10

THE ORGANISM AS A FUNDAMENTAL UNIT IN A POPULATION

The individual organism is of fundamental significance in ecological analyses because every organism lives and dies as an individual. It has many relationships with other individuals in the community, of course, and is influenced by them in many ways. These other organisms are an integral part of the environment of each individual whenever there are functional relationships between them, just as physical factors that have functional relationships with an organism are a part of its environment. Each individual, however, relates to both the biological and the physical factors in its own unique way.

There is a tendency to consider groups of individuals as the smallest unit that can be analyzed ecologically. The key point in this chapter is that even in a group the individual's productivity is its own, and the variation between individuals in a community is an exciting part of ecology! The "averaging" of several individuals in a group, describing the group with a single number or by a mean with a standard deviation, masks the drama within the community as each organism meets the ecological forces in its day to day existence.

Analysis of the effect of variation on different individuals reveals something about what they must do to cope successfully with ecological forces. Thus a parasite-laden white-tailed deer may need a larger fat reserve going into winter to cope with the extra demands that the parasites place on it. A pregnant deer may need a larger fat reserve to survive the winter, or it may benefit more from an early spring than a nonpregnant deer would. Both the pregnant and the nonpregnant deer may live in the same area, but the effect of winter on each of them is different because they are different. To be sure, they are both *Odocoileus virginianus*, but that is a similarity based on several gross features that man has

decided upon as standards for identifying the species. Ecologically, they can be described in terms of their own energy and matter characteristics in relation to the energy and matter characteristics of their environment.

Analysis of the individual, however, is not an analysis of a single animal per se, but of individual characteristics. The purpose of such analyses is the determination of the importance of individual characteristics for the survival and productivity of the individual first, and then of the population. Pregnancy, for example, may have an effect on the ability of the pregnant individual to survive. If the individual survives and the pregnancy is successful, there is an addition to the population.

10-1 ENERGY, MATTER, AND TIME

One of the significant features of the existence of an individual organism is its energy and matter configuration through time. The energy requirements of individuals are constantly changing. The requirements are generally greatest per unit body weight during the early part of life. Adults have lower requirements for energy while resting, but higher requirements for productivity, especially for reproduction. Energy and matter is being reorganized at a rapid rate during gestation (especially the last two-thirds of the gestation period) and during lactation or egg-laying. These processes result in a synthesis of new tissue uniquely organized to become self-sufficient as a separate individual. The ability of this individual to survive depends on its success in coping with the forces of nature.

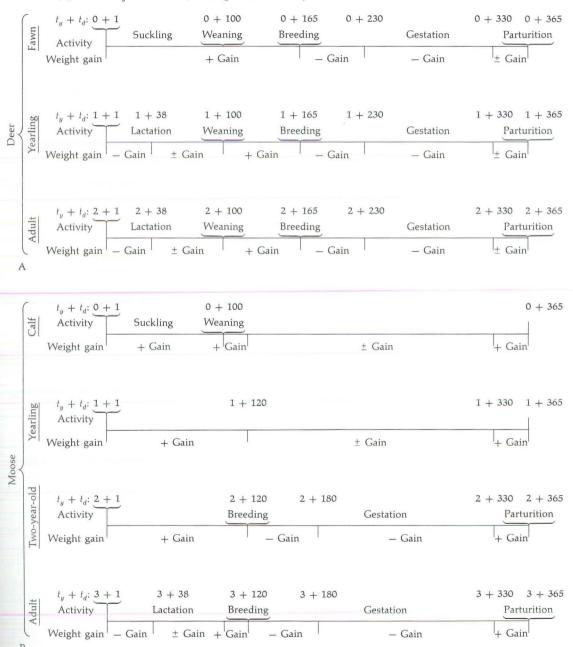
How can the differences between individuals in a population be analyzed? First of all, individuals can be represented by "points" on gradients between maximum and minimum values for different biological functions. For example, white-tailed deer may weigh between 2 kg and 120 kg. We all know that small, newborn deer are different from larger adult deer in many ways. They have spots rather than a solid coat color and are therefore a different part of a predator's visual environment than a solid-colored deer would be. They are lower to the ground, living in a different wind environment from that of the larger deer. A newborn fawn does not have as distinctive an odor as a larger, older deer. The younger deer are growing at a faster rate than the older deer, requiring more energy and protein on a relative or per-unit-weight basis. The older and larger deer have a higher absolute requirement though, since they need a considerable amount of energy just for maintenance. The pregnant adult deer need energy and protein for pregnancy, too. Thus the younger, smaller deer have different ecological roles from those of the older, larger deer, and each makes different contributions to the population.

Individual characteristics can be analyzed by studying the biological characteristics of deer ranging in weight from one extreme to the other, say, at 5-kg intervals up to 120 kg. This procedure demands a bit of knowledge about deer biology, of course, since the changing characteristics of deer of different weights must be known. Examples of such knowledge, expressed mathematically for use in computer analyses, are included in Parts 5 and 6.

10-2 BIOLOGICAL CHRONOLOGY

The chronological format for displaying the biological functions through an annual cycle are shown in Figure 10-1. Note that time is expressed in years (t_y) and days (t_d) . The sum of those two, with the age in years converted to days $(t_y \times 365)$, gives the total age in days. For deer, the chronology begins with parturition, with

FIGURE 10-1. Format for displaying biological functions through the annual cycle for (A) white-tailed deer and (B) moose: $t_y = \text{time in years}$; $t_d = \text{time in days}$.



the fawn weaned 100 days later, bred at the age of 165 days, and giving birth to its own young on its first birthday. This is an idealized chronology, of course. It is not meant to be precise for all deer since the primary function of such a chronology is to provide a time base in a computer program. A similar example of chronology for moose is also shown in Figure 10-1.

Given such a time base, the computer program can be written with equations for calculating the energy or protein costs of pregnancy during the periods of 165 to 365 days. The program can be written to include decision-making capabilities so that any analysis outside of that time period will not include the pregnancy cost calculations. The effect of variation in the timing of biological functions can be analyzed with this approach. Suppose female fawns were not capable of reproduction until the age of 195 days (30 days later than that shown in Figure 10-1). This would delay conception by one month, with the fawn being dropped one month later in the spring (about July 1). Suppose that fawn was bred on day 225, delaying the birth of its fawn by yet another month (to August 1). Continuing that pattern for the late-born, it would be bred in February—a time when the bucks may not be capable of servicing a female. If she was not bred then, she would breed for the first time as a long yearling. At this older age, she probably would come into heat early in the breeding period, resulting in an early fawn the following summer. Her fawn might very well breed that fall, starting the cycle all over again.

The foregoing example illustrates the use of the chronology as a base, with a shift in the breeding time. This procedure can be used to test a hypothesis about the time of fawn or calf drop and the age of reproductive maturity, comparing the theoretical results with observed field data. This background knowledge about the significance of the time of breeding may help in interpreting the field data. Many other relationships can be tested in a similar way. The time base is used to test the effect of time variation on nutritive relationships in Part 6.

The biological or life-history characteristics of waterfowl can be expressed on a time base that includes significant reference points in their annual cycle. Let us illustrate the annual cycle of several species of waterfowl by first identifying their main biological activities (Figure 10-2). Note that both males and females are present on the wintering grounds and both participate in breeding activity during the flight northward. After arriving at the marsh, the male participates in territorial defense, "loafing," and molting prior to southward migration. The female builds a nest, lays eggs, incubates, rears the brood, molts, and then flies south. If the first nest is destroyed, the reproductive activities may be repeated.

The next step is to identify the period of time in which each of these biological activities occurs. Data for northward flight, arrival at Delta Marsh, and the beginning of nesting for five species of ducks described in Sowls (1955) have been positioned on chronology scales (Figure 10-3). The average date of arrival is shown along with earliest and latest recorded dates of arrival. The peak for beginning the building of nests is shown, along with earliest and latest days on which nests were started. Note that the distribution is skewed to the left because of renesting attempts. Other significant days in the annual cycle can be determined

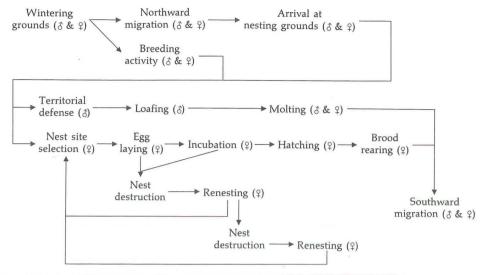


FIGURE 10-2. Significant reference points in the annual cycle of waterfowl.

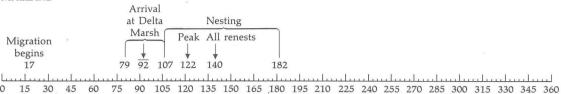
from the data in Figure 10-3. One egg is laid per day, for example, so the number of days of egg-laying is equal to the number of eggs in the clutch. Incubation is from 21 to 23 days for ducks, which establishes the date of hatching. Thus, there are certain constraints in the chronology; nesting begins only after arrival at the marsh, egg-laying takes at least as many days as there are eggs in the clutch, brood-rearing cannot begin before the end of the 21-day incubation period, and so forth.

These characteristics of the biological cycle through time can be expressed mathematically for use as a time base for computer calculations of the nutrient requirements, behavioral interactions, and other characteristics of the animal throughout the year. The symbols used to designate biological events are listed in Table 10-1. The values for different characteristics of the five species are shown

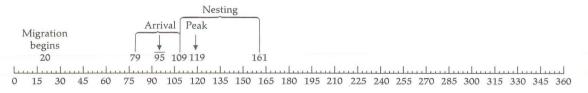
TABLE 10-1 SYMBOLS USED IN THE CHRONOLOGY OF WATERFOWL $d_{nf} = \text{day northward flight begins}$ $d_{am} = \text{day of arrival at marsh}$ $d_{lb} = \text{day laying begins}$ $d_{nd} = \text{day nest destroyed}$ $d_{le} = \text{day laying ends}$ $d_{ib} = \text{day incubation begins}$ $d_{ie} = \text{day incubation ends}$ $d_{ln} = \text{day leave nest} = d_{ie} + 2$ $d_{fb} = \text{day flight begins} = d_{ie} + 42$

 $d_{st} = day$ southward flight begins

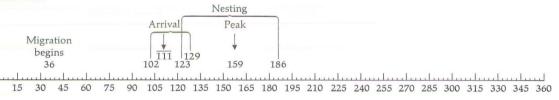




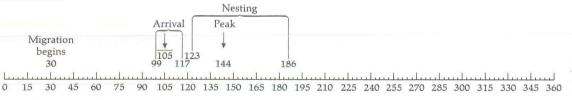
PINTAIL



GADWELL



SHOVELLER



BLUE-WINGED TEAL

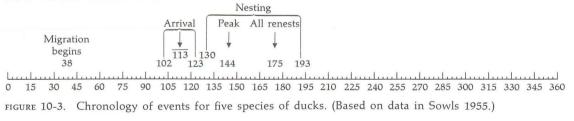


TABLE 10-2 VALUES (days) USED TO CALCULATE THE EXPECTED DATE OF OCCURRENCE OF THE BIOLOGICAL EVENTS DESCRIBED IN THE TEXT

Event	Mallard	Pintail	Gadwell	Shoveller	Blue-winged Teal
$d_{nf}^{*} = d_{am} -$	75	75	75	75	75
$d_{lb(1)} = d_{am} +$	30	24	48	39	31
$d_{le(1)} = d_{am} +$	40	33	58	51	42
$d_{ib(1)} = d_{am} +$	41	34	59	52	43
$d_{ie(1)} = d_{am} +$	62	55	80	73	64
$d_{ln(1)} = d_{am} +$	64	57	82	75	66

^{*}A constant flight time is shown here for all species. Variations can be added for different weather conditions and other factors affecting migration time.

in Table 10-2 for the first nest. All of these are related to $\emph{d}_{am'}$ the day of arrival at the marsh, with the rationale shown below using blue-winged teal as an example.

$d_{nf} = d_{am} - 75$	d_{am} is considered the biologically significant day in the program. The northward flight from the wintering grounds to Delta Marsh is assumed to take 75 days.
$d_{lb(1)*} = d_{am} + 30$	Laying is assumed to begin 30 days after
	arrival at Delta. It cannot begin before arrival, and Sowls uses arbitrary dates for the latest date on which the first nests were begun by each of the five species.
$d_{le(1)} = d_{am} + 42$	The number added here is 30, taken from the preceding event, plus the number of eggs laid in the first clutch. Sowls states that one egg is laid each day until the clutch is complete.
$d_{ib(1)} = d_{am} + 43$	Incubation is assumed to begin the day after laying ends.
$d_{ie(1)} = d_{am} + 64$	For ducks, incubation ends 21 days after it begins. Published incubation periods vary from 21 to 23 days. The extra two days are considered in part in the next entry since not all ducks spend two full days at the nest after hatching.
*The 1 indicates the first nest.	

$d_{ln(1)} = d_{am} + 66$	The ducklings leave the next two days after hatching, hence 2 days are added to d_{ie} .
$d_{fb(1)} = d_{am} + 108$	Forty-two days are allowed for growth after the ducklings leave the nest and begin to fly.

A renesting attempt can be added to the chronology for the blue-winged teal by using the following information:

$d_{lb(2)*} = d_{am} + 30 + n \text{ eggs laid}$ $+ 5 \text{ if } d_{nd} < d_{am} + 41$	Five days are added to the number of eggs laid before nest destruction. This is a recovery period during which the hen locates a new nest site and builds the nest.
$\begin{aligned} d_{lb(2)} &= d_{am} + (d_{nd} - d_{am}) + 5 \\ &+ \{ [d_{nd} - (d_{am} + 42)] \ 0.644 \} \\ &\text{if } d_{am} + 42 > d_{nd(1)} < d_{am} + 66 \end{aligned}$	Five days are allowed first, then a 0.644-day delay in the beginning of a renest is allowed for each day the duck was into the incubation period. This is based on a linear regression equation in Sowls.
$\begin{aligned} d_{le(2)} &= d_{nd(1)} + 5 \\ &+ \{ [d_{nd} - (d_{am} + 42)] \ 0.644 \} + 9 \end{aligned}$	Nine days are added to the day on which laying begins, based on data from Sowls indicating that blue-winged teal lay 9 eggs in a renest.
$d_{ib(2)} = d_{le} + 1$	See $d_{ib(1)}$.
$d_{ie(2)} + d_{le(2)} + 22$	Twenty-two days are added to the end of egg laying, including 1 day for the interval between the end of laying and the beginning of incubation and 21 days for incubation.
$d_{ln(2)} + d_{ie(2)} + 2$	See $d_{ln(1)}$.
$d_{tb(2)} + d_{ln(2)} + 42$	See $d_{fb(1)}$.

^{*}The 2 indicates the second nest.

$$\begin{aligned} &d_{sf} = 244 \text{ if } d_{fb(1)} \text{ or } d_{fb(2)} < 244 \\ &d_{sf} = d_{fb(2)} \text{ if } d_{fb(2)} > 244 \end{aligned}$$

This assumes that they begin southward migration on the day that they learn to fly. This is the earliest possible date; it is likely that migration would begin after a few days of "practice."

The other four species included in the chronology of the first nesting attempt can be described for the second nesting attempt if the number of eggs in the second clutch is known. These are [based on data in Sowls (1955)]: mallard (9), pintail (9), gadwell (7), and shoveller (9).

This rather complex chronology is useful if a computing system is used to calculate biological characteristics over time. Thus to obtain information on the protein requirement of blue-winged teal on May 30, an input of day 150 (May 30, Julian calendar) into a computer program with the chronology stored in it, along with equations for calculating protein requirements for maintenance, activity, and production, will result in an output including egg-laying as a protein cost. In other words, the computer is programmed to make decisions resulting in the acceptance of equations for calculating cost items present at the time of year being analyzed and rejecting the irrelevant ones.

An interesting variation to test would be to vary the day of arrival at the marsh by intervals on either side of the average date, with concomitant variations in the span for the beginning of nesting, after which egg-laying, incubation, and brood-rearing follows at set intervals. For example, suppose nesting was delayed 30 days for blue-winged teal because of very cold, stormy weather. Other functions following the onset of nesting would also be delayed, since only 1 egg a day is laid, 21 days are required for incubation, and the growth rate of the ducklings has an upper limit. These delays may result in higher mortality should the marshes dry up while the birds are still young or should there be a large proportion of immature birds later in the fall, rendering them less capable of completing southbound migration. Thus the effect of changes in the phenology of the bird can be related to the effects of weather conditions, water levels, and other natural phenomena to develop predictive capabilities when different combinations of events occur.

The information necessary to develop chronological models of different species is available in research reports, in life-history books, and through observation in the field. The behavior of turkeys in Texas has been described by Watts and Stokes (1971), with a chronological display (Figure 10-4) similar to that shown earlier in this chapter for ducks (Figure 10-2). These events for turkeys can be quantified if additional data on clutch size, energy, protein and mineral contents of eggs, incubation period, requirements for brood-rearing, and others are determined. Some of this information is available in books such as Hewitt's *The Wild*

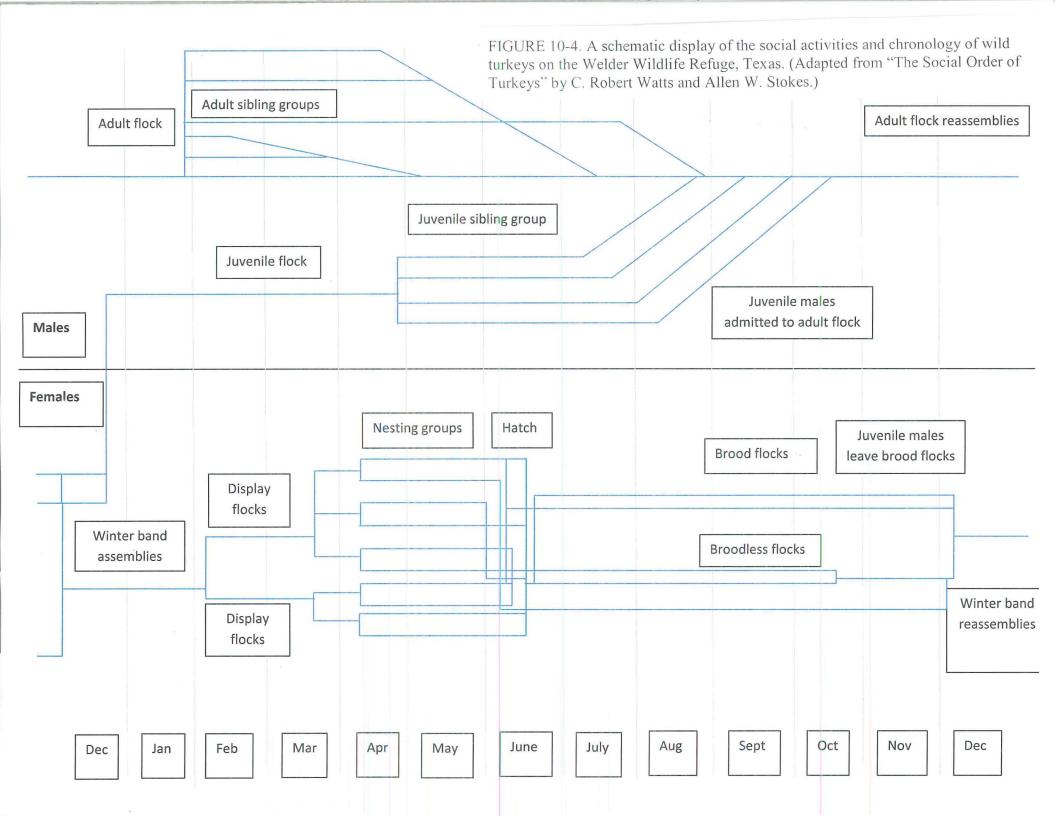


TABLE 10-3 YEARLY AVERAGE HATCHING DATES IN WISCONSIN—STATEWIDE AND GREEN AND MILWAUKEE COUNTIES

Year	Statewide			Green Co.			Milwaukee Co.			Weighted Avg.	
	June Avg.	No. Broods	Std. Err. (days)	June Avg.	No. Broods	Std. Err. (days)	June Avg.	No. Broods	Std. Err. (days)	June Avg.	No. Broods
1947	21	43	3.2	-		The mile	23	53	4.0	22	96
1948	18	60	2.4	17	56	1.6	18	78	1.6	18	194
1949	16	218	1.2	16	148	1.4	18	147	1.1	17	513
1950	21	166	1.1	24	147	1.3	24	148	1.2	23	461
1951	16	157	1.4	23	102	1.3	22	17	2.0	18	276
1952	15	238	1.0	13	112	1.3	17	60	1.8	15	410
1953	15	378	0.8	13	94	1.5	14	71	1.9	15	543
1954	20	306	0.9	21	77	1.8	21	48	1.1	20	431
1955	12	338	0.5	12	52	1.7	21	23	2.5	13	413
1956	21	261	1.0	18	29	3.1	26	8	6.2	21	298
Un-											
weighted	June		June				June			June	
mean	18			17			20			18	

SOURCE: Wagner, Besadny, and Kabat 1965.

Turkey (1967), with additional information in basic books on avian physiology [e.g., Sturkie (1965)].

Chronologies for pheasants, with variation within the earliest and latest hatching dates reported, can be established from data in Table 10-3 for Wisconsin (Wagner, Besadny, and Kabat 1965). The authors provide additional data on the observed "week of peak hatch," so variation of the data in Table 10-3 could realistically simulate previously observed conditions. The mortality of chicks in a brood is shown in Figure 10-5; note the decline in the average brood size from birth through 16 weeks. The data in Figure 10-6 show the relationship between average brood size and week of hatch; broods hatched later are smaller. Further, changes in brood size vary according to the time of hatching (Figure 10-7). Broods hatched early are larger, but they also suffer a higher mortality rate through the age of 16 weeks.

The pheasant data shown in Table 10-3 and Figures 10-5—10-7 are nonlinear over time. The technique of using first approximations that are mathematically simple can be usefully employed here. For example, the effect of hatching dates in Table 10-3 on the ecology of pheasant populations should be analyzed from June 12 through June 24, the earliest and latest yearly averages reported. The data in Figure 10-5 can be expressed in either one or three linear regression equations, calculating the change in average brood size with age. The data in Figure 10-6 can be expressed with a single linear regression equation. Figure 10-7 can be expressed with three or more simple equations approximating the data.

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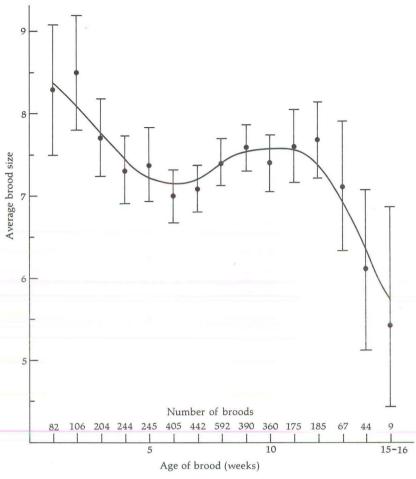


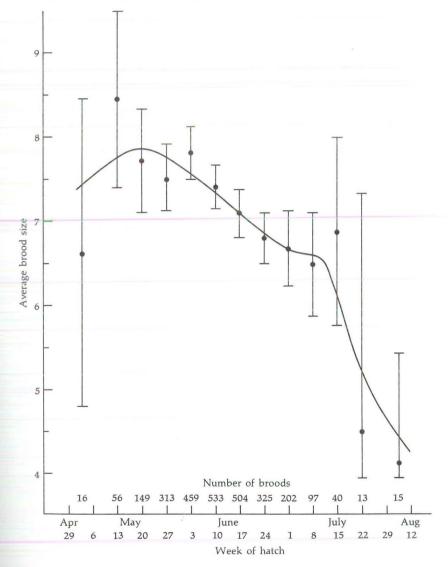
FIGURE 10-5. Relationship between brood age and brood size, 1946–56. The limits on each side of the mean represent twice the standard error of the mean. The line was drawn with three-point moving averages. (From Wagner, Besadny, and Kabat 1965.)

Once these first approximations are determined, they can be synthesized into a working model that begins with the onset of egg-laying, continuing through incubation and brood-rearing, with an analysis of brood mortality throughout the summer. After the techniques for relating these biological parameters in an ecological analysis have been worked out, the first approximations can be improved where necessary.

Many books containing life-history data of other species are available, including Taylor's The Deer of North America (1956), Allen's Pheasants in North America (1956), Mech's The Wolves of Isle Royal (1966), Errington's Muskrats and Marsh Management (1961), Peterson's North American Moose (1955), Jackson's Mammals of Wisconsin (1961), Palmer's Fieldbook of Natural History (1944), Leopold's Game Management

(1933), Jackson's *The Clever Coyote* (1951), Burrows's *Wild Fox* (1968), Stoddard's *Bobwhite Quail* (1931), Young's *The Bobcat of North America* (1958), Young's and Goldman's *The Puma, Mysterious American Cat* (1946), and many others. All of these are valuable in providing life-history information that can be expressed mathematically, including such things as reproductive phenology, growth rates, ingestion rates of different foods, activity regimes, and others.

FIGURE 10-6. Relationship between time of hatch and size of broods 4–10 weeks of age, 1946–56. The limits on each side of the mean represent twice the standard error of the mean. The line was drawn with three-point moving averages. (From Wagner, Besadny, and Kabat 1965.)



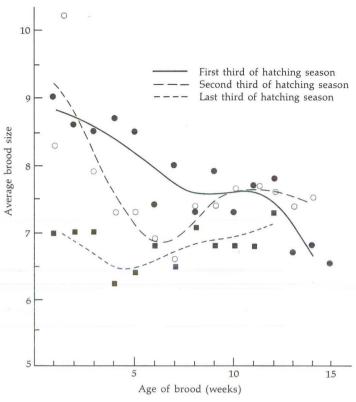


FIGURE 10-7. Week-by-week changes in sizes of broods hatched in the first, second, and last third of the hatching season. The graphs include data from all sources, 1946–56. The lines were fitted by the use of three-point moving averages. (From Wagner, Besadny, and Kabat 1965.)

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IDEAS FOR CONSIDERATION

Tabulate the life-history information about free-ranging animals in a chronological format, relating these biological functions to each other through time. Which factors are controlled internally, which are controlled externally, and how does variation in either or both of these sets affect the ecological productivity of the individual?

Prepare equations describing the cost of various activities and productive functions (see Chapter 16, for example), and calculate the specific "cost of living" throughout the animal cycle.

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