



## Can the Population Regulation Controversy Be Buried and Forgotten?

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## Can the population regulation controversy be buried and forgotten?

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For more than half a century ecologists have been debating whether a population's size, numbers, and density were determined or not determined by density-dependent regulatory processes. The lack of consensus among ecologists and the apparent lack of progress in this important field are a result of inexplicitly stated (and, therefore, falsifiable) hypotheses, a preponderance of ad hoc hypotheses (also falsifiable), an apparent lack of rigorous debate among disputants supporting alternative hypotheses, and a shortage of relevant data.

Wolda (1995) suggests that the "regulation versus non-regulation controversy [of the past 60 years] should be quietly buried and quickly forgotten" because "No one has been able to prove beyond doubt that one side or the other was right and the other wrong", because "there is no absolute well-definable difference between regulated and non-regulated populations", and because "Continuing the debate on regulation is futile and is not leading anywhere". Wolda (1995) suggests further that the "question to be asked, then, should no longer be 'is this population regulated or not', but 'how much is this population regulated', 'how strong are the regulatory versus the disruptive forces in this population'".

I doubt that the debate regarding the significance of density-dependent and density-independent processes in population dynamics is going to go away because I think that Wolda is wrong regarding the reasons for ecologists' failing to reach some kind of consensus on the problem. I also think that he is asking the wrong questions. The first question to be asked of and answered by the proponents of the "density-dependent regulation hypothesis" (DDRH) is, What is the DDRH? Seemingly, there is no one answer (Murray 1994), and without an explicit statement, we cannot be sure that disputants are discussing the same hypothesis.

Let us begin, then, with, What is the DDRH?

(1) Classically (e.g., Nicholson 1933, 1954, 1958, 1959, Lack 1954, 1966, Solomon 1958a, b, Andrewartha 1958, 1959, Huffaker et al. 1984), the DDRH involved the idea that a population's numbers are regulated by one or more factors that act as negative-feedback loops on the population's growth rate. The regulating factors, such as predation, disease, or competition for food and other resources, act linearly or curvilinearly on birth and death rates throughout (most of) the range of a population's density (Fig. 1). If this is the hypothesis, then I think it can be refuted by pointing out that at low densities, often, birth rates decrease and death rates increase with decreasing density, the so-called Allee effect.

(2) Some ecologists, such as Lack (1966) and Royama (1977, 1992), proposed that the idea of density dependence was a priori true – no empirical evidence was necessary. As Lack (1966): 291 put it, "the absence of field evidence does not, and will not, make the advocates of density-dependent regulation change their minds ... because, given certain assumptions about the persistence of natural populations, the existence of density-dependent regulation becomes a logical necessity". Royama (1977): 33 wrote, "The concept of density-de-

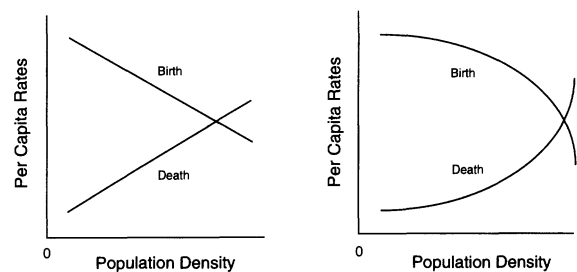


Fig. 1. Linear (left) and curvilinear (right) relationships between birth and death rates and population density, which characterize density-dependent regulation hypotheses.

pendent regulation ... is derived through pure logical deduction from one major premise, namely the persistence of populations in the wide sense. It is knowledge obtained a priori. There is no need to test its validity against observations ...” Berryman (1991): 142) agrees: “Royama (1977) has argued convincingly that tests for density-dependence are unnecessary”. The idea, I guess, is that a population grows when its birth rate is greater than its death rate and can stop growing only when its birth rate decreases, its death rate increases, or both change with increasing density (presumably by density-dependent negative feedback loops) such that the death rate eventually exceeds the birth rate. According to Lack, Royama, Berryman, and others, the DDRH is the *only* possible logical explanation for the persistence of populations.

A priori hypotheses, however, are not necessarily true. I agree with Feynman (1995), who stated that a fundamental hypothesis of science is that “the sole test of the validity of any idea [i.e., hypothesis] is experiment”, an interpretation that is consistent with at least some philosophers of science (e.g., Popper 1968, 1979). Is it conceivably possible for a population’s birth rate to decline and its death rate to increase with increasing density in the absence of density-dependent regulatory processes? I think so (see below).

(3) For some ecologists, the DDRH is descriptive rather than explanatory. For example, Turchin (1995): 22, his italics) suggests that, “The best way to define population regulation (and regulation in any dynamic system) is to equate it with the presence of a *long-term stationary probability distribution of population densities*”. The size of regulated populations fluctuates within bounds, whereas fluctuations in unregulated populations are unbounded (Murdoch 1994). The only requirement now for the demonstration of “density-dependence” seems to be the long-term persistence of a population. Accordingly, inasmuch as all extant populations are fluctuating within bounds in the long term, all populations must exhibit density-dependence, and persistence implies the existence of density-dependent regulation.

Turchin (1995): 36) goes on to write that “we should not be carried away and claim universal applicability of regulation, since there are numerous counterexamples demonstrating that regulation does not always operate in all populations at all times”. Unfortunately, if a hypothesis is not universally applicable, it is not testable, in the sense that the hypothesis cannot be refuted (Popper 1968, 1979). The DDRH is applicable to those populations in which it works and is not applicable to those populations in which it does not work. Thus, the DDRH is testable in the sense that it can be *verified* by finding examples of populations that appear to be regulated. The DDRH, however, is not testable in the sense that it can be *falsified* (Popper 1968, 1979) because whenever contradictory evidence is

discovered, it can be dismissed on the grounds that “density-dependence” is simply not operating in that population at that time.

If the DDRH is applicable to one population but not to another, the ecologists’ explanation of population dynamics is logically tautologous, that is, it is a hypothesis in the form “*P* or not-*P*” (Sober 1984, 1993). The population dynamics hypothesis would be that a population’s numbers are regulated by density-dependent factors (*P*), or they are not regulated by density-dependent factors (not-*P*). This explanation of population dynamics is not testable (i.e., falsifiable) because it is logically tautologous.

(4) In recent years the search for density dependence has not been to identify the alleged density-dependent factors and processes that bring about the end of a population’s growth but to detect density dependence itself in a series of population counts over a period of time (e.g., Turchin 1990, Greenwood and Baillie 1991, Woiwod and Hanski 1992, Murdoch 1994). Apparently, the correlation between growth rate and population density is so obscure that it requires “healthy doses of mathematics” to find it (Turchin 1995), such as the mathematical methods proposed by, for example, Bulmer (1975), Slade (1977), Pollard et al. (1987), and Turchin and Taylor (1992). Woiwod and Hanski (1992) and Murdoch (1994) report finding evidence for density-dependence of this sort in long time-series of population counts. The difficulty in finding direct evidence for density dependence is rather surprising, considering that every ecologist (on either side of the argument) agrees that birth rates should decline and death rates increase with increasing density (the issue that divides ecologists is how these changes come about).

The question is (or should be), *Why* does the birth rate decrease and death rate increase with increasing density (at least at high densities)? The mere demonstration that these relationships exist does not answer this question (after all, these relationships are mathematical imperatives – they are a priori so; that they come about by density-dependent factors or processes, however, is not a priori so). Our problem is to understand how these changes in birth and death rates with changing density come about in a population. We need to know the specific interactions among animals, plants, and their environments that result in decreasing birth rates and increasing death rates with increasing density.

Without having an explicit answer to the question, What is the DDRH?, we cannot begin to attempt falsifying the DDRH. Any criticism of the DDRH can be deflected by asserting that the critic does not know what the DDRH is, or that the DDRH is not applicable in the studied population at the time it was studied. The supporters of the DDRH must do more than describe what a “regulated” population should look like. They must provide us with a description of the hypothetical processes by which a population’s numbers are kept from increasing indefinitely.

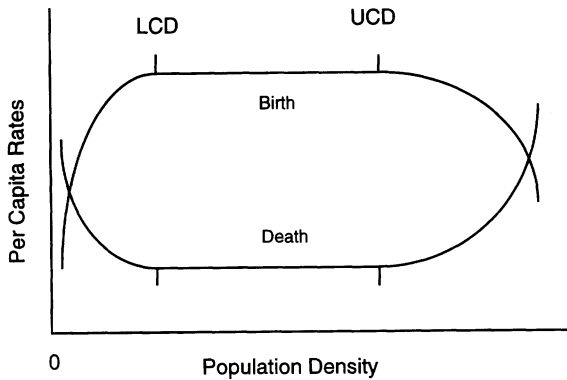


Fig. 2. Relationship between birth and death rates and population density, which characterize population limitation hypotheses.

### Population limitation hypothesis

The alternatives to density-dependent regulation hypotheses are population limitation hypotheses (PLH), not density-independent regulation hypotheses, as the proponents of DDRHs often mischaracterize them. For example, Turchin (1995): 29 suggests that proponents of density dependence have reached agreement regarding “the appropriate null model for density independence”. He continues, “Of the two possibilities, the unbiased random walk,  $f(N_{t-1}) = 0$ , is a special case of the stochastic growth/decline model  $f(N_{t-1}) = a$ . Both of these models are density independent, but the second one is more general and thus should be used as the explicit alternative to density dependence”. This explicit alternative to density dependence, however, bears no resemblance whatsoever to the population limitation hypotheses of, for example, Andrewartha and Birch (1954), Milne (1958, 1962), Reddingius (1971), den Boer (1968, 1991), Strong (1984, 1986), or me (Murray 1979, 1982, 1986). The “random walk” models showing the unboundedness of populations being regulated by density-independent factors are irrelevant to the discussion of population limitation hypotheses.

We may ask, then, What is the PLH? Like the DDRH, it is a collection of hypotheses, proposed by, among others, Andrewartha and Birch (1954), Milne (1958, 1962), Reddingius (1971), den Boer (1968, 1991), Strong (1984, 1986), and me (Murray 1979, 1982, 1986). Again, we need an explicit description of the relationship between a population’s growth rate and density and of the hypothetical processes by which a population’s numbers are kept from increasing indefinitely. A clear difference between the DDRH and the PLH is the relationship between birth and death rates and the population’s density, as illustrated in Fig. 1 (DDRH) and Fig. 2 (PLH). This difference should be easily testable empirically by those who have the data. Another difference between the two hypotheses is the processes by which a population’s size is prevented

from increasing indefinitely. In the DDRHs, presumably, density-dependent processes result in a density-dependent effect. In the PLHs, presumably, density-independent processes have a density-dependent effect (e.g., Andrewartha and Birch 1954). Let us now consider some density-independent processes that have the density-dependent effect of reducing the birth rate or increasing the death rate with increasing density.

I will present here only my version of the population limitation hypothesis (others may speak for themselves). As a biologist, I am more interested in describing the biological interaction of individual organisms with their environment than I am in fitting data to abstract mathematical models. In my descriptive model of population growth (Murray 1979, 1982, 1986), there is a range of densities between the lower critical density (LCD) and upper critical density (UCD) in which birth and death rates (and, thus, the growth rate) are essentially constant (Fig. 2). Below the LCD the birth rate may decrease, the death rate may increase, or both may occur with decreasing density. The LCD is the minimum density at which individuals may easily find mates or cooperatively protect themselves. The phenomenon is sometimes referred to as the Allee effect. The LCD, however, is not an essential feature of the model because the Allee effect may or may not occur.

We are interested in why populations stop growing. The essential part of the model is the UCD, which is the density above which, for example, per capita availability of resources declines, resulting in a decreasing birth rate, increasing death rate, or both. Thus, the relationships of birth, death, and growth rates with population density are quite different from those usually attributed to density dependence (compare Fig. 1 with Fig. 2). The rationale is that the resource requirements of individuals are independent of the total amount of resource.

Suppose that each individual in a population requires 50 g per day of food, and that 10000 g per hectare are available each day. When the population size is 10, 50, or even 100 per hectare, each individual is able to obtain all the food necessary for surviving and breeding maximally. There is no competition among them for nutrient resources. At population sizes 10, 50, and 100 per hectare, the population’s per capita growth rate ( $r$ ) is at its maximum and is a constant. Competition does not begin until, let us say, the population numbers 150 per hectare (i.e., at 66.7 g of food per individual), when each individual must hunt longer or exert more energy in the search for food and, therefore, has less to invest in survival and reproduction. The population’s birth rate declines, and its death rate increases. The population continues to grow, the birth rate continues to decline, and the death rate continues to increase until the population stops growing when the death rate exceeds the birth rate.

Suppose instead that there are 20000 g per hectare of food available to this population every day. There is no competition until the population numbers 300 per hectare (i.e., at 66.7 g per individual). In this population the growth rate at population sizes 150, 200, and 250 per hectare is the same as it was at 10, 50, and 100 per hectare. Above 300 per hectare the growth rate begins to decline as a result of competition for food, as it did above 150 per hectare in the population living with a smaller amount of food.

About this population we could say that, above the UCD (the point at which not all individuals can obtain all the food necessary for maximum survival and reproduction), intraspecific competition for food reduces the rate of growth until the population stops growing. We could say that intraspecific competition was a density-dependent factor (*above the UCD*) limiting further growth of the population because it intensifies with density. Nevertheless, the final mean size of each population was determined by the amount of food available to it, not by density-dependent competition above the UCD, which occurred at different densities in these populations. Therefore, population size is limited by the amount of food available, whereas the process that stopped the population's growth was competition above the UCD. The competition, however, was independent of what is usually considered to be density (i.e., numbers per hectare). What matters is the density at which per capita resource availability decreases (the UCD).

Alternatively, one could imagine that as the population becomes larger it attracts predators, which increase the mortality rate. In this case, we have density-dependent predation above the UCD (the point at which the prey population becomes sufficiently common to attract predators), which affects the rate of population growth and may or may not limit a population's size (Murray 1986).

Instead, the individuals in a population could be territorial. If there is a minimum territory size, and if that size sequesters more than 50 g of food per day per individual living in that territory (for the animal in the above example), and if age-specific death rates and the fecundity of breeding females on territories are constants, the population nevertheless stops growing because the habitat can only sustain a maximum number of breeders with territories. When that number is filled (the UCD), the birth rate begins to decline and the death rate begins to increase, mainly because of the changing ratio of breeders to total population size and changing age structure (Murray 1979, 1982). In this case the size of the *breeding* population is determined by the territorial behavior of the animals or the number of breeding sites within an area and remains *unchanged* even as the population continues to increase (temporarily) with non-breeders and even as intraspecific competition for territories or breeding sites intensifies and

correlates with a decreasing birth rate and an increasing death rate (Murray 1979, 1982). Although the population maintains a constant population size (Murray 1979, 1982), I fail to see anything here that might be what Berryman (1989, 1991) would call a density-induced negative feedback loop.

The descriptions of population dynamics given here are only a sampling of many imaginable permutations (Murray 1986). In none of these examples is density dependence, in what seems to be its classical sense (Fig. 1), involved. As far as I can tell from my reading and discussions, classical density dependence does not recognize, much less discuss, the role of the UCD in population dynamics. Nevertheless, the DDRH, as a concept, is so vague that, despite the rather striking differences (compare Fig. 1 with Fig. 2), several reviewers of my population dynamics papers have claimed that my model is a DDRH.

I doubt that the complex interactions among individual organisms and their predators, pathogens, competitors, and physical environment can possibly be teased out by a simple (or even complex) statistical analysis of a time-series of population counts.

## Conclusion

The debate regarding the determination of population size is not going to disappear by fiat. It will be around as long as ecologists (1) do not write their hypotheses in explicit and testable (i.e., falsifiable) form, (2) practice a verificationist philosophy (accepting any hypothesis for which a single piece of supporting data can be discovered) rather than a falsificationist philosophy (rejecting hypotheses when a single piece of contrary data is found), and (3) continue to search for biological examples of ad hoc mathematical models rather than to write equations that are consistent with biological reality.

Feynman (quoted in Gleick 1993: 324, original emphasis) suggested that "whatever we are *allowed* to imagine in science must be *consistent with everything else we know...*". The problem with the density-dependent regulation hypothesis for me is that it seems *inconsistent* with almost everything else that I know.

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