

## N-DIMENSIONAL POPULATION STRUCTURES

A population is a collection of organisms of the same species located within a prescribed area. This suggests that a population has the characteristics of *number* and *area*, from which the *density* or number per unit area can be calculated. This is a useful calculation for determining how many organisms are present at a point in time, and the number present at one time can be compared with the number present at another time. Since the numbers are usually not stable for any length of time, biologists and mathematicians may begin to calculate the rate of change and other characteristics of the change in numbers.

The analytical ecologist is interested in *cause and effect* relationships. Observed responses by organisms, both plant and animal, must be caused by something. These responses may range from mortality, at one extreme, to maximum productivity at the other. Within the productivity gradient there is room for an infinite number of combinations of responses, and these responses constitute the observed population dynamics through time.

The many possible observed responses are due to the many different characteristics of the members of a population. Some of these characteristics have been discussed in preceding chapters; variations in weight have been related to a number of different biological functions, for example. The significance of many of these variations between individual animals cannot be determined without a detailed "systems analysis" of the individual on one hand and of the individual in relation to its environment, including both physical and biological factors, on the other. Biological factors include internal, intraspecies, and interspecies relationships, implying that the variation associated with one individual may be a

function both of itself and of the entire community in which it lives. This community is a very complex entity that cannot be described analytically without an understanding of how its component parts function.

Various characteristics of a population will be examined in this chapter, with an indication of how they might be used in predicting population dynamics given in Chapter 19. Both of these chapters contain examples of the kinds of considerations that can be made, but without a full complement of considerations for the many different kinds of wild organisms that could be analyzed. Many of the characteristics of a population are based on data in a descriptive article by Taber and Dasmann (1957) on the dynamics of a mule-deer (*Odocoileus hemionus columbianus*) population in shrubland habitat in California (Table 18-1). Students are urged to apply the same principles to species in which they are interested in their own localities.

### 18-1 SEX AND AGE RATIOS

The sex ratio is the expression of the number of males in relation to the number of females present. Sex-ratio data from Taber and Dasmann for a mule-deer population inhabiting 100 square miles of shrubland are shown in Table 18-2. The unbalanced ratio in favor of females is in part a result of selective hunting of the male deer; this is reflected in the drop from 66 to 47 males per 100 females between July and December.

Expressing sex ratios without considering age ratios results in a masking of certain factors since different age classes respond differently to mortality factors. There were more male fawns born than female fawns (Table 18-3), but differential mortality apparently resulted in a reversal of that balance by December, inasmuch as there were fewer male than female fawns at that time. The ratio of male to female deer dropped further in the one-year age group, and then dropped drastically in the two-year age group after the hunting season.

The cost of life is related to the weight of an organism. The productivity of an organism is dependent on the ability of that organism to meet the cost of life

**TABLE 18-1** DYNAMICS OF A DEER POPULATION INHABITING 100 SQUARE MILES OF SHRUBLAND IN CALIFORNIA

Season	Males				Females				Total
	3+ yr	2 yr	1 yr	Fawns	3+ yr	2 yr	1 yr	Fawns	
Late May (fawn-drop)	616	482	556	2042	1935	706	858	1810	9005
July herd-composition count	616	482	556	1692	1906	706	858	1586	8402
December herd-composition count	467	182	536	836	1791	669	838	1039	6358

SOURCE: Data from Taber and Dasmann 1957.

**TABLE 18-2** SEX RATIOS OF A MULE-DEER POPULATION IN CALIFORNIA

<i>Season</i>	<i>Males</i>	<i>Females</i>	<i>Males per 100 Females</i>
Late May	3696	5309	70
July	3346	5056	66
December	2021	4337	47

SOURCE: Calculated from data in Taber and Dasmann 1957.

both for itself and for its offspring. Thus it is logical to calculate the weight of deer in different age groups to determine the cost of life for each age group as a whole and on a per animal basis.

The weights of mule deer in the California shrubland population are shown in Table 18-4, calculated using an equation from Wood, Cowan, and Nordan (1962; see Figure 9-8). This procedure results in only an approximation of the weight, of course, but it illustrates the effect of analyzing a population by weight rather than by number. The average weights of 1- to 4+-year-old males increased from late May to July to December, but the total weight of the male portion of the

**TABLE 18-3** SEX RATIOS FOR EACH AGE CLASS IN A MULE-DEER POPULATION IN CALIFORNIA

<i>Age</i>	<i>M</i>	<i>F</i>	<i>M/100F</i>
Late May			
3+	616	1935	32
2	482	706	68
1	556	858	65
Fawns	2042	1810	113
July			
3+	616	1906	32
2	482	706	68
1	556	858	65
Fawns	1692	1586	107
December			
3+	467	1791	26
2	182	669	27
1	536	838	64
Fawns	836	1039	80

SOURCE: Calculated from data in Taber and Dasmann 1957.

**TABLE 18-4** CONVERSION OF THE AGE STRUCTURE OF A MULE-DEER (*Odocoileus hemionus hemionus*) POPULATION TO A WEIGHT STRUCTURE

Season	Age Classes									
	Males					Females				
	4+	3	2	1	Fawns	3+	2	1	Fawns	Total
	NUMBER OF DEER AT DIFFERENT AGES*									
Late May (fawn drop)	434	182	482	556	2,042	1,935	706	858	1,810	9,005
July	434	182	482	556	1,692	1,906	706	858	1,586	8,402
December	350	117	182	536	836	1,791	669	838	1,039	6,358
	WEIGHT OF DEER IN EACH AGE CLASS*									
Late May										
Individual weights (lbs)	210	195	169	124	9	195	169	124	9	
Individual weights (kgs)	95	89	77	56	4	89	77	56	4	
Total weight (lbs)	91,140	35,490	81,458	68,944	18,378	377,325	119,314	106,392	16,290	914,731
Total weight (kgs)	41,230	16,198	37,114	31,692	8,168	172,215	54,362	48,048	7,240	416,267
July										
Individual weights (lbs)	244	207	200	154	20	198	174	132	20	
Individual weights (kgs)	111	94	91	70	9	90	79	60	9	
Total weight (lbs)	105,896	37,674	96,400	85,624	33,840	377,388	122,844	113,256	31,720	1,004,642
Total weight (kgs)	48,174	17,108	43,862	38,920	15,228	171,540	55,774	51,480	14,274	456,360
December										
Individual weights (lbs)	271	255	233	191	92	205	185	152	92	
Individual weights (kgs)	123	116	106	87	42	93	84	69	42	
Total weight (lbs)	94,850	29,835	42,406	102,376	76,912	367,155	123,765	127,376	95,588	1,060,263
Total weight (kgs)	43,050	13,572	19,292	46,632	35,112	166,563	56,196	57,822	43,638	481,877

SOURCE: Age data from Taber and Dasmann 1957.

\*Male weights calculated by using an equation from Wood, Cowan, and Nordan 1962; female weights calculated with their equation for minimum male weights.

population decreased because of a loss of number. The females increased slightly in average weight and decreased slightly in total weight. The fawns increased the most in weight (from 4 to 42 kg) but decreased about 60% in number. Numerically, the fawn portion of the population went down, but the amount of animal tissue in deer fawns increased over four times for males and six times for females.

All of the animal tissue in the population, including both adults and young, is supported metabolically in a nonlinear fashion in relation to weight. A unit weight of larger adult deer can be supported at less cost to the range than a unit weight of smaller deer. This was discussed in Chapter 17 in relation to carrying capacity. Using the fractional exponent 0.75, the metabolic weights are shown in Table 18-5. Multiplication of the metabolic weight by 70 gives the energetic cost of life under basal conditions, with the ratios expressing this cost showing an increase in efficiency with increases in body weight.

Free-ranging animals do not live at a basal rate, but rather at an "ecological metabolic rate" that is a reflection of the maintenance and production factors present at a given point in time. Thus it is necessary to calculate the cost of the biological functions specific to each group of animals in order to come up with a total energy cost. The total energy cost can be expressed as a multiple of BMR by dividing the total by  $(70)W_{\text{kg}}^{0.75}$ .

**TABLE 18-5** AVERAGE WEIGHT, AVERAGE METABOLIC WEIGHT, AND BASAL METABOLISM OF A MULE-DEER POPULATION

Age	Males			Females		
	$W_{\text{kg}}$	$W_{\text{kg}}^{0.75}$	$\text{BMR day}^{-1}$	$W_{\text{kg}}$	$W_{\text{kg}}^{0.75}$	$\text{BMR day}^{-1}$
Late May						
4+	95	30.4	2128			
3	89	29.0	2030	89	29.0	2030
2	77	26.0	1820	77	26.0	1820
1	56	20.5	1433	56	20.5	1433
Fawns	4	2.8	196	4	2.8	196
July						
4+	111	34.2	2394			
3	94	30.2	2114	90	29.2	2044
2	91	29.5	2065	79	26.5	1855
1	70	24.2	1694	60	21.6	1512
Fawns	9	5.2	364	9	5.2	364
December						
4+	123	36.9	2583			
3	116	35.3	2471	93	29.9	2093
2	106	33.0	2310	84	27.7	1939
1	87	28.5	1995	69	23.9	1673
Fawns	42	16.5	1155	42	16.5	1155

**TABLE 18-6** THE ENERGY COST OF LACTATING ADULTS AND YEARLINGS IN JULY

	<i>Adults</i>	<i>Yearlings</i>
Number	2612	858
Average weight (kg)	87	57
Number with 2 fawns	1698	0
Number with 1 fawn	914	858
Energy cost per doe with 2 fawns*	4586 kcal day <sup>-1</sup>	—
Energy cost per doe with 1 fawn†	3709 kcal day <sup>-1</sup>	2701 kcal day <sup>-1</sup>
Energy cost for does with 2 fawns	7,787,028 kcal day <sup>-1</sup>	—
Energy cost for does with 1 fawn	3,390,026 kcal day <sup>-1</sup>	2,317,458 kcal day <sup>-1</sup>
Total	11,177,054 kcal day <sup>-1</sup>	2,317,458 kcal day <sup>-1</sup>
Average cost per deer	4279 kcal day <sup>-1</sup>	2701 kcal day <sup>-1</sup>

Note: Reproductive rate is 1.65 fawns per adult doe and 1.00 fawns per yearling doe.  
\*  $Q_r = (2.30)(70)W_{kg}^{0.75}$   
†  $Q_r = (1.86)(70)W_{kg}^{0.75}$

Estimates of the cost of homeothermy were discussed in Part 5, and of growth, activity, gestation, and milk production for deer earlier in Part 6. The cost of activity ranged from 1.23 to 1.98 × BMR for several different activity regimes. The cost of activity for a 60-kg deer was 1.42 × BMR in one case (see Figure 16-12), increasing to 1.86 at the peak of lactation with one fawn and to 2.30 with two fawns. Applying these data to an analysis of the energy cost of a female population results in the costs shown in Table 18-6. The cost of lactation in different age classes includes consideration of the reproductive rates of yearlings and adults. Taber and Dasmann state that the former produce about 1.0 fawns per year and the latter 1.65.

Another population dimension that varies between geographical areas and between ages of deer is the conception date. The data in Figure 18-1 show that more adult deer breed at an earlier date in the northern part of New York than in the southern part. Conception normally occurs the second week of November in the northern part, and the third week of November in the southern part of the state. Thus the high energy and protein costs at the termination of pregnancy would be expected about a week earlier for the deer in the northern part, but wintery weather conditions are likely to be present a week or two longer there. This essentially alters the pregnancy-period-winter-period relationship by two to three weeks and may have significance in terms of productivity. Further, the earlier fawns in the northern part have a greater chance of being born in cold, wet weather. The effects of wet weather may be greater than those of cold; data are lacking on the survival of fawns in the wild that are exposed to different weather conditions, but data on sheep show that wet weather can cause higher mortality.

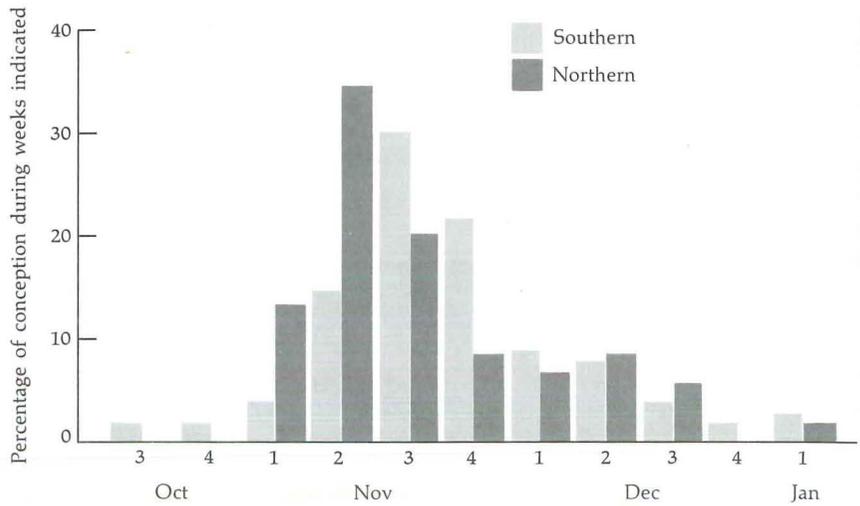
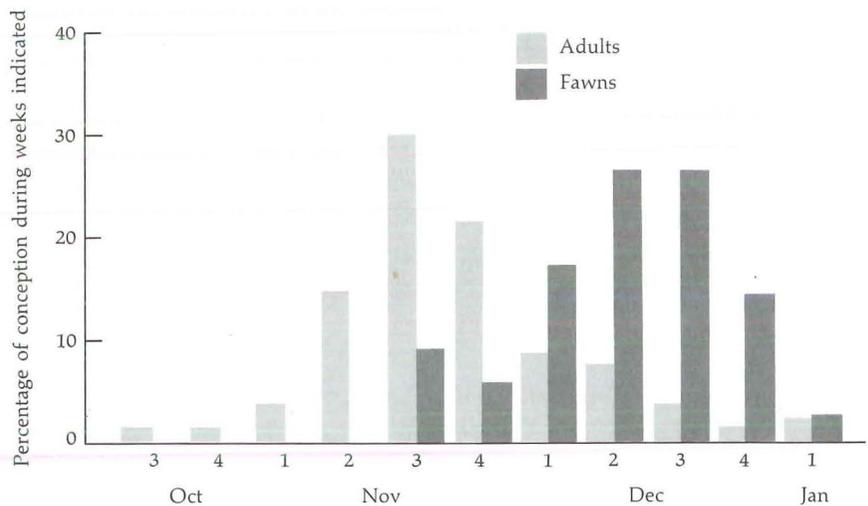


FIGURE 18-1. Weeks of conception for adult whitetails in the northern and southern part of New York State. (Data from Cheatum and Morton 1946.)

Differences in the breeding dates of white-tailed adults and fawns (Figure 18-2) are of interest in terms of productivity because the fawn bred in the middle of December will drop a fawn during the first week in July. If the second fawn were 3 kg at birth and gained 0.2 kg day<sup>-1</sup>, it would weigh 6 kg (13 pounds) less than the first fawn in the fall if growth rates of both fawns were equal. Given these assumptions, the predicted weights on November 15 would be about 65 pounds for the offspring of a late-bred fawn, and 78 pounds for the offspring of the earlier bred adult. The critical weight necessary for fawn breeding to occur in western New York seems to be about 65 pounds (Hesselton, personal communication)

FIGURE 18-2. Weeks of conception for white-tailed adults and fawns in the southern part of New York State. (Data from Cheatum and Morton 1946.)



so the fawns born later might consistently be in a precarious balance between breeding and nonbreeding. These are oversimplifications of the real situation, of course, but they do illustrate the possible role of these dimensions in the productivity of particular members of a deer herd.

They also raise the question of compensatory growth. Assuming equal birth weight and growth rates, the distribution of fawn weights would be identical to the distribution of conception dates. Since there is variability in both birth weight and growth rate owing to range quality and other factors, it is logical to consider whether that variability has a beneficial effect consistently or if it is more or less random.

The variability of birth date in relation to conception date may be compensated for by the physiological stage of development at birth. White-tailed fawns born earlier than expected at the BioThermal Laboratory are less developed physiologically; they are "premies" and it takes one to two weeks for them to develop to the same point at which a later-born fawn might be at birth. These considerations are discussed further in Chapter 19.

## 18-2 PARASITISM

The dynamic relationships between parasite and host have not been analyzed as a system except in a few instances such as the work of Whitlock et al., which was discussed in earlier chapters. There are several basic relationships between parasite and host populations that can be expressed, however, at least in dimensionless form.

The number of parasites present in a host is partially dependent on age (Figure 18-3). Newborn animals are not infected, but as time passes the number of parasites increases up to a maximum. The shape of the parasite-number curve is very likely that of the typical sigmoid-growth curve.

The number of parasites present may not be strictly related to the effect of the parasites. The effect might be suspected to be greater on young adults that have

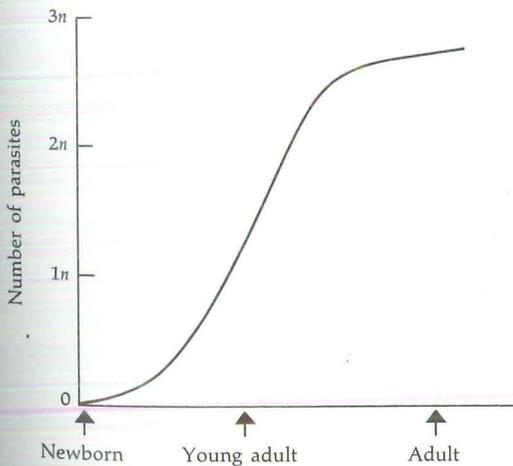


FIGURE 18-3. Nondimensional display of the relationship between the number of parasites and the age of the host.

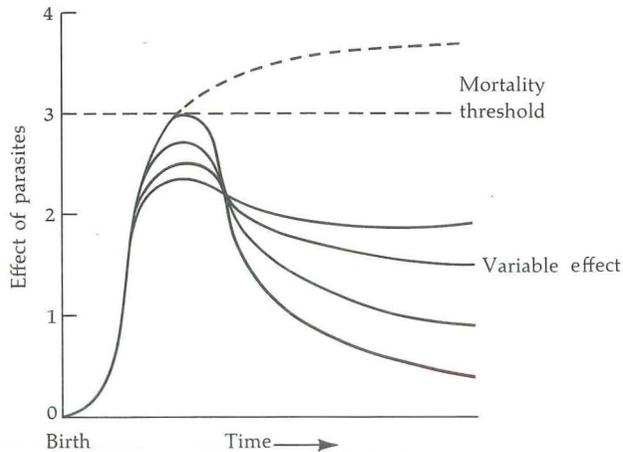


FIGURE 18-4. Nondimensional display of the relationship between the effect of parasites and the age of the host.

not built up a physiological resistance to the parasite(s) than on older adults that have reached a kind of equilibrium between parasite and host (Figure 18-4). The effect of parasite productivity is difficult to measure because of its subtle characteristics, as well as its interaction with other factors, such as nutrition, weather, and intraspecific relationships due to density-related factors, and the temporal physiological rhythms of the host itself. Somewhere within the effect of variables on productivity a "normal" physiological load due to parasites might be recognized since they are a part of the life of every animal, except those raised in sterile environments.

### 18-3 GEOMETRY AND POSTURE

The geometric characteristics of animals in a population affect the animals' relationships to certain physical factors in the habitat. The depth of snow, for example, is important in determining its effectiveness as a barrier to travel. The heights of the bellies of deer of different weights are given in Figure 18-5.

The energy cost of traveling through snow of different depths is very likely not linearly related to snow depths. There may be little effect from snow depths up to about two-thirds of the length of the legs. However, the energy cost increases in snow depths that equal the length of the legs, and it increases sharply if the belly is resting on the snow, forcing the deer to leap from one spot to another. The energy cost varies for different types of locomotion and for different snow characteristics. Loose fluffy snow is less a barrier than more dense snow, and a hard wind-pack may support the weight of the deer, presenting no barrier. Very deep, soft snow may be almost a complete barrier. One of the most costly combinations may be that of a running deer on a snow pack that supports the animal's weight only part of the time. If such a situation exists, dogs can become a problem in some areas.

Another geometric factor of possible importance in a population is the height

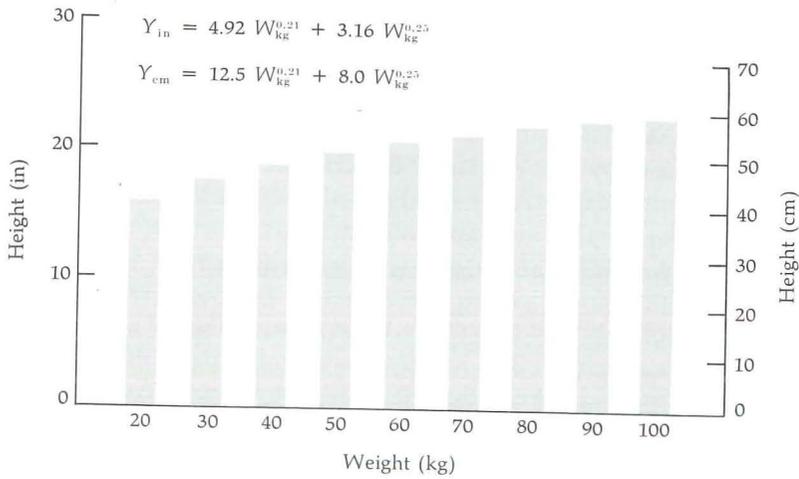
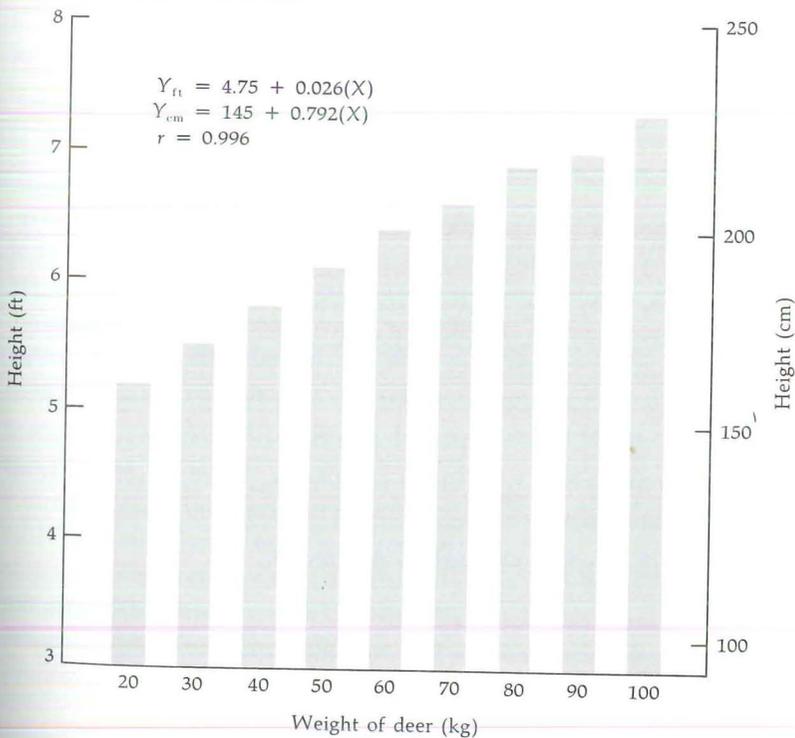


FIGURE 18-5. The height of the bellies of white-tailed deer in relation to deer weight.

to which a deer can reach. This may be especially critical in areas in which overbrowsing has occurred, since a large deer may be able to reach a supply of food that is unavailable to smaller deer. The estimated heights reached by deer of different weights are shown in Figure 18-6, calculated from data used in determining the relationships between surface area and weight that were discussed in Chapter 13. These geometric considerations have an effect on the deer's ability

FIGURE 18-6. The height of forage that white-tailed deer can reach while standing on their hind legs.



to select and ingest forage. This is important in determining how well the requirements for protein and energy are met by ingestion and how much of these requirements must be met by urea recycling, mobilization of the fat reserve, and other physiological compensations during depressed nutritive conditions.

#### 18-4 POPULATION REQUIREMENTS FOR PROTEIN

The protein requirement of a herd of animals is the sum of the protein requirements of individuals in the herd. The average requirement per animal can be determined as a weighted mean. An arithmetic mean is not appropriate since the total protein requirement is nonlinear in relation to weight. The time dimension must also be considered, since the rate of gain changes, females are pregnant or lactating for a part of the year, males have seasonal changes in activity, and so forth. Further, the total requirements change as the weight structure of the population changes.

The mean-protein requirement of a population can be determined for a given time by multiplying the sum of the protein requirements for specific body functions (see Table 16-7) by the percentage of the population in each weight class under consideration. This can be illustrated by equation (18-1).

$$Q_p = [(Q_{pw1})(\%W_1) + (Q_{pw2})(\%W_2) + \cdots (Q_{pwn})(\%W_n)]/100 \quad (18-1)$$

where

$$\begin{aligned} Q_p &= \text{mean protein requirement} \\ Q_{pw1,2,\dots,n} &= \text{protein requirement for each weight class} \\ \%W_{1,2,\dots,n} &= \text{percentage of animals in each weight class} \end{aligned}$$

The number of combinations of conditions is large because activity, weight gains, pregnancy, and lactation can all vary.

#### 18-5 POPULATION REQUIREMENTS FOR ENERGY

The energy requirement of a herd of animals is the sum of the energy requirements of the individuals in the herd. As with protein, the mean requirement of each individual is not a simple arithmetic mean, since energy requirements are nonlinear with respect to weight. The effects of growth, pregnancy, and lactation on the total energy requirement must also be considered. The average energy requirement of individuals in a population can be calculated by using equation (18-2). Each  $Q_e$  is the sum of the energy costs listed in Table 16-11.

$$Q_e = [(Q_{ew1})(\%W_1) + (Q_{ew2})(\%W_2) + \cdots (Q_{ewn})(\%W_n)]/100 \quad (18-2)$$

#### 18-6 OTHER POPULATION DIMENSIONS

The population characteristics mentioned thus far in this chapter illustrate the kinds of considerations that can be made in dividing a population into functional biological groups. Many others have been mentioned in earlier chapters without

expressing them directly as population characteristics. All of the dependent relationships in which weight was shown as an independent variable are population dimensions whose distributions are dependent on the weight distribution within a deer population. Many thermal factors were shown in relation to weight, and several nutritive considerations were also shown to be related to weight.

Many of these characteristics are very subtle. The bedding posture of a deer or the amount of head extension of a grouse are both difficult to detect in the field, yet both can be demonstrated to be heat-conservation responses that may be important if the animal is in a critical thermal environment. On the other hand, some members of a population may employ these heat-conservation responses although other members may not need to, resulting in no differences among the animals because of their capabilities to compensate. These examples illustrate that populations have internal labile characteristics that may not appear to be of consequence except in analyses of factors affecting productivity.

Whenever one of these parameters has a negative effect on productivity, another factor (or more) has to compensate or else there will, in fact, be a reduction in productivity. Thus the different age classes in a population are in a constant state of change inasmuch as factors and forces affect biological functions in both negative and positive ways.

Population ecologists have recognized the effects of the existence of many of these factors. Chapman, Henny, and Wight (1969) discuss the vulnerability of Canada geese to hunting in relation to age, sex, harvest areas, time periods, and all-day hunting. They also discuss mortality in relation to age, sex, and hunting regulations. These are valuable considerations, but the potential for population growth lies not so much with the number and characteristics of animals removed from a population as it does with the productivity of the remaining members. Wildlife biologists have been saying this for some time. Hunting is not as important as hatching and rearing in determining a fall population of game birds, for example; but there has been a dearth of information on the real, fundamental causes of high production, with too much emphasis on the causes of mortality and on the characteristics of the dead.

One reason for the lack of information and understanding of factors affecting productivity is that many biological investigations are short-term and limited in scope—too short and too small to observe changes over many generations. There are exceptions, such as the ruffed-grouse project at the Cloquet Forest in Minnesota, under the direction of Dr. W. H. Marshall, University of Minnesota. Gullion (1970) discusses the factors influencing grouse populations there, pointing out that although predation is the ultimate fate of more than 80% of the grouse in the Cloquet Forest, it is seldom a limiting factor per se. This indicates the  $n$ -dimensional characteristics of the population, and he concludes that “. . . periodic fluctuations are not so much the result of any ‘die-off’ or accelerated losses among living grouse as they are the failure to recruit young grouse [i.e., productivity] each season to replace birds lost through ‘normal’ attrition.” He also suggests that annual reproductive success has been largely determined before nesting begins, indicating that it is the physiological condition of the bird prior

to nesting that determines its productivity and, subsequently, the current season's production. He also points out that the red-phase grouse do not live as long as the grey-phase, especially in unfavorable snow conditions. The color itself may be of some importance in predation, but Gullion suggests that data for the entire continent indicate that the red phase may be less tolerant to cold than the grey phase. He also discusses nutritive factors and social behavior, both of which affect productivity.

The roles of the many population dimensions that might be considered are difficult to identify, but they can be conceptualized, given the right philosophical approach to the prediction of population dynamics. Some suggestions are discussed in Chapter 19.

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#### IDEAS FOR CONSIDERATION

Examine the characteristics of individual members of different populations, identifying as many differences as possible. Then relate these different characteristics to productivity, predicting the production of each individual based on its own characteristics and its relationship to other members of the population. This can be done from the literature and in the field.

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