PATTERNS OF GROWTH IN BIRDS. V.
A COMPARATIVE STUDY OF DEVELOPMENT IN THE STARLING, COMMON TERN, AND JAPANESE QUAIL

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ABSTRACT.—This study compares developmental changes in the behavior, morphology, and body composition of three species of birds with different types of development: Starling (*Sturnus vulgaris*) (altricial), Common Tern (*Sterna hirundo*) (semi-precocial), and Japanese Quail (*Coturnix coturnix japonica*) (precocial). The Starling grows four times and the tern, two and one-half times more rapidly than the quail. Although the adult weights of the three species are similar, the tern neonate is about twice as large (12.8% adult weight) as Starling (6.7%) and quail (5.8%) hatchlings.

Both the tern and quail move about and regulate their body temperatures at hatching. The quail chick begins to fly when it is half-grown, the Starling and tern when they are nearly full-grown. At hatching, the tern and quail have larger proportions of nonlipid dry matter and less water in their bodies than does the Starling, indicating greater maturity. The body proportions of neonates are similar, except that the integument and legs of the Starling are smaller than those of the tern and quail. During development, proportion of pectoral muscles and, to a lesser extent, wings, increases in all three species, proportion of legs in the tern decreases and, proportion of head in the quail and, to a lesser extent, the Starling and the tern decreases. Development of homeothermy in the Starling is accompanied by the development of plumage and maturation of the leg muscles to provide a source of heat.

In most tissues, increasing function is accompanied by decreasing water content and decreasing growth rate. The functional maturity of the leg appears to set the overall pace of development of the chick. In the tern, rapid body growth is consistent with slow leg growth because the relative size of the legs decreases continually during development. Adult terns have small legs compared both to other adult birds and to newly hatched chicks. Large egg size in the tern results in large hatching size and further reduces the postnatal growth increment of the legs, thereby reducing the postnatal development period.

The results of this study support the hypothesis that rate of increase in body weight is inversely related to degree of functional maturity. Several refinements of this general pattern are also evident: (1) the growth rate of the organism is limited by the most slowly growing component, (2) the relative proportions of body components must remain within limits determined by their function during the development period, and (3) post-hatching growth rate may be increased under certain circumstances by increasing embryonic growth of organs that are functionally mature at hatching. *Received 17 May 1976, accepted 5 September 1978.*

ORNITHOLOGISTS have paid little attention to growth rate (here meaning the rate of increase in body weight during the development period) except where variation in growth rate between species either is associated with differences in clutch size or reflects differences in the nutrition of the young (Lack 1968). The adaptive basis of growth rate traditionally has been viewed as a balance between selection of faster growing individuals, because they are vulnerable to predators for shorter periods, and selection of slower growing individuals, because they require less energy per unit time and thereby permit larger family size. According to this view, optimum growth rate is determined by selection directly upon growth rate and is independent of other aspects of development.

The hypothesis that growth rate represents an optimum balance between selection for low rates of energy requirement and short development time would predict that variation in growth rate between species should be related to predation rate and pattern of energy utilization. Lack (1968) found a direct relationship between nestling

period, which he used as an index of growth rate, and clutch size in passerines and other orders of birds having altricial development. A limitation to Lack's analysis is that nestling period need not correspond to growth rate; in passerines and, to some extent, in larger altricial species, age at fledging varies with respect to the body weight growth curve (Ricklefs and Hainsworth 1968, Ricklefs 1973). Furthermore, defining the age at fledging for nidifugous species presented such problems that Lack could not include their growth rates in his discussion of adaptations for reproduction.

The application of curve-fitting techniques to growth curves (Laird 1965, Ricklefs 1967, Taylor 1968) has permitted more direct analysis of variation in growth rate than afforded by comparison of nestling periods. I have found that the characteristic growth rates of species are related to adult body weight, nestling period, food availability (particularly in seabirds with broods of one chick and possibly in tropical birds, especially those that feed fruit to their young), and type of development pattern (altricial versus precocial and intermediate types) (Ricklefs 1968, 1973). But I failed to find any relationship between growth rate and nesting mortality rate, which would be expected in accordance with the traditional view of growth rate (Ricklefs 1969a). Tropical passerines grow more slowly than temperate-zone passerines, even though they suffer twice the nest mortality on average (Ricklefs 1968, 1969b, 1976). Among temperate-zone passerines, growth rate and nest mortality rate are positively, but not significantly, correlated (Ricklefs 1969a), although growth rate and length of the nestling period are strongly related (Ricklefs 1968). Raptors, which as a group have low nest mortality, grow several times more rapidly than galliforms of similar body weight, which suffer relatively high mortality during the early development period. Additional examples further emphasize the lack of empirical relationship between growth rate and mortality.

According to a mathematical model of factors influencing growth rate in altricial species (Ricklefs 1969a), the optimum growth rate is the most rapid that can be supported by the parents' ability to feed their young. The model, based solely on the relationship of growth rate to energy requirement and nestling mortality, predicts that birds will always sacrifice family size to reduce development period and therefore will rear a single offspring at a rate limited only by the parents' capacity to satisfy the energy and nutrient requirements of the growing chick. The inconsistency of this theoretical result with the breeding behavior of birds, particularly the prevalent characteristic of laying more than one egg per clutch, illustrates the inadequacy of the model, particularly the assumption that growth rate evolves without internal constraints.

I have proposed two types of internal constraints on growth rate based on the requirement of growth processes for energy and nutrients, on one hand, and for tissue capable of embryonic activity, on the other (Ricklefs 1969a, 1973). First, the allocation of energy by precocial birds to such mature functions as activity and temperature regulation could limit the energy available for growth. Total energy intake may also be limited by the development of feeding behavior. Second, the acquisition of functional maturity through cellular differentiation could limit the proportion of a tissue that is capable of cell proliferation and growth. If these processes were themselves limited by cellular (biochemical and molecular) constraints whose nature is determined without regard to selection on the growth rate of the organism, the proportion of embryonic tissue in an individual could determine its rate of growth.

Hypotheses based on internal constraints do not exhaust the potential factors underlying variation in growth rate among birds (see Dunn 1973, in press; O'Connor 1975, 1977 for further discussion of growth rates). Nor are the two hypotheses described above necessarily mutually exclusive or even distinguishable by experimental analysis. At this point, our understanding of the factors that determine growth rate is limited by our understanding of growth and development patterns themselves, particularly the internal changes in body proportions and constituents that accompany the transition from egg to adult (Ricklefs 1967, 1975; O'Connor 1977).

This paper examines developmental changes in the behavior, morphology, and anatomy of the Starling (*Sturnus vulgaris*), Common Tern (*Sterna hirundo*), and Japanese Quail (*Coturnix coturnix japonica*). The species were chosen for their varied types of development. The Starling is altricial, lacking mature function and self-sufficiency at hatching (Nice 1962), and grows rapidly. The Japanese Quail is precocial, that is, highly self-sufficient in feeding and temperature regulation at hatching (Wetherbee 1961, Spiers et al. 1974), and grows slowly. The Common Tern mixes altricial and precocial traits. Tern chicks are nearly self-sufficient in temperature regulation at hatching (LeCroy and Collins 1972) but are fed by their parents. Like the quail chick, the newly hatched tern has open eyes, well-developed down, and runs about (though neither can fly at hatching), but it grows almost as rapidly as the Starling (Ricklefs 1968). The tern's rapid growth is inconsistent with the idea that growth rate is constrained by maturity of function. One purpose of comparing tern chicks with those of species having different types of development is either to resolve this inconsistency or to reject the hypothesis about growth rate variation that is based on a precocity-growth rate trade off.

MATERIALS AND METHODS

Starlings were studied between 1970 and 1974 at a colony of free-living birds attracted to nesting boxes at the Stroud Water Research Laboratory of the Academy of Natural Sciences of Philadelphia near Kennett Square, southeastern Pennsylvania. Japanese Quail eggs obtained from Truslow Farms, Chesterton, Maryland, were incubated, and the chicks raised, in my laboratory. Common Terns were studied in 1972 at the Great Gull Island, New York, field station of the Linnean Society of New York City.

Capacity for temperature regulation in the Starling and quail was determined from the body temperatures of chicks exposed to ambient temperatures of 17–23°C for 30–45 min. Temperatures were obtained with a telethermometer probe (Yellow Springs Instruments) inserted through the mouth into the proventriculus. During the test, the young were suspended in small cheese-cloth bags, within which their motion was restricted. Measurements were made during the middle of the day; none of the subjects had been deprived of food. LeCroy and Collins (1972) used a similar technique to measure temperature regulation in 1 to 4 day-old Common Terns. A coefficient of temperature regulation was calculated by the expression $(T_{young} - T_{ambient})/(T_{adult} - T_{ambient})$ where T is temperature; the body temperature of adults was designated as 42°C. The coefficient of temperature regulation thus measures the fraction of the temperature gradient between an adult and its environment that can be maintained by a young bird.

Pedal activity was determined for the Starling and quail in a circular pen 1 m in diameter with sides 20 cm in height. The floor of the pen was marked in squares 10 cm on a side. Young were placed in the pen and the number of squares entered in a 30-s trial period was counted. Activity was expressed as number of squares per minute.

Flight capability in the Starling and quail was determined by dropping young from a height of 5 ft (1.52 m) onto a soft mat. The horizontal distance covered by the bird before landing was measured, and the angle of descent, measured from the horizontal, was calculated as arctan (h/d) where h is the height from which the chick was dropped and d the horizontal distance. Birds less than 10 days old were not tested.

The length of the wing, tarsus, and a primary feather (outer for the tern, and fifth for the Starling and quail), and the area of the wings were measured on all the birds collected for anatomical analysis. Wing

area was measured by tracing the outline of the outspread wings onto paper and comparing the weight of the outlined area to a piece of paper of known area.

Series of chicks of each species were dissected into 10 components, each of which was analyzed separately to determine amounts of water, lipid, and nonlipid dry constituents. Although all the specimens were frozen and stored for variable periods before analysis, the difference between the fresh weight and the summed weights of the constituents were generally less than 5% of the fresh weight for the smallest young and less than 2% for adults.

The components analyzed were integument (skin and feathers together), leg, wing, pectoral muscle, heart, liver, stomach, intestine, head, and remainder of body (primarily the back, neck, rib cage, pelvic girdle, lungs and kidneys). Components were dried to constant weight in a vacuum oven at 50–60°C. Lipids were extracted with a 5:1 mixture of petroleum ether (30–60°C b.p.) and chloroform (see Ricklefs 1975). Components were placed in pre-weighed aluminum pans and weighed on a Sartorius analytical balance.

Although the ages of all young used in the analysis were known to within 1 day, a developmental chronology was constructed from wing length and, for younger birds, partly from body weight and tarsus length. Because this study examined differences between species rather than variation within a species, developmental age was used so as to minimize the deviations of individuals from the average development pattern of the population.

The growth rate of each species was determined by fitting the growth curve by a logistic equation, having the form

$$W(t) = A/(1 + \exp[-K(t - t_i)])$$

where $W(t)$ is the weight at age t, A is the asymptote, or weight plateau, of the growth curve, K is the growth rate constant, and t_i is the age at the inflection point of the growth curve—the point of maximum growth rate—which occurs at one-half the asympotic weight on a logistic curve. The logistic equation and methods used to fit the equation to growth data are described by Ricklefs (1967, 1968).

A growth index was calculated for each species from the age at inflection and the growth rate constant. The growth index is a time scale adjusted by the growth parameters so as to make the growth curves of all species coincide when plotted as a function of their particular growth indices. The growth index is 0 at the age of inflection; its absolute value increases in both directions along the time axis by units equal to the time required for growth between 10 and 50% of the asymptote. This growth unit may be calculated directly from the growth rate constant by the expression, growth unit (days) = $2.20/K$ (Ricklefs 1967). The growth index allows one to portray the growth of body components, the acquisition of mature function, and the timing of such discrete events as hatching and fledging with respect to growth in body weight, yet retain their proper temporal relationships. The growth index thus reveals differences in the development patterns of species independently of differences in rate of increase of body weight.

Growth indices used in this analysis are based on logistic equations fitted to data of Kessel (1957) for Starlings obtained from early broods of one season near Ithaca, New York, data of LeCroy and Collins (1972) for Common Terns obtained on Great Gull Island in 1968, and unpublished data for Japanese Quail raised in the laboratory. The first day of post-hatching life was designated as day 1; young aged 1 day were thus between 0 and 24 h old.

RESULTS

Growth rate.—Constants of the logistic equation fitted to the growth curve of each species are listed in Table 1. The growth rate constant (K) varied from 0.401 for the Starling to 0.265 for the Common Tern and 0.106 for the Japanese Quail. The growth equations are compared graphically in Fig. 1. Although growth constants are known to vary individually, seasonally, and geographically within species (Ricklefs 1968, 1976), this variation is generally negligible compared to differences between the species in this study.

Adult weight.—Among birds, growth rate (K) is inversely related to adult body weight (W) by the expression $K = aW^b$ where a and b are constants. Depending upon the taxonomic order, b varies between -0.26 and -0.42 (Ricklefs 1973).

Adult Starlings weigh about 30% less than adult Common Terns and Japanese Quail, hence the more rapid growth of the Starling is exaggerated by the differences
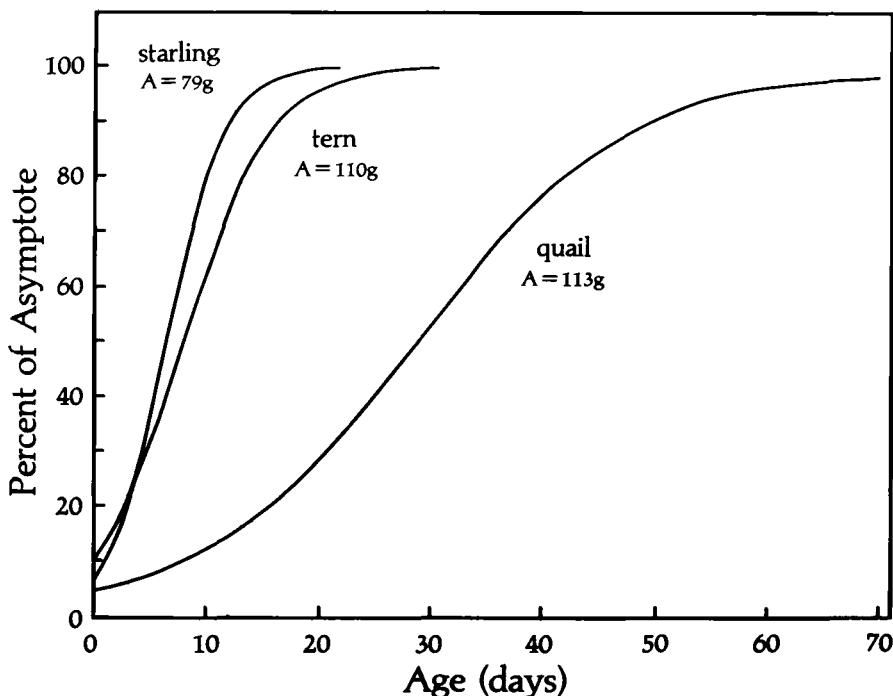
Fig. 1. Curves for logistic equations fitted to growth data for Starlings, Common Terns, and Japanese Quail. Body weights are normalized to asymptote (Starling 79 g, tern 110 g, quail 113 g). First recorded weights are designated day 1; hatching occurs between age 0 and 1.

in adult weight. Adult body weight averages about 79 g among Starlings (Stegeman 1954), 116 g among Common Terns (LeCroy and Collins 1972), and 113 g among Japanese Quail (Hartman and Brownell 1961, this study). When the growth rate of the Starling is scaled to an adult body weight of 115 g, using the relationship $K_2 = K_1 (W_2/W_1)^b$ and $b = -0.28$ (Ricklefs 1968), K becomes 0.361, rather than 0.401. Adult body weight therefore accounts for little of the variation among growth rates of the species considered in this study.

TABLE 1. Constants of growth equations fitted to growth data for the Starling, Common Tern, and Japanese Quail.

Species and locality	Number of chicks	A	K	t_i[a]	Source
Starling					
Scotland	5	79.0	0.396	—	Dunnett (1955)
Czeckoslovakia	44–104	70.4	0.412	—	Hudek & Folk (1961)
New York		79.0	0.401	6.55	Kessel (1957)
Pennsylvania	191	70.1	0.411	6.40	Ricklefs & Peters (unpubl.)
Japanese Quail[b]	20	113.0	0.106	29.0	This study
Common Tern					
England	9	130	0.300	8.3	Pearson (1968)
England (b/1)[c]		125	0.254	8.6	Langham (1972)
(b/2)		122	0.249	9.5	Langham (1972)
New York	15	110	0.265	8.2	LeCroy & Collins (1972)

[a] Day of hatching is designated day 1.
[b] *Coturnix c. japonica*, laboratory raised birds; pen-reared *Coturnix c. coturnix* (Dement'ev and Gladkov 1952, quoting Heinroth) had growth curves best fit by a Gompertz equation (Ricklefs 1973) and thus not comparable to the data presented here.
[c] Brood size.

TABLE 2. Weights of newly hatched chicks of the Starling, Common Tern, and Japanese Quail.

Species	Number	Average weight (g)	Standard deviation	Source
Starling	18	5.27	—	Wetherbee & Wetherbee (1961)
	4	5.19[a]	0.71	This study
Common Tern	13	14.8[b]	—	LeCroy & Collins (1972)
	5	12.1	—	Wetherbee & Wetherbee (1961)
Japanese Quail	8	6.50[c]	0.89	This study

[a] Range 4.36–6.07 g.
[b] Range 12.0–17.7 g.
[c] Range 5.12–8.05 g.

Hatching weight.—Weights obtained immediately after hatching (often while the young were still wet) and before feeding are presented in Table 2. The hatching weight of the Starling (5.27 g) is 6.7% of adult weight, that of the Common Tern (14.8 g), 12.8% of adult weight, and that of the Japanese Quail (6.5 g), 5.8% of adult weight.

Because the growth index is directly related to percent of asymptote achieved, the hatching weight has a corresponding value of the growth index (G), calculated by the expression

$$G_{\text{hatching}} = 0.455 \log_e[W/(1 - W)]$$

where W is the fraction of the asymptote attained at hatching; the constant 0.455 is derived from conversion factors for the logistic curve from Ricklefs (1967). Hatching weights as decimal fractions of the asymptote in the Starling (0.067), tern (0.135), and quail (0.058) correspond to growth indices of -1.20, -0.85, and -1.27.

The growth index can also be calculated from the age at which 50% of asymptotic weight (t_i) is attained and the growth unit (t_{10-50}), an inverse measure of growth rate (K). Assuming that young weighed during the first day of post-hatching life are 0.5 days old on average, the growth index,

$$G_{\text{hatching}} = (t_i - 0.5)/t_{10-50}$$

is -1.10 for the Starling, -0.93 for the tern, and -1.37 for the quail.

TABLE 3. Proportions of components in adults and newly hatched young of the Starling, Common Tern, and Japanese Quail.[a]

Component	Starling		Common Tern		Japanese Quail	
	chick[b]	adult	chick	adult	chick	adult
Integument	9.0	12.6	13.5	19.6	14.3	9.9
Body	34.0	23.3	29.5	24.6	27.8	27.8
Intestine	7.4	6.4	5.9	4.7	3.4	8.0
Heart	1.0	1.4	1.3	1.6	1.5	1.3
Liver	3.9	5.3	4.8	6.3	2.6	3.9
Head	19.6	8.9	20.0	10.2	19.7	3.6
Pectoral muscle	2.4	20.2	1.3	16.3	1.7	19.4
Legs	10.2	11.6	15.8	4.5	18.1	16.5
Wings	3.0	6.8	3.7	10.1	2.2	4.9
Stomach	6.8	3.7	4.4	2.3	7.3	4.7
Total	98.0	100.2	100.2	100.2	98.6	100.0

[a] Data are presented as percentages of the nonlipid wet weight.
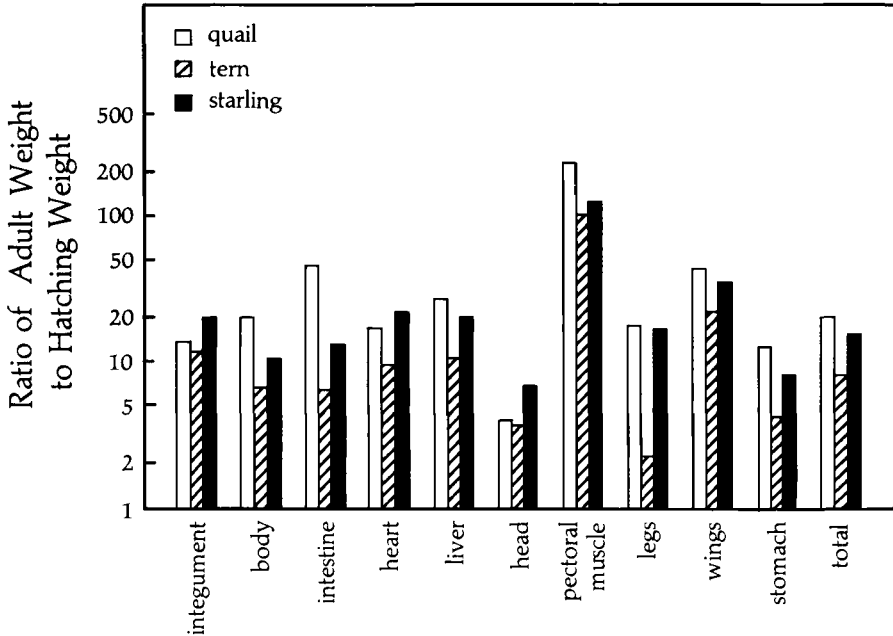[b] Several measurements based on one chick only.

Fig. 2. Ratios of the nonlipid wet weights of components in adults to the weights of those components in newly hatched young. The ratios are plotted on a logarithmic scale and thus indicate relative periods required for the growth of the components, assuming equal growth rates.

Condition of the young at hatching.—Differences in the precocity of Starling, tern, and quail chicks at hatching are reflected in the composition of their tissues (Table 3) and the proportions of the various components and organs of their bodies (Table 4). In calculating these values for quail chicks, the yolk sacs, which were removed and analyzed separately, were not included. The yolk sacs weighed 0.44 g on average. Neither the tern nor the Starling had large yolk reserves at hatching; where present, these were included with the body component.

TABLE 4. Characteristics of newly hatched chicks and adults of the Starling, Common Tern, and Japanese Quail.

	Starling		Common Tern		Japanese Quail	
	chick	adult	chick	adult	chick	adult
Number of individuals	4	22	1	2	8	3[a]
Weight (excluding yolk)	5.19	76.3	14.9	111.5	5.83	113
Percent water	86.8	64.4	78.7	59.9	75.9	64.2
Percent nonlipid dry material	10.4	31.2	19.4	34.1	17.6	26.8
Percent lipid	1.6	4.4	1.9	6.0	6.4	9.0
Water index[b]	8.35	2.07	4.06	1.76	4.31	2.39
Lipid index[c]	0.15	0.14	0.10	0.18	0.36	0.34
Water index of:[b]						
integument	7.10[d]	0.74	2.42	0.67	2.41	0.94
stomach	5.82	2.58	3.84	2.64	4.11	2.52
leg	6.79[d]	1.90	3.80	1.82	4.11	2.26
pectoral muscle	7.72	2.76	7.05	2.91	6.42	2.94
head	8.02[d]	2.57	5.75	2.60	6.04	3.02

[a] Fully grown individuals 64–71 days old.
[b] Water content divided by nonlipid dry weight (dry weight for Starling chick).
[c] Lipid divided by nonlipid dry weight.
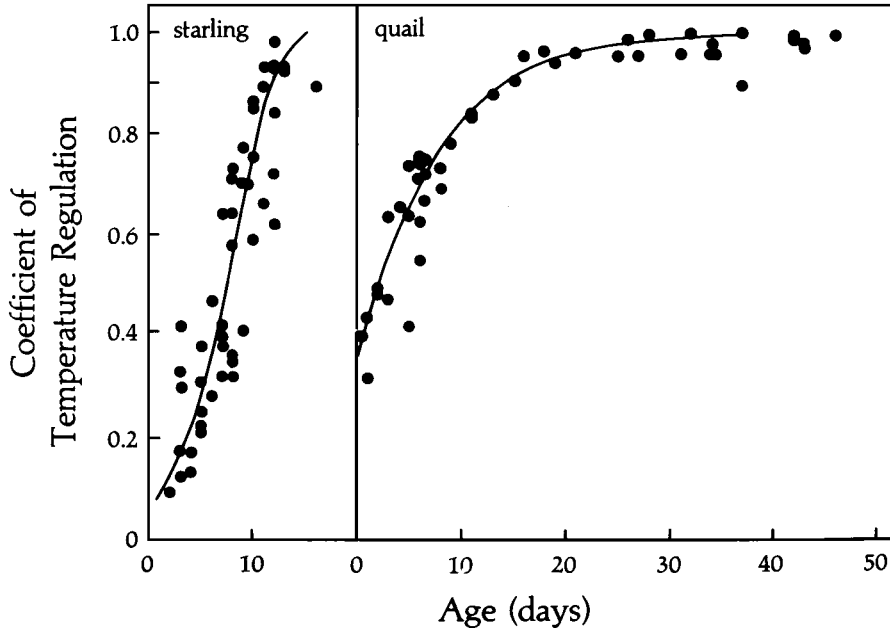[d] One chick only.

Fig. 3. Development of homeothermy in Starlings and Japanese Quail. The coefficient of temperature regulation is the percentage of the gradient between adult body temperature and air temperature that the chick maintains after 30 min at 20°C. Plotted data represent individual measurements; curves were fitted by eye.

Newly hatched quail and tern chicks had a higher proportion of nonlipid dry material and less water than Starling chicks. The water level of the chicks, expressed as the water index (water divided by nonlipid dry weight), emphasized the similarity of the tern (4.06) and quail (4.31) and distinguished them from the Starling (8.35). Water indices of the adults of each species were similar (1.76–2.39); the small differences were related to the proportion of integument, which has a low water content (see Tables 3 and 4).

Only the quail chicks had a substantial lipid reserve at hatching (6.4% of fresh body weight). Under natural conditions, this reserve presumably supplements energy intake during the days immediately following hatching. Under laboratory conditions, the lipid content of quail remained high, reaching 9.0% by 10 weeks of age. Adult Common Terns and Starlings had lipid deposits amounting to 6.0 and 4.4% of adult body weight.

The water levels of most body components of tern and quail chicks differ from those of Starling chicks; water levels of the pectoral muscles and, to a lesser extent, the head of the three species are similar (Table 3). Similar water indices for the pectoral muscles underscore the fact that neonates of all three species are unable to fly.

The body proportions of the newly hatched Starling, tern, and quail were similar, although the integument and legs of the Starling were relatively smaller than those components of the tern and quail (Table 4). Among adults of the three species, the tern had relatively small legs, large wings, and a heavy integument; the quail had a relatively small head. The most striking changes in body proportions during the development period were an increase in the pectoral muscles and, to a lesser extent,
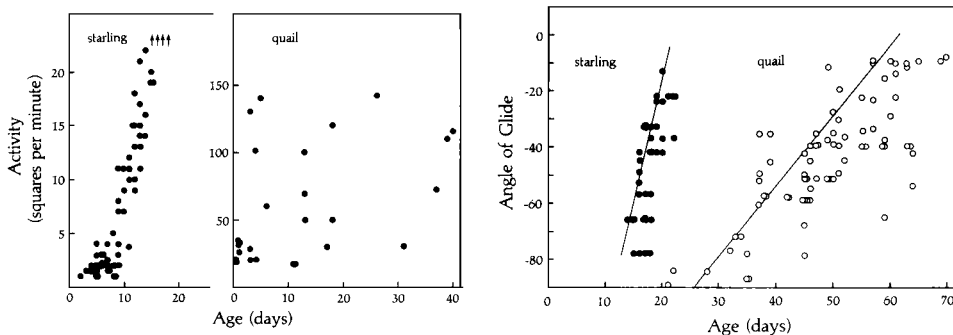
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Fig. 4. Left: Rate of pedal movement as a function of age in young Starlings and Japanese Quail. Activity was measured in a pen 1 m in diameter, the floor of which was marked off into 10-cm² squares. Activity was monitored by the number of squares entered per min. Plotted data represent individual measurements. Arrows indicate that the birds hopped out of the pen before the end of the test. Note the difference in scale for the Starling and quail. Right: Development of flight capability in the Starling and Japanese Quail. Flight was tested by dropping the young from a height of 5 ft (1.5 m) and calculating the angle of descent. Plotted data are individual measurements.

wings of all three species, a decrease in the legs in the tern, and a decrease in the heads of the quail and, to a lesser extent, the Starling and tern.

The factor by which each component increases from hatching to adulthood is compared among species in Fig. 2. In all species, the pectoral muscles showed the greatest increase and the head, least (excluding the leg component of the tern). The postnatal growth increments of all components of the tern were smaller than those of the Starling and quail, reflecting the larger size of the tern at hatching. The intestine of the quail exhibited a 45-fold increase, but the contents of the intestines were not removed during processing and their size may have increased partly through accumulation of gut contents in addition to tissue growth.

Development of mature function.—Pedal motion and temperature regulation are both well developed in newly hatched tern and quail chicks, but not in Starling chicks. In all three species, flight does not appear until well after hatching.

In the Starling, the coefficient of temperature regulation increased gradually during the nestling period and attained adult level for ambient temperatures of 20°C at about 12 days. One-half of adult thermoregulatory capacity was reached by day 7 or 8 (Fig. 3). The quail neonate exhibited a thermoregulatory capacity of about 40% of the adult. Further increase was slow compared to the Starling because the quail grows more slowly. In the Common Tern, the coefficient of temperature regulation increased from about 50% to 70%, 85%, and 90% during the first 4 days of post-hatching life (LeCroy and Collins 1972).

The development of pedal activity in the Starling and quail is shown in Fig. 4. Starlings could not lift themselves off their tarsi before day 10. Activity increased rapidly thereafter until by 15 days most young were able to hop out of the test enclosure. Quail could run rapidly on the first day of post-hatching life, but they were not active in the test enclosure until the third day. Because quail tend to remain quiet when alarmed, few of the birds exhibited their potential level of activity during the tests. Experience with young terns indicated that their pedal locomotion develops as precociously as that of the quail chick.

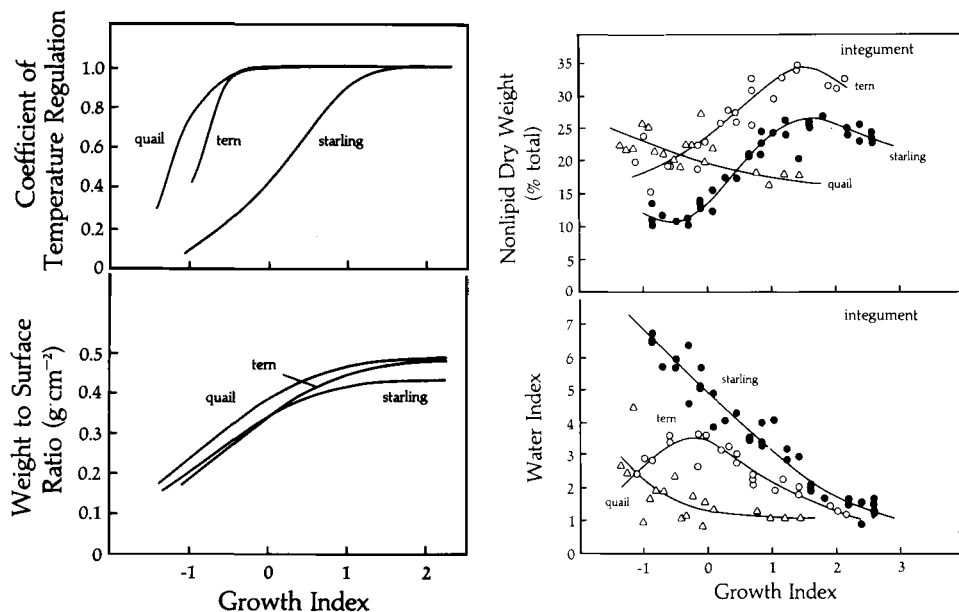In the Starling, flight capability developed rapidly between 15 and 20 days of age.

Fig. 5. Left: Coefficient of temperature regulation (above) and ratio of body weight to body surface area (below) as a function of the growth index. Surface area was estimated by the expression, $S(\text{cm}^2)$ = $10W(\text{g})^{2/3}$ (Meeh's formula). Right: Proportion of integument in the nonlipid dry weight of the chick (top) and water index of the integument (bottom) as a function of the growth index. Curves are fitted by eye.

Quail chicks began to fly at 30 days and could maintain level flight at 60 days (Fig. 4). Quail prefer running to flying and they were reluctant subjects for the flight tests. However the data in Fig. 4 may underestimate their ability, quail clearly do not develop flight as precociously as megapodes and some other galliforms (see Nice 1962). LeCroy and Collins (1972) reported that most Common Tern chicks were flying by 28 days of age.

Development with respect to the growth index.—Development of mature function parallels increase in body weight, but there are obvious differences among species in morphology and functional maturity at a given body weight. These differences are clarified when the development of function and changes in body proportion are related to the growth index.

Relative to increase in body weight, homeothermy was acquired earliest by the quail (Fig. 5). It was delayed in the tern because terns complete more of their growth prior to hatching. Compared to the quail, the appearance of thermogenesis in the starling was delayed by nearly 1.5 growth units, and its development was more gradual.

To maintain a high temperature, the body must be insulated to reduce heat loss across its surface and it must have a large mass of mature muscle tissue to generate heat. Homeothermy is also facilitated by a high ratio of body weight to body surface area. Quail chicks acquired 50% of adult homeothermic capacity when the ratio of their weight to surface area was $0.19 \text{ g} \cdot \text{cm}^{-2}$. In the tern, the ratio was $0.23 \text{ g} \cdot \text{cm}^{-2}$. But in the Starling, it was $0.36 \text{ g} \cdot \text{cm}^{-2}$. Clearly the earlier acquisition of homeothermy of precocial chicks bears no relation to the ratio of weight to surface area.
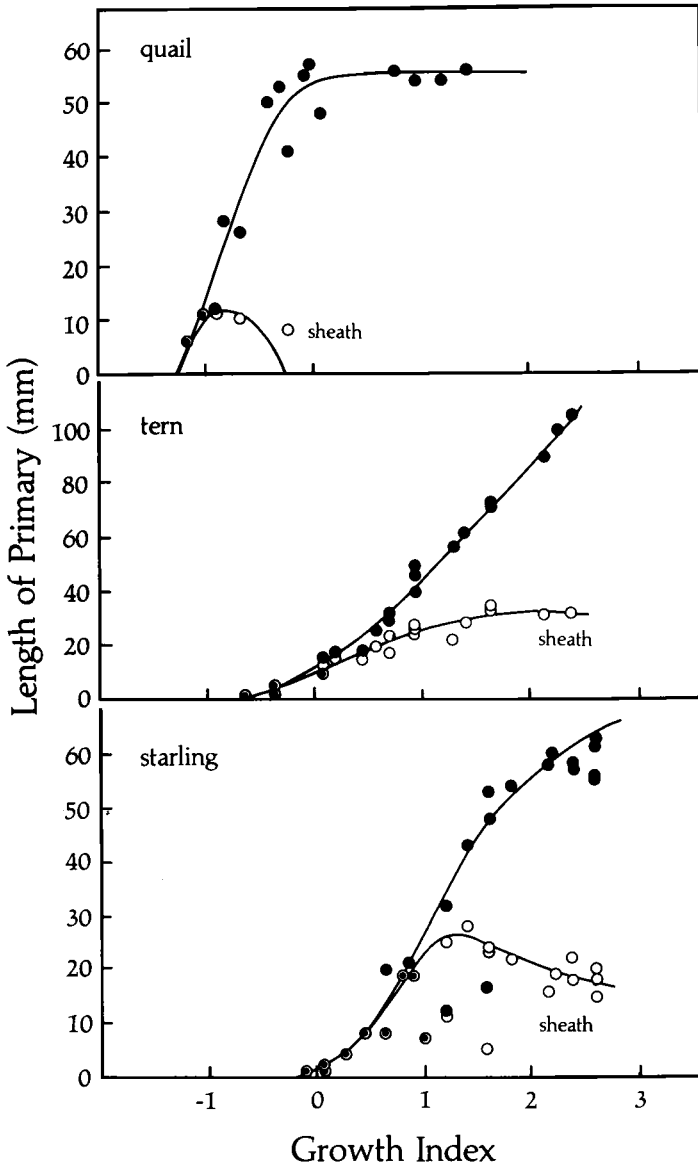
Fig. 6. Length of the fifth primary (Starling and quail) and outer primary (tern) as a function of the growth index. The length of the sheath surrounding the base of the growing feather is also shown. Lengths of the fully grown feathers are tern, 202 mm; quail 55 mm; and Starling, 77 mm. At maximum length, the sheaths are 16% (tern), 20% (quail) and 35% (Starling) of the final length of the feather.

Insulation is reflected in the size and water level of the integument (Fig. 5). The Starling neonate has only a few tufts of down. Its integument is mostly skin and both comprises a small proportion of the total and has a high water level. The integument of the tern neonate has a lower water level, but as the contour and flight feathers begin to grow, the water index of the integument increases with the development of blood-filled feather sheaths until a level close to that of the Starling is reached. The integument of the quail neonate resembled that of the tern, but sub-
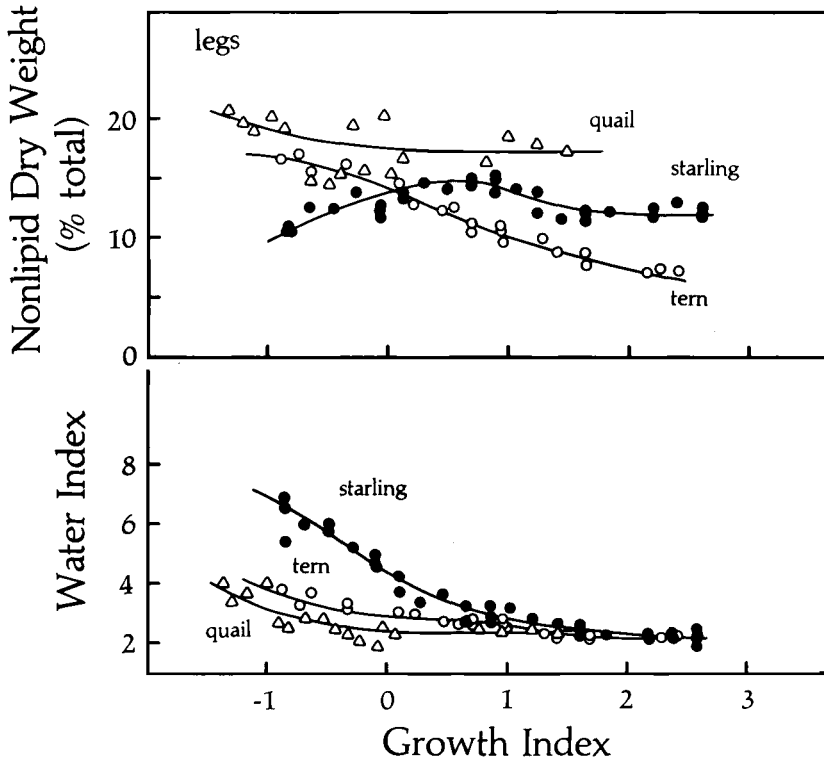
Fig. 7. Changes in the relative size and water index of the leg as a function of the growth index.

sequently its proportional weight and water index did not increase. The quail's lighter plumage may be explained in part by the smaller surface area of its wings (see Fig. 9).

The water index of the quail's integument did not increase during the period of feather growth because (1) feathers grew slowly, (2) the development of feathers was staggered, and (3) each growing feather had a small volume of feather pulp. Of the three species, the Starling's primaries grew most rapidly (6.1 mm · day^{-1}), the tern's intermediate (5.1 mm · day^{-1}), and the quail's, least (2.51 mm · day^{-1}) (Fig. 6). Conversely, with respect to the growth of the feather, the primaries of the quail unsheathed earliest and those of the Starling latest. By unsheathing when it is a small fraction of its final length, a feather has a small proportion of growing pulp and consequently grows slowly and has a low water content. Because the surfaces of blood-filled feather sheaths are avenues of heat loss from the body, insulation probably varies inversely to the water content of the plumage.

The retarded development of pedal locomotion in the Starling, compared to the tern and quail, was accompanied by a relatively small leg component with a high water index during the early part of the development period (Fig. 7). The ability of Starlings to use their legs (Fig. 4) increased rapidly between 9 and 15 days (growth index 0.5 to 1.5), at which time the water index decreased to the same level as that of the quail and tern at hatching.

The proportion of the body weight in the leg component of the Starling increased prior to the leg's rapid increase in function, and then decreased slightly thereafter
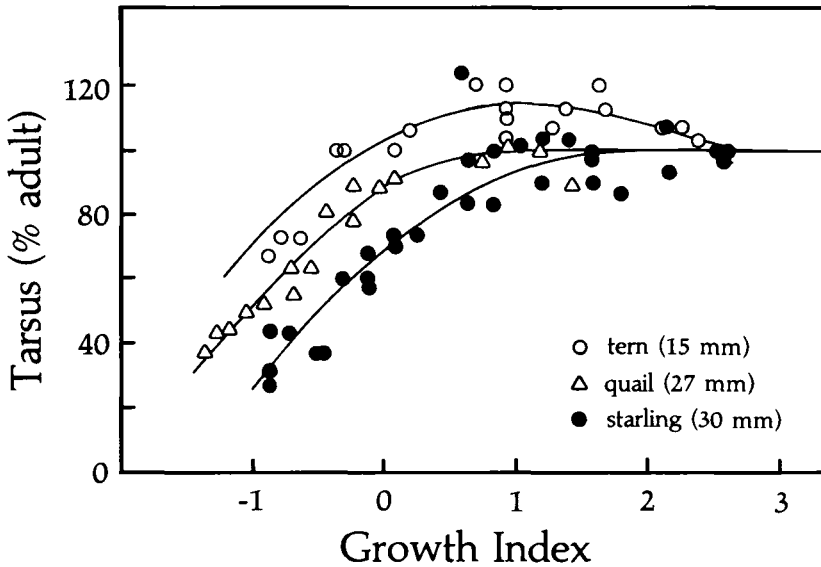
Fig. 8.   Increase in the length of the tarsus (percent of adult tarsal length) plotted as a function of the growth index. The tarsal length of tern chicks exceeds that of the adults owing to the fleshiness of the growing leg. If the length of the tern's tarsus were recalculated as a percent of the maximum length, its growth curve would nearly coincide with that of the quail.

(Fig. 7). The proportion of the body weight in the leg of the tern, however, decreased steadily with age. Increase in the length of the tarsus was more similar among the species than the development of mobility, although tarsal growth in the Starling lagged somewhat behind that in the tern and quail (Fig. 8). The elongation of skeletal elements evidently is more narrowly constrained than the development of skeletal muscle masses.

The development of flight (Fig. 4) was related to increase in wing area and growth and maturation of the pectoral muscles (Fig. 9). The quail developed flight earliest relative to growth in body weight. Associated with this precocious development of function, wing area and proportion of body weight in the pectoral muscles increased, and the water index of the pectoral muscle decreased, early in development. In the quail, the ratio of wing area to body weight reached a peak near a growth index of zero (50% adult body weight, 29 days of age) and thereafter declined to adult levels. The large wing area presumably allows small chicks to achieve some flight capacity without having to develop powerful flight muscles. Both the Starling and the tern eventually attained ratios of wing area to body weight much larger than that of the quail, but first flight occurred when all three species had achieved about the same wing area, and weight and water index of the pectoral muscles. I assumed that the rapid development of flight capability began at 15 days (1.6 growth units) in the Starling and 23 days (1.55 growth units) in the tern.

The water index of the pectoral muscle generally decreases as flight capability increases. But the pectoral muscle of the tern has a lower water index at hatching than one would expect from the late development of flight in that species. Perhaps water level reflects the development of connective tissues as well as the contractile muscle fibers themselves.
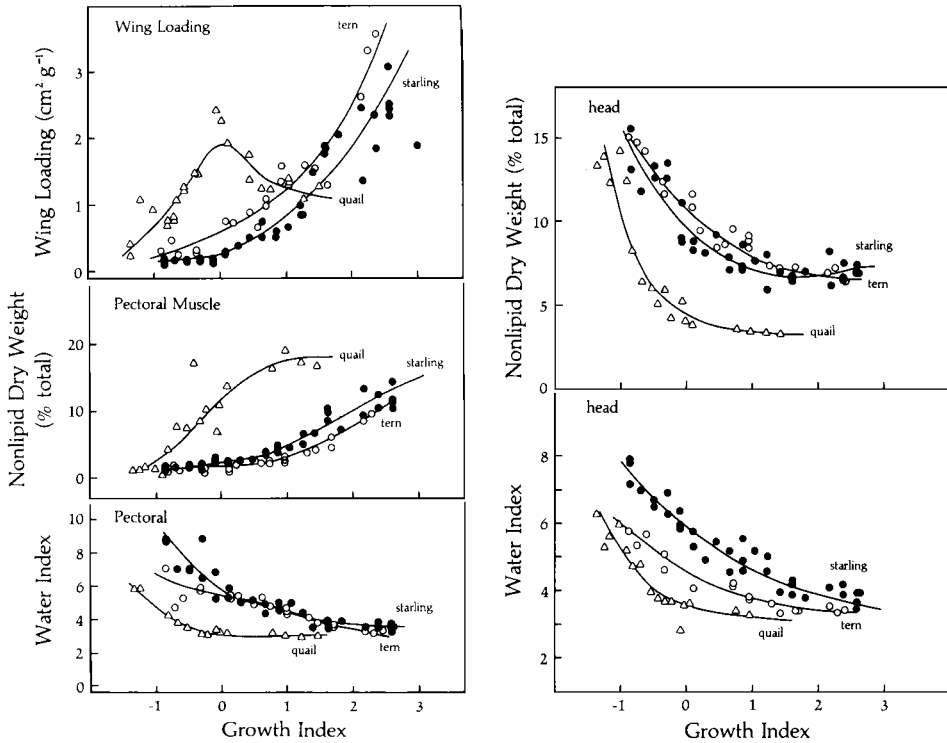
Fig. 9. Left: Changes in the ratio of wing area to weight (top), relative size of the pectoral muscle (middle), and water index of the pectoral muscle (bottom) as a function of the growth index. Right: Changes in the relative size (top) and water index (bottom) of the head as a function of the growth index.

Relative sizes and water indices of the visceral organs (heart, stomach, intestine, and liver) are not considered in detail here because in all three species they are functional and constitute a similar proportion (15 to 20%) of the hatchling. In contrast to the visceral organs, the head is a complex component made up of diverse tissues, including bone, brain, and muscle. Changes in the size of the head and its water index are shown in Fig. 9. At hatching, the heads of the three species are nearly identical in size (Table 4) but the heads of the tern and quail have lower water indices (Table 3). The relative size of the head of the quail decreases during development until it is less than half that in adult terns and Starlings. With respect to body weight growth, decrease in water index and attainment of adult proportions occurred earliest in the quail and latest in the Starling.

DISCUSSION

I began this study to determine the relationships between the rate of increase in body weight, change in body proportions and composition, and acquisition of homeothermy and capacity for walking and flight in three species with different patterns of development. I also intended to determine the extent to which these observations were consistent with the hypothesis that growth rate is constrained by compromise in the allocation of tissue to embryonic and mature functions. As the data presented in this paper do not bear on the several alternative hypotheses con-

cerning the significance of variation in growth rates, these hypotheses will not be discussed here.

The tissue-allocation hypothesis predicts that growth rate should be inversely related to degree of functional maturity: as more tissue is allocated to mature function, less is available for embryonic growth, and vice versa. In general, this relationship holds true: as birds acquire mature function, their growth slows; birds that are mature at hatching (precocial) grow more slowly than those that are dependent at hatching (altricial) (Ricklefs 1973).

The rapid growth of the Common Tern, a species whose young are precocial although fed by their parents (a type referred to as semi-precocial by Nice 1962), seems to present a fundamental challenge to the tissue allocation hypothesis. But the tern's growth rate is reconciled with the tissue-allocation hypothesis when one considers the roles of different tissues in development. Terns acquire homeothermy and pedal locomotion shortly after hatching, but they cannot fly until near the end of the growth period. Tissues associated with the flight apparatus remain undifferentiated and thus retain a capacity for rapid growth throughout most of the development period. By having completed before hatching a large fraction of the growth of tissues that attain full function early in postnatal development (particularly leg and integument), the tern is able to take full advantage of the potential for rapid growth of tissues whose maturation is deferred until near the end of the development period. Two factors are important to this strategy. First, tern neonates weigh almost 13% as much as adults. By comparison Japanese Quail neonates are 6%, and Starlings 7%, of adult weight. Second, the leg, one of the most mature body components of the neonate, comprises only 4.5% of adult weight in the tern compared to 16.5% in the quail and 11.6% in the Starling (Table 4). As a result, during postnatal development the weight of the leg increases only 2.2 times in the tern, compared to 17.7 times in the quail and 16.9 times in the Starling (Fig. 2).

When a large fraction of the growth of tissues destined for early maturation is accomplished during the embryonic period, one would expect the embryonic growth rate of the tern to be slow and the incubation period long relative to altricial species, and, perhaps, to precocial species with eggs of similar size. The 23-day incubation period of the Common Tern is 6 days longer than that of the Japanese Quail and 12 days longer than that of the Starling. Even the precocial domestic hen, with a much larger egg, hatches in 21 days.

Because terns have large eggs and small legs, the slow post-hatching growth rate of the leg need not constrain the growth rate of the body as a whole. Growth is multiplicative, and so the increment of growth is properly expressed as the difference between the logarithm of weights at the beginning and end of the growth period. This is equivalent to the logarithm of the ratio of the weight at the end to that at the beginning of the growth period. For the leg component, this index in the quail (2.87) is 3.6 times that of the tern (0.79). If the growth rates of the tissues were identical, the post-hatching growth of the quail's legs would require a period 3.6 times longer than that of the tern. Because the legs of the tern at fledging (7.3 g) are larger than the legs of the adult (5.2 g), the logarithmic index of growth accomplished during the nestling period is more properly 1.14 than 0.79. With this ratio, the growth period of the quail should be 2.52 (2.87/1.14) times that of the tern, which is almost precisely the ratio (2.50) of the growth rate constant (K) of the tern (0.265) to that of the quail (0.106).

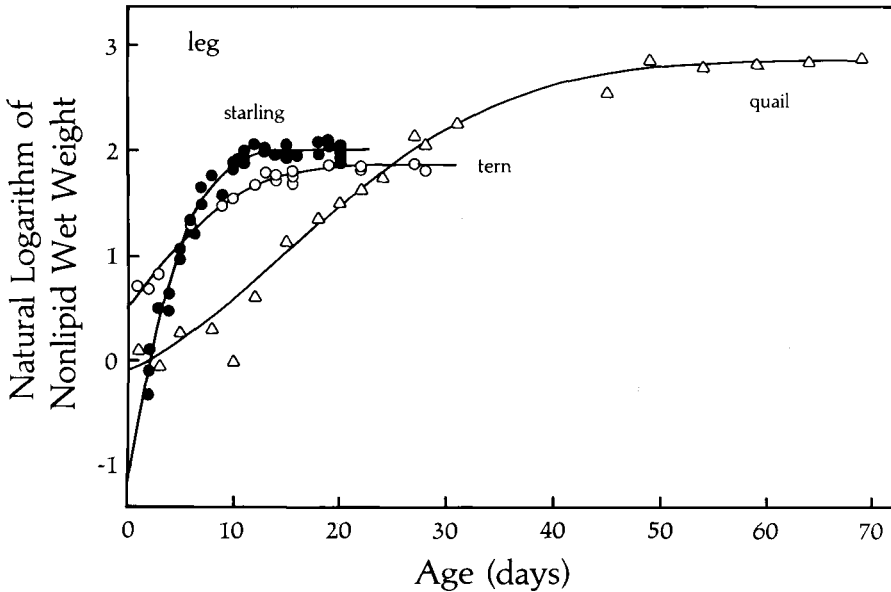Water content is an index to functional maturity. The development of function

Fig. 10.   Increase in the weight of the leg as a function of age. Weight is plotted on a logarithmic scale, hence the slope of the growth curve is the percentage rate of increase.

by a cell is accompanied by the accumulation of structural proteins and enzymes—e.g. the contractile proteins of muscle—that increase the dry weight component of the cell. Deposition of extracellular materials also may contribute to this drying trend in maturing tissues. Regardless of the cause, water content decreases in direct correspondence to increasing functional maturity in all species that have been studied (Ricklefs 1967, 1968, 1975). The water indices of the tissues of adult birds do not differ markedly among species; the minor variation that does occur is related to the proportions of bone and feather in the component. Thus the integument of the Common Tern has a lower water index than that of the Japanese Quail because terns have a heavier plumage relative to the weight of the skin; the leg of the tern has a lower water index than that of the quail because it contains less muscle, hence relatively more bone.

The similar water indices of the legs of the tern and quail (Fig. 7) indicate a similar course of development of mature function. Weight increase of the tern's leg also parallels that of the quail during the most rapid growth phase (Fig. 10). In contrast, the Starling's leg grows very rapidly, accomplishing in about 10 days an increase requiring 50 days in the quail.

Because the growth rate of the tissue is inversely related to its functional maturity, the growth rates of the pectoral muscles of the Starling, tern, and quail should be more similar than are the growth rates of their legs. Using the water index of the pectoral muscles (Fig. 9) as a measure of their capacity for embryonic growth, we expect that growth rate at hatching will be most rapid in the Starling, that growth rates in the Starling and tern will converge midway through the growth period, and that the growth of the quail's pectoral muscle will quickly slow, nearly ceasing when the water index has decreased to a level approximately that of the adult (at about 30 days of age). These predictions are generally borne out by Fig. 11. In addition,
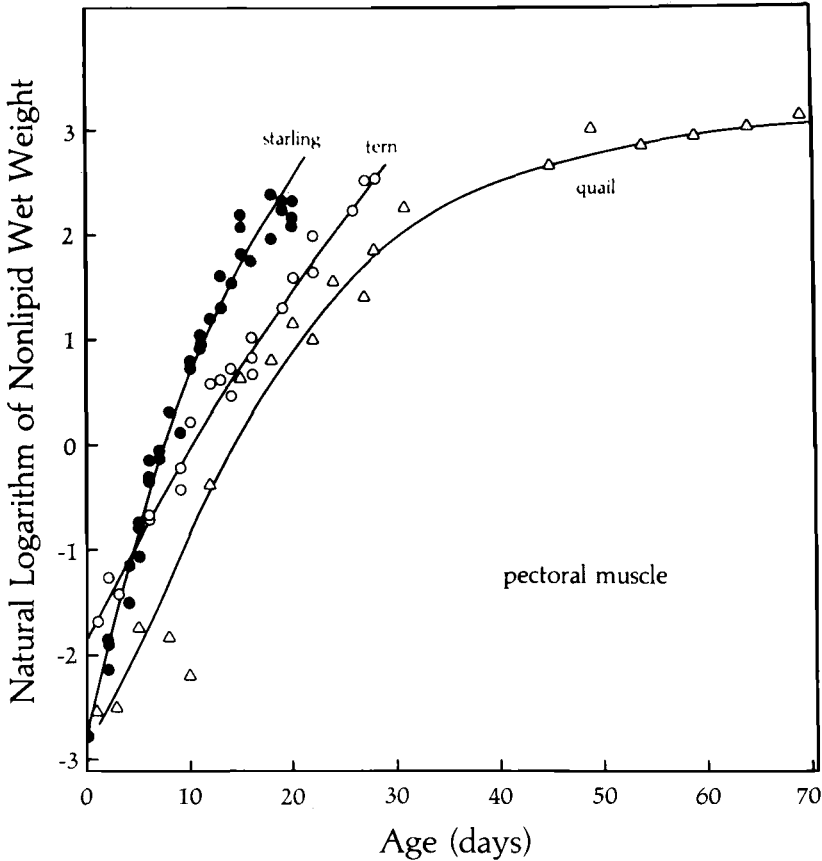
Fig. 11.   Increase in the weight of the pectoral muscles as a function of age. Weight is plotted on a logarithmic scale, hence the slope of the growth curve is the percentage rate of increase.

in the Starling and tern, the pectoral muscles continue to grow rapidly at the end of the nestling period. In marked contrast, the legs, which are used prior to the acquisition of flight, cease to grow well before fledging (Fig. 10).

Although I have indicated that development of the legs may control growth rate in the tern and quail, the head also has achieved much of its function by hatching and grows slowly. Water indices suggest earlier maturity in the tern and, particularly, the quail compared to the Starling (Fig. 9). Growth of the head is slowest in the quail, intermediate in the tern, and most rapid in the Starling (Fig. 12).

Sacher and Staffeldt (1974) determined that gestation period of mammals is related more closely to brain weight at birth than to body weight at birth and concluded that growth rate of the brain determines the fetal development period. Their hypothesis clearly could not apply to postnatal growth in birds unless one included the functional maturity of the brain. Even so, the growth rates of the heads of terns and quail differ sufficiently to make doubtful any application of Sacher and Staffeldt's ideas. In the quail, the relative size of the brain decreases from 32% of the head hatching to 24% in adulthood; in the Starling, it increases from 15% to 26% (brain weight data from Sutter 1943). This difference is consistent with the quail's early acquisition of mature function and, presumably, need for nervous control and
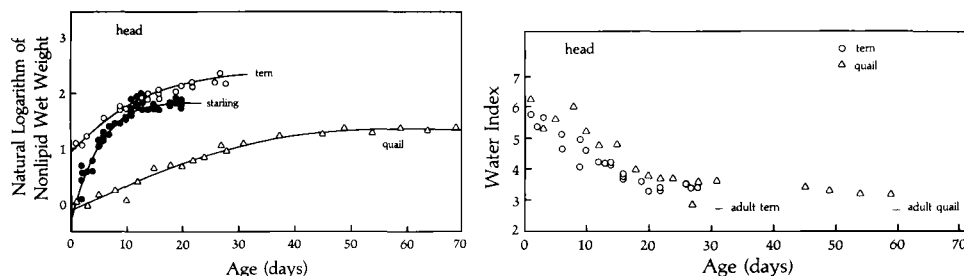
Fig. 12.   Left: Increase in the weight of the head as a function of age. Weight is plotted on a logarithmic scale, hence the slope of the growth curve is the percentage rate of increase. Right: Decrease in the water index of the head as a function of age in the Common Tern and Japanese Quail.

integration of behavior. It also accentuates the difference between the Starling and quail in growth rate of the brain compared to the entire head.

The visceral organs, especially the stomach, are relatively large at hatching compared to their size in adults. Presumably, these organs attain similar levels of function in neonates of the three species. But the growth rates of the viscera parallel the growth of the body as a whole. The heart probably varies little among species in level of function. Water indices of the heart at hatching (Starling 5.57, tern 4.87, quail 4.79) reflect this. Yet, presumably because the optimum size of the heart relative to the body changes little during development, the growth rate of the heart is closely tied to the growth rate of the body as a whole.

CONCLUSIONS

Patterns of growth and development in the Japanese Quail, Common Tern, and Starling suggest that growth rate is constrained by the proportion of tissue capable of cell proliferation—that is to say, growth rate varies inversely with functional maturity. The data further suggest that (1) the growth rate of the organism is generally determined by the most slowly growing component, (2) the relative sizes of body components must remain within limits determined by their function, and (3) post-hatching growth rate may increase when organs that are functionally mature at hatching accomplish a greater proportion of their growth during the embryonic period.

Development of the legs appears to determine the growth rate of the Japanese Quail and may set the pace of development more generally in birds. Precocial chicks need a large, functioning muscle mass at hatching both for locomotion and as a source of heat; birds generate heat primarily by shivering (West 1965). Compared to altricial species, like the Starling, precocial and semi-precocial chicks have a thick down, which is fully grown and functional at hatching. Subsequent growth of the plumage probably does not affect overall growth rate. Post-embryonic feather development is more closely related to acquisition of flight than to growth rate or mode of development.

The size of an organ must be consistent with its function. The heart pumps blood to the body from an early embryonic stage and its relative size varies little with age. The leg muscles and other skeletal muscles generate heat for temperature regulation in addition to providing mobility, and they must be well developed at hatching. In the tern, the contribution of leg muscles to heat production, hence their size, can

decrease only as the relative size of the pectoral muscles increases (Aulie 1976). In the quail, the legs are the primary locomotory organs throughout life and they remain large.

Because the pectoral muscles do not begin to function in most species until near the end of the development period, their relative size remains small during the early part of the growth period. And unlike the legs, the growth rate of the pectoral muscles remains rapid until most of the growth is completed.

In the Common Tern, the legs are well-grown at hatching. During post-embryonic development, the legs increase by a factor of only 3.1 (based on fledging weight) compared to factors of 16.9 in the Starling and 17.7 in the Japanese Quail. Because the postnatal growth increment of the slowly growing leg component is so small, the growth rate of the tern's body is determined by more rapidly growing components in which the acquisition of mature function is delayed.

The tern neonate is about twice the relative size of the Starling and quail neonates. Large hatching size reduces the post-embryonic growth increment of the legs in the tern and presumably reduces the post-embryonic development period. If the degree of functional maturity of the hatching were unchanged, doubling the size of the tern neonate would reduce the period of subsequent development by 38% (compare the logarithm of 3.1 to the logarithm of 6.2). Doubling hatching weight should, however, lengthen the incubation period (e.g. tern 23 days, quail 17 days). But the incubation period should increase less than the post-hatching development period decreases because the acquisition of function by the leg is delayed until hatching regardless of its size at hatching.

Species with semi-precocial development have two advantages of precocial species: young can maintain their own body temperatures and presumably escape some predation, and one advantage of altricial species: rapid growth. Why is this mode of development not adopted more widely? Among species in which parents feed their young, and hence in which precocity of development is not prerequisite to self-feeding, semi-precocial development is restricted primarily to the Charadriiformes—gulls, terns, and alcids. These species characteristically have small legs and lay few eggs. The first trait permits rapid post-hatching growth by reducing the growth increment of the leg component. The second permits large egg size, further reducing the growth increment of the leg. For species like the quail, in which the adults have large legs, doubling egg size would reduce the growth increment less than in the tern. The log of 17.7/2 (2.18) is only 24% less than the log of 17.7 (2.87). In addition, such an increase would result in a smaller clutch if the ability of the adult to produce or incubate eggs were limited. Any benefit from rapid growth in a species whose young are self-feeding and capable of escaping predators at an early age may be quite small relative to the lower fecundity and greater nest predation during the lengthened incubation period that would likely accompany any increase in neonatal size. For an altricial species like the Starling, the decreased fecundity and increased egg loss that would accompany an increase in egg size would not be balanced because post-hatching growth rate is already rapid and function is not achieved until well after hatching.

Finally, we must inquire about the advantage of semi-precocial development to such species as the Common Tern. A consequence of semi-precocial development is that parents are freed of having to brood their young at an early age. In the Common Tern, adults rarely brood young beyond the fourth day (LeCroy and Col-

lins 1972). Increased feeding time probably does not itself constitute an advantage since small young require proportionately less food than large young and the total number of young that the parents can feed is likely independent of whether small chicks are brooded. But if parents fed at a distance from the nest site and traveling time between the nest and feeding locality approached half the average interval between brooding spells—most gulls, terns, and alcids fall into this category—brooding would require full commitment of time by one adult and reduce the feeding capacity of the pair by one-half. In this case, brooding could reduce the number of young that could be fed. This factor may explain the precocial development of the Charadriiforms (other than shorebirds) and Procellariiforms, most of which feed at great distance from their nesting colonies. But measurements of energy requirements of precocial and altricial young will be needed before the issue is resolved.

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