

chicks with adults, but older chicks were not seen with adults. They also noted that at 25 days Sora chicks had almost full juvenal plumage and were independent.

Irish (Jack-Pine Warbler 52:115–124, 1974) interpreted Virginia Rail and Sora responses to tape-recorded calls in July and August as defense of a postbreeding territory, though little evidence is presented to support this hypothesis. By contrast, we observed that chasing and posturing in response to taped calls, the primary means of territory defense (Kauffmann 1983), were rare within several weeks after territory establishment. The frequency of responses to taped calls declined as hatching approached (Johnson 1984). The observations made by Irish (1974) may correspond to the second peak in calling activity observed by Pospichal and Marshall (1954), Glahn (Wilson Bull. 86:206–214, 1974), and Kauffmann (1971). No clearly defined second peak was observed in this study.

Adult Virginia Rails and Soras made a previously unreported dispersal from the vicinity of the home range used for brood-rearing. We believe the stimulus for this emigration is the maturation and increasing independence of the brood. The adult male may stimulate the breakdown of the family group with increasing aggressiveness toward the chicks and his mate. Kauffmann (1971), noting that juvenile and adult rails were always observed alone during late summer, suggested that this solitary behavior was due to increasing aggressive behavior of the chicks. We were unable to determine which sex emigrated from the home range first.

When emigration or dispersal does occur, it appears to involve a fairly long-distance movement between wetlands. Pospichal and Marshall (1954) noted that, in late summer, rails left wetlands for short periods to feed on uplands. Upland areas, including row crops, may serve as initial dispersal habitat. A female Virginia Rail and her brood used a weedy cornfield for 2 days before returning to wetland habitat. A Sora, located after dispersal near an isolated seasonal wetland 5 km from his home range, must have made extensive use of row crops in the 12 days after dispersal and, indeed, was relocated in a soybean field.

The significance of this dispersal is unclear. It may simply act to segregate family members because of increasing aggressiveness, it may be a limited molt migration, or it may be a shift to a fall migration staging area. The extent and pattern of this emigration deserves further investigation if we are to understand the impact of the loss of small private wetlands.

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Growth rates and development of Redhead ducklings.—Variation in avian growth rates has been found to be related to adult body size (Ricklefs, *Ibis* 110:419–451, 1968), feeding ecology (Lack, *Ecological Adaptations for Breeding in Birds*, Methuen, London, England, 1968; Ricketts and Prince, *Ornis. Scand.* 12:120–124, 1981), predation pressure (Lack, 1968; Clark and Wilson, *Quart. Rev. Biol.* 56:253–277, 1981) and precocity of development

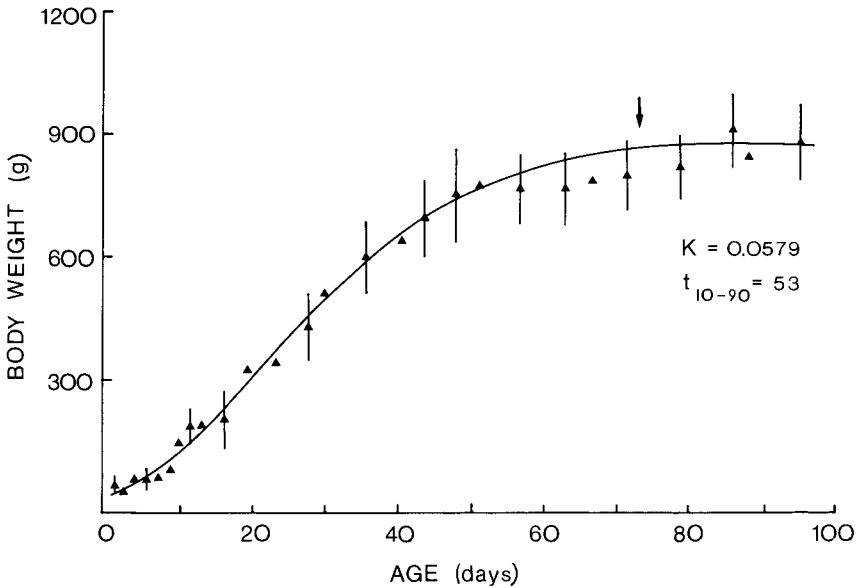


FIG. 1. Growth of Redhead ducklings ($N = 11$) raised in captivity. Individual points are means, and the arrow indicates the mean age at fledging. The curve was best fit by the Gompertz equation. Vertical bars are standard deviations.

(Ricklefs, *Ibis* 115:177–201, 1973; *Biol. Rev.* 54:269–290, 1979). Lightbody and Ankney (*Auk* 101:121–133, 1984) suggested that there also may be a seasonal influence on growth rate. Variation in patterns of growth is difficult to assess adequately unless there are sufficient, similarly collected and analyzed data. Ricklefs (1968, 1973) synthesized the results of many growth studies, but most were not directly comparable to one another owing to differences among the studies in methods of obtaining growth data (e.g., wild vs penned birds; if penned, by how they were reared; if wild, by how they were aged).

Ricklefs (*Ecology* 48:978–983, 1967) presented a simple graphical method for determining growth rate (K), asymptote (a), and the type of equation by which the data are best described (logistic, Gompertz, von Bertalanffy). Other methods (Richards, *J. Exp. Bot.* 10:290–300, 1959; Fendley and Brisbin, *Proc. XIII Int. Congr. Game Biol.* 337–350, 1977) produce estimates of K that differ from one another and from Ricklefs' estimate. The time required to grow from 10 to 90% of asymptotic size (t_{10-90}) is a less ambiguous value than K for comparing growth of body parts fitted to different forms of growth curves because it represents the linear part of the growth curve and is roughly comparable among the types of curve (Ricklefs 1967). Curves plotted as a function of the species' Growth Index (a time scale that makes the curves coincide along the abscissa; the growth index at time t is $G_t = [t - t_{50}]/[t_{50} - t_{10}]$ where t_{10} and t_{50} are the ages at 10 and 50% of asymptotic size) permit comparisons of relative growth of a body part (component) among species.

It is instructive to examine patterns of growth in closely related species, preferably intra-generic, so that a partial separation of environmental influences from phylogenetic differences can be achieved. Growth rates of waterfowl (Anatidae), particularly diving ducks (tribe

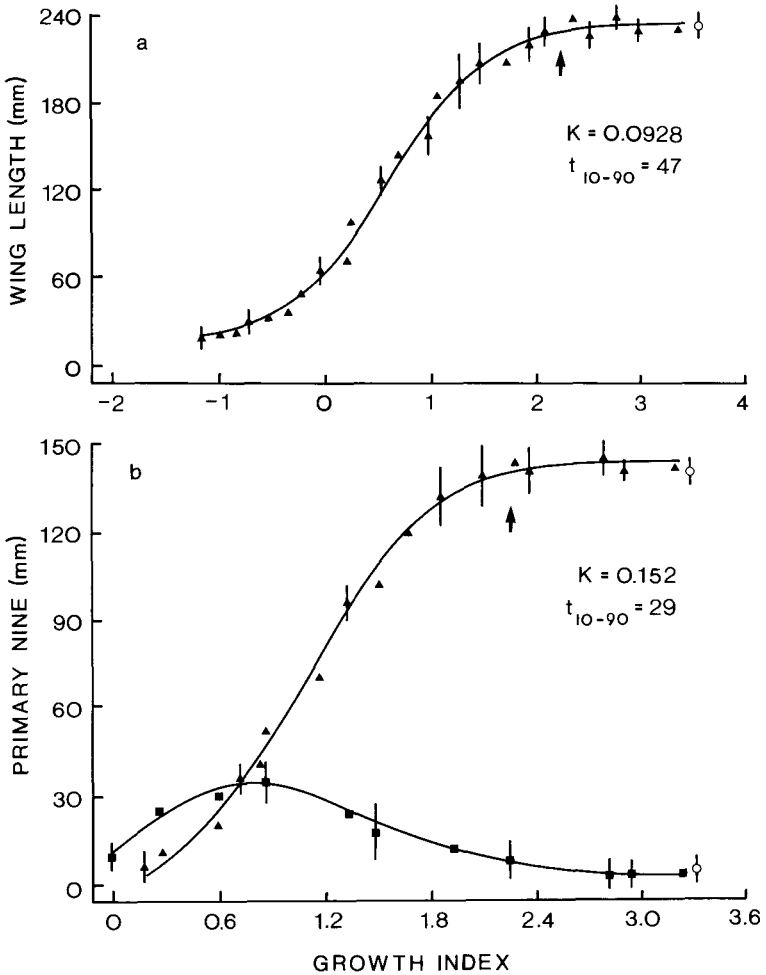


FIG. 2. Growth of (a) the wing and (b) the ninth primary shaft (squares) and feather excluding shaft (triangles) of Redhead ducklings ($N = 11$) raised in captivity. Solid points are mean values, and open circles are mean values at one year. The arrows indicate the age at fledging. Both curves were best fit by the Logistic equation. Vertical bars indicate standard deviations.

Aythini), have not been investigated frequently. Herein I describe the pattern of growth and development of captive Redheads (*Aythya americana*) in the same manner as I described growth patterns of two other species of diving ducks, the Canvasback (*A. valisineria*) and the Lesser Scaup (*A. affinis*) (Lightbody and Ankney 1984). Redheads are intermediate in size between the larger Canvasback and the smaller Lesser Scaup, and they nest at the same

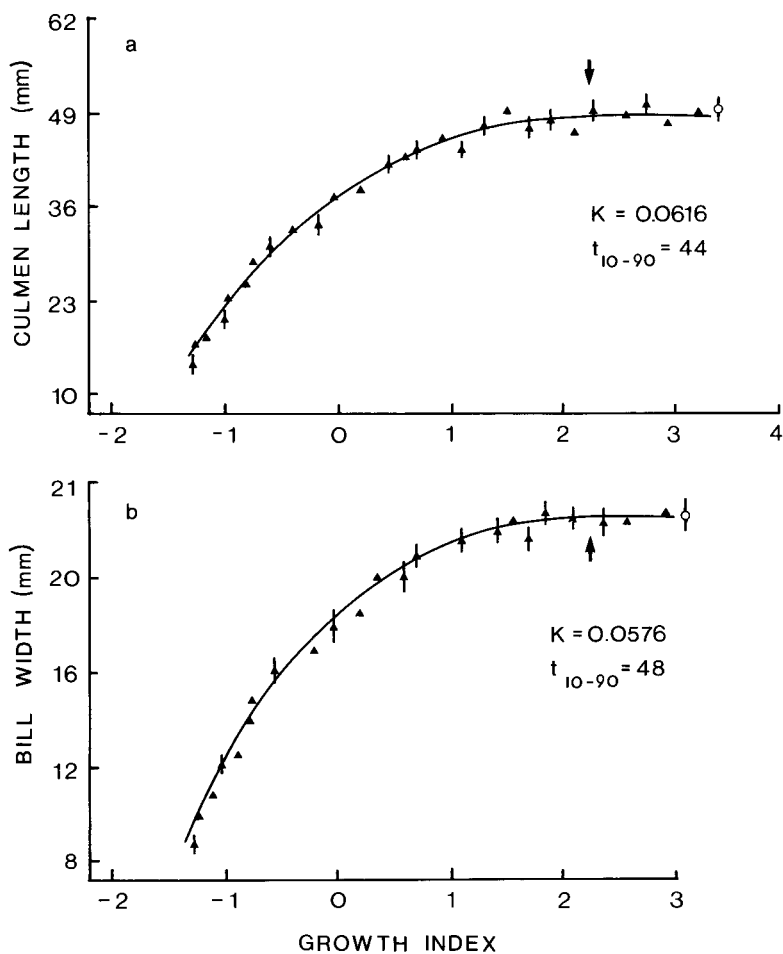


FIG. 3. Growth in (a) length and (b) width of the bill of Redhead ducklings ($N = 11$) raised in captivity. Solid points are mean values; open circle is the mean value at one year. The arrow indicates the age at fledging. Both curves were best described by the von Bertalanffy equation. Vertical bars indicate standard deviations.

time as Canvasbacks; thus a comparison of the growth rates of these three species is useful in investigating the seasonal influence of growth suggested by Lightbody and Ankeny (1984). Growth curves of some body components (see below) are compared to values reported by Weller (Wilson Bull. 69:5-38, 1957) for Redheads, and growth rates are determined for each component using Ricklefs' (1967) method; growth rates for body components have not been reported previously for this species.

As Redheads commonly parasitize Canvasback nests, I was able to collect Redhead eggs

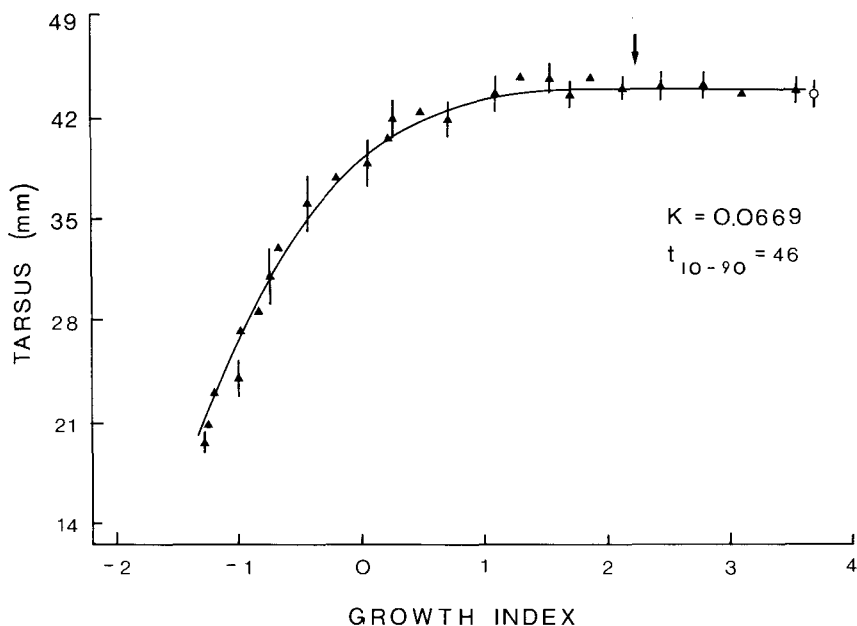


FIG. 4. Growth of the tarsus of Redhead ducklings ($N = 11$) raised in captivity. Solid points are means, and the open circle is the mean value at one year. The curve was best described by the von Bertalanffy equation. Vertical bars indicate standard deviations.

from parasitized nests (one egg per nest) while collecting Canvasback eggs near Minnedosa, Manitoba, during May 1981. Each Redhead egg probably came from a different female as parasitized nests were several miles apart. Eleven eggs were hatched in incubators, and the resulting seven males and four females were reared according to standard procedures (Ward and Batt, Propagation of Captive Waterfowl, Delta Waterfowl Res. Station and Wildl. Manage. Inst. Publ., Washington, D.C., 1973).

Measurements were made on the ducklings at hatching, every other day until they were two weeks old, and then every four days until they were several weeks past fledging, which occurred when the young were about 10 weeks old. Birds were considered fledged when the shafts of all primaries were firm and clear (Weller 1957). The ducks were measured again in June 1982 at one year of age. Weight, wing length, ninth primary shaft length and feather length excluding the shaft, tarsus, culmen length, and bill width were measured (see Lightbody and Ankney 1984 for details).

Growth curves were plotted for each component using the means for all ducklings, and (K) and t_{10-90} were derived from each curve following Ricklefs' (1967) method. Growth curves were plotted vs Growth Index.

As there were no significant differences in size of males and females (t -tests at each week of age, $P > 0.05$) up to one week after fledging, data from both sexes were pooled for analyses. I did not calculate values for each duckling; only mean values were used for the analyses. The growth rate I calculated ($K = 0.058$) (Fig. 1) was higher than that which Ricklefs (1973) calculated using Weller's (1957) data ($K = 0.041$). Body weight is affected by many factors

(e.g., food quality, ambient temperature, activity level). Differences in these factors may make the growth rates variable, so the range of values in both studies may overlap. Ducklings fledged at 92.6% of the estimated asymptotic weight and reached that asymptote at day 85 (Fig. 1). A decline in weight was evident beginning two weeks before fledging. Similar declines have been reported for Mallards (*Anas platyrhynchos*) (Sugden et al., *Can. J. Zool.* 59:1567–1570, 1981; J. M. Rhymer, pers. comm.), Canvasbacks (Dzubin, *J. Wildl. Manage.* 23:279–290, 1959), Lesser Scaup (Sugden et al. 1981), and Redheads (Weller 1957); although Lightbody and Ankney (1984) found no such decrease for Canvasbacks or Lesser Scaup. Flight and muscle growth and development are energetically expensive, so it is not surprising that the birds lost weight at that time. That Lightbody and Ankney (1984) found no weight loss for Canvasbacks or Lesser Scaup may be due to lower levels of activity of individuals of these species compared to Redheads (pers. obs.).

Wing length increased rapidly and attained adult size at the time of fledging (Fig. 2a). Primaries emerged on day 28. The ninth primary grew rapidly, reaching adult length by the time the birds fledged (Fig. 2b). Primary shafts started to clear on day 54, and ducklings flew short distances over 1-m high dividers into the next section in the pen as early as day 63, when seven shafts were clear. Redheads seemed incapable of, or unwilling to attempt, sustained flight at that age, and they did not fly when tossed into the air. Ducks fledged on day 73 ± 2 [SD] (Fig. 1), which is near the upper end of the range of values reported by Smart (57–75 days, *J. Wildl. Manage.* 29:533–536, 1965) and Weller (56–73 days, 1957).

The bill grew faster in length than in width, and at the time of fledging, it had obtained adult length and width (Fig. 3), as reported by Weller (1957). The tarsus grew at a moderate rate (Fig. 4), yet reached adult size well before fledging. Weller (1957) found similar growth curves for these components. One-year-old birds had not grown since the time of fledging (Figs. 2–4).

Overall, body growth may be limited by tissue constraints (Ricklefs 1973, 1979), but the pattern of development and growth rates of various components may depend upon the allocation of energy at the organism level. Pattern of development, growth, and fledging age of Redheads were similar to those of Canvasbacks (Lightbody and Ankney 1984), which are exposed to the same environmental conditions in the wild (e.g., temperature, daylength, habitat characteristics). Growth rate is usually related inversely to body size within a phylogenetic family (Ricklefs 1968), and because Redheads are smaller than Canvasbacks, they should grow faster. That they do not, suggests that either Redheads grew relatively slower or that Canvasbacks grew relatively faster than expected, or both. Redheads fledged older and grew slower in all components than did Lesser Scaup (Lightbody and Ankney 1984), which hatch later in the season under different environmental conditions. This was true even after accounting for differences in body size. Thus, there may be a seasonal influence on growth rates.

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