Population Regulation

I. The effects of density-dependent factors may regulate populations
   A. The logistic equation has been applied successfully to describe the growth of populations in the laboratory and in some natural habitats. It suggests that factors limiting growth exert stronger effects on mortality and fecundity as a population grows.
   B. What are these factors, and how do they operate?
      1. Many things influence rates of population growth, but only density-dependent factors, whose effects increase with crowding, are thought to be able to regulate the size of a population.
      2. Of prime importance among these factors are limitations on food supply and places to live, as well as predators, parasites, and diseases whose effects are felt more strongly in large than in small populations (Figure 1).

![Figure 1. Basic features of population regulation by density-dependence factors.](image)

3. Other factors, such as temperature, precipitation, and catastrophic events, alter birth and death rates largely without regard to the number of individuals in a population. Such density-independent factors may
influence the exponential growth of a population, but they generally do not regulate the size that the population will attain in the environment.

C. Examples of density-dependence in animals.

1. Density dependence in the Mandarte Island song sparrow (*Melospiza melodia*) population (Figure 1; Smith et al. 1991).

Figure 1. The Mandarte Island song sparrow.

Figure 2. Mandarte Island, British Columbia.
a. Mandarte Island is a rocky, 6-ha island off the coast of British Columbia (Figure 2).
b. The island is home to a population of song sparrows that has been studied for many decades.
c. On average, only 1 new female migrant joins this population each year (i.e., immigration is minimal), so most of the changes in population size are due to local births and deaths.
d. Over a 30 year period of time, the population has varied between 4 and 72 breeding females and between 9 and 100 breeding males.
   1) The sparrow population of Mandarte Island does not conform to a simple logistic growth model; population size is variable and there have been periods of increase followed by rapid declines (Figure 3).
   2) An unusually cold winter and an increased death rate caused some of these population changes, such as the crash beginning in 1985.

[Graph showing population size of the song sparrow on Mandarte Island]

3) Other declines were not correlated with any obvious change in the environment.
4) Although this population is clearly buffeted by density-independent changes, there is good evidence of underlying density dependence (Figure 3).
   a) Male song sparrows defend territories that determine their breeding success, but limited food resources and space prevent many males from ever establishing territories.
   b) These nonterritorial “floaters” are behaviorally submissive individuals.
   c) Their proportion increased in a density-dependent fashion as the population became more crowded (Figure 4a).
   d) When the resident territory holders were experimentally removed, floater males quickly took over their territories, so the total breeding population size remained relatively constant.

5) Density dependence is also seen in the number of surviving young produced/female, and in the survival of juveniles, both of which decreased as the population size increased (Figure 4b,c).

6) Experimental studies confirmed that food limitation was the controlling factor: when food levels for sparrows were artificially enhanced, female reproductive output increased 4-fold (Arcese and Smith 1988).

7) Thus, both territoriality and food limitation generated density-dependent birth and death rates in song sparrows.

2. Density dependence in the fecundity of white-tailed deer (*Odocoileus virginianus*) as a function of food quality.
   a. The reproduction and survival of deer depend directly on the quality of their food.
   b. Deer browse herbaceous vegetation, and they require large quantities of new growth with high nutritional content to maintain high growth rates and normal reproduction.
   c. In white-tailed deer in New York, the proportion of females pregnant and the mean number of embryos/pregnant female were found to be directly related to range conditions (Table 1).
   d. The number of corpora lutea and number of embryos seem to indicate poor range conditions, which resulted in poor nutrition of pregnant females and embryo death and resorption.
e. In the central Adirondack area, where habitat for deer was very poor even ovulation was greatly reduced.

f. Selective hunting to thin dense populations can often reverse range deterioration caused by overgrazing.

g. When DeBar Mountain, an area of very poor range, was opened to hunting, the population of white-tailed deer decreased, range quality recovered, and reproduction improved dramatically (Table 2).
Figure 4. Density dependence in the Mandarte Island song sparrow population. As the population becomes crowded (a) the proportion of nonterritorial “floater” males increases; (b) the number of surviving young produced per female decreases; (c) juvenile survival decreases. Data from Arcese and Smith 1988 and Smith et al. 1991.

Table 1. Reproductive parameters of white-tailed deer in 5 regions of New York State, 1939-1949. From Chaetum and Severinghaus (1950).

<table>
<thead>
<tr>
<th>Region</th>
<th>Percentage of females pregnant</th>
<th>Embryos per female</th>
<th>Corpora lutea per ovary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western (good range)</td>
<td>94</td>
<td>1.71</td>
<td>1.97</td>
</tr>
<tr>
<td>Catskill periphery</td>
<td>92</td>
<td>1.48</td>
<td>1.72</td>
</tr>
<tr>
<td>Catskill central</td>
<td>87</td>
<td>1.37</td>
<td>1.72</td>
</tr>
<tr>
<td>Adirondack periphery</td>
<td>86</td>
<td>1.29</td>
<td>1.71</td>
</tr>
<tr>
<td>Adirondack center (bad range)</td>
<td>79</td>
<td>1.06</td>
<td>1.11</td>
</tr>
</tbody>
</table>

1Arranged by decreasing suitability of range.

Table 2. Reproductive parameters of white-tailed deer in the Debar Mountain area of the Adirondack Mountains of New York State before hunting and after hunting. From Chaetum and Severinghaus (1950).

<table>
<thead>
<tr>
<th></th>
<th>Percentage of females pregnant</th>
<th>Embryos per female</th>
<th>Corpora lutea per ovary</th>
</tr>
</thead>
<tbody>
<tr>
<td>1939-1943 (prehunting)</td>
<td>57</td>
<td>0.71</td>
<td>0.60</td>
</tr>
<tr>
<td>1947 (after heavy hunting)</td>
<td>100</td>
<td>1.78</td>
<td>1.86</td>
</tr>
</tbody>
</table>

II. Summary
   A. Density-dependent factors tend to bring populations to $K$, which is set by the availability of resources and conditions in the environment.
   B. Changes in these conditions and resources continually establish new equilibrium values toward which populations grow or decline.
   C. Furthermore, catastrophic changes in the environment brought about by a sudden freeze, a violent storm, or a shift in an ocean current often reduce
populations far below their carrying capacities and initiate periods of population recovery.
D. Although density-dependent factors seem to be able to regulate population size, variations in the environment also cause populations to fluctuate about their equilibrium sizes.