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# A new equation relating population size and demographic parameters: some ecological implications

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A simple equation relates mean population size ($\overline{N}$), mean initial size of cohorts ($\overline{n}_0$), and life expectancy at birth ($\sum_0^\infty l_x$) in persisting populations that are fluctuating between upper and lower boundaries: $\overline{N} = \overline{n}_0 \sum_0^\infty l_x - \overline{n}_0$. This equation indicates that the study of differences in size between two populations, of global and local commonness and rarity, and of the limitations to population growth should focus on ecological factors affecting $\overline{n}_0$ and $\sum_0^\infty l_x$. The equation also has a potential practical application for those countries, such as China, interested in designing policies for limiting population growth.

## Introduction

Two fundamental equations of population dynamics are the exponential and the logistic. In the exponential equation, $N_t = N_0 e^{rt}$, $N_0$ is population size at time 0, $N_t$ is population size at time $t$, $r$ is the per capita rate of change in numbers, and $e$ is the base of the natural logarithms. With this equation, $N_t$ cannot be calculated without knowledge of $N_0$ and $r$, the latter itself being determined from two or more values of $N$ at different times (e.g., $t_1$, $t_2$, $t_3$, etc.). In the logistic equation, $\Delta N/\Delta t = N_t r_m[(K - N_t)/K]$, $\Delta N$ is the difference between $N_t$ and $N_{t+1}$, $K$ is the "carrying capacity of the environment" or the "equilibrium population size," and $r_m$ is the intrinsic rate of increase, that is, the maximum unimpeded growth rate. With this equation, $\Delta N$ cannot be calculated without knowledge of $N_t$, $K$, and $r_m$, the latter two parameters being fitted constants. Thus, population size ($N$) or change in population size ($\Delta N$) cannot be determined from parameters that are independent of population size itself.

In this paper, I present a simple equation relating mean population size ($\overline{N}$), mean number of eggs laid or young born in each cohort ($\overline{n}_0$), and mean life expectancy at birth ($\sum_0^\infty l_x$): $\overline{N} = \overline{n}_0 \sum_0^\infty l_x - \overline{n}_0$. This novel equation allows the calculation of mean population size from independently determined demographic parameters and has both theoretical and practical applications. The two parameters, $\overline{n}_0$ and $\sum_0^\infty l_x$, are rarely, if ever, calculated by ecologists, much less discussed in the ecological literature. Nevertheless, these may be useful in understanding the commonness, rarity, and dynamics of populations. After explaining the rationale of the equation, I provide some examples of how this equation could be used in the study of populations.

## Relationship between population size, survival, and reproduction

A census of a population of living individuals occurs on some date of interest within some area of interest to the counter. A census at time $t$ may be a simple count of the population ($N_t$), or it may be more elaborate, including counts of individuals by age and by sex, in which case,

$$N_t = \sum_{1}^{\infty} n_{m,x,t} + \sum_{1}^{\infty} n_{f,x,t}, \qquad (1)$$

where $n_{m,x,t}$ is the number of males and $n_{f,x,t}$ the number of females of age $x$ alive at time $t$. For ease in presenting the following equations, I have assumed a sex ratio at birth of 1.0 and no difference between males and females in survival. The equation may be rewritten to accommodate differences between the sexes should the need arise (*see* Eqs. 11 and 14).

Let us assume, for purpose of discussion, that populations comprise individuals that can be identified by age and by sex. If we first imagine an idealized population with a stable age distribution, that is, a population in which the proportion of individuals of each age class is constant in time, then the number of individuals ($n_{x,t}$) of a cohort surviving to age $x$ at time $t$ is,

$$n_{x,t} = n_{0,t-x}\, l_x, \qquad (2)$$

where $n_{0,t-x}$ is the number of eggs laid or young born in that cohort between time $t - x$ and time $t - x + 1$, and $l_x$ is the probability of members of a cohort surviving from birth to age class $x$. Survival from birth to age class $x$ ($x > 0$) is given by,

$$l_x = \prod_{0}^{x-1} s_x, \qquad (3)$$

where $l_0 = 1.0$, and $s_x$ is the probability of surviving from age class $x$ to age class $x + 1$.

A population's size at time $t$ ($N_t$) is the sum of the individuals of all cohorts, excluding individuals of age class 0,

$$N_t = \sum_{x=0}^{\infty} n_{0,t-x}\, l_x - n_{0,t-x}. \text{ Erratum} \qquad (4)$$

Age class 0 is excluded from $N_t$ because it represents the number of births between times $t$ and $t + 1$. Natural populations, however, seem never to be in the idealized state described above. Typically, populations fluctuate between an upper and lower bound with a long-term per capita growth rate ($r$) of zero, and the number in each age class varies between censuses, as shown in Table 1. In such populations, however, a good estimate of the mean population size ($\overline{N}$) over a period of time is given by,

$$\overline{N} = \overline{n}_0 \sum_{0}^{\infty} l_x - \overline{n}_0, \qquad (5)$$

where $\overline{n}_0$ is the mean initial size of cohorts.

In the illustrative population (Table 1),

**Table 1.** Annual censuses of a hypothetical population. The age-specific survival rates ($s_x$) are determined from, $s_x = \sum_{t=1}^{14} n_{x+1,t} \Big/ \sum_{t=0}^{13} n_{x,t}$; $l_x$ is calculated with Eq. 3.

| Age | Time | | | | | | | | | | | | | | | $s_x$ | $l_x$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $x$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | | |
| 0 | 53 | 92 | 69 | 79 | 51 | 79 | 15 | 77 | 85 | 80 | 39 | 85 | 25 | 48 | 54 | 0.5245 | 1.0000 |
| 1 | 27 | 7 | 74 | 50 | 33 | 17 | 69 | 14 | 7 | 43 | 20 | 25 | 45 | 20 | 36 | 0.4812 | 0.5245 |
| 2 | 7 | 18 | 0 | 60 | 15 | 29 | 11 | 23 | 10 | 0 | 19 | 15 | 5 | 12 | 0 | 0.3482 | 0.2524 |
| 3 | 0 | 5 | 16 | 0 | 2 | 14 | 13 | 5 | 2 | 3 | 0 | 1 | 3 | 3 | 11 | 0.2836 | 0.0879 |
| 4 | 2 | 0 | 1 | 3 | 0 | 1 | 4 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0.2632 | 0.0249 |
| 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2857 | 0.0066 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0.0000 | 0.0019 |
| $\sum_0^\infty n_{x,t}$ | 91 | 123 | 160 | 192 | 101 | 140 | 112 | 128 | 107 | 127 | 78 | 126 | 78 | 84 | 103 | | |
| $\sum_1^\infty n_{x,t}$ | 38 | 31 | 91 | 113 | 50 | 61 | 97 | 51 | 22 | 47 | 39 | 41 | 53 | 36 | 49 | | |
| $\sum_0^\infty l_x$ | | | | | | | | | | | | | | | | | 1.8981 |

lacking a stable age distribution, $\bar{n}_0 = 62.1$ and $\sum_0^\infty l_x = 1.8981$. Thus, from Eq. 5, $\bar{N} = 62.1 \times 1.8981 - 62.1 = 55.7$. The mean population size, determined directly from the census data $(\bar{N} = \sum_{t=0}^{14} \sum_{x=1}^{\infty} n_{x,t} / 15)$, is 54.6.

Equation 5 may be useful for understanding some theoretical and practical ecological problems.

## Implications

### Demography of common and rare species

If we have two species, one of them abundant, the other scarce, they may each have identical birth, death, and growth rates, generation time, life expectancy, and age structure. In Table 2, population B is 50 times larger than Population A. Nevertheless, both populations have the same age-specific survival rates ($s_x = n_{x+1,t+1}/n_{x,t}$), and the same mean age-specific fecundity ($m_x = n_{0,t} / \sum_\alpha^\omega n_{x,t}$, where $\alpha$ is age of first breeding, and $\omega$ is age of last breeding), and the same empirical age structure (Table 2). With the same age-specific survival rates and mean fecundity, the two populations must have identical life tables (Table 3), and, thus, have the identical birth ($b$), death ($d$), and growth ($r$) rates, life expectancy at birth ($\sum_0^\infty l_x$), generation time ($T$), and proportion of individuals in each age class ($c_x$). The difference in size between the two populations is a result only of their having different initial size of cohorts, $n_0$.

This result indicates that when studying why these two populations differ in size, ecologists should be looking for factors that limit the size of $n_0$, a parameter that is not now calculated by ecologists. Of course, two populations with the same $\bar{n}_0$ but different $\sum_0^\infty l_x$ should also be of different size (Eq. 5). Thus, in trying to determine why one species is rare and another common, we should be looking for the causes of differences between populations in $\bar{n}_0$ or $\sum_0^\infty l_x$, or both.

$\sum_0^\infty l_x$ is affected by all those factors causing mortality: predation, parasites, disease, accident, food shortage, competition, etc. This seems fairly straightforward. If two populations have the same mean initial size of cohorts, and if a population suffers greater mortality from any cause than another population, then we might expect that it would be smaller in size. Alternatively, if they do not differ in life expectancy at birth (i.e., they have the same survivorship schedule and, thus, same $\sum_0^\infty l_x$), then they must differ in the mean initial size of cohorts ($\bar{n}_0$).

**Table 2.** Censuses, age-specific survival ($s_x$), proportion of age class in population ($c_x$), and mean age-specific fecundity ($m_x$) for two populations of different size (assume no differences between males and females in each population). Mean fecundity = $n_{0,t} / \sum_2^\omega n_{x,t}$ = 2.8018, when breeding begins at two years of age. Population size = $N_t = \sum_1^\infty n_{x,t}$.

| | Population A | | | | Population B | | | |
|---|---|---|---|---|---|---|---|---|
| Age class $x$ | $n_x$ ($t$ = 0) | $n_x$ ($t$ = 1) | $s_x$ | $c_x$ | $n_x$ ($t$ = 0) | $n_x$ ($t$ = 1) | $s_x$ | $c_x$ |
| 0 | 622 | 622 | 0.2508 | 0.6220 | 31 100 | 31 100 | 0.2508 | 0.6220 |
| 1 | 156 | 156 | 0.5962 | 0.1560 | 7 800 | 7 800 | 0.5962 | 0.1560 |
| 2 | 93 | 93 | 0.6022 | 0.0930 | 4 650 | 4 650 | 0.6022 | 0.0930 |
| 3 | 56 | 56 | 0.6071 | 0.0560 | 2 800 | 2 800 | 0.6071 | 0.0560 |
| 4 | 34 | 34 | 0.5882 | 0.0340 | 1 700 | 1 700 | 0.5882 | 0.0340 |
| 5 | 20 | 20 | 0.6000 | 0.0200 | 1 000 | 1 000 | 0.6000 | 0.0200 |
| 6 | 12 | 12 | 0.5833 | 0.0120 | 600 | 600 | 0.5833 | 0.0120 |
| 7 | 7 | 7 | 0.0000 | 0.0070 | 350 | 350 | 0.0000 | 0.0070 |
| Sum | 1 000 | 1 000 | | 1.0000 | 50 000 | 50 000 | | 1.0000 |
| Population size | 378 | 378 | | | 18 900 | 18 900 | | |
| Number breeders | 222 | 222 | | | 11 100 | 11 100 | | |
| $m_x$ (as eggs) | 2.8018 | | | | 2.8018 | | | |

The number of eggs laid or young born between $t$ and $t + 1$ (i.e., $n_{0,t}$) is a function of the number of breeding females alive at time $t$ (some fraction of $N_t$), the mean clutch or litter size, and the number of clutches or litters produced per female. The question: Why so many eggs or young?, however, ultimately means: Why so many females? The number of females in a population is affected by many environmental factors, such as the total amount of living space (nesting sites, territories) available, the total amount of available food, and the amount of both required for a female and her mate to survive and to rear their offspring, the abundance of competitors, predators, and pathogens, and the quality of the physical environment. The clutch or litter size and the number of clutches or litters produced per female are also affected by many environmental factors. Most populations of different size may often differ in both $\bar{n}_0$ and $\sum_0^\infty l_x$.

For a simple example, if there were twenty cavities acceptable to females for breeding in an area, then a maximum of twenty females could breed at any time. If females produced a maximum of twelve eggs or young in a breeding season, then the maximum $n_0$ for the population would be 240. If the number of breeding females, the clutch or litter size, and the number of clutches or litters produced vary in response to other environmental variables, then the mean number of breeding females should be < 20 and $\bar{n}_0 < 240$. Over a period of years Eq. 5 should hold.

Hart (2001) reported that two populations of a Hawaiian honeycreeper (Aves: Drepanidinae), the Hawaii Akepa *Loxops coccineus coccineus*, living in close proximity on the island of Hawaii, have maintained different densities (one three times greater than the other) for more than fifteen years, despite similarities in annual adult survival, reproductive success, age structure, mean fat level, mean weight, external indicators of disease, and sex ratios. Data on predation, disease, and the availability of food failed to support hypotheses that these factors might be responsible for the differences between the high and low density populations (Hart 2001). Hart (2001) and Freed (2001) proposed the hypothesis that the number of large trees with suitable nest holes limited the number of breeders in each population, the big trees with suitable nest holes being more abundant where the akepa was more dense. This hypothesis and data, then, are consistent with the implications of Eq. 5.

## Distribution and abundance

There are several predictions that follow from Eq. 5, which seem consistent with empirical evidence. Globally (total number in the world), a population's numbers should be a function of habitat availability. A species occupying a geographically widespread habitat or a wide range of habitats should likely be a globally numerous species because there could be many breeding females and, thus, large $\bar{n}_0$. A species of limited range and habitat should be less numerous because it would likely have fewer breeding females and a smaller $\bar{n}_0$ than a widespread

**Table 3.** Life table for populations A and B.

| Age class $x$ | $s_x$ | $l_x$ | $m_x$ | $l_xm_x$ | $xl_xm_x$ | $l_xm_xe^{-rx}$ | $l_xe^{-rx}$ | $c_x$ |
|---|---|---|---|---|---|---|---|---|
| 0 | 0.2508 | 1.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 1.0000 | 0.6220 |
| 1 | 0.5962 | 0.2508 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.2508 | 0.1560 |
| 2 | 0.6022 | 0.1495 | 2.8018 | 0.4189 | 0.8378 | 0.4189 | 0.1495 | 0.0930 |
| 3 | 0.6071 | 0.0900 | 2.8018 | 0.2523 | 0.7568 | 0.2523 | 0.0900 | 0.0560 |
| 4 | 0.5882 | 0.0547 | 2.8018 | 0.1532 | 0.6126 | 0.1532 | 0.0547 | 0.0340 |
| 5 | 0.6000 | 0.0322 | 2.8018 | 0.0901 | 0.4505 | 0.0901 | 0.0322 | 0.0200 |
| 6 | 0.5833 | 0.0193 | 2.8018 | 0.0541 | 0.3243 | 0.0541 | 0.0193 | 0.0120 |
| 7 | 0.0000 | 0.0113 | 2.8018 | 0.0315 | 0.2207 | 0.0315 | 0.0113 | 0.0070 |
| Sum | | 1.6077 | | 1.0000 | 3.2027 | 1.0000 | 1.6077 | 1.0000 |

$R_0 = \sum l_xm_x = 1.0000$, $T = \sum xl_xm_x/\sum l_xm_x = 3.2027$, $r = \ln(R_0)/T = 0.0000$

species. Locally, within a habitat, a colonial species, with nests close together, should be more numerous than a population with large territories because it is likely to have more breeding females and a greater $\bar{n}_0$. These are only broad generalizations. Each species should be analyzed separately because there is much variation. For example, despite a limited breeding range (sometimes a single island or limited number of small islands) and low fecundity (less than a single egg per female per year), some seabirds may be extremely numerous because they are colonial (allowing a large number of females to breed and eggs to be laid in a small space — a large $\bar{n}_0$) and subject to low mortality (a large $\sum_0^\infty l_x$). Alternatively, a species could have a limited suitable habitat within a wide geographic range, in which case it could be locally abundant but globally scarce. The situation for each species could be different, and these demographic differences should be of interest in investigating the distribution and abundance of species. Regardless of the complexity of pattern in the distribution and abundance of habitats, within any small area the more numerous species should have a greater $\bar{n}_0$, greater $\sum_0^\infty l_x$, or both. The difficult job for ecologists remains to determine why $\bar{n}_0$ and $\sum_0^\infty l_x$ differ among populations and species.

Another simple inference regards the relative numbers of predator and prey. Predatory species tend to be longer lived than their prey (greater $\sum_0^\infty l_x$), but their prey are more numerous (greater $\bar{N}$). Thus, the mean initial size of cohorts ($\bar{n}_0$) should be greater in the prey species than in the predator population.

These inferences are hardly surprising. What is interesting is that they are all consistent with a simple, universally applicable mathematical equation. Thus, the equation may be useful in analyzing differences between populations and species.

## Population dynamics

Equation 5 describes an empirical relationship (i.e., one that could be shown directly to be true or false by population censuses over a period of time because there are no hypothetical terms) and provides us with two new parameters ($\bar{n}_0$, $\sum_0^\infty l_x$) to study in our investigation into the deeper issues of population dynamics, such as the debate about the role, or even the existence, of density-dependent negative-feedback loops between a population's size, $N$, and its growth rate ($r$), which has been a central problem for population ecologists for much of the past century (e.g., Nicholson 1933, 1954, Andrewartha & Birch 1954, Lack 1954, 1966, Murray 1979, 1982, 1994, 2000a, Berryman 1991, 1997, den Boer 1991, Turchin 1995, 1999, White 1993, 2001, Berryman *et al.* 2002).

In this regard, we should note that the relationship between one count ($N_t$) and the next ($N_{t+1}$) in a population is,

$$N_{t+1} = N_t + B_t - D_t + V_t - W_t, \qquad (6)$$

where $B_t$ is the number of births (note that $B_t = n_{0,t}$), $D_t$ is the number of deaths, $V_t$ is the number of immigrants, and $W_t$ is the number of emigrants, occurring between times $t$ and $t + 1$. Dividing both sides of this equation by $N_t$, we have,

$$\frac{N_{t+1}}{N_t} = \frac{N_t + B_t - D_t + V_t - W_t}{N_t}, \qquad (7)$$

$$\lambda_t = e^{r_t} = 1 + b_t - d_t + v_t - w_t, \qquad (8)$$

$$r_t = \ln(1 + b_t - d_t + v_t - w_t), \qquad (9)$$

where $e$ is the base of the natural logarithms, $r_t$ is the per capita growth rate, $\lambda_t$ the finite growth rate, $b_t$ the birth rate, $d_t$ the death rate, $v_t$ the immigration rate, and $w_t$ the emigration rate between times $t$ and $t + 1$. Furthermore, from Eq. 6,

$$\Delta N = N_{t+1} - N_t = B_t - D_t + V_t - W_t. \qquad (10)$$

According to population regulation theory (e.g., Berryman *et al.* 2002, Sibly & Hone 2002), a population's density ($N$) feeds back negatively on its per capita growth rate ($r$). Presumably, as the population's density increases, the increasing competition for resources, or increasing exposure to predation and disease, or other factor decreases the probability of individuals' successfully breeding or increases the probability of their dying. Eventually, a population stops growing because the death rate exceeds the birth rate. Although a decreasing $r$ with increasing $N$ is a necessary condition for regulation, it is not a sufficient condition (Berryman *et al.* 2002).

Suppose that a population's $B$, $D$, $V$, $W$, and, therefore, $\Delta N$ (Eq. 10) are constants over some period of time. Suppose that $\Delta N$ is $> 0$. The population would grow additively by $\Delta N$ individuals per year and nevertheless have decreasing birth ($b$), death ($d$), immigration ($v$), and emigration ($w$) rates. The growth rate ($r$), too, would be decreasing with increasing $N$, despite the facts that $\Delta N$ is constant and the population is growing toward infinite size. The growth rate is decreasing not because of feedback between population size ($N$) and $B$, $D$, $V$, or $W$, according to the theory, but because $N$ is getting bigger relative to $B$, $D$, $V$, or $W$. The point here is that a decreasing $r$ with increasing $N$ can occur in the absence of regulation.

In order to understand the dynamics of this population, we must determine whether the decreasing $r$ with increasing $N$ is a consequence of decreasing $B$ or $V$ or increasing $D$ or $W$. This would require plotting $B$, $D$, $V$, and $W$ against $N$. These plots are not done by ecologists, so we do not know how these parameters vary with $N$. Nevertheless, Lack (1966) showed that the mean clutch size at time $t$ ($C_t$) in the great tit *Parus major* decreased with increasing population size. Because the great tit at Marley Wood begins breeding at age one, is essentially single-brooded, and lays few replacement clutches, its mean clutch size is close to its birth rate (i.e., $B/N$). Calculating $B_t$ from $N_t \times C_t$ and then plotting $B_t$ *vs.* $N_t$, however, shows that the number of eggs laid ($B$) increases with increasing $N$ (Murray 1999). Thus, the decreasing clutch size is an ineffective regulating factor, as Lack (1966) himself recognized. A plot of $B$ against $N$ would be more informative about feedback than the usual plot of $b$ against $N$. The plot of $B_t$ *vs.* $N_t$ is the equivalent of a plot of $n_{0,t}$ *vs.* $N_t$.

## A practical application: managing population growth in China

In an effort to control the country's population growth, the government of the People's Republic of China in the mid-1960s began to promote a policy of later marriage, longer intervals between births, and fewer children per female. This resulted in a precipitous decline in China's fertility rate (Coale *et al.* 1991). Nevertheless, in 1979 the government imposed a one child per family policy, which, if continued indefinitely, should result in extinction. Thus, the population policy will have to change again. A government's changing policy every few years on such an important social issue would not inspire confidence. Equation 5 may provide a means to manage population growth for those governments with a desire to do so. Equation 5 is simple, and the alternatives easily understood. Although I use data on China for illustration, I emphasize that the discussion is not about China and its population problem. I have chosen China for illustrative purposes because the necessary data were readily available.

Equation 5 tells us that the mean steady-state size of a population ($\bar{N}$) is a function of the mean number of babies born each year ($\bar{n}_0$) and mean life expectancy at birth ($\sum_0^\infty l_x$). If a study of resource availability and consumption shows that the maximum population size that could be sustained by its most limiting factor was $N$ persons, and if a consensus among the people was to maintain or increase current mean life expectancy, then Eq. 5, modified to reflect differences between males and females in their frequency at birth and subsequent survival, could tell us exactly how many babies should be born in each year in order to maintain a sustainable population at a given size,

$$\bar{N} = \bar{n}_{0(m)} \sum_0^\infty l_{x(m)} - \bar{n}_{0(m)} + \bar{n}_{0(f)} \sum_0^\infty l_{x(f)} - \bar{n}_{0(f)}, \quad (11)$$

where $\bar{n}_{0(m)}$ and $\bar{n}_{0(f)}$ are the mean numbers of males and females, respectively, born per year, and $l_{x(m)}$ and $l_{x(f)}$ are the probabilities of males and females, respectively, born alive and surviving to subsequent ages $x$. Furthermore, if the male/female ratio at birth is $a$, then

$$\bar{n}_{0(m)} = a\bar{n}_{0(f)} \quad (12)$$

and

$$\bar{N} = \left( a\bar{n}_{0(f)} \sum_{0}^{\infty} l_{x(m)} - a\bar{n}_{0(f)} \right) + \left( \bar{n}_{0(f)} \sum_{0}^{\infty} l_{x(f)} - \bar{n}_{0(f)} \right), \quad (13)$$

$$\bar{N} = \bar{n}_{0(f)} \left( a \sum_{0}^{\infty} l_{x(m)} + \sum_{0}^{\infty} l_{x(f)} - a - 1 \right). \quad (14)$$

In order to illustrate the consequences of alternative population policies, let us consider age-specific survival data from Beijing in the Peoples Republic of China, obtained in 1981 (CASS 1989), which were extrapolated by me beyond age 90 to age 100 by extending a regression of age-specific survival rates from age 80 to 90. Beijing has the best survivorship in China, and females have better survival than males. From these data the mean life expectancy of males ($\sum_0^\infty l_{x(m)}$) is 71.0 years and of females ($\sum_0^\infty l_{x(f)}$) is 74.0 years. The male/female ratio ($a$) at birth is 1.068 (Song *et al.* 1985).

The number of births recorded each year between 1962 and 1975 in China varied between about 21 and 30 million with a mean of 25.8 million (Coale 1984). If the mean number of babies born each year ($\bar{n}_0$) over a prolonged period of time were 25.8 million (13 324 178 males and 12 475 822 females; $\bar{n}_0 = a\bar{n}_{0(f)} + \bar{n}_{0(f)}$), then, from Eq. 11 or Eq. 14, the steady-state size should be about 1.859 billion, if it could be sustained.

Suppose, however, that the experts in evaluating the resources (e.g., food, water, wood products, energy) available to the Chinese population decide that, for a sustainable and desirable quality of life, the population of China should not exceed 650 million (Song *et al.* 1985). In order to maintain a population of 650 million, Eq. 11 or Eq. 14 tells us that the average number of babies born each year should be only about 9.1 million in a steady-state population of 650 million people with the life expectancies of 71.0 years for males and 74.0 years for females. This population could be sustained at 650 million with more babies but a shorter life expectancy or fewer babies and a longer life expectancy.

The difference between 25.8 million and 9.1 million babies born each year indicates the magnitude of change that must occur in China to bring a growing population of more than 1.2 billion down to a sustainable steady-state size of 650 million. The methods of implementing such a policy are beyond the scope of this paper.

## Discussion

A simple equation relates mean population size ($\bar{N}$) to mean initial size of cohorts ($\bar{n}_0$) and mean life expectancy at birth ($\sum_0^\infty l_x$): $\bar{N} = \bar{n}_0 \sum_0^\infty l_x - \bar{n}_0$. Thus, two populations of different size must differ in $\bar{n}_0$, $\sum_0^\infty l_x$, or both. Comparing two populations of the same size, the population with a greater $\bar{n}_0$ must have a smaller $\sum_0^\infty l_x$; that with a greater $\sum_0^\infty l_x$ must have a smaller $\bar{n}_0$. Because $\bar{n}_0$ and $\sum_0^\infty l_x$ are not now calculated or reported by ecologists in their work, completely evaluating the usefulness of Eq. 5 cannot be determined by a review of the literature and relating those parameters to a plethora of empirical work. The few examples discussed above indicate the potential for the wide applicability of the equation.

My greatest disappointment has been my failure to find relevant data ($\bar{n}_0$ and $\sum_0^\infty l_x$) on non-human populations in the literature. Nevertheless, almost any long-term study of populations of marked, long-lived (> 1 yr.) individuals should have the raw data for the calculation of, at least, good estimates for these parameters. Ecologists probably know the demography of birds better than the demography of any other taxon. Nevertheless, what ornithologists know is limited. They know mean clutch size for many species but mean annual fecundity of breeding females for few species. They know the number of fledglings per successful nest, but not per successful breeding female, much less per female of breeding age (Murray 2000b). They know minimum age of first breeding but rarely mean age of first breeding. They know whether a population is single-brooded or multibrooded but not the mean number of broods reared, or even attempted (Cody 1971, von Haartman 1971, Ricklefs 1973). They know the maximum life expectancy of many species (e.g., Klimkiewicz & Futcher 1989) but not the mean life expectancy. I hope that investigators will begin to calculate values for these demographic parameters for different species and in different situations.

Even without data, however, the equation tells us something about all populations that meet the stated criteria (persisting populations fluctuating between upper and lower bounds with long-term $r = 0$), much as Newton's Laws tell us something about the orbits of the billions of unknown planets in the universe. Without data, we can be sure that two populations of different size also differ in the mean initial size of cohorts (number of babies born or eggs laid) or mean life expectancy at birth of individuals, or both. Differences between persisting populations in size cannot be determined by comparing per capita birth rate, per capita death rate, clutch or litter size, and other population parameters.

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## References

Andrewartha, H. G. & Birch, L. C. 1954: *The distribution and abundance of animals*. — Univ. Chicago Press, Chicago, Illinois.

Berryman, A. A. 1991: Stabilization or regulation: what it all means! — *Oecologia* 86: 140–143.

Berryman, A. A. 1997: On the principles of population dynamics and theoretical models. — *Amer. Entomol.* 43: 147–151.

Berryman, A. A., Lima Arce, M. & Hawkins, B. A. 2002: Population regulation, emergent properties, and a requiem for density dependence. — *Oikos* 99: 600–606.

CASS 1989: *Almanac of China's population*. — Population Research Institute, Beijing.

Coale, A. J. 1984: *Rapid population change in China, 1952–1982*. — National Academy Press, Washington, D.C.

Coale, A. J., Feng, W., Riley, N. E. & De, L. F. 1991: Recent trends in fertility and nuptiality in China. — *Science* 251: 389–393.

Cody, M. L. 1971: Ecological aspects of reproduction. — In: Farner, D. S. & King, J. R. (eds.), *Avian biology,* vol. 1: 461–512. Academic Press, New York.

den Boer, P. J. 1991: Seeing the trees for the wood: random walks or bounded fluctuations of population size? — *Oecologia* 86: 484–491.

Freed, L. A. 2001: Significance of old-growth forest to the Hawai'i 'Ākepa. — *Studies Avian Biol*. 22: 173–184.

Hart, P. J. 2001: Demographic comparisons between high and low density populations of Hawai'i 'Ākepa. — *Studies Avian Biol*. 22: 185–193.

Klimkiewicz, M. K. & Futcher, A. G. 1989: Longevity records of North American Birds, Supplement 1. — *J. Field Ornithol*. 60: 469–494.

Lack, D. 1954: *The natural regulation of animal numbers*. — Oxford University Press, London.

Lack, D. 1966: *Population studies of birds*. — Clarendon Press, Oxford.

Murray, B. G. Jr. 1979: *Population dynamics: alternative models*. — Academic Press, New York.

Murray, B. G. Jr. 1982: On the meaning of density dependence. — *Oecologia* 53: 370–373.

Murray, B. G. Jr. 1994: On density dependence. — *Oikos* 69: 520–523.

Murray, B. G. Jr. 1999: Is theoretical ecology a science? A reply to Turchin (1999). — *Oikos* 87: 594–600.

Murray, B. G. Jr. 2000a: Dynamics of an age-structured population drawn from a random numbers table. — *Austral. Ecol*. 25: 297–304.

Murray, B. G. Jr. 2000b: Measuring annual reproductive success in birds. — *Condor* 102: 470–473.

Nicholson, A. J. 1933: The balance of animal populations. — *J. Anim. Ecol*. 2: 132–178.

Nicholson, A. J. 1954: An outline of the dynamics of animal populations. — *Austral. J. Zool*. 2: 9–65.

Ricklefs, R. E. 1973: Fecundity, mortality, and avian demography. — In: Farner, D. S. (ed.), *Breeding biology of birds*: 366–435. National Academy of Sciences, Washington, D.C.

Sibly, R. M. & Hone, J. 2002: Population growth rate and its determinants: an overview. — *Phil. Trans. R. Soc. Lond. B* 357: 1153–1170.

Song, J., Tuan, C.-H. & Yu, J.-Y. 1985: *Population control in China: theory and applications*. — Praeger, New York.

Turchin, P. 1995: Population regulation: old arguments and a new synthesis. — In: Cappuccino, N. & Price, P. W. (eds.), *Population dynamics: new approaches and synthesis*: 19–39. Academic Press, San Diego, California.

Turchin, P. 1999: Population regulation: a synthetic view. — *Oikos* 84: 153–159.

von Haartman, L. 1971: Population dynamics. — In: Farner, D. S. & King, J. R. (eds.), *Avian biology,* vol. 1: 391–459. Academic Press, New York.

White, T. C. R. 1993: *The inadequate environment: nitrogen and the abundance of animals*. — Springer-Verlag, Berlin.

White, T. C. R. 2001: Opposing paradigms: regulation or limitation of populations? — *Oikos* 93: 148–152.