in egg mass of 1 SD (11.6 g) was associated with a 3.0-day (0.35 SD) decrease in the length of the fledging period. (3) Asymptote was negatively related to growth rate in all four species. (4) When egg mass was added to the regression of A on K, a significant positive relationship between A and egg mass was revealed for *G. japonensis* and *G. antigone*. The slopes of the regressions indicate that 1-SD increases in egg mass were associated with 594-g (0.52 SD) and 807-g (0.65 SD) increases in asymptote, in spite of the fact that egg mass and asymptote did not bear a simple correlation to one another. (5) In the multiple regres-

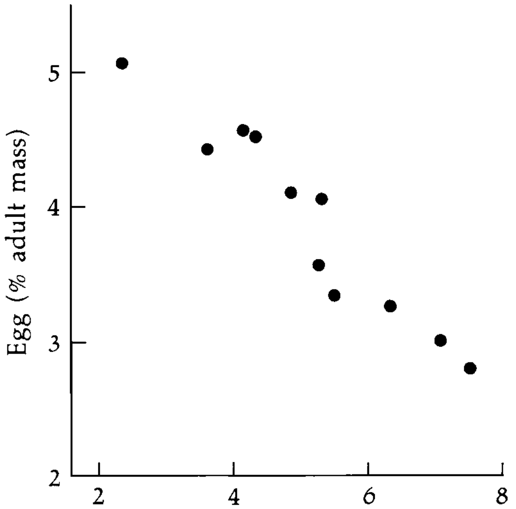

Fig. 1. Relationship between the relative mass of the egg and the mass of the adult among cranes.

sion of K on A, egg mass, and incubation period, K and egg mass were significantly related in *G. japonensis* and K and incubation period were significantly related in *G. vipio*. In the first case, the slope of the relationship indicated that a 1-SD increase in egg mass produced a 0.89-SD increase in K. In the second case, a 1-SD increase in incubation period was associated with a 0.44-SD increase in K. (6) In *G. vipio*, the simple regression of K on incubation period revealed a similar slope to that of their relationship in the multiple regression.

Interspecific relationships of variables.—Among species of cranes, the relative size of the egg (mass as a percent of adult mass) was related inversely to adult mass, and declined from 4.5% in the smallest species to about 3% in the largest (Fig. 1). Incubation and fledging periods also were strongly, positively related, even though the range of variation in the fledging period was almost 10 times as great as that of the incubation period (Fig. 2A). The relationship between incubation and fledging periods appears not to be mediated through the rate of postnatal growth (K), which was not correlated with fledging period among the smaller species of cranes (Fig. 2B). Fledging age also was not strongly related to the asymptote of the growth curve, although the two largest species, *G. japonensis* and *G. antigone*, have the longest fledging periods (Fig. 2C).

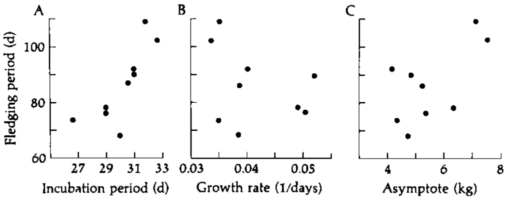

Fig. 2. Relationship of the fledging period to the incubation period (A), growth rate of the chick (B), and asymptote of the growth curve (C) among cranes.

As in most groups of birds, growth rates and asymptotes of cranes had an inverse relationship (Fig. 3). The size-adjusted growth rates of most of the cranes fell within the range of 55–65% of the K-values of large, altricial landbirds with broods of two or more chicks (mostly raptors, herons and egrets; Ricklefs 1982). Three of the species, *G. leucogeranus*, *G. rubicundus*, and *G. americana*, grow more rapidly, however, averaging 86% of the rate of large altricial species.

DISCUSSION

Cranes grow more rapdily than do galliforms of similar adult body size. This difference is consistent with the state of development of the crane chick at hatching. The fact that crane chicks are fed and brooded by their parents for several weeks suggests that they do not achieve a level of functional development comparable to hatchling galliform chicks until they are partly grown. This delay of tissue maturation, particularly of the skeletal muscles required for locomotion and thermogenesis, enables the chick to retain the rapid growth characteristic of earlier stages of development well into the postnatal growth period (Ricklefs 1979b). Thus, the data on growth rates of cranes are consistent with the hypothesis that growth rate is determined by the degree of differentiation and functional maturation of certain tissues. But because other hypotheses, e.g. based on the allocation of metabolizable energy between growth and maintenance, may explain the data equally well in the absence of additional information, we conclude only that cranes are consistent with the general inverse relationship between precocity of development and growth rate (Ricklefs 1973, 1979a, b, 1983).

The growth-rate constants of fitted equations are well suited for broad comparisons among species, but because growth often does not follow the curve of a particular model precisely, curve fitting may not be useful for comparisons within species or among closely related species. Crane chicks exhibit a lag phase of growth during the first week after hatching, during which mass initially decreases. Hence, fitted Gompertz equations depart considerably from the observed data at this period. Even after mass increase accelerates after the end of the first week, the fitted asymptotes of the growth curves are not correlated with masses, at least through the first month. According to the Gompertz, and other, growth equations, variations in *A* should be expressed in masses at all ages.

In contrast to the asymptote, variation in the growth rate was strongly correlated with variation in mass during the first month. These results suggest that early and late growth in crane chicks are somewhat independent and, therefore, that fitted three-parameter equations do not provide a model of growth processes. Apparently, the asymptote is relatively independent of growth performance during the early part of the development period, although asymptote was related to egg mass in two species.

Correlations of variables describing growth and development within species enable us to examine the organization of variation in breeding parameters and to elucidate functional interrelationships that might constrain the evolution of breeding adaptations. For example, it is reasonable to suppose that larger eggs produce chicks of higher quality (i.e. chicks that exhibit higher survival, grow more rapidly, or attain larger adult size). Simple correlations between pairs of variables showed that egg size was related only to the mass of the hatchling. However, because some of the variables showed strong intercorrelations, particularly growth rate (*K*) and asymptote (*A*), the unique relationship between any two variables sometimes could be revealed only by multiple regression analysis, which adjusts values according to their covariation with other variables.

The relationship between growth rate and asymptote within species probably reflects the correlations between the two variables in the curve-fitting procedure. Variation in the estimate of the asymptote produces inverse variation in the estimate of the growth rate. Unless the data are closely matched by the Gompertz equation, there may be considerable variation in the estimate of the asymptote. Even when the fit is good, any ambiguity in estimating *A*, because data were not gathered well into the mass plateau of the growth curve, produces equal ambiguity in the inverse direction in *K*. In the European Starling (*Sturnus vulgaris*), *A* and *K* were not correlated, perhaps because there was so much independent variation that the inverse correlation expected from the curve-fitting procedure was swamped (Ricklefs and Peters 1979). Furthermore, nestlings had exhibited well-developed mass plateaus before weighing was discontinued at fledging.

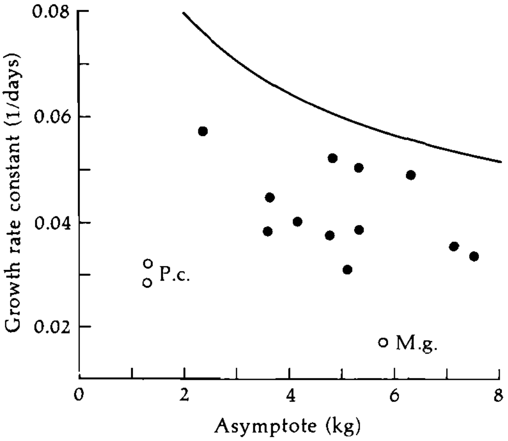

Fig. 3. Relationship of growth rate (*K*) to the asymptote of the growth curve (*A*) among cranes. The solid line is the allometric regression of *K* upon *A* for large altricial birds (Ricklefs 1982). The open circles are two species of large galliforms [Ring-necked Pheasant (*Phasianus colchicus*) and Wild Turkey (*Meleagris gallopavo*), Matthew 1982)].

When asymptote was related to egg mass, after first adjusting for the relationship of *A* to *K*, egg mass was positively related to *A* in two species, *G. japonensis* and *G. antigone*. Furthermore, the slopes of the relationships, 40–50 g of asymptote per gram of egg mass, indicated that a change in 1 SD in egg mass was associated with a change of 0.52 and 0.65 SD in asymptote.

Egg mass bore a weak ($P = 0.11$) negative relationship to the length of the incubation period in *G. monacha* and a barely significant ($P = 0.05$) negative relationship to the length of the fledging period in *G. vipio*. These results suggest that large egg size may be associated with an acceleration of both embryonic and post-hatching growth rates. To test these relationships directly, we used a multiple regression to examine the dependence of growth rate on asymptote, egg mass, and incubation period. With values adjusted for the relationship between K and A, K was positively related to egg mass in *G. japonensis* and positively related to the length of the incubation period in *G. vipio*. The first relationship is consistent with the hypothesis that larger eggs produce more rapidly growing chicks. The second is more puzzling because it suggests that more rapid embryonic growth was associated with slower post-hatching growth.

Few of the relationships revealed by the regression analyses are either strong or generalizable to all species of cranes. It is also not possible to assign causality to the relationships in the absence of experimental work. Hence, particular measures of growth are insufficient as predictors of other aspects of growth performance in captive propagation programs.

ACKNOWLEDGMENTS

Computer time was provided by the School of Arts and Sciences, University of Pennsylvania. RER was supported by NSF grant DEB80-21732.

LITERATURE CITED

ARCHIBALD, G. W., Y. SHIGETA, K. MATSUMOTO, & K. MOMOSE. 1981. Endangered cranes. Pp. 1-12 *in* Crane research around the world (J. C. Lewis and H. Masatomi, Eds.). Baraboo, Wisconsin, International Crane Foundation.

———, & D. L. VIESS. 1978. Captive propagation at the International Crane Foundation 1973-78. Pp. 51-73 *in* Proc. 1978 Crane Workshop (J. C. Lewis, Ed.). Fort Collins, Colorado State Univ. Printing Serv.

HEINROTH, O., & M. HEINROTH. 1926. Die Vogel Mitteleuropas, vol. 3. Berlin, Lichterfelde.

HELWIG, J. T., & K. A. COUNCIL (Eds.). 1979. SAS user's guide, 1979 ed. Raleigh, North Carolina, SAS Inst.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96: 73-77.

JOHNSGARD, P. A. 1983. Cranes of the world. Bloomington, Indiana Univ. Press.

LARUE, C. 1981. Techniques for breeding cranes in captivity. Pp. 15-18 *in* Crane research around the world. (J. C. Lewis and H. Masatomi, Eds.). Baraboo, Wisconsin, International Crane Foundation.

MATTHEW, K. K. 1982. Growth and development in Galliformes. Unpublished Ph.D. dissertation, Philadelphia, Univ. Pennsylvania.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York 8: 1-211.

RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983.

———. 1969. Preliminary models for growth rates of altricial birds. Ecology 50: 1031-1039.

———. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201.

———. 1979a. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. Auk 96: 10-30.

———. 1979b. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54: 269-290.

———. 1982. Some considerations on sibling competition and avian growth rates. Auk 99: 141-147.

———. 1983. Avian postnatal development. Pp. 1-83 *in* Avian biology, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

———, & S. PETERS. 1979. Intraspecific variation in the growth rate of nestling Starlings (*Sturnus vulgaris*). Bird-Banding 50: 338-348.

SERAFIN, J. A. 1982. The influence of diet composition upon growth and development of Sandhill Cranes. Condor 84: 427-434.

SOKAL, R. R., & J. F. ROHLF. 1981. Biometry, 2nd ed. San Francisco, W. H. Freeman.

WALKINSHAW, L. H. 1949. The Sandhill Cranes. Bloomfield Hills, Michigan, Cranbrook Inst. Sci.

———. 1973. Cranes of the world. New York, Winchester Press.