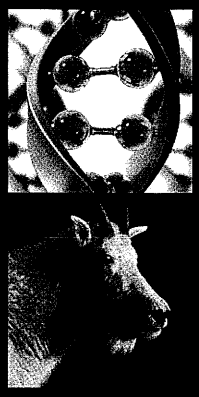
Conservation of Wildlife Populations

Demography, Genetics, and Management



$$\hat{N} = \frac{n_1 n_2}{m_2}$$

L. Scott Mills

Blackwell Publishing

LITERATURE

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Density-Dependence

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Blackwell
Publishing

BLACKWELL PUBLISHING
350 Main Street, Malden, MA 02148-5020, USA
9600 Garsington Road, Oxford OX4 2DQ, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

First published 2007 by Blackwell Publishing Ltd

1 2007

Library of Congress Cataloging-in-Publication Data

Mills, L. Scott.
Conservation of wildlife populations : demography, genetics, and management / by L. Scott Mills.
p. cm.
Includes bibliographical references (p.) and index.
ISBN-13: 978-1-4051-2146-0 (pbk. : alk. paper)
ISBN-10: 1-4051-2146-7 (pbk. : alk. paper) 1. Wildlife management. 2. Animal populations. I. Title.

SK355.M55 2006
639.9–dc22
2006009953

A catalogue record for this title is available from the British Library.

Set in 10.5 on 13pt Minion
by SNP Best-set Typesetter Ltd, Hong Kong
Printed and bound in Singapore
by C.O.S. Printers Pte Ltd

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4

Estimating population vital rates

> *If I were an animal, I'd choose to be a skunk: live fearlessly, eat anything, gestate my young in just two months, and fall into a state of dreaming torpor when the cold bit hard. Wherever I went, I'd leave my sloppy tracks. I wouldn't walk so much as putter, destinationless, in a serene belligerence – past hunters, past death overhead, past death all around.*
>
> **Louise Erdrich (1993), in *The Georgia Review***

Introduction

How many leopards are in a National Park, and how fast are they dying and reproducing? Are deer in Colorado few and declining, or many and increasing? How is the proportion of male and female turtles changing due to global warming?

Population characteristics estimated from field data form the skeleton on which the body of applied population biology rests. These **vital rates**, within and among populations, are united by the famous BIDE equation:

$$N_{t+1} = N_t + B + I - D - E \tag{4.1}$$

Abundance (N) at time $t + 1$ equals the abundance the previous time step, t, plus the number of animals that arrive due to birth (B) or immigration (I), and minus those dying (D) or emigrating (E). Because males and females often have different dispersal and mortality patterns, sex ratio also affects and is affected by these vital rates.

In this chapter I will discuss within-population vital rates, including abundance and density, survival, reproduction, and sex ratio. Later in the book (Chapter 10) I will describe how to estimate immigration and emigration, key vital rates for the dynamics of multiple populations.

Estimating abundance and density

Abundance is probably the piece of information most sought after in wildlife population biology: it is key for determining harvest regulations, for deciding on protection

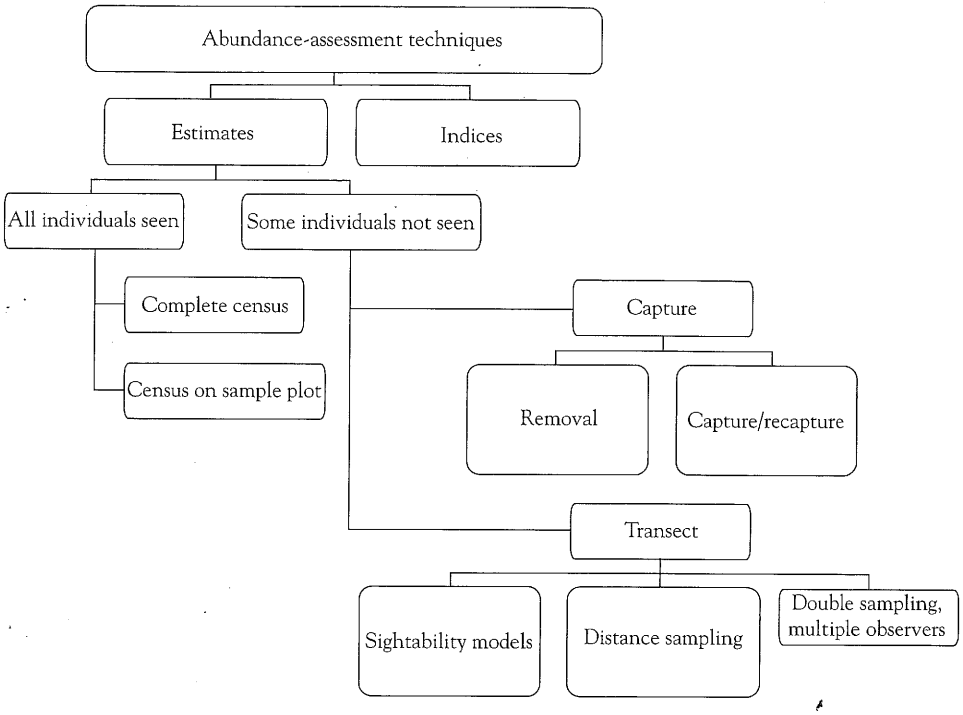

Fig. 4.1 Schematic of various measures mentioned in text to assess abundance of wildlife populations. The major groupings are based on indices or estimators, and whether all animals can be seen ($\hat{p} = 1.0$) or not ($\hat{p} < 1.0$). Modified from Lancia et al. (2005). Reproduced by permission of The Wildlife Society.

for species, and for evaluating the effects of predation or human actions, to name just a few. On the face of it, animal abundance might seem to be trivial: why not just count them? And yet, abundance estimation is one of the most mathematically sophisticated and conceptually challenging components of wildlife population biology. I will cover the basics of some of the most widely used approaches (Fig. 4.1). Throughout, I will use **abundance** and **population size** interchangeably to refer to the number of animals, and **density** to refer to abundance per unit area.

Abundance estimate versus census versus index

Here is one of the most important take-home messages of the chapter: all estimates of animal abundance, no matter how wild the math or intimidating the equations, can be reduced to a simple equation with profound implications:

$$\text{Estimate of abundance} = \hat{N} = \frac{\text{Count of animals}}{\text{Estimated probability of detection}} = \frac{\text{Count}}{\hat{p}} \qquad (4.2)$$

When all animals are detected ($\hat{p} = 1$), the count equals the estimate. But as the probability of detection declines, our estimate will increase.

This equation for abundance estimation has been called canonical (Williams et al. 2002), in the sense that it is a simple yet axiomatic and universally binding principle. The estimated probability of detection ($\hat{p}$) is a function of both detectability (e.g. capture, sighting) within the sampled area and the proportion of the area sampled relative to the total population. Setting aside for the moment the second of these components – the fact that time and money often limit us to sampling only subsections of a population's range (Chapter 2) – we will focus on the implications of detecting fewer than 100% of the animals within a sampled area.

In nature animals are elusive and sometimes downright uncooperative when we try to detect them. They avoid traps, turn their reflective eyes from spotlights, hide under trees when biologists fly overhead, and pass rub pads without leaving hairs behind. In short, detection probabilities will nearly always be less than 1.0 in wildlife studies, so eqn. 4.2 shows that if we use the count alone without accounting for detection probability the resulting measure of abundance will be too small. For example, if we count 40 rabbits on a spotlight transect and ignore the fact that detection probability is, say, 0.5, then we would report 40 animals when really $\hat{N}$ should be (40/0.5) = 80. Detection probability can change over time, space, and even among individuals, and these complexities are why so many articles and books describe mathematical ways to estimate this probability. As we will see, accounting for detectability is also relevant for estimating other vital rates such as survival and movement.

In wildlife applications, the word **census** is reserved for the special and unusual case where detection probability equals 1.0; that is, all animals are counted. This might occur when studying a visible species on a small island, or with surveys in a narrow open transect where all individuals are seen. Botanists quite appropriately census numbers by counting all the plants in a plot, but a true census is rare for wildlife (and sometimes even for plants, where seeds or young plants can be missed). In fact, even the census of humans conducted by many governments is actually not a census at all but rather a count index with unknown detection probability (Box 4.1).

An **index** is a field count of animals or their sign that (hopefully) contains information about the relative number or density, but is not in itself an abundance or density estimate. Examples include mammal captures uncorrected for detection probability, as well as pellet counts, bird-call counts, track counts, numbers of burrow entrances or lodges, harvest numbers at check stations, questionnaires of wildlife sightings, and many others. Because they are typically cheaper to implement than formal estimators of abundance or density, indices are usually favored when money is tight, the species is difficult to observe directly, and/or when the questions are of such broad scale that more intensive estimators are impractical.

As an indirect assay of abundance, the utility of indices must be judged against how well they track changes in absolute or relative abundance across time, space, habitat types, or management treatments. An index can reliably indicate trends over time or relative difference across space only if its relationship to true abundance remains linear and constant, or at least does not change systematically (Bart et al. 2004).

If the relationship between the index and abundance does vary, you will not know whether you are seeing real changes in abundance or changes in the index/abundance relationship (Nichols & Pollock 1983, Tallmon & Mills 2004). For example, fur-

Box 4.1 Example of a non-census: the US "census"

The US Constitution mandates a count of the population in each state every 10 years to apportion the 435 seats in the US House of Representatives and to distribute federal funds to the states. Although it is called a census, the logistics are just too daunting for it to have a detection probability of 1.0; even Thomas Jefferson, who initiated the first census, noted that some persons had been missed. Ignoring that detection probability is less than 1.0 and relying on the count alone means that it is really a US index, with no known relationship to true census population size.

Statisticians proposed for the year 2000 census a transition from index to population estimate. Prior to the traditional census (where an intensive count is followed by random sampling of non-responding housing units) a totally independent set of 750,000 housing units would be picked. After determining the number of housing units present in both counts, the abundance estimate would be:

(Count 1 * Count 2)/number of matching housing units

The census bureau calls this the one number census or dual system estimation, but we will recognize it as the Lincoln–Petersen estimator described later in this chapter.

The fascinating part of this story is that this straightforward proposal to move beyond an uncorrected count index has stirred enormous political debate, because of the possibility that different groups of citizens may have differing detection probability, which would adjust the estimates of numbers and thereby shift political power. Even the US Supreme Court ruled that a 1976 federal census law "directly prohibits the use of sampling in the determination of population for the purposes of apportionment." Apparently we have a way to go to educate some that a complete count – a census – is impossible with hundreds of millions of people, and that a solid sampling strategy is the best way to move from an index to a reliable population estimate.

Source: Wright (1998).

trapping data are probably a poor index of abundance because the number of trapped animals will in large part reflect trapper effort, which in turn will be driven by economics and social norms. Obviously, some control on the constancy of the relationship between the index and abundance can be exerted by the researcher; in a bird-call index survey, for example, sampling could be restricted to the same time of day or year, and steps taken to minimize observer bias. Also, some indices better lend themselves to testing for constancy of the relationship between index and abundance; for example, bird calls or counts of captured animals can be tested statistically for constant detection probability (MacKenzie & Kendall 2002).

Clearly, then, some indices will perform better than others at portraying changes over time or relative differences across habitats or treatments. However, a growing movement argues that instead of hoping that an abundance index will reliably indicate relative differences in abundance over time and space, it is better to either directly estimate abundance (see below) or to switch to a different state variable such as pro-

portion of area occupied (MacKenzie et al. 2005). Certainly, indices will almost always fail as descriptors of absolute abundance, because the relationship between index and abundance will rarely be both constant and known. In short, if the goal is to estimate how many individuals are actually in a population, an index will not do it; you need to use a statistically based estimator (Fig. 4.1), perhaps based on transect sampling or capture–mark–recapture (CMR).

Transect methods for estimating abundance

It is easy to envision counting animals on either side of a line that you sample by walking, driving, riding a horse, or flying. These transects have some known width. If all animals in a series of transects were detected, the abundance in the study area would simply be the number counted divided by the proportion of area sampled in all the transects (Thompson 2002). But if some animals are likely to be missed in a transect, the probability of detection must be estimated (eqn. 4.2). One way to do this is **double sampling** (or ratio estimates): incomplete counts are made over an extensive area (e.g. counts on transects in a helicopter or airplane) while a simultaneous complete census on the ground at a subset of the transects provides an estimate of detection probability (which equals mean aerial count/mean ground count) for the aerial count. Similarly, **multiple observers** can count animals, with the estimated detection probability based on overlap in observations (Lancia et al. 2005). Two of the most widely used approaches to estimate abundance on transects include distance sampling and sightability models.

Distance sampling

Distance-sampling techniques are based on the idea that detection probability decreases with distance from the observer, so detections at various distances can be used to estimate detection probability as well as abundance and density (Buckland et al. 2001). The most common applications of distance sampling include sighting animals at various distances from a line during a transect count, and sighting (or listening to calls) from the center point of a circle. The essential data needed to conduct distance sampling are the measured perpendicular distances from the center line of the transect to each animal seen. To minimize flushing animals as the observer draws close, you can estimate the straight-line distance from where you first see the animal, then use trigonometry to calculate the perpendicular distance (Fig. 4.2).

The distance data are used to estimate the probability of detection ($\hat{P}$). It is easiest to first see how this works graphically (Fig. 4.3) and then summarize the calculus. If all animals could be seen equally at all distances, we could draw a **perfect sightability rectangle** with a $\hat{P}$ value of 1.0 across all distances. Because the sightability is assumed to decline with distance, the curve showing animals sighted at different distances would only occupy a portion of the perfect sightability rectangle. Therefore, the overall $\hat{P}$ in Fig. 4.3 is the proportion of the perfect sightability rectangle under the curve.

Mathematically, we first estimate the probability of observing an animal, given that it is found at distance x from the line $[g(x)]$. Then the computer software (such as the

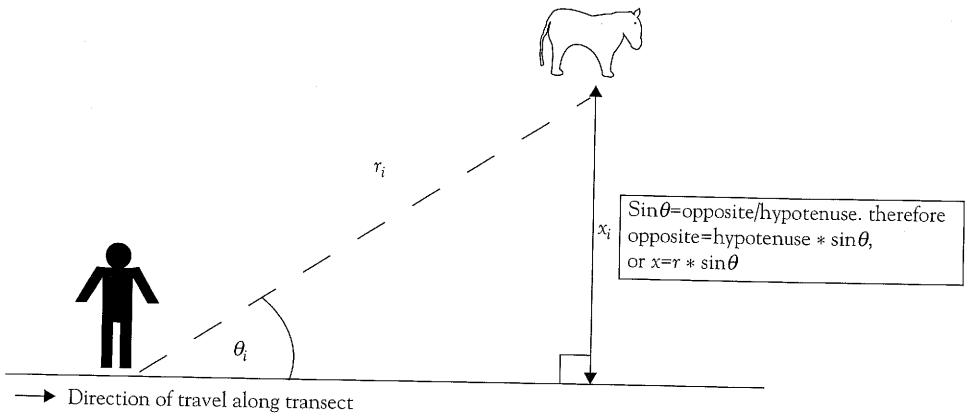

Fig. 4.2 How perpendicular distance for line-transect sampling can be calculated if the observer is not able to directly measure it. As the observer moves along the transect, they record the distance r_i from the line to where the animal is in the field. They also record the angle θ_i formed by the line of sight and the transect line. From these measures, the perpendicular distance (x_i) is $x_i = r_i(\sin \theta_i)$. Trigonometry really does have some interesting applications in applied biology!

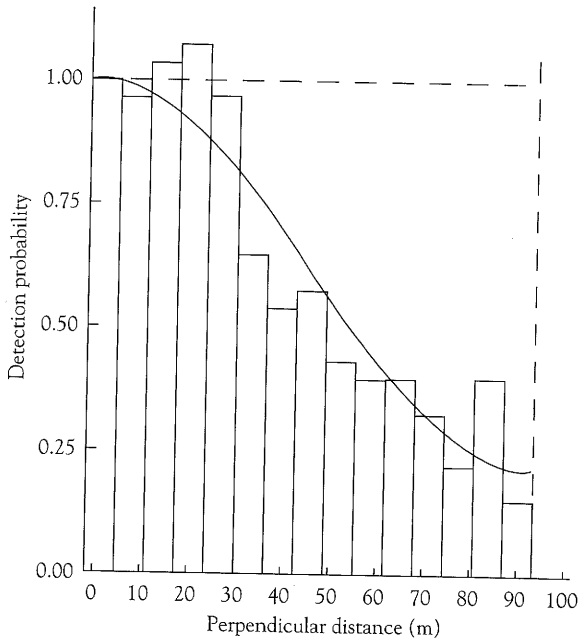

Fig. 4.3 Detection probabilities calculated from perpendicular distance-sighting data using line-transect sampling of wood ducks in forested habitat. The curve shows the fitted Fourier series estimator from the program DISTANCE. The dashed line shows what the overall detection probability would be if it were perfect at all distances (the perfect sightability rectangle); an intuitive estimator of overall detection probability for these data is the proportion of the perfect sightability rectangle under the curve. The increased detections at 15 and 20 m are assumed to be sampling anomalies. Modified from Kelley (1996). Reproduced by permission of The Wildlife Society.

program DISTANCE) integrates the detection function across all distances. In symbols, the probability of detection $\hat{p}_w$ is roughly the average of the detection probabilities across all distance categories from 0 to the maximum distance w:

$$\hat{p}_w = \frac{\left[\int_0^w g(x)\mathrm{d}x\right]}{w} \tag{4.3}$$

With an estimate of detection probability, abundance ($\hat{N}$) may be estimated using the canonical formula (eqn. 4.2), and with the known transect length (L) and width ($2w$; because you are sampling both sides of the transect line) density, D, can be estimated[1]:

$$D = \hat{N}/(2 * L * w) \tag{4.4}$$

Here are some key assumptions for distance sampling.

- All animals directly on the line are seen (this assumption can be relaxed).
- Animals are counted only once, and do not move before being sighted.
- Perpendicular distances are measured exactly. It is permissible to lump estimates into categories (for example, 10-m intervals) to deal with uncertainty in distance estimation[2].
- Sightings are independent, such that one animal does not cause others to be more or less likely to be sighted (more complicated models can account for this, as in herding animals).

As a rough guideline for required sample sizes, Buckland et al. (2001) recommend measuring distance to at least 40, and preferably 60–80 animals.

A common variant of distance sampling uses a single point instead of a line. For example, in point counts of birds the observer records over a specified time period (e.g. 5 minutes) all birds that are seen or heard, along with their estimated distance. Rather than perpendicular distances, radial distances are recorded, but the approach again assumes a monotonic decline in detection with distance. The detection curve is then exactly like line-transect sampling, with similar assumptions and analysis. Considerable error can arise in estimating distance when you can hear but not see the birds (Nichols et al. 2000a).

Sightability or observation probability models

Given that accounting for detectability is critically important yet hard to do for every time and place, sightability models can be developed and the resulting detection probabilities used to estimate abundance in future surveys. Often coupled with aerial

[1]Note: I have derived the density estimate in a way that connects distance sampling to the canonical approach to estimating abundance. Buckland et al. (2001) provide an excellent treatment of variance estimators, and show how density can be directly estimated without going through these steps.

[2]In practice, the most important part of the sightability curve is near the center line of the transect. As such, Buckland et al. (2001) recommend having smaller or more numerous distance categories nearer the line than away from the line.

transect surveys, a known population (usually radio-marked) is observed while additional variables likely to influence sighting probability (for example, snow conditions, group size, animal activity, vegetation type, etc.) are recorded simultaneously. The sightability model is developed from the relevant variables coupled with the proportion of known animals detected. In subsequent surveys, observers record data on the sightability variables and use the formula to convert the raw counts into an abundance estimate with variance (Unsworth et al. 1994).

As an example, Samuel et al. (1987) used radio-marked elk to develop a sightability model for aerial surveys in Idaho. Observers flew over the sampling area and documented whether they actually observed radio-marked individuals. Sightability for a group of a given size was modeled with logistic regression, where the radio-marked elk were either observed or not, with covariates that affect the sightability. They found that sightability increased with group size and decreased with vegetation cover. Specifically:

$$\text{Sighting probability} = \hat{p} = \frac{1}{1+e^{-[1.22+1.55\ln(\text{group size})-0.05(\%\,\text{vegetation cover})]}} \qquad (4.5)$$

Thus for a future survey following similar protocols and in similar conditions to the Idaho study, a survey detecting a group of five elk in 70% vegetation cover would have a sighting probability of 0.55 (arrived at by putting 5 and 70 into the equation above). Each group count divided by its sighting probability (eqn. 4.2) gives an estimate of abundance for that group, and the sum of all abundances gives the overall abundance estimate for the sampled area.

The appeal of this approach is that after the sightability model has been developed and tested, future efforts require only counts and data on the model variables, without the need to directly estimate detection probability. Although one must be aware that the sightability model may only work well under the particular conditions for which it was developed, a sightability model thoughtfully applied from one place to another is better than a guess at numbers not framed in statistical sampling (Box 4.2).

CMR methods for estimating abundance

A different class of abundance estimators relies on capturing and marking, and recapturing again (with **capturing** and **marking** defined broadly and not necessarily literally; see Box 4.3)[3]. A **capture history** for each animal is generated, with a 1 denoting capture on a sample occasion and a 0 denoting no capture.

Two broad classes of CMR model may be distinguished: **closed-population models**, where the population is assumed to experience neither losses (by death or emigration) nor additions (by birth or immigration) during the period sampled, and **open-population models**, where losses and additions occur and can, in fact, be measured. The more complicated open models build on concepts and definitions from closed models.

[3]I will not cover **removal** abundance estimators whereby captured animals are permanently removed from the population (these are often used for fisheries or game animals where the harvest can be used to help estimate abundance).

Box 4.2 Application of a sample-based population survey to resolve a debate over numbers of mule deer

The Colorado Division of Wildlife (CDOW) used harvest, sex, and age data to estimate a relatively stable population of approximately 7000–9000 mule deer through the 1990s for a population of deer residing in northwest Colorado. Some sportsmen in Colorado believed that mule deer in the state were in serious peril, and used casual methodology (e.g. personal observations, outfitter guesses) to estimate the number of deer in this particular population at closer to 1750. The discrepancy led some sportsmen to accuse the CDOW of misleading the public by inflating estimates of deer population size. In a mediation process, it was agreed that an intensive aerial survey system developed in Colorado would be used to estimate numbers of deer in this population and, additionally, a sightability model developed for mule deer in Idaho would be applied to counts of deer using the CDOW survey system (Freddy et al. 2004). The CDOW system used intensive censuses of deer on randomly selected sample units or quadrats and assumed 100% detectability of deer on each sampled quadrat. In the area having the contested numbers of deer, the CDOW method led to an estimated population size of 6782 ± 2497 (90% confidence interval), whereas adjusting the counts using the Idaho sightability model led to an estimate of $11{,}052 \pm 3503$. Thus the original CDOW estimate of approximately 7000 deer was supported by two approaches to estimating deer population size, but no statistical support could be found for the sportsmen's estimate of 1750. This case study demonstrates that intuitive guesses at wildlife abundance without a formal sampling framework can be very wrong. It also shows the potential of under-estimating numbers of deer even when intense counts are conducted on relatively small parcels of land having complex cover and terrain features, underscoring the need to estimate detectability through sightability models or other approaches.

Closed CMR models of abundance

The simplest and most well-known closed-population model is the Lincoln–Petersen (LP) estimator of abundance based on two sampling periods. The LP method has a deep history, with applications stretching back to estimates of the human population of France in 1786 and of waterfowl of North America in 1930 (Williams et al. 2002:290). I will explain the LP in depth, both because it is commonly used to estimate abundance and because it forms the basis for understanding most other CMR estimators.

LP estimator with two samples

Suppose you want to estimate the abundance (N) of mice on a grid. You open traps in the afternoon, and the next morning you check traps and mark some mice uniquely (n_1 marked mice). You release them, and then a short time later (say, the next day) repeat the process. In the second sample you capture a total of n_2 mice, of which m_2 of these are marked. The best way to understand the LP abundance estimator without having to memorize it is to remember eqn. 4.2 and think of the first capture and marking session as the count and the second as the means for estimating the probability of detection:

Box 4.3 Methods of marking animals

Individual marks for wildlife studies usually conjures images of bird leg bands, turtle shell notches, and mammal ear tags. Although these traditional methods continue to be useful and widely applied, a number of other approaches are now available to mark animals (Silvy et al. 2005). Radio transmitters can be implanted in animals as small as shrews, worn as backpacks in birds, and equipped with global positioning satellite location monitors for larger animals. Telemetry has the benefit of being able to help a researcher differentiate movement from mortalities. Passive integrated transponder (PIT) tags are rice-grain-sized glass and metal cylinders that are injected under the skin; they do not transmit a signal but individual tags are recorded by an electronic reader passed over the animal. For amphibians, elastomer (rubbery paint) of different colors can be injected under the skin. If the mark does need not be permanent or individuals do not need to be distinguished (e.g. in short studies using two-sample Lincoln–Petersen methods), options could include paint balls, dyes, or hair clipping.

In some cases animals can be distinguished with noninvasive methods whereby the animal does not have to be captured. Animals with stripes, spots, or other patterns can be individually identified (e.g. body patterns on species ranging from salamanders to tigers), as can animals with distinctive scars from wounds (e.g. manatees scarred by boat propellers; Langtimm et al. 1998). As discussed in Chapter 3, noninvasive individual identification can also be obtained via genotype marks from bits of hair, feather, feces, or other material.

In all cases the choice of tag should result from careful deliberation, weighing possible negative effects on the animal against the efficiency of the method and the information to be gained from the particular study design. The ideal mark is humane, does not affect the response being studied (e.g. abundance, survival, reproduction, or behavior), is not prone to misidentification, and lasts reliably for the length of the study. Some can be used for multiple purposes; for example, toe clips provide an instant DNA sample as well as a mark that is permanent for small mammals and for some (but not all) amphibians.

$$\hat{N} = \frac{n_1}{\hat{p}} = \frac{n_1}{\left(\frac{m_2}{n_2}\right)} \tag{4.6}$$

This rearranges to give the intuitive abundance estimate:

$$\hat{N} = \frac{n_1 n_2}{m_2} \tag{4.7}$$

Although eqn. 4.7 shows the intuitive form of the LP estimator, it turns out that it is negatively biased, so the operational forms of the LP formula for abundance (the one to use in actual application) and its variance are:

$$\hat{N} = \left[\frac{(n_1+1)(n_2+1)}{(m_2+1)}\right] - 1. \tag{4.8}$$

$$\mathrm{var}\left(\hat{N}\right) = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \tag{4.9}$$

The square root of the variance gives the SE of the estimate, and the 95% confidence interval of the abundance estimate is:

$$\hat{N} \pm 1.96(\text{SE}) \tag{4.10}$$

An example of abundance estimation using the LP method is shown in Box 4.4.

Three key assumptions underlie the LP and other closed-population estimators of abundance.

1. The population is closed, so that $\hat{N}$ applies to both capture occasions. If deaths or emigration occur between the two periods, the LP estimate refers only to the population at the time of the first sampling period[4]. Immigration or births can also violate closure, in which case the LP estimate refers to population size at the time of the second sample (see Kendall 1999). Closure in CMR studies is usually biologically reasonable if the trapping sessions are close together in time (e.g. consecutive nights of trapping).
2. Marks are not lost or overlooked by observers. If tags are lost between the two samples, the LP estimate will be positively biased (because fewer of the n_1 animals will be available to become m_2 animals, so $\hat{p}$ will be biased low and therefore $\hat{N}$ will be biased high).
3. All animals are equally likely to be captured in each sample. For any CMR study, capture probability might vary in three primary ways: over time, among individuals, or in response to the animal having been trapped (Box 4.5). For LP, a change in capture probability over time is not a problem (the first sample merely introduces marked animals to the population to facilitate an estimate of $\hat{p}$ at the next session), but individual heterogeneity or trap response can bias the LP estimator. As an example of the effects of individual heterogeneity, remember from Chapter 3 that noninvasive genotyping of hair or scat to mark individuals can in some cases lead to a shadow effect whereby certain individuals share the same genotype (the same mark). These shadows are essentially genotypes more likely to be detected, biasing $\hat{p}$ high which causes a negative bias in $\hat{N}$ (Mills et al. 2000b). Finally, a trap-shy response leads to a positive bias in $\hat{N}$ while a trap-happy response leads to a negative bias.

A few other practical points about the LP estimator are worth mentioning. First, because it is a two-sample estimator, marks are only applied once and checked once which means that animals do not have to be individually identified. This makes LP unusual among CMR estimators in that simple batch marks – perhaps a dab of paint on the back – are sufficient to identify the marked animals. The one-time mark also means that the second capture session can be based on any method that obtains an estimate of (m_2/n_2), including the use of hunters or anglers to obtain the sample.

A related feature arising from the two-sample construction of the LP estimator is that the mark–recapture can often be improved by using different methods for the two

[4]Deaths during the second trapping event will not affect LP. If a death occurs during the first session (due to trapping or handling), the dead animal(s) should not be included with the n_1 animals but rather added to the abundance after $\hat{N}$ is estimated; the variance estimate is unaffected (Williams et al. 2002:293).

Box 4.4 An example of abundance estimation using the LP method and noninvasive sampling

Eastern North Pacific humpback whales can be uniquely (and noninvasively) identified from natural markings including pigmentation, scars, and ridging of the flukes. Population closure over 1–3 years can be assumed because the whales have high site fidelity to distinct feeding aggregations off the coast of California, Oregon, and Washington before migrating to wintering grounds off Baja California, mainland Mexico, and Central America. Some humpback whale data and abundance estimates are shown below. Many animals were captured (photographed) several times in a year, so the number of photographs is much greater than the number of uniquely identified whales (n_1 and n_2; Calambokidis & Barlow 2004).

Years for n_1 and n_2	Number of identification photographs in first year	n_1	Number of identification photographs in 2nd year	n_2	m_2	$\hat{N}$	95% Confidence interval around $\hat{N}$
1991 and 1992	668	269	1023	398	188	569	537–601
1992 and 1993	1023	398	512	254	173	584	547–620
1993and 1994	512	254	402	244	108	572	512–633
1994 and 1995	402	244	661	331	100	804	704–904
1995 and 1996	661	331	564	331	144	759	690–829

n_1, The number of individuals identified in photographs in the first year; n_2, the number of individuals identified in photographs in the second year; m_2, the number of individuals in the second year that had been identified in the first year.

capture sessions. With **mark–resight** methods, potential logistical advantages accrue with using a different method (sighting) for the recapture, and trap response and individual heterogeneity should be reduced if capture probabilities of the two samples are independent. Finally, two samples does not necessarily mean only 2 days of trapping. Multiple days can be collapsed into two samples of unequal length, so for example the first three nights of trapping could be sample one and the second two nights sample two. Collapsing multiple days into two samples can help deal with population closure (Kendall 1999), and has the benefit of increasing sample size per trapping event. However, if you can conduct sampling over more than 2 days, other CMR models such as those discussed next may be more appropriate.

Box 4.5 Three ways that CMR studies can violate the assumption of equal catchability (and how field researchers try to minimize the violations)

1. **Time** may change capture probabilities for all animals in different capture sessions. Weather, moon phase, or time of year could cause capture probability to change. Researchers attempt to minimize this violation of equal catchability by closing down traps when weather patterns are likely to affect capture probability.
2. **Heterogeneity among individuals** indicates that different animals have different capture probabilities. It can be caused by an animal's age, sex, dominance status, home-range location relative to trap locations, and so on. A possible solution to heterogeneity is to estimate abundance separately for classes of animals thought to have different capture probabilities (e.g. males and females). Individual heterogeneity can also be minimized by making sure that each animal is likely to encounter more than one trap during the course of daily movements; although the traps do not need to be in a uniform grid pattern (e.g. Karanth & Nichols 1998), regular trap spacing is usually used with at least four per home range. It can also be minimized by using different techniques – such as marking, telemetry, sighting, and so on – on different occasions (for example, mark the first session, resight the second).
3. **Behavioral response** arises when an animal becomes more or less likely to be captured after the first capture. Trap-happy animals are more likely to be captured again (perhaps due to the novelty or security of the trap, or the allure of free food). Trap-shy animals are less likely to be trapped after first exposure. Trap happiness can be decreased by pre-baiting traps (which is also a good idea because it tends to increase capture probability in general), trap shyness by minimizing the time and severity of handling.

Closed-population estimates requiring three or more samples

Although the LP method is robust to some forms of unequal trappability it is not robust to all. If you are able to employ more than two capture sessions, then you will have a sufficient data stream to first test which forms (if any) of unequal trappability are apparent in the data, and then be able to employ an estimator robust to the identified deviations from equal catchability. You will not be doing this by hand; the approaches were originally codified in the computer program CAPTURE in the late 1970s (Otis et al. 1978, White et al. 1982), and more recently in the program MARK (Cooch 2001). For a particular data-set, the model whose assumptions of capture-probability structure most closely approximate the trapping data is chosen to provide the most accurate (least biased, most precise) estimate of abundance. Briefly, here are the models:

- Model M_0: equal catchability. Every animal has the same probability of capture for each sampling period in the study (no behavioral response, individual heterogeneity, or temporal variation).

- Model M_h: individual heterogeneity. Individuals have different capture probabilities.
- Model M_b: behavioral response. All animals initially have the same capture probability but after first capture may become trap happy or trap shy.
- Model M_t: time-variation model. Probabilities of capture change from trap period to trap period but within a period all animals have an equal chance of capture. Essentially an extension of the LP model.
- Models M_{bh}, M_{th}, M_{tb}, and M_{tbh}: various forms incorporating multiple deviations from equal trappability.

Open CMR models of abundance

In many cases, the length of the study makes it impossible to assume that the population is closed to additions and losses. In the mid 1960s Richard Cormack, followed closely and independently by George Jolly and George Seber, developed a modeling framework to provide estimates of vital rates in open populations. Abundance estimates in open populations are therefore based on **Jolly–Seber** (JS) models, while survival estimates are called Cormack–Jolly–Seber (CJS) models.

The Jolly–Seber model for estimating abundance is analogous to the LP estimate, except that the pieces are generalized to more than two sessions (with subscript i referring to the session) and capture probability focuses on marked animals only, to account for the open population (Pollock et al. 1990). As with LP, a total of n_i animals are caught at time i. Although m_i marked animals are captured at time i, in an open population with a probability of detection of less than 1.0 we know that other marked animals are alive but not caught at i while others have died. Therefore $\hat{M}_i$, the number of marked animals alive and in the population at occasion i, is estimated using information on animals captured both before and after i (and therefore known to be alive at i)[5]. Thus, the Jolly–Seber abundance estimate for sample i is:

[5]While I am trying to avoid gory details I do not want to leave a big black box. $\hat{M}_i$, the number of marked animals in the population at time i, is estimated based on the following (Pollock et al. 1990).

- R_i, The number of the n_i animals caught at i that are successfully released with marks (this could be less than n_i if there were losses during capture).
- r_i, The number of the R_i subsequently recaptured after i.
- m_i, The number of marked animals caught in the ith sample.
- z_i, The number of marked animals not captured at i but recaptured after i.

If we assume the probability of ever seeing again a marked animal that has just been released is the same as the chance of seeing again a marked animal that was not captured at time i then $\frac{r_i}{R_i} = \frac{z_i}{(M_i - m_i)}$, which rearranges to: $\hat{M}_i = m_i + (R_i z_i / r_i)$. So in words, we estimate the number of marked animals alive in a sample based on both the marked animals captured (m_i) and the number of animals not captured but known to be alive because they were captured later ($R_i z_i / r_i$).

Robust design

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A note on density

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$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i} \tag{4.11}$$

Robust design

In 1982, wildlife biometrician Ken Pollock made the simple but profound observation that closed- and open-population models could be combined to take advantage of each of their strengths. Closed-population models can be robust to unequal capture probabilities among individuals or over time, but are only valid over relatively short periods of time during which no additions or losses to the population occur. Open-population models allow estimates of abundance in the face of gains and losses, but are not as precise, or as easily accommodating to unequal catchability in the form of individual heterogeneity or behavioral responses (Lebreton et al. 1992, Burnham & Anderson 2002). Pollock's suggestion was to use a **robust design** such that a long-term study of an open population is implemented as a sequence of short-term studies of closed populations (Pollock et al. 1990). The robust design is implemented with several primary sampling occasions, between which the population is likely to be open to gains and losses (Fig. 4.4). Each primary session includes several secondary sampling periods (preferably four or more), analyzed using closed models. For example, there may be four nights of mark–recapture trapping once a month for 5 months (Fig. 4.4). Abundance is estimated with closed-population models within each month. Cormack–Jolly–Seber survival estimates (described below) are based on pooled data across the secondary periods (e.g. each animal is recorded if it was captured at least once during a four-night set of secondary periods).

The robust design provides a powerful engine for estimating vital rates (Box 4.6). In addition to good estimates of survival and abundance, with two age classes you can estimate new individuals entering the population from both immigration and *in situ* reproduction (Nichols & Pollock 1990, Nichols & Coffman 1999), as well as temporary movement into and out of the study area (Kendall et al. 1997, Bailey et al. 2004a, 2004b; Chapter 10 will show the application of this method to estimating dispersal).

A note on density estimation in capture-mark-recapture studies

Often the density of animals per unit area is of more interest than abundance per se. Intuitively, density is simply the abundance estimate divided by the area of the trapping grid. However, animals whose home range barely overlaps the trapping grid, or animals that come onto the grid from outside its perimeter, make the effective size of the trapping grid larger than the actual grid. The size of the **effective trapping grid** depends on the animal, the grid shape, and the study design, so it should be estimated for each study.

A practical approach assumes that animals off the grid are just as likely to move toward the grid as away, and that the distance moved can be indexed by the maximum distance between captures for animals on the grid. A boundary strip equal to half

Box 4.6 Some insights using the robust design

The robust design provides a powerful framework for estimating abundance and survival within populations, and for connectivity (movement) among populations. I will save examples of quantifying movement for Chapter 10. Here are two case studies to show how detection and survival can be quantified with robust design.

Case study 1: how many salamanders are missed during monitoring counts? (Bailey et al. 2004a, 2004b)

Concerns about global amphibian declines have led to widespread efforts to monitor amphibians over time and space. Plethodon salamanders have received special attention because they may be particularly susceptible to human-caused stressors, and therefore may be good indicator species (Chapter 13). But how good are raw counts of salamanders as a tool for population monitoring? Working in Great Smoky Mountains National Park, Larissa Bailey and colleagues were interested in the likelihood of being able to actually detect salamanders present in an area, and in the stability of detection probability over time and space. For salamanders that spend a lot of time underground, the probability of capture or detection is a product of the probability that the salamander is near the surface and thus available to be captured multiplied by the probability of catching a salamander given that it is near the surface during a set of secondary samples. The first bit is the probability that the salamander has not temporarily emigrated, or is otherwise temporarily unavailable for sampling; this is a problem for lots of species that pop up briefly but then seem to disappear for a while (e.g. marine mammals that only visible when they come to the surface or snow geese that are only detectable when they are breeding). The second bit is simply the capture probability.

The robust design of sampling involved four primary periods 6–10 days apart and lasting for 3–4 consecutive daily secondary samples, repeated for 3 years. What did they find? The average probability of a salamander being available near the surface (that is, not temporarily emigrated to the soil depths) was only 13%, and the average probability of catching a salamander near the surface was 30%. Together, that means that the probability of detecting a salamander that occurs in a particular plot is only 4%. Furthermore, the capture probability varied across years, across habitat type, and across species. Therefore, actual population size could decline quite a bit with relatively little change in a count-based index. Conversely, a count index could fluctuate a lot because of changes in detection probability, while actual abundance (what we care about) changed very little. Therefore, count indices are not reliable in this case and if abundance is of interest, formal CMR estimators should be used.

Box 4.6 Continu

Case study 2: s fragments (Tal

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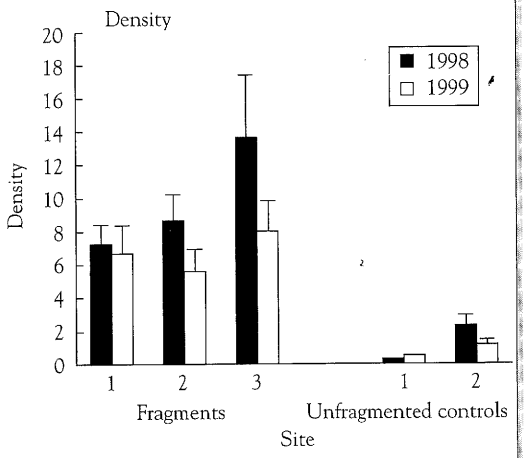
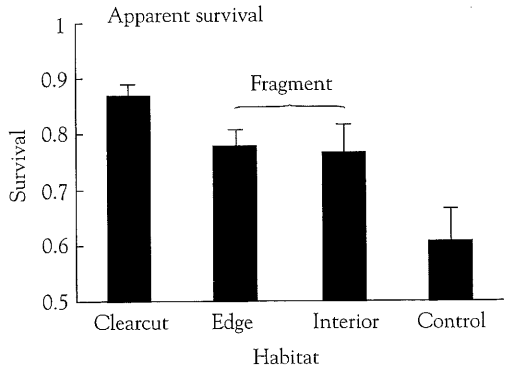
Estimates of dee density and surv landscape. From Reproduced by pe

Box 4.6 Continued

Case study 2: survival of voracious deer mice on clearcuts and forest fragments (Tallmon et al. 2003)

Deer mice can be voracious seed predators, and are known to respond positively to many human perturbations, so it is of interest how forest fragmentation affects their density and survival. In a study in southwest Oregon, David Tallmon and colleagues used a robust design to trap four primary periods in each of two summers. The first primary session consisted of eight consecutive nights of secondary samples, whereas the other three primary periods were four consecutive nights each. A 16-day interval separated primary sessions (except for one year where 20 days separated two sessions). From this robust design coupled with 340 mouse captures it was possible to calculate density in forest fragments compared with unfragmented controls during the last primary session of each summer (closed models), as well as apparent survival in different fragmentation habitat types over 20-day intervals (see figure). So, deer mice love forest fragmentation!





Estimates of deer mouse population density and survival in a fragmented landscape. From Tallmon et al. (2003). Reproduced by permission of the ESA.

LITERATURE INDEX Density-Dependence

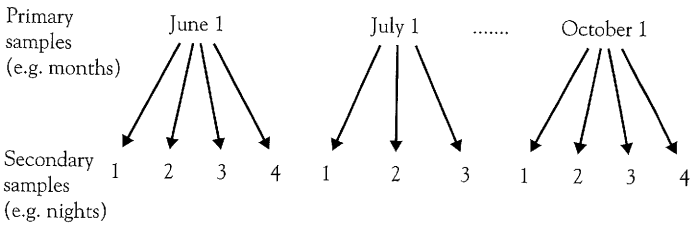


Fig. 4.4 Pollock's robust design. Here I use five monthly primary sampling periods (June–October, with the dots indicating August and September) and three- or four-night secondary periods. Notice that the number of secondary periods can differ among primary periods, which is nice because rain shuts down trapping efforts, trucks break down, field assistants get sick, and so on. Apparent survival (and recruitment and movement) can be estimated between primary periods (e.g. monthly survival using Cormack–Jolly–Seber methods), and abundance and capture probabilities can be estimated using closed models across secondary periods (e.g. abundance for each month).

the mean maximum distance moved is added all the way around the grid to provide an effective grid size (Wilson & Anderson 1985, Karanth & Nichols 1998)[6]. The density estimate is based on estimated abundance divided by estimated effective area, with its variance accounting for uncertainty in both abundance and effective grid size.

Survival estimation

Three main classes of survival estimator can be distinguished by whether or not all animals can be relocated (known fate) or whether survivors are recorded (CMR) or deaths are recorded (band recovery or return)[7]. The computer program MARK (Cooch 2001) is the workhorse for all of these analyses.

Known-fate models

In cases where a method such as radiotelemetry allows for certainty in relocating or detecting an animal that is alive and part of the study, **known-fate models** or **complete follow-up models** can be used. The simplest way to think about survival estimation using known-fate models is to start with the ideal case where the surviving animals (x) relative to the total number (n) are known unambiguously. The estimated

[6]Alternative approaches for estimating effective grid size include **nested grid** analysis and direct measurement using radio-collared animals (Lancia et al. 2005).

[7]Many other methods combine and extend the categories (see Further reading at the end of the chapter, and Lebreton et al. 1992, Winterstein et al. 2001).

proportion surviving is like a coin-tossing game (with life and death on each side of the coin):

$$\hat{S} = \frac{x}{n} \tag{4.12}$$

The estimated variance (based on a binomial probability model) is:

$$\hat{\text{var}}(\hat{S}) = \frac{\hat{S}(1-\hat{S})}{n} \tag{4.13}$$

This simple bionomial model can be elaborated for time intervals of different lengths, and for cases where animals must be **censored** because their fates become unknown when a transmitter stops working or falls off, or a marked animal leaves the study area, or the study ends. For example, some extensions take advantage of **failure-time** or **hazard** methods used in engineering (estimating the lifetimes of machine components) and medicine (estimating survival time of patients). One of the most widely used failure-time models is the **Kaplan–Meier** method (Pollock et al. 1989, Winterstein et al. 2001). The Kaplan-Meier approach accommodates limited censoring, as well as staggered entry whereby animals are released gradually into the sample over time. The estimate of survival for t units of time from the start of the study is:

$$\hat{S}(t) = \prod_{i=1}^{t}\left[1 - \left(\frac{\text{Number of deaths at time } i = d_i}{\text{Number at risk at time } i = r_i}\right)\right] \tag{4.14}$$

where the number at risk in each time step (r_i) includes everybody tagged, alive, and not censored at the start of an interval (remember that Π means product).

The variance is[8]:

$$\text{var}\left[\hat{S}(t)\right] = \frac{\left[\hat{S}(t)\right]^2\left[1-\hat{S}(t)\right]}{r_t} \tag{4.15}$$

An example of the Kaplan–Meier estimator for bobwhite quail with both censoring and staggered entry is given in Box 4.7.

Like all estimates of survival based on marked animals, the Kaplan–Meier method assumes that marked animals are representative of the population (for example, across sex and age classes, habitat types, or other characteristics), and that the mark does not affect survival. Also, it is assumed that whatever reason caused the animal to be censored is not related to their fate; this assumption will be violated if, for example, radios are destroyed only when animals are killed. The final assumption is that survival times are independent for the different animals (one animal dying does not

[8]As with abundance (e.g. eqn. 4.10), the 95% confidence interval is $\pm 1.96\sqrt{\text{var}\left[\hat{S}(t)\right]}$.

Box 4.7 An example of how to use the Kaplan–Meier method to estimate survival from the start of a study through time period t

The data used here are from a study of northern bobwhite quail (*Colinus virginianus*) radio-tagged in North Carolina (Pollock et al. 1989). As an example, let's estimate survival through week 15 using the data in the table. The quail had survived from the start of the study through week 14 with a probability of 0.235. During week 15, an additional four quail died out of 23 at risk. Therefore:

$$\hat{S}(15) = 0.235 * \left(1 - \frac{d_{15}}{r_{15}}\right) = 0.235\left(1 - \frac{4}{23}\right) = 0.235 * 0.826 = 0.194$$

with variance of 0.0013 (95% confidence interval, 0.123–0.265). Because six new animals were added to the study during week 15, but one animal was censored and four died, the number at risk going into week 16 was $(23 + 6 - 1 - 4) = 24$.

Week (t)	Dates	No. at risk (r_i)	No. of deaths (d_i)	No. censored	No. of new individuals added	Survival ($\hat{S}[t]$)	95% CI
1	17–23 Nov	20	0	0	1	1.000	1.000–1.000
2	24–30 Nov	21	0	0	1	1.000	1.000–1.000
3	1–7 Dec	22	2	1	0	0.909	0.795–1.024
4	8–14 Dec	19	5	0	0	0.670	0.497–0.843
5	15–21 Dec	14	3	0	0	0.526	0.337–0.716
6	22–28 Dec	11	0	0	0	0.526	0.312–0.740
7	29 Dec–4 Jan	11	0	0	0	0.526	0.312–0.740
8	5–11 Jan	11	2	0	0	0.431	0.239–0.623
9	12–18 Jan	9	1	0	0	0.383	0.186–0.579
10	19–25 Jan	8	0	1	0	0.383	0.174–0.591
11	26 Jan–1 Feb	7	0	0	3	0.383	0.160–0.606
12	2–8 Feb	10	0	0	6	0.383	0.196–0.569

Box 4.7 Continued

13	9–15 Feb	16	4	0	10	0.287	0.168–0.406
14	16–22 Feb	22	4	0	5	0.235	0.149–0.321
15	23 Feb–1 Mar	23	4	1	6	0.194	0.123–0.265
16	2–8 Mar	24	4	0	0	0.162	0.103–0.221
17	9–15 Mar	20	2	0	0	0.146	0.087–0.205

CI, confidence interval. Data from Pollock et al. (1989). Reproduced by permission of The Wildlife Society.

affect others). If this assumption is violated – for example when predators tend to kill off entire litters of newborn radiocollared snowshoe hares (O'Donoghue 1994), – the Kaplan–Meier estimate of survival is not biased but the variance will be too low.

Notice that survival does not need to be constant among individuals or over time, making this method a good choice when survival probabilities change due to hunting pressure, weather, and other events. Precision of the estimate is a function of the number of animals at risk, so it is important to maximize the number of animals followed and to minimize censored animals, with a suggested minimum sample of 25, and preferably 40–50, marked animals in the population at all time steps (Pollock et al. 1989, Winterstein et al. 2001). The Kaplan–Meier approach is easily extended to relate survival to covariates, or to statistically test for differences in survival among treatment (e.g. harvest compared with no-harvest) or other classes (sex, age, etc.; see White & Garrot 1990, Winterstein et al. 2001).

CMR using the Cormack–Jolly–Seber method

Suppose you have animals that are marked but whose fates cannot be known with certainty: the probability of detection complicates assessment of whether they are dead or alive but not captured. A naïve estimate of survival using such marked animals would be the number of marked animals captured at time $i+1$ (m_{i+1}) divided by the number of animals released with marks at time i (R_i). By now I hope that such a naïve estimator for survival, $\frac{m_{i+1}}{R_i}$, sends shivers down your spine, because you know that it will almost always be biased low. Why? Because some of the marked animals not caught at $i+1$ are very much alive, just not captured!

So we need to estimate the number of marked animals that make it from one interval to the next, following an approach similar to that used for the Jolly–Seber abundance estimate (see footnote 5). At time i, the number of marked animals include the R_i animals caught in i and released with marks back into the population, plus the marked animals alive but not caught in $i(\hat{M}_i - m_i)$. Of these, a total of $\hat{M}_{i+1}$ survive through to the next interval. Therefore, apparent survival (ϕ_i) is the simple proportion of marked animals that have survived and remained in the population from the end of one trapping event to the start of the next[9]:

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i + R_i - m_i} = \frac{\text{Estimated number of marked animals that make it to } i+1}{\text{Number marked animals leaving trapping event } i} \quad (4.16)$$

Variances for all of these estimators are available, as are power curves showing expected precision of estimates for various population sizes and capture probabilities (Pollock et al. 1990, Krebs 1999).

Band-return approaches

Band-return approaches are conceptually closely related to CMR methods in that a form of detection probability is accounted for and estimated as part of estimating survival. The big difference, of course, is that you are not tracking marked animals that live to each time step, but rather those that die with bands being returned to the researcher. Because the band returns come from people hunting or fishing, a recovery depends on the animal being killed and reported. The recovery rate becomes loosely analogous to detection probability, in that we must tease its effects out of the data in order to estimate what we care about: survival (Williams et al. 2002).

Other approaches

Many approaches extend the methods described above, such as the development of known-fate telemetry models with a relocation probability less than 1.0 (as might occur if movement or topography precludes detection of telemetry signals on certain sampling occasions; Pollock et al. 1995). Also, approaches have been combined and incorporate auxiliary information. For example, survival of an open population of wood thrushes that were both radiocollared and banded for recapture was estimated by linking Kaplan–Meier estimates with Cormack–Jolly–Seber methods (Powell et al. 2000); elk survival and abundance was estimated by combining known-fate survival models for radiocollared elk with age-at-harvest data from hunter check stations (Gove et al. 2002).

In contrast to the approaches discussed so far, one common approach derives survival estimates solely from **life-table** survivorship curves or other age-distribution

[9] $\hat{\phi}_i$ is called **apparent survival** because it does not separate death from the probability of permanently leaving the area. The probability of survival alone is harder to estimate, requiring telemetry or sampling at different spatial scales (Citta 2005).

methods based on unmarked animals. A cohort is followed through time, with the drop in numbers indicating survival through each age class (the horizontal life-table approach). For example, a cohort of 100 2-year olds that is reduced to 60 by the time they become 3-year olds implies a survival of 0.6. It can be logistically very challenging to follow a cohort from birth to the death of the last individual, and the process must be repeated to capture the variation in survival that occurs through time (i.e. good and bad years). Alternatively, if the current age structure is assumed to reflect the past (and population growth is either stationary or known), then the changes from age class to age class could again indicate survival through each age (the vertical life-table approach). A serious limitation of life-table or age-distribution methods is that we are not accounting for age-specific detection probabilities and so must assume that all individuals are equally detected across age classes and time. This problem, coupled with the restrictive assumptions, makes this a much weaker method for estimating survival than radiotelemetry or CMR-based approaches (Lebreton et al. 1992, Williams et al. 2002).

Estimation of reproduction

Reproductive output is another essential within-population vital rate estimated from field data. Sometimes reproductive output refers to females alone, and sometimes to either-sex offspring born to either-sex adults; the important thing is to keep the accounting straight. To be clear in meaning about various terms related to reproduction, I'll begin with some pedantic definitions.

- **Maternity** and **paternity** refer to the mother and father of an animal, respectively.
- **Natality** is the average number of live offspring born (or eggs laid) per female that reproduces, often called **litter size** for mammals and **clutch size** for birds, amphibians, reptiles, and fish. (Again, sometimes only female offspring are counted.)
- **Fecundity** is the average number of offspring born per individual of a given age (or stage) in one time step, so it is a product of natality and the proportion of the cohort that breeds (note that if focusing only on females, fecundity is the product of female natality multiplied by the proportion of females that breed).
- **Recruitment** often gets tossed in with reproduction, but I will use this term (in later chapters) to refer to net population production after both births and deaths have been taken into account.
- Finally, the **average reproductive contribution** of individuals of a given age or stage to the population next year is a product of fecundity and either the survival of young to be counted the next year or the survival of parents to have the young[10] (Box 4.8 shows an example of calculating reproductive rates from field data).

Natality of females has traditionally been determined by observation (for a review see Harder & Kirkpatrick 1994). In some cases, mammal litter size is inferred from counts

[10]Some call this **fertility**, but often in the ecology and wildlife biology literature fertility and fecundity are interchanged and used differently. That is why I am making what might seem to be gruesomely detailed and even arcane distinctions for these terms. The meaning of the terms are especially important in population-projection models (Chapter 7).

Box 4.8 Example of calculating reproductive rates from field data

For adult common frogs (*Rana temporaria*) in Europe, reproductive data may be assembled from a number of studies (see Biek et al. 2002). Here we are evaluating reproduction by females of females.

Measured from the field:

- Clutch size = natality: 650 female eggs per female that reproduces (SD, 133)
- Probability of females laying eggs: 1.0, all females breed annually
- Sex ratio: 0.5 (SD, 0)
- Adult survival: 0.43 (SD, 0.035)

Calculated from field data:

- Fecundity: $650 \times 1.0 = 650$ female eggs laid per adult female in the population

We'll come back to this example in Chapter 7.

made *in utero*. Mammals have corpora lutea scars that form in the ovaries after release of the egg; a count of corpora lutea scars – for example, in an ungulate brought in to a hunter check station – reveals the number of ova shed per estrus for that female. Fetal counts *in utero*, as well as uterine scars marking sites of previous placental attachment, can also be counted in necropsied mammals. Ultrasound is emerging as an increasingly field-friendly tool to count embryos *in utero* (Griffin et al. 2003). Birds do not have corpora lutea or uterine scars but do have postovulatory follicles that sometimes persist long enough to be counted.

Remember that measures of reproductive output taken at different times in the birth process must be scaled by survival: an ova must be both fertilized and implanted in the uterus to become a fetus, and a fetus must not be reabsorbed or aborted to be born alive. Thus to serve as an estimate of natality a count of corpora lutea scars or fetus numbers must account for the probability of making it from that stage to birth.

The proportion of the population likely to breed can also be determined in the field. For mammals, vaginal smears assessing the proportion of epithelial cells and leukocytes can indicate female mating receptivity, fecal steroid hormones can indicate pregnancy (Berger et al. 1999), and lactation can indicate likely nursing. Reproductive status of males is more difficult, with possible assessment based on sperm counts, hormonal levels, or testis size. In birds, the same approaches apply to males; for example, the testis of a mature male white-crowned sparrow goes from less than 10 mg to more than 600 mg during the height of the breeding season. For females, a laparotomy incision to expose the left ovary can indicate the proportion of birds nearing the egg-laying stage, and also confirm the sex of live birds where the sexes cannot easily be distinguished morphologically. Also, necropsied female birds in some families (such as the Columbidae, doves and pigeons) will have distinguishable crop

glands filled with a curd-like material fed to young. For a harvested bird such as mourning doves, crop glands can indicate the proportion of birds incubating or rearing young.

Genetic markers can clarify maternity and paternity, and establish reproductive patterns that are not intuitive from observation alone (Jones & Ardren 2003). For example, over 4 years in Yellowstone National Park there was usually concordance between parentage estimates from nuclear DNA markers (microsatellite loci) and visual observation or telemetry data for 11 wolf packs (K. Murphy, personal communication). However, the DNA matches showed two surprising deviations from the behavioral observations of maternity and paternity. First, a putative mother identified via observation was not the biological mother of pups that she nursed; second, a 10-month-old male and an 11-month-old female wolf reproduced, although wolves of less than 1 year old had never been known to reproduce in free-ranging gray wolves. Similarly, in African lions, DNA fingerprinting complemented intensive behavioral observations by determining that a single male was the father for the entire litter in 23 out of 24 cases despite the fact that females had been observed accepting multiple copulatory partners (Gilbert et al. 1991).

Sex ratio

Marilyn Monroe, the famous American actress, is said to have quipped, "What do I think about sex? Oh, I think it's here to stay." As long as Marilyn Monroe is right, as long as we applied biologists deal with creatures that have sexual reproduction (as virtually all wildlife populations do), then the ratio of males to females will always be an important population descriptor.

Although the sex ratio of a population is most commonly given as the ratio of males to females (e.g. 60 : 40) or the percentage of males (e.g. 60%), it may also be described as the ratio of females to males or the percentage of females. The sex ratio often changes with time, with the following conventional distinctions: (i) **primary sex ratio** means conception[11]; (ii) **secondary sex ratio** means birth; (iii) **tertiary sex ratio** means some later date, usually at the end of parental care (weaning/fledging); and (iv) **quarternary sex ratio** means the older breeding adult population. Finally, one should be clear on whether the ratio is referring to a head count or to a breeding sex ratio. The two can be very different, depending on the mating system. For example, in a **polygynous** system, where one male mates with more than one female, a head-count sex ratio may be 1 : 1 (males/females) while the breeding sex ratio may be as extreme as 1 : 20 (for example, in the case of elephant seals where males violently maintain exclusive harems). The flip side of a polygynous mating system is **polyandry**, where one female mates with multiple males, again skewing the breeding sex ratio compared with the head count (this is relatively rare, but can be found, for example, in emus). In a

[11]Sometimes researchers use the primary sex ratio to refer to the youngest juveniles they can easily observe and sex.

monogamous mating system, a pair bond between one male and one female leads to more similar breeding and head-count sex ratios.

As an aside, when there is a skewed sex ratio (polygyny or polyandry) there will tend to be increased competition within the sexes for mates. This is called **sexual selection** and it explains crazy things like huge antlers on ungulates which seem impossibly maladaptive (try walking through dense trees with an elk rack on your head) except in the light of increased mating opportunity. Sexual selection also helps to drive selection of sexual dimorphism, as with the elephant seals mentioned above: competition for their large harems leads to selection for massive males that are perhaps five times as large as females.

Sex ratios in the wild

What drives sex ratios in wildlife? The mechanisms leading to primary sex ratios are complex (see Hardy 2002). One much-discussed branch of **sex allocation theory** posits that, although selection should favor equal primary sex ratio under most conditions, females in better physical condition (with more access to resources) should produce more offspring of the sex that would most benefit from the improved condition (Trivers & Willard 1973). For example, consider polygynous systems where males compete for mates or territories and where big strong males mate the most: when food resources are plentiful mothers might invest more in males, increasing their reproductive success; when resources are poor mothers would invest more in females because females would have mating opportunities even with poor food availability. A fair amount of data now support these theoretical predictions (Hardy 2002, Suorsa et al. 2003), including a fascinating application where supplemental feeding affects sex ratios in the critically endangered kakapo (Box 4.9).

In many reptiles, amphibians, and fish, primary and secondary sex ratios may depend on temperature (temperature-dependent sex determination). With a 4°C increase during incubation, painted turtles and loggerhead turtles may produce nearly all females (Mrosovsky 1982, Janzen 1994), whereas a mere 1°C shift can push tuatara to produce all males (Cree et al. 1995). Ignorance of temperature-dependent sex determination can undercut conservation efforts: for years, well-meaning people took the eggs from threatened marine turtles out of the sand and put them into Styrofoam boxes so they could hatch away from predators. It turns out that the boxes were a few degrees cooler than the beach sand, leading to severe masculinization of the hatchlings in boxes (Mrosovsky 1982).

Quarternary sex ratios differ from primary ratios in fairly predictable patterns for mammals and birds because survival between the sexes changes with time. The primary drivers of changes in sex ratio over time arise from behavioral, physiological, and genetic differences between the sexes. As an example of these factors in play, let's get personal and consider human sex ratios (Holden 1987, Williams 2003). At conception the primary human sex ratio is skewed toward males, with 53% : 47% males/females. But males are slightly more likely to be lost *in utero* due to spontaneous abortions, miscarriages, and stillbirths, so by birth the secondary sex ratio is less male-

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Box 4.9 Sex ratios and kakapo conservation

The kakapo is a large flightless parrot once common in New Zealand but nearly driven to extinction by introduced black rats and weasels. By 1997 only about 60 kakapo remained in the world.

The exceptionally small numbers and vulnerability of this flightless, ground-nesting bird to ever-increasing introduced predators led managers in 1982 to capture and move all remaining birds to mammal-free islands. Adult survival increased substantially, but reproduction and chick survival was poor. Kakapo have a polygynous mating system, with males congregating in leks every 2–5 years in synchrony with the episodic mass fruiting of podocarp trees. Males display vocally to attract females and compete intensely among themselves; larger males are more likely to mate.

To increase reproduction, supplemental food (nuts, apples, and sweet potatoes) was provided to the kakapo beginning in 1989. Paradoxically, this reasonable and intuitive attempt to save the species by supplemental feeding appears to have backfired. Females provided with supplemental food produced 67% males, compared with 29% males for birds not given supplemental food. Thus kakapo sex allocation followed the Trivers–Willard hypothesis, with females producing more sons than daughters when resources were high. The male bias under supplemental feeding is problematic not only because females are needed for the population to grow, but also because the population was already heavily skewed toward males (41 : 21 males/females) because introduced predators kill females as they incubate the nest.

In a terrific example of ecological theory guiding management, in 2002 the New Zealand Department of Conservation acted on predictions of sex allocation theory. While food was provided to all females after mating to increase chick survival, only lighter females (which might most need food and yet would tend to produce more female young than heavier females) were given supplementary food before mating. So far, the strategy appears successful: all but one of the 21 adult females laid eggs, leading to the highest kakapo recruitment in at least 20 years; furthermore, of the 24 young fledged that year, more than half (15 of 24) were females.

Sources: Clout et al. (2002), Sutherland (2002), Robertson et al. (2006).

dominated, at about 51 : 49. Males have higher death rates, so by age 30 the sex ratio is even (50 : 50) and by age 65 it is 45 : 55. Why the strong skew toward females between childhood and older age? In large part, male behaviors are to blame. Male humans kill each other and themselves more than females, and are twice as likely as females to die from lung cancer, pulmonary disease, accidents, liver damage, heart damage, and suicide. Males are more likely to drink heavily, use seat belts less often, and die in motor vehicle accidents. In addition to behavioral differences, human sex ratio may be affected by physiological factors including the potential role of estrogen in lowering so-called bad cholesterol levels and reducing heart attacks. And finally, recall that sex determination in mammals depends on the sex chromosome, with females being XX and males XY. An X-linked gene that has negative effects will automatically be expressed in a male (as men only have one X-chromosome), while the same deleterious gene could be masked by the second X in a female. Thus, for example, males are

far more prone to X-linked genetic problems such as muscular dystrophy and color blindness.

What do we see in wildlife populations? Many mammal populations follow the trends described for humans, with the same general mechanisms likely to come into play. Parasitism may also play a role, as male-biased parasitism is the general rule among mammals (Moore & Wilson 2002). The heavier parasite load for males is most pronounced in species where male–male competition for mates or territories is most severe, leading to reduced immunocompetence to defend against parasites (perhaps because testosterone is an immunosuppressant or perhaps just because intraspecific competition leads to larger male size, which in turn attracts a larger parasite load). By the way, the parasite-burden hypothesis can also be linked to humans, as men are about twice as vulnerable to parasite-induced death in the USA, UK, and Japan, and more than four times as vulnerable in countries with higher parasite-induced death, such as Kazakhstan and Azerbaijan (Owens 2002).

Birds show a pattern opposite to mammals, with females tending to die earlier and sex ratios becoming more male-biased with age. Behavioral risks typically differ from mammals, most obviously when egg-laying exposes females to high predation risks and energetic drains. Females are also the heterogametic sex in birds (ZW; see Chapter 3), exposing them to deleterious alleles expressed on the sex chromosome. And in some species, notably raptors and polyandrous bird species, size dimorphism is reversed, with females being larger and therefore potentially carrying heavier parasite loads.

Over time, if the myriad interacting factors affecting sex ratios stay relatively constant, then we would expect to see a stable and characteristic sex ratio for particular species. Despite considerable debate as to the adaptive significance of stable sex ratios, for applied purposes knowing why sex ratios are as they are allows us to consider what might happen when we intentionally alter the sex ratio under different scenarios of harvest, translocation, or intensive management (Wedekind 2002), or when the sex ratio is inadvertently altered when environments change due to fragmentation (Suorsa et al. 2003) or global climate change (Janzen 1994).

Summary

Vital rates are the skeleton upon which the body of population biology hangs. Both models and management actions dealing with factors such as harvest, endangered species, and control of exotics rest on estimates of abundance, survival, reproduction, and sex ratios (as well as connectivity – to be discussed in a later chapter).

Although indirect indices of abundance (e.g. snow tracks, call counts, or fur returns) may have some utility for assaying relative abundance over time and space, they are constrained by the fact that a change in the index could be caused either by a change in true abundance (which is what we care about) or by a change in the relationship between the index and true abundance (a bothersome confounding effect). The reliability of information about populations will be improved by estimating abundance. The dizzying blizzard of abundance estimators is unified by the simple idea that all involve some count of animals divided by an estimated probability of detecting (or

capturing) an animal during the count period. In rare circumstances all animals are counted, a true census. In most other cases, however, probability of detection is less than 1.0 and must be estimated; two common approaches include transect-based and CMR approaches.

Survival can be based on models that either can reasonably assume a probability of detection of 1.0 – that is, that the fate of the animal is known at all times, usually with the help of radiotelemetry – or that the detection probability is less than 1.0 so that survival must be estimated from recorded deaths (band-return models) or recorded live marked animals (Cormack–Jolly–Seber models). These approaches and others can be mixed and matched to estimate survival, but the commonality is to avoid the naïve estimator of (number encountered/total), which ignores the fact that animals not captured or sighted may be very much alive but simply not detected.

Reproduction is often easier to determine than survival, with a suite of methods to detect reproductive output both before and after birth. Determination of maternity and paternity of offspring, and therefore reproductive output of parents, can benefit from DNA markers.

Because there is a mortality component from conception through old age, and this mortality can be sex-specific, sex ratios should specify the time at which they are taken. Primary (at conception) and secondary (at birth) sex ratios may be affected by resources and in some amphibians, reptiles, and fish by temperature; human-caused changes in resources (through habitat fragmentation) or temperature (under global warming) could severely affect populations by skewing sex ratios. Later in life the sex ratio in mammals tends to become more female-biased because male mammals tend to die faster due to behavioral, physiological, and genetic differences; birds tend to follow the opposite trend.

Further reading

Lancia, R.A., Nichols, J.D., Pollock, K.H., and Kendall, W.L. (2005) Estimating the number of animals in wildlife populations. In: *Techniques for Wildlife Investigations and Management*, 6th edn. (ed. C.E. Braun), pp. 106–53. The Wildlife Society, Bethesda, MD. Describes the fundamentals and wide variety of approaches to estimating animal abundance.

Thompson, S.K. (2002) *Sampling*, 2nd edn. John Wiley and Sons, New York. A good overview of sample design, plus information on a variety of abundance estimators. A good overview of sample design, plus information on a variety of abundance estimators.

Williams, B.K., Nichols, J.D., and Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA. The most detailed, complete single source for the theory and mathematics of vital-rate estimation.

5

The simplest way to describe and project population growth: exponential or geometric change

I think I may fairly make two postulata. First, that food is necessary to the existence of man. Secondly, that the passion between the sexes is necessary and will remain nearly in its present state . . . Population, when unchecked, increases in a geometrical ratio: Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will show the immensity of the first power in comparison of the second.

Thomas Malthus (1798), *An Essay on the Principle of Population*

The buffalo herds also vanished before the great pilgrimage . . . Scarce by 1867, those "wild cattles of the prairies" were all but gone by the 1870's. . . . The prairies were repopulated with domestic animals brought in by the settlers. In 1833 Charles Larpenteur drove four domestic cows and two bulls into Montana from the Green River country. A conservative count in 1880 showed 48,287 horses, 1,632 mules, 249,888 sheep, and 274,321 cattle in Montana territory.

Bud Moore (1996:55), *The Lochsa Story*

The burial mound was outside the city walls, in a field dotted with cow pies and large stones. The stones had been arranged geometrically in patterns that were supposed to mean something to the gods; presumably, the cow pies had fallen at random, although then, as now, the division between what is random in nature and what is purposeful is extremely difficult to determine.

Tom Robbins (1984:28), *Jitterbug Perfume*

Introduction

The quotation by Thomas Malthus describes a profound paradox between the increases in human population size and the ability to harvest enough food to feed us; the paradox catalyzed Charles Darwin's theory of natural selection as a driver of evolutionary change. Whether or not Malthus was right is a matter of hot debate that we

will not wade into (at least 20 books address the topic in my local university library). Rather, the quotation helps us in the transition from considering conceptual pieces (e.g. study design, genetic tools, and measurements of vital rates) to understanding the process of population biology.

In the last chapter we saw that at the most basic level change in abundance (N_t) over time is driven by dynamics both within populations (births and deaths) and among populations (immigration and emigration). In this chapter we will examine the simplest way to quantify population growth: geometric or exponential change unaffected by density, individual qualities, or other factors. Later chapters will add more complexity, including changes in population growth due to density (density dependence) and characteristics of the individuals in the population (e.g. age structure). Importantly, I should note at the outset that **population growth** refers to any trajectory in abundance over time, including increases, decreases, or no change.

At the heart of Malthus' concern is that an arithmetic process generates a straight line over time whereas multiplicative (geometric or exponential) growth creates a curved line (Fig. 5.1). **Arithmetic change** involves adding or subtracting a fixed number at each time interval (or step). Malthus posited that food supply ("subsistence") increases by a fixed absolute amount each time step; for example, an additional 900 tonnes of wheat available to humans each year.

In contrast, **geometric** or **exponential growth** means that a constant fraction of the current number is added to the population each time step. Said differently, this means that the current population is multiplied by a constant number each time step. Money in your interest-bearing bank account grows exponentially (or, equivalently, geometrically) because each dollar contributes to future income; more dollars multiplied by a fixed rate means more of an increase. Likewise, population growth is a multiplicative process which can lead to geometric or exponential increase (or decrease). Geometric and exponential are best considered as the same type of multiplicative growth: the only difference is that one occurs on a discrete time scale while the other happens on a continuous scale (more on this later in the chapter).

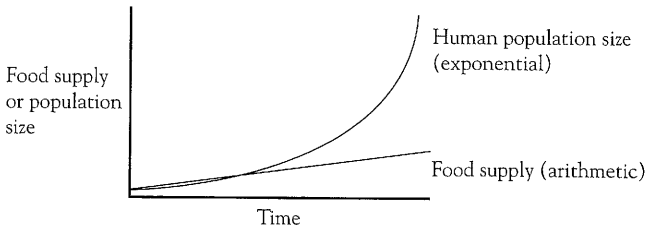

Fig. 5.1 The distinction between arithmetic and geometric (or exponential) growth posited by Thomas Malthus in his famous 1798 essay. His key claim was that food supply was growing arithmetically (the straight line) while the human population was growing exponentially (the curve).

Fundamentals of geometric or exponential growth

Discrete (geometric) growth

Suppose we want to characterize population growth over time for a species that breeds annually and is sampled annually. The growth rate of the population over discrete time steps, otherwise known as the population multiplication rate or **geometric growth rate** (λ; called **lambda**), describes abundance next year as a multiple (or proportion) of the abundance this year. A population with $\lambda=1.0$ is **stationary**, meaning that it neither increases nor decreases. A population with a λ value of 2.0 will double in 1 year. If $\lambda=0.75$ the population will be three-quarters the size that it was last year; that is, the population will decline by 25%. Mathematically, the abundance of a population (N) at time $t+1$ is a function of both abundance at time t and the population growth rate:

$$N_{t+1}=N_t\lambda \tag{5.1}$$

If the population continues to grow at the rate λ for t time steps from an initial abundance at time 0 (N_0), then at time t we would expect N to be:

$$N_t=N_0*\lambda_1*\lambda_2*\ldots\lambda_t$$

$$N_t=N_0\lambda^t \tag{5.2}$$

So to estimate population growth, λ, as a function of a change in abundance over one time step, we just rearrange eqn. 5.1:

$$\lambda=N_{t+1}/N_t \tag{5.3}$$

And to estimate the constant annual growth rate over t time steps, rearrange eqn. 5.2:

$$\lambda=\sqrt[t]{\frac{N_t}{N_0}}=\left(\frac{N_t}{N_0}\right)^{\frac{1}{t}} \tag{5.4}$$

As an example, consider wolves (specifically, the population in the US northern Rocky Mountain states after reintroduction). Minimum counts for 3 years were $N_{1998}=275$, $N_{1999}=322$, and $N_{2000}=433$ (US Fish and Wildlife Service et al. 2001). Using eqn. 5.3, annual λ estimates were: $\lambda_{1998-9}=322/275=1.17$; $\lambda_{1999-2000}=433/322=1.34$. These can be interpreted as 17 and 34% increases per year. If we only had the abundances in 1998 and 2000 (spanning 2 years) and wanted to calculate the average annual λ value, we would use eqn. 5.4: $\lambda_{1998-2000}=\sqrt[2]{\frac{433}{275}}=1.25$, which gives an average 25% increase per year.

Because λ is a *rate* of change, two different-sized populations with the same λ will have different *absolute* changes in abundance. For example, if $\lambda=0.80$ a population of 1000 rabbits will change by 200 rabbits in one time step (from 1000 to 800) whereas a population of 100 will decrease by only 20 rabbits.

Continuous (exponential) growth

In some ways it would be easier just to stop at the discrete form of population growth described by geometric change. It is, after all, an intuitive and easy way to explain population growth: "My newt population decreased by 3% per year ($\lambda=0.97$) from 1999 to 2001." But suppose the species of interest does not reproduce seasonally, or we want to compare population growth in an elephant population (which undergoes yearly intervals of population change) with that in a mouse population (monthly or bimonthly intervals of population change). It turns out that discrete growth represented by λ has some awkward mathematical properties, so to really understand population growth requires understanding the calculus-based continuous-time analog of λ, defined by r and interchangeably called the **exponential growth rate** or the **instantaneous per capita growth rate**.[1]

With your help, our little venture showing how r relates to λ will be fairly painless. On Fig. 5.2(a), sketch lines up from 2007 and 2008 on the x axis to the curved line, then from each of these points across to the y axis; the lower intersection with the y axis is N_{2007}, the upper is N_{2008}. The lines show the change in abundance (ΔN) over a 1-year change in time (Δt) from 2007 to 2008. Now, we can shorten the interval, making Δt smaller and smaller, so ΔN gets smaller too (try it on the graph). Make a smaller and smaller interval, converging to a point on the curve. At this point, the change in the population per unit time has gone from the world of discrete time to the world of continuous time described by a derivative, where a tiny (infinitesimal or instantaneous) change in population size (dN) occurs over a tiny interval of time (dt):

$$dN/dt=rN \tag{5.5}$$

where r is the instantaneous growth rate per capita (per individual).

Because dN/dt is a derivative, you can also think of rN as the slope of the tangent of the curve of N plotted against time (Fig. 5.2a). To isolate r, abundance over time can be plotted on a logarithmic scale, which makes the curved line of abundance straight, with the slope of the line equaling r (Fig. 5.2b)[2].

[1]The instantaneous per capita growth rate, r, is sometimes called the **intrinsic** growth rate because it represents growth of the population without density dependence.

[2]A reminder: logarithms, regardless of what base they are in (e.g. base 10 or base e) convert multiplicative processes (such as exponential growth) to additive processes. Thus, a multiplicative geometric growth curve becomes a straight line when plotted as the logarithm of abundance.

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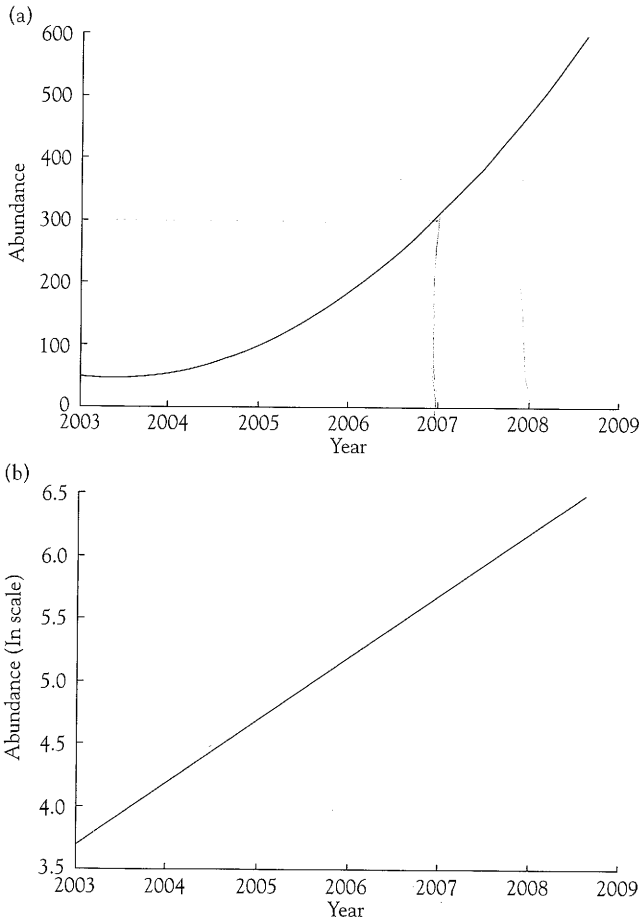


Fig. 5.2 Constant exponential growth of a hypothetical population (r=0.5 or the equivalent λ=1.65), showing how the curve of abundance over time (a) becomes a straight line when plotted against the natural logarithm, ln, of abundance (b). The slope of the line in (b) is equal to r in a constant environment.

How does the instantaneous per capita growth rate, r, relate to λ? The two are interchangeable, after a simple conversion:

$$r=\ln \lambda$$

or

$$\lambda=e^{r} \tag{5.6}$$

The ln is the **natural logarithm**, with the base e (which is about 2.718).

The property of being able to substitute λ for r, or r for λ, means that eqn. 5.2 can be rewritten as:

$$N_t = N_0 e^{rt} \quad (5.7)$$

A population with an $r>0$ is increasing, and one with $r<0$ is decreasing.

To get familiar with converting between λ and r, let's convert the previous calculations of wolf λ values to values of r:

$$\lambda_{1998-9} = 1.17 \text{ converts to } r_{1998-9} = \ln 1.17 = 0.16$$

$$\lambda_{1999-2000} = 1.34 \text{ converts to } r_{1999-2000} = \ln 1.34 = 0.29$$

As a convenient shortcut for converting between λ and r, it turns out that when r is close to 0, as it usually is for most wildlife populations, $\lambda \cong 1 + r$. This means that when population growth is a relatively small increase or decrease you can approximate λ by adding 1 to whatever r is: an r value of 0.2 gives a λ value of about 1.2, and an r value of −0.2 gives a λ value of about 0.8. This rule of thumb breaks down as the absolute value of r gets further from 0 (e.g. try it for $r=0.6$ or −0.6); in that case you need to use your calculator and eqn. 5.6: $\lambda = e^r$.

Overview of λ and r

Exponential or geometric population growth, described by λ or r, find application in an enormous number of management applications ranging from harvest or endangered species programs to monitoring regimes. These approaches are based on two important assumptions. First, the growth rate over time is assumed to be independent of density. Second, growth is based on population sizes that can be adequately represented by the total number of individuals, ignoring differences between sexes, ages, and so on.

Which is better to use, λ or r? The answer depends on what you are doing. If you are just describing constant growth over time for a population with regular breeding seasons, λ is intuitively easier because it is based on familiar percentage changes. On the other hand, r has many useful properties, as listed here.

- The parameter r is centered on 0, whereas λ is centered on 1. Therefore population change is more intuitive with r, because a positive value indicates an increase and a negative value a decrease. Also, being centered on 0 leads to a symmetry that is lacking for λ: for example, a population going from 100 individuals to 165 and back to 100 over 2 years first has an r value of 0.5 and then an r value of −0.5; the same abundance change described by λ would be 1.65 (=165/100) followed by 0.61 (=100/165).
- If you want to compare species whose biology is based on different time steps, r transforms to other time scales easily whereas λ does not. For example, suppose we want to compare the growth rates of a tortoise and a hare. The tortoise has a growth rate of $\lambda = 1.3$/2 years, whereas the hare has $\lambda = 1.03$/month. Which is increasing faster? To make the comparison on the same time scale, we'll use a monthly growth rate. First convert both λ values to r ($r = \ln \lambda$): 0.26/2 years for the tortoise and 0.029/month for

Box 5.1 Analogy between λ versus r and annual yield versus annual rate in financial circles

For better or worse, few of us in wildlife or conservation biology got into this field because we want to make a lot of money. Still, you can use your knowledge about λ and r to help you make more sense of advertisements for savings and money market accounts, just in case you do make some money and wonder how to save it. Notice that the annual rate (sometimes called the interest rate) is always lower than the annual yield (sometimes called the annual percentage yield). That's because the annual rate means that your money will be compounded instantaneously over the whole year, just like r compounds population size. The annual yield is compounded just once a year, like λ.

So, suppose the annual rate is 5.75%; a population of money growing at $r=0.0575$ (they state r as a percentage to make it more palatable to people). Using $\lambda=e^r$, that is the same as a λ value of 1.0592, or an annual yield (proportional change) of our money of 5.92%. Just as wildlife population growth can be described interchangeably with r and λ, so too can your riches. Investing \$100 today at these rates would give you, 1 year later, $\$100*e^{0.0575}=\$105.92$, which is the same as $\$100*1.0592=\$105.92$. Just as the annual rate and annual yield produce the same amount of interest earned, population growth using r and λ give the same rate of population change after you have transformed them appropriately.

Source: (after Case 2000).

the hare. Converting the tortoise r to a monthly rate (0.26/24) we get 0.011/month, much slower than the hare. Note that if we had simply and incorrectly divided the $\lambda_{tortoise}$ by 24 months (without first converting it to r) we would have calculated $\lambda=1.3/24=0.05$, an absurd answer implying a screaming decline of 95% per year!

- Similarly, you can add r values of a population over successive time intervals to get total growth over the whole period, but you cannot add λ values.
- Finally, if the growth rates over time are variable, the expected growth rate can be estimated by a simple average, or arithmetic mean, of the r values in consecutive time periods, but not of the λ values. We'll develop this idea much more in the upcoming section on the implications of variation in population growth (see below).

In short, Caughley (1977:52) states it nicely: "Although the replacement of the simple statistic λ by the more complex e^r may seem barbaric, it leads to simplified algebra and a better appreciation of the nature of a rate of increase." To make this comparison less abstract, Box 5.1 shows that the advertisements for money market or savings interest rates also use the concepts embodied by λ and r.

Before wrapping up this overview of geometric and exponential growth, we should address a common mistake, where exponential or geometric growth gets confused with "really big growth." Without a doubt, constant geometric or exponential change can propel abundances rapidly upward. For example, suppose you offered to give your

roommate $1 million at the end of the month if he or she will give you just 3 cents today, then double the amount each day for the next 30 days. The population of pennies begins with $N_0=3$ and $\lambda=2$. After $t=30$ days, at the end of the month your roommate would have paid you (eqn. 5.2):

$$\text{Pennies}_{(\text{day } 30)}=3*2^{30}=3{,}221{,}225{,}472 \text{ pennies}$$

After paying back your roommate the $1 million you promised, you would still make more than $31 million!

Notwithstanding such striking examples, exponential or geometric growth is characterized not by how big the population gets or how rapidly it increases, but rather by population change being unaffected by density. For example, a population with $\lambda=1.001$ could grow exponentially for 100 years and only increase from 10 individuals to 11. Simply put, exponential growth may or may not be really large, and a huge population may or may not be growing with exponential growth.

Doubling time

As a way of reviewing and synthesizing the use of simple exponential or geometric growth models, consider how the equations discussed so far can help predict the time it would take a population increasing at a certain exponential rate to double in size. The formula can be memorized, but instead let's derive it from first principles based on eqn. 5.2 ($N_t=N_0\lambda^t$) or eqn. 5.7 ($N_t=N_0e^{rt}$). Given an observed λ or r value, how many time steps (t) would it take for N_t to be twice N_0 if that exponential growth continued? Going through the procedure for λ and using eqn. 5.2:

$$N_{t(\text{double})}/N_0=2=\lambda^t \tag{5.8}$$

To solve for the number of time steps (t) we get t out of the exponent by taking the ln of both sides:

$$\ln 2=t(\ln \lambda) \tag{5.9}$$

Then solve for t:

$$t=\ln 2/\ln \lambda \text{ (recall that } r=\ln \lambda)$$

$$t_{\text{double}}=0.69/r \tag{5.10}$$

Thus the time that it takes to double in size is shorter when population growth is larger. To see how doubling time is affected by growth rate, calculate for yourself the time it would take to double if $r=0.10$ (6.9 years), and compare that with the doubling time for a population in which $r=0.05$ (13.9 years). Once you see how it works for doubling time, you should be able to plug in the right numbers to calculate tripling time, the time to decrease by half, and so forth.

Box 5.2 Doubling time of Olympic mountain goats

Approximately 12 mountain goats were introduced to the Olympic Peninsula of Washington state during the late 1920s (Houston et al. 1994). In 1935, the central mountainous portion of the peninsula (including most of the prime goat habitat) was designated as Olympic National Park, with a mission to conserve the natural biota. The estimated exponential growth rate per year (r) of goats from the late 1920s to the early 1980s was 0.08. In the early 1980s, with more than 1100 goats distributed across the mountains of the park, biologists documented damage to native flora from the goats and the park authorities initiated exploratory efforts for decreasing or removing this introduced species. Suppose that in 1980 we were asked how long it would take for the goat population to double in size if no efforts were taken to reduce numbers and the past growth rates continued.

We're assuming no control in numbers and that population growth will continue as it had in the past. Using eqn. 5.10 from the text:

$$t_{double} = 0.69/0.08 = 8.6 \text{ years}$$

Therefore, our starting point under the assumptions above would be that the population would double in size from 1100 to 2200 goats in about 9 years. In this case, that doubling time did not happen because the park began removing goats in the early 1980s (see Chapter 14).

Box 5.2 gives an example of calculating doubling time in a real population. It also reminds us that by projecting into the future we must assume that conditions in the past hold into the future.

Causes and consequences of variation in population growth

Factors that cause population growth to fluctuate

Population change in the real world will never be constant. Consider the time series in Fig. 5.3. Why aren't the changes in abundance constant over time? Obviously, a big reason will be steady impositions on population growth arising from other interacting species (predation, competition, parasitism, habitat loss due to humans, etc.), or from within the species (e.g. competition and other forms of density dependence). These are **deterministic factors** that change population growth in predictable ways (or at least somewhat predictable; see the Robbins quote at the start of the chapter).

But plots of wildlife abundance over time bounce around a lot more than can be explained by deterministic factors increasing or decreasing population growth rate. Some of the bounce is an artifact of **sample variance**, arising from the process of sampling abundance (see the SE bars in Fig. 5.3, which quantify the precision

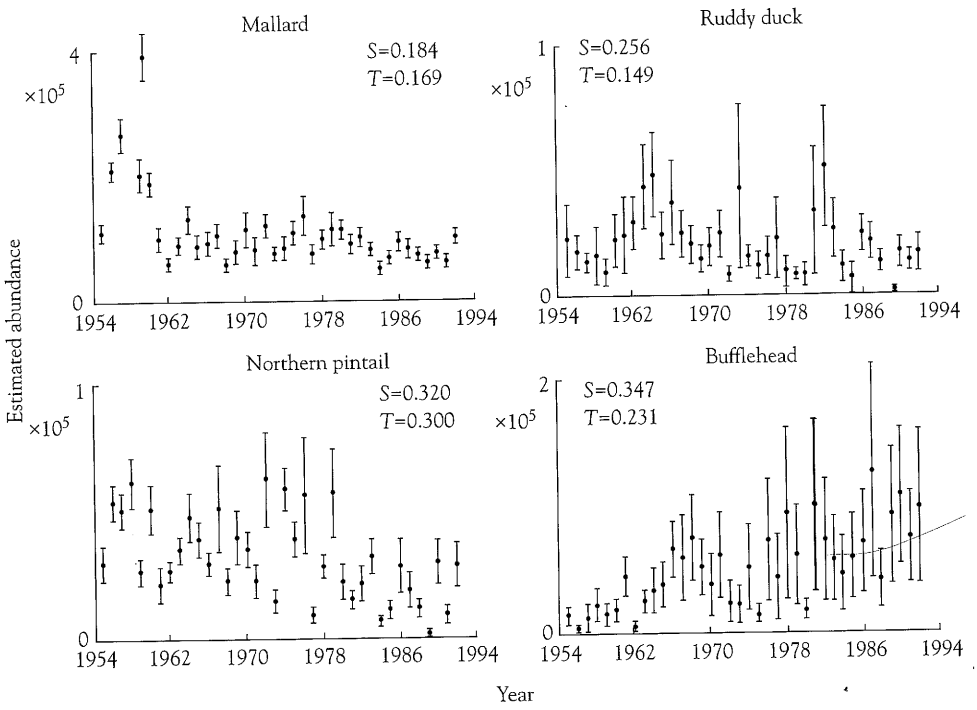


Fig. 5.3 Plots of estimated abundance over time (called **time series**) for four waterfowl species (from Link & Nichols 1994; reproduced by permission of Oikos). Abundance estimates ($\times 10^5$) during the period 1955–92 were obtained by aerial survey corrected for visibility bias, for a stratum of the May Breeding Waterfowl Survey in southern Manitoba. The bars around each abundance estimate represent 1 SE. Total variation in the time series is given by *S* for each species. This includes true process variance (environmental stochasticity over time) as well as sampling variance of the individual abundance estimates (see Chapter 2). The smaller value, *T*, for each species represents true temporal (process) variance, after sample variance is subtracted out. Note that total variation is up to 50% larger than true process variance, reminding us that sampling variance makes the trend in the populations look more variable through time than they really are.

of the annual abundance estimates). Notice, for example, that if I had just plotted the mean abundance estimates (without error bars) for the bufflehead in Fig. 5.3, it would appear that the population bounced around a great deal. But the overlap of the standard error bars arising from sample variance means that true population size actually may have been nearly constant across the time series, especially after 1980. Fortunately, there are ways to mathematically remove the noise contributed to time series by sample variance (Meir & Fagan 2000, White 2000, Holmes 2001).

Thus, deterministic changes could modify population growth over time for any population, and sampling error could make a time series appear to have fluctuations simply because we are making estimates of abundances. But imposed on these are true random fluctuations, otherwise known as **stochastic process variance**, affecting

population growth[3]. The two main forms of stochasticity in population growth are demographic and environmental stochasticity.

Demographic stochasticity includes the inevitable deviation in birth and death rates arising from the mean rates being probabilities across a population. For example, if the mean annual survival rate is 0.8, each animal can only live through a given year, or die. It cannot 0.8 live. For small populations, demographic stochasticity causes variation in population growth even when mean birth and death rates remain absolutely constant.

One of the easiest ways to understand demographic stochasticity is by example. If you toss a coin, you would reasonably expect the probability of heads to be 50%. But if you toss the coin only three times, you cannot possibly get 50% heads: you will get 0, 33, 67, or 100% heads, by chance, even when the mean expectation is 50%. Even if you tossed it 10 times you would not be terribly surprised to get 3, 4, 6, or 7 heads, all of which are deviations from the expected 50:50. However, if you tossed the coin 100 times you would expect the percentage of heads to be much closer to 50%, and with 1000 tosses you would expect it to closely converge on 50%, the expected probability of heads (see Box 5.3).

Consider how this analogy would apply to sex ratios, which are often expected to be close to 50:50 at birth. In a small population, say with only 20 births, by chance only five or six females might be born in a given year. Such chance events – demographic stochasticity – can hamper the ability of a population to increase. Similarly, when numbers are small there could be large deviations from the expected survival rate or birth rate. So demographic stochasticity can affect sex ratio, reproduction, and survival, causing each to be more or less than the mean expectation.

The result of demographic stochasticity is that a population trajectory for a small population will vary even in a constant environment, with no change at all in mean birth or death rates. In particular, even if average population growth should be positive, demographic stochasticity in a small population could cause a decline towards extinction. An often-cited example is the extinction of the dusky seaside sparrow, for which all of the last five survivors happened to be males. Just as you would be more confident that your coin toss would be close to 50:50 when repeated many times, demographic stochasticity is minimized when abundance exceeds about 100 individuals (see Box 5.3).

In contrast to demographic stochasticity, which produces random variation around the mean rates, **environmental stochasticity** produces random changes in the mean vital rates for the population. Environmental stochasticity arises from extrinsic factors, often driven directly or indirectly by weather (Fig. 5.4). For example, if a salamander requires a certain level of moisture to breed, then a particularly hot dry spring may lower the mean reproduction of adults and survival of juveniles across the population. For many wildlife populations, food supplies may affect average survival of young in

[3]To be precise, a lot of the stochastic or random, fluctuations we see in populations may in fact actually be driven by deterministic factors, but can more easily be treated as stochasticity. Given how limited our knowledge is of many things impacting most wild populations, we are usually left treating a lot of variability as randomness even though it might be predictable with more complete information. See the quote about stones and cow pies at the start of the chapter.

Box 5.3 An example of demographic stochasticity based on reintroduced woodland caribou

Although woodland caribou formerly ranged over much of the northern USA, by the early 1980s habitat degradation, poaching, and vehicle collisions had reduced their US distribution to only about 25 animals in the Selkirk Mountains of northern Idaho and northeastern Washington. One recovery strategy for this federally listed endangered species was to translocate caribou back into their historic range (see Chapter 10 for more on caribou translocations). The estimated survival for 60 caribou translocated over 5 years was 0.74 (Compton et al. 1995).

Although of course survival varies over space and time from environmental stochasticity, let's see how much variation we might expect from demographic stochasticity alone. If only two caribou (one female and one male) were released and the environment was constant (environmental stochasticity was 0), the expected number in the next year would be $2 * 0.74 = 1.48$. Of course, as in the coin-toss example there would be three possible outcomes: both caribou survive (survival = 1.0), only one does (survival = 0.5), or neither does (survival = 0). The binomial probabilities of each of these outcomes can be calculated[1], and the table shows that for two individuals we would expect neither caribou to survive about 7% of the time, one of two to survive (for a survival rate of 0.5) about 38% of the time, and for both to survive about 55% of the time. A survival rate of 0.74 is not even possible! Even with the actual reintroduction sizes of 12 and 24, lots of survival rates other than 0.74 are possible. As the population gets close to 100 individuals, the variability due to demographic stochasticity decreases and the expected survival rate converges on the annual survival rate of 0.74 for all individuals.

Percent chance that different population sizes would have particular observed survival rates. (Survival rates centered on the true mean of 0.74 are highlighted.)

		Chance of observed survival rate (%)									
Population size	**Survival rate . . .**	**0–0.1**	**0.1–0.2**	**0.2–0.3**	**0.3–0.4**	**0.4–0.5**	**0.5–0.6**	**0.6–0.7**	**0.7–0.8**	**0.8–0.9**	**0.9–1.0**
2		7	0	0	0	38	0	0	0	0	55
6		0	1	0	4	14	0	30	0	35	16
12		0	0	0	0	6	12	20	26	22	14
24		0	0	0	0	1	6	20	52	18	3
48		0	0	0	0	0	1	24	59	16	0
96		0	0	0	0	0	0	20	70	10	0

[1]The binomial probability of y successes in n trials with a probability of success of z per trial is $\left[\left(\frac{n!}{y!(n-y)!}\right)z^{y}(1-z)^{n-y}\right]$ where ! refers to the factorial (e.g. $4! = 4*3*2*1 = 24$).

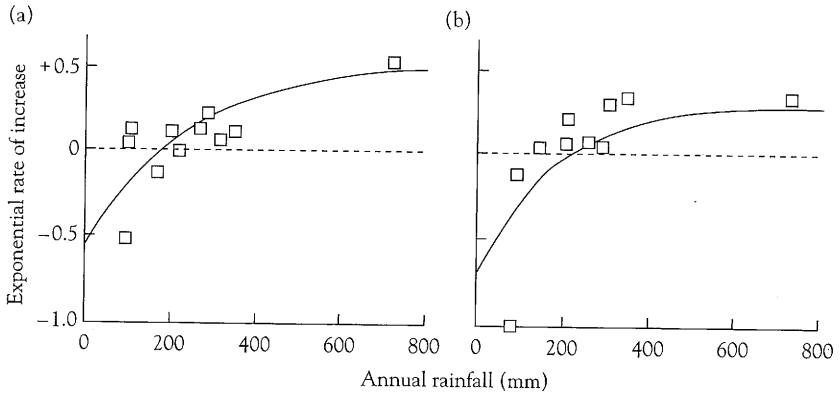


Fig. 5.4 Stochasticity in rainfall patterns explains variation in population growth rates in kangaroos. (a) Red kangaroos; (b) western grey kangaroos. Modified from McCallum (2000). Reproduced by permission of Blackwell Publishing Ltd.

a given year, as do random changes in predators or parasites. In all of these cases, mean vital rates for animals in the population – and therefore population growth rate – vary over time and space in unpredictable ways. Unlike demographic stochasticity, the occurrence of environmental stochasticity is not necessarily dependent on population size: for example, a year where λ fluctuates from 1.2 to 1.1 will reduce population size by about 10% for 50 or 500 animals.

A population exposed to environmental stochasticity (as all are) will inevitably have some very bad years and some very good years (Shaffer 1987). In many cases these stochastic fluctuations may seem extreme to us (perhaps because homes are damaged or human lives are lost), but they are really just somewhere away from the mean. In other cases true outliers can be referred to as **catastrophes** or **bonanzas** because they are outside the range (or at least far out in the tails of the distribution) of normal environmental stochasticity. Volcanic eruptions, avalanches (in some cases), and the plague come to mind as factors leading to catastrophes. Here are some specific wildlife-related examples of catastrophes: in 1973 a hurricane decimated the last Laysan teal population; volcanic eruptions in Japan almost destroyed the last colony of the short-tailed albatross; and a severe winter coupled with overbrowsing wiped out all but 50 of the 6000 reindeer on St. Matthew Island (Simberloff 1988).

Implications of variation in population growth

What happens when numbers of an exponentially increasing population bounce around through time due to stochastic variation? One outcome is fairly obvious: as variance in population growth increases, future population size outcomes become more uncertain and more variable. You can see this if you let a computer play "what if" scenarios of population growth many times (Fig. 5.5). Greater variation in future population sizes leads to an increase in extinction probability (Boyce 1977), even if average population growth is positive. In Fig. 5.5, you can see that a few replicate populations increase to very large sizes while most end small, or even extinct; from this

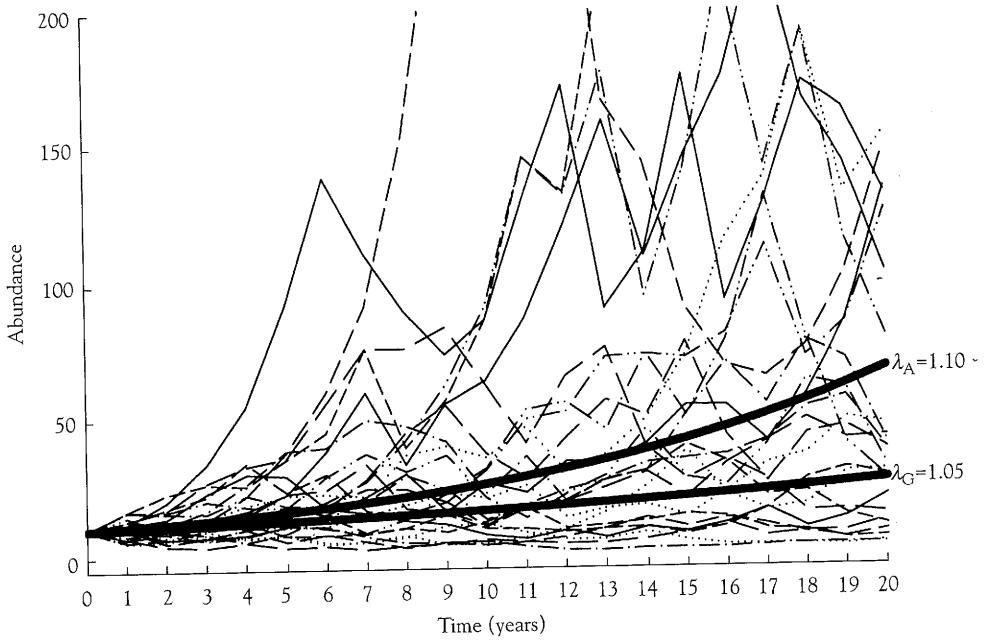
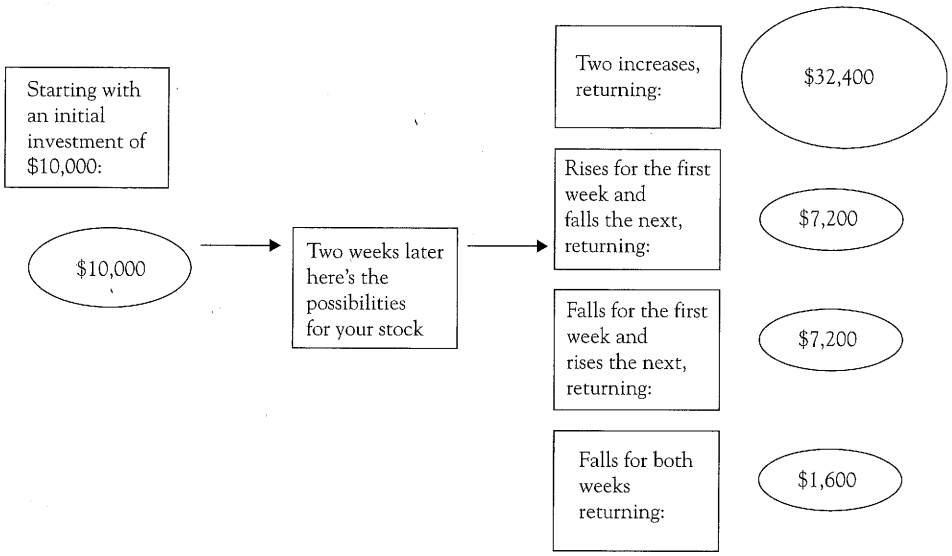


Fig. 5.5 Stochastic geometric growth showing 25 possible population growth trajectories for hypothetical snail kite populations (e.g. Beissinger 1995) beginning with 10 individuals. For each replicate, λ at each of 20 time steps varied randomly between 0.5 and 1.7 (σ^2_λ=0.12). λ_A is therefore 1.1 and λ_G approximately 1.05 (represented by thick lines). Because λ_G represents median population growth, about half of the final abundances fall above the λ_G line and half below.

we can take home the generalization that the greater the environmental stochasticity relative to mean population growth, the higher the chance of extinction.

The second outcome of stochastic variation in population growth is related but less intuitive. In a stochastic environment, the likelihood (or probability distribution) of any particular population size at time t in the future becomes more and more skewed, with most populations being relatively small (their numbers can't go below zero) but with a tiny fraction having huge abundance. The few really big populations inflate the average population size, making it much larger than the most likely future population size. Another way to say this is that without variation, the most likely outcome is the same as the average, but with stochasticity the few big winners make the average become larger than the most likely population size. With stochasticity, the most likely trajectory of population size over time is captured by the geometric mean growth rate (λ_G) – which is mathematically identical to the arithmetic mean, r – not the arithmetic mean growth rate (λ_A; Morris & Doak 2002).

Before exploring this idea with wildlife populations, let's think about uncertainty in outcomes using the stochastic world of playing the stock market (Fig. 5.6). Suppose you were offered a stock that each week either gains 80% of its value or loses 60% of its value: in half of all weeks it gains and in half it loses. You could estimate the average change in value as the **arithmetic mean**, which is a 10% gain (calculated from [80+−60]/2=10). Wouldn't that be an awesome buy for a starving wildlife population



So, the average return per week is still 10% for an arithmetic mean return of $ 12,100 after 2 weeks), but there is a loss in three of the four possible scenarios, indicating the most likely outcome is that you will lose money.

Extending the outcome of the investment to 1 year:

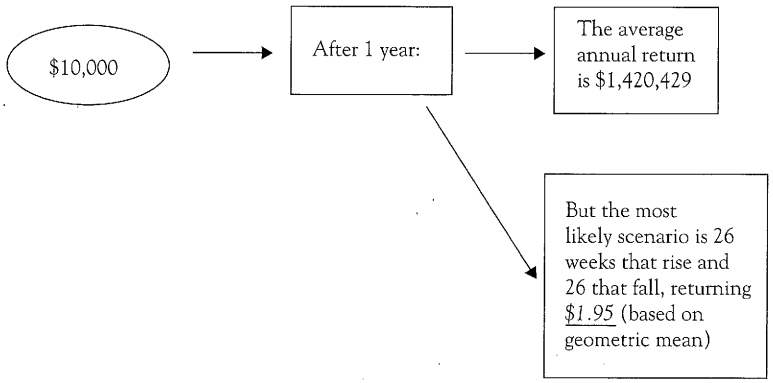


Fig. 5.6 The impacts of stochasticity. This is a deal too good to be true (Chang 2003, Paulos 2003). Suppose I offered you a stock that is updated in value each week: half the time it increases by 80% of its current value, and half the time it loses 60% of its current value. Although the arithmetic mean indicates a 10% gain, if you bought it you would most likely lose a lot of money. In a stochastic world with multiplicative growth (of dollars or populations), go with the geometric mean, not the average from the arithmetic mean.

ecologist? After a year of average growth of 10% per week, a $10,000 investment would be worth more than $1.4 million dollars! So why not quit your job and just buy this stock? Because the arithmetic mean, or average, is driven by the few lucky winners who make a lot of money (due to a rare string of many weeks with 80% gains), while most investors will lose in a big way. If you want to know the most likely outcome you would calculate the **geometric mean** (λ_G or $\bar{r}$; see Box 5.4): in this case you would learn that

Box 5.4 Calculating the geometric mean

The geometric mean differs from the arithmetic mean because instead of adding a total of "t" numbers and dividing by t, you instead multiply the t numbers and take the tth root of the product. To put these words into an equation for the geometric mean population growth rate (λ_G) over time:

$$\lambda_G = \sqrt[t]{(\lambda_1 * \lambda_2 * \lambda_3 * \ldots \lambda_t)}$$

or equivalently

$$\lambda_G = (\lambda_1 * \lambda_2 * \lambda_3 * \ldots \lambda_t)^{\frac{1}{t}}$$

The geometric mean will be less than the arithmetic mean when there is stochasticity. Let's run through an example. Suppose an endangered population grows at a constant $\lambda = 1.05$; we would expect a 5% increase per year, so that in 16 years a population of 100 would have an expected size (from eqn. 5.2) of

$$N_{16} = 100 * 1.05^{16} = 218$$

Now suppose instead that the population growth alternated each year between $\lambda = 1.55$ and $\lambda = 0.55$. The arithmetic mean of the growth rate is still 1.05 [from (1.55+0.55)/2]. But the growth of the average population is governed by the geometric mean, which is

$$\sqrt{1.55 * 0.55} = 0.923$$

After 16 years the expected population size would be

$$N_{16} = 100 * 1.55^8 * 0.55^8 = 28$$

This is the same as projecting all 16 years with the geometric mean: $100 * 0.923^{16} = 28$.

A population of 28 is a lot less than the 218 expected from the arithmetic mean! The variation in population growth leads to a likely decline for the population, even though the deterministic growth rate implies that the population should increase substantially.

Similarly, look back at Fig. 5.6, the stock market example, with a variable growth rate of 80% increase ($\lambda = 1.8$) and 60% decrease ($\lambda = 0.4$). The arithmetic mean is (1.8+0.4)/2 = 1.1, which is what led to the predicted average of

$$\$_{52\ \text{weeks}} = \$10{,}000 * 1.1^{52\ \text{weeks}} = \$1{,}420{,}429$$

By contrast, the geometric mean ($\sqrt{1.8 * 0.4} = 0.849$) gave the predicted most likely earning of

Box 5.4 Continued

$$\$_{52\ \text{weeks}} = \$10{,}000 * 0.849^{52} = \$1.95$$

An equivalent way to calculate the geometric mean population growth rate from a time series takes advantage of the mathematical properties of $r = \ln \lambda$:

- calculate r for each interval by $\ln(N_{t+1}/N_t)$;
- take the arithmetic mean of all of the r values to obtain $\bar{r}$;
- convert the $\bar{r}$ back to λ (by way of $\lambda = e^r$) and you've got your λ_G.

you and the majority of other buyers will lose almost all of your money, ending the year with \$1.95 of your original \$10,000 (Fig. 5.6). This is barely enough for a big mug of coffee with which to console yourself. The average population growth leading to the average earnings (\$1.4 million) is much less informative than the geometric mean leading to the most likely (median) earnings over time.

Bringing this back to wildlife population biology, how would you feel about the fate of a population that increased by 80% half the time and declined by 60% half the time? Just as mean stock market earnings are dominated by a very few big winners, the average population size in a stochastic environment with multiplicative population growth is driven by the likelihood that a few populations would by small chance become very large while most populations would not. Typically we are interested in the geometric mean – indicating the most likely trajectory and its associated population size – not the growth rate of the average population size.

Thus, the real biological variation around λ will make populations grow more slowly than they would under a constant arithmetic mean growth rate. This leads to the counterintuitive finding that a population whose average growth rate is positive could be most likely to decline over time. The magnitude of the decrement in the long-term growth rate of a population depends on how variable the growth rates are (Fig. 5.7).

Specifically, increasing the variance in growth rate (σ^2_λ) causes the geometric mean (λ_G) to be less than the arithmetic mean (λ_A; Case 2000, Lande et al. 2003)[4]:

$$\lambda_G \cong \exp(\ln \lambda_A - [\sigma^2_\lambda/(2 * \lambda^2_A)]) \tag{5.11}$$

In short, λ_G (or its cousin $\bar{r}$, which we'll discuss next section) tells us what the typical population with stochastic growth is likely to do in the future[5]. Because λ_G predicts the

[4]If you like thinking in terms of $\bar{r}$, an analogous approximation uses variance in the r values (σ^2_r) instead of σ^2_λ (Lande et al. 2003:11): $\bar{r} \cong \ln \lambda_A - \sigma^2_r/2$. The applied result is simple: if variance in r is more than twice as big as $\ln \lambda_A$, then $\bar{r} < 0$, and the long-term growth rate becomes a decline towards extinction.

[5]Often in the literature on population viability analysis you will see λ_G or $\bar{r}$ denoted with the symbol μ and called the long-run growth rate.

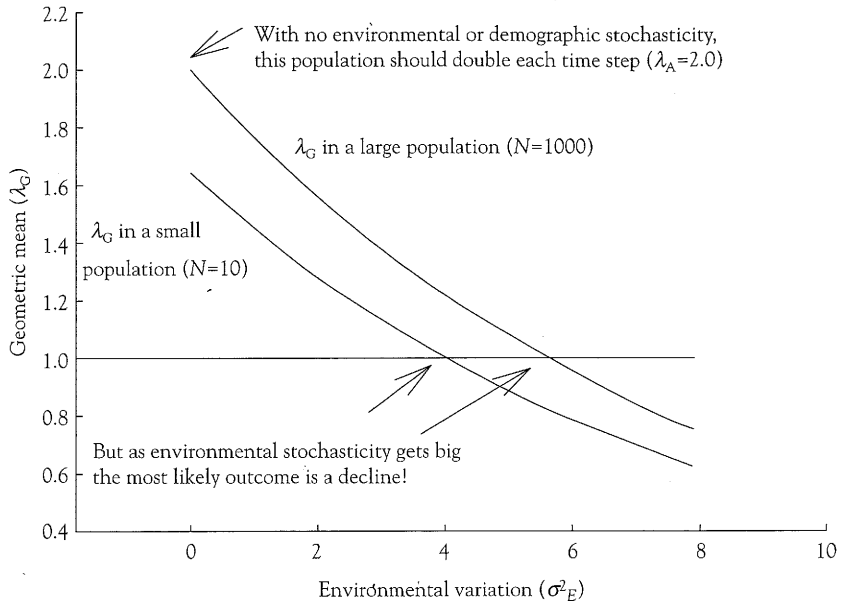


Fig. 5.7 As environmental stochasticity increases there is a reduction in geometric mean growth rate (λ_G). The upper curve shows the reduction in a large population (N= 1000). The lower curve shows that in a small population (N= 10) the added fluctuations due to demographic stochasticity further decrease expected population growth. The arithmetic mean growth rate (λ_A) is 2.0. Notice that the most likely population trajectory is a decline (λ_G< 1.0; horizontal line) as environmental variation increases. Modified from Case 2000.

median population size along the curve (i.e. at any point approximately half the replicates have population sizes above and half below the line for λ_G in Fig. 5.5), a population with $\lambda_G < 1$ or $\bar{r} < 0$ will be more likely to decline than to increase. Next we'll describe how to estimate the exponential population growth rate.

Quantifying population growth in a stochastic environment

So far I have emphasized that population growth for a time series cannot be estimated by a simple arithmetic mean of the λ values (λ_A), but rather should be based on the geometric mean population growth rate. What is the best way to estimate λ_G (or $\bar{r}$) and its associated estimate of uncertainty from field data (J.Y. Humbert & L.S. Mills, unpublished work)?

One way is described in Box 5.4. This straightforward approach of simply taking the geometric mean of all λ values in the time series (or the arithmetic mean of the r values)[6] works fine if estimates of abundance are available for each and every time interval. Unfortunately, for most studies holes creep into the time series because trucks

[6]The variance for $\hat{\bar{r}}$ across q estimates of r with no missing values is $\sigma^2 = \frac{1}{q-1}\sum_{i=1}^{q}(r_i - \bar{r})^2$.

break down, field assistants get sick, weather keeps us from getting to the study site in a particular year, or funding fluctuates. If any breaks occur in the time series, so that some of the λ or r values refer to more than a single year (or time step), the values cannot be simply summed or averaged.

Because holes in the time series are an inescapable part of wildlife studies, how do we estimate the exponential growth rate ($\hat{\bar{r}}$) and its variance (σ^2) in their presence? A simple and intuitive trend estimate, recommended by several papers and books (e.g. Caughley & Sinclair 1994, Caughley & Gunn 1996) is to plot the natural logarithm of all of the abundance estimates ($\ln N$) against time; the slope of the line is an estimate of $\hat{\bar{r}}$ (as in Fig. 5.2b). This method has several problems. First, there is no valid estimate of the variance in $\hat{\bar{r}}$; the variance of the slope actually represents variance of the ln(abundance) values, not of the r_i, and will be less than the actual σ^2 of the population growth rate (Eberhardt & Simmons 1992). This is critical, because it means we can't test whether changes up or down are significant (and if you are trying to convince angry people that you have to change management based upon changes in population numbers, you'd like to have statistics on your side). Second, because successive abundances in a time series are not independent – when a particular abundance deviates from the mean regression line it will likely deviate in the next year too, causing what is known as autocorrelation – a basic assumption of linear regression is violated.

A much better way to estimate exponential trend ($\hat{\bar{r}}$) and its variance (σ^2) is the **density-independent diffusion approximation method** (let's just call it the DA method) championed by Brian Dennis and colleagues (1991; see also Morris & Doak 2002). Essentially, you first transform time elapsed and population change for each interval to account for holes in the time series, then you do a regression of the transformed population changes against the transformed time intervals to estimate $\hat{\bar{r}}$ and σ^2 (Box 5.5 gives a worked example). Specifically, the explanatory variable (x_i) is the transformed time interval between each successive pair of abundance estimates:

$$x_i = \sqrt{t_{i+1} - t_i} \tag{5.12}$$

The response variable (y_i) is the population change corrected for its time interval:

$$y_i = [\ln(N_{i+1}/N_i)]/x_i \tag{5.13}$$

By using population change (y_i) over the interval instead of the raw $\ln N$ values, the autocorrelation problem of the previous method is minimized. For ease in presentation I'll use a year as a time interval, but it could be any unit, such as months or days. Notice that if we had been able to obtain estimates of abundance each year, so that each interval of population change equals one ($x_i = 1$), then the response variable (y_i) would simply be the consecutive r_i estimates.

With the x_i and y_i calculated (easy to do in any spreadsheet program; try it with Box 5.5), you next perform a linear regression of the y values against the x values, forcing the regression intercept through 0. The slope of the regression is an estimate of $\hat{\bar{r}}$. The estimated variance ($\hat{\sigma}^2$) for the estimated growth rate is the mean square error (called the residual mean square in some statistics packages) for the regression.

Box 5.5 How to calculate $\hat{r}$ and its variance ($\hat{\sigma}^2$) using the DA method

An isolated population of adders (a type of pit viper) in Sweden declined dramatically about 40 years ago, and has been studied intensively since 1981 by Thomas Madsen and colleagues (Madsen et al. 1996, 1999). The time series for adult male adders (1981–95) can be used to demonstrate how to calculate $\hat{r}$ and its variance ($\hat{\sigma}^2$) using the DA method. Because the snakes bask in the open in a small study area, so that virtually all adult males adders can be captured in each annual survey, sampling variance is nearly 0, so virtually all variance in the time series is process variance. Although the original data set is complete, I omitted 2 years (1987 and 1988) to show the common case of dealing with missing counts.

Year	Number of adult males	$\ln(N_{t+1}/N_t)$	$x_i = \sqrt{t_{i+1} - t_i}$	$y_i = \ln(N_{t+1}/N_t)/x_i$
1981	19	−0.0541	1	−0.0541
1982	18	0.201	1	0.201
1983	22	0.128	1	0.128
1984	25	−0.0834	1	−0.0834
1985	23	0.0000	1	0.0000
1986	23	−0.191 across three intervals	1.732	−0.110
1987	No count			
1988	No count			
1989	19	−0.111	1	−0.111
1990	17	−0.125	1	−0.125
1991	15	−0.511	1	−0.511
1992	9	−0.406	1	−0.406
1993	6	0.154	1	0.154
1994	7	−0.560	1	−0.560
1995	4			

Both the explanatory variable (time interval x_i) and the response variable (growth rate y_i) are transformed to account for the different number of years spanned by the growth rates. A linear regression of y_i against x_i, forcing the intercept through 0 (yes, it will look odd because so many of the x_i values are equal to 1), gives a slope of −0.11, a SE of the slope of 0.067, and a variance (error mean square) of 0.063. Therefore:

$$\hat{r} = -0.11 \text{ and } \hat{\sigma}^2 = 0.063$$

A confidence interval (CI) is calculated from the SE and the Student's t value. Specifically, a 90% CI is specified by $\hat{r} \pm [t_{0.10,\ q-1} * \mathrm{SE}(\hat{r})]$, where q is the number of y_i in the regression (12 in this case). For these data the 90% CI of $\hat{r}$ is:

Box 5.5 Continued

upper: $-0.11+(1.796*0.067)=0.01$

lower: $-0.11-(1.796*0.067)=-0.23$

Although these count data imply a declining population (with 90% CI barely overlapping 0), the story has a happy ending: the inbreeding depression that contributed to the decline was reduced by translocations, with a considerable population increase after 1996 (see Chapter 9).

A confidence interval (CI) for $\hat{\bar{r}}$ can be calculated from the standard error (SE), usually supplied by the statistics package and labeled as the SE of the slope; if not, you can hand-calculate SE from $\sqrt{\frac{\hat{\sigma}^2}{\text{Number of years spanned}}}$, where $\hat{\sigma}^2$ is the estimated variance and number of years spanned means the duration of the time series (unaffected by missing values in the time series). The confidence interval is: $\hat{\bar{r}} \pm [t_{\alpha,q-1} * \text{SE}(\hat{\bar{r}})]$ for the upper and lower intervals.

The $t_{\alpha,q-1}$ values are the critical values of the two-tailed Student's t distribution (available in any statistics book[7]) with a significance level of α (for example, $1-0.95=0.05$ for a 95% CI, or $1-0.90=0.1$ for a 90% CI) and q equaling the number of transitions used in the regression. As you recall, the 95% CI tells us that if we were to do this study several times using the same population and same sample size, 95% of the time the true growth rate would fall within the range of the estimated confidence interval. As I preached in Chapter 4 (on estimating vital rates), confidence intervals are essential because they help indicate whether an apparent trend is actually likely to be different from zero; whether or not our $\hat{\bar{r}}$ confidence interval contains zero becomes especially important in management applications, for example in deciding whether to delist an endangered species that appears to be increasing[8].

The DA method does an excellent job of estimating density-independent trends, and their variance, in a variety of conditions (Humbert & Mills, in preparation)[9]. Other insights that can be gained from this regression method include confidence intervals for variance (σ^2), tests for outliers, tests for changes in trend in different segments of the time series, and tests for temporal autocorrelation in the population growth rate (i.e. whether a good or bad year for growth is correlated with whether previous or successive intervals were good or bad; see Morris & Doak 2002). The estimates of $\hat{\bar{r}}$ and $\hat{\sigma}^2$ can also be used to predict probabilities of extinction from time-series data (see Chapter 12).

[7]You can also get the t statistic in Microsoft Excel by using =TINV (your probability, your $q-1$).

[8]A reminder: the variation in the time series should represent true process variation and not sample variance arising from estimating abundance (Chapter 2); if sample variance is not accounted for in the time series, the variance of the growth rate would be artificially large.

[9]Although the previous method, plotting ln N against time, performs well under some conditions the DA method always outperforms it; because the two methods can give qualitatively different results (one says increase while the other says decrease), you should always use the DA method.

How long a time series is needed to estimate trends reliably? The answer depends on many factors, of course, but a rule of thumb is at least 10–15 years or so (Swanson 1998, Holmes 2001, Morris & Doak 2002). However, here's a surprising but useful bit of mathematical trivia that can affect how you sample across the time series: the DA method for estimating $\hat{\bar{r}}$ is absolutely equivalent to a form where only the first and last data points are used to estimate trend[10]:

$$\hat{\bar{r}} = \frac{1}{\text{Total duration of survey}} * \ln\left(\frac{N_{last}}{N_{first}}\right)$$

Although this means you could quickly determine $\hat{\bar{r}}$ with just this first-and-last-points method, it has no measure of variance so you'll still need to fall back to using all data points with the DA method to get a proper variance[11]. The fact that the DA method reduces to using just the first and last points to estimate trend – and that it estimates both $\hat{\bar{r}}$ and σ^2 really well, even when up to half of the data points in a time series are missing (Humbert & Mills, in preparation) – suggests that if there is no reason to suspect cycles or other factors that would change the trend, the best strategy is to place more effort and money into fewer data points (with improved accuracy), even if it means lots of holes in the time series. Thus to estimate trend for a 15-year time series you might put more effort into only seven really good estimates of abundance rather than 15 mediocre ones.

Other approaches may also be used to estimate trends of wildlife populations over time. For example, Bayesian analyses (e.g. Taylor et al. 1996) are becoming more popular. Also, if mark–recapture data are available both λ and its variance can be calculated directly (see Nichols & Hines 2002 for nice overview and Cam et al. 2003 for an application based on marbled murrelets).

Summary

Population growth (and decline) is a multiplicative process, not an additive one, leading to exponential or geometric changes in the absence of density or individual-level effects. Although the bounce, or variation, that accompanies population changes over time can arise from deterministic factors coming and going, in part the variation in numbers will be an illusion arising from the fact that we typically have to sample (not census) a population; thus, nuisance sampling variation makes it look like the population varies more over time than it really does.

Even with these two sources of variation accounted for, however, there will be process variance in population growth due to demographic and environmental stochasticity. Stochastic variation in growth rates causes the long-term most-likely

[10] You've seen this before – this is mathematically identical to the estimate of λ in eqn. 5.4.

[11] Although some have suggested that the DA method wastes data because it reduces to only using two points in the time series, the alternative approach (least-squares regression of ln N against time) also weights more heavily the first and last data points in estimating the slope of the line.

abundance – based on the geometric growth rate – to be lower than that based on the arithmetic average λ. This leads to the counterintuitive finding that a population which has, on average, a positive growth rate may be most likely to decline. The best way to estimate population growth rate and its variance from a field-based time series is via a regression on transformed growth rate and time.

Although exponential and geometric growth are based on a number of assumptions, and no population can grow without limit for long, understanding this simple form will make it easier to understand more complicated models of population growth. Furthermore, we can learn a lot about mechanisms of population growth (increases or decreases) for real populations by comparing trajectories with what might be expected under simple geometric or exponential growth. The next two chapters will add complexity to our tools for assessing and predicting population change over time.

Further reading

Case, T. (2000) *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, Oxford. An excellent overview of theory, clearly and cleverly explained.

McCallum, H. (2000) *Population Parameters: Estimation for Ecological Models*. Blackwell Science, Oxford. Provides a thorough background for estimating population growth rate.

Morris, W.F. and Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA. The "go- to" source for time-series analysis, matrix modeling, and many other important topics.

6

Density-dependent population change

> *The elephant is reckoned the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase; it will be safest to assume that it begins breeding when thirty years old, and goes on breeding till ninety years old, bringing forth six young in the interval, and surviving till one hundred years old; if this be so, after a period of from 740 to 750 years there would be nearly nineteen million elephants alive, descended from the first pair.*
>
> **Charles Darwin (1859), *On the Origin of Species***

Introduction

So far we have learned how to describe and predict population change when additions and deletions to a population are unaffected by its own density. Of course, Darwin's quotation reminds us that it would be silly to expect populations to increase exponentially for long periods. Eventually, there will be feedback between the density of the population and its growth rate. **Density dependence** refers to the profound influence that a population's density has on the vital rates of individuals in the population; changes in vital rates, in turn, lead to changes in population growth rate[1].

This chapter will first cover classic negative density dependence, where high numbers lead to negative feedback on vital rates and population growth. We will then discuss positive density dependence, where survival or reproduction actually improves with higher density. Finally, we will explore some ways to incorporate density dependence in models that can be useful both for prediction and to show how surprisingly complex dynamics can emerge from simple processes.

[1] As in the last chapter, remember that population growth refers to increasing, decreasing, and constant populations.

Negative density dependence

Increases in density can exacerbate competition among members of a population and heighten susceptibility to predation, parasites, and disease. As long as humans have been observing other species (or their own species; see the quotation at the start of Chapter 5 from Malthus) we have noticed the occurrence and consequences of intraspecific competition among individuals of a species. Sometimes this competition occurs as direct **interference** or **contests** among individuals, as in fights for food, mates, or territories; winners get sufficient resources to survive and reproduce while losers may not. In other instances the competitive interaction is **exploitative**, or based on scrambles for resources, with simultaneous use of a common resource (often food) lowering the amount of that resource available to each individual without direct interference; this is like sharing a single pie with more and more people.

Obviously, the mechanisms and outcomes of competition can operate simultaneously, a fact nicely demonstrated with black-throated blue warblers that show clear negative density dependence (Fig. 6.1a). As abundance increases the warblers experience scramble competition, with reduced average fecundity across individuals. At the same time, contest competition occurs on a broad scale because increases in warbler abundance force additional individuals into areas of lower quality (Rodenhouse et al. 2003).

Competition is not the only mechanism that can lead to negative density dependence. For example, larger groups may be more conspicuous to predators, or have an increased probability of contracting parasites or contagious disease. In short, under negative density dependence births or survival – and the associated observed population growth rate – decrease as the population size increases (Fig. 6.1). Negative density dependence thus **regulates** population numbers within some equilibrium size range (carrying capacity) by decreasing population growth at high density and increasing it at low density.

Although regulation is a density-dependent process, **limiting factors** that determine the actual equilibrium population size range may be density-dependent or density-independent (Sinclair 1989, Caughley & Sinclair 1994, Hixon et al. 2002). As an example of both density dependence and environmental stochasticity (a density-independent factor) acting simultaneously as limiting factors, arctic ground squirrels experience strong density dependence on the proportion of females weaning a litter and the proportion of females surviving winter hibernation, but the weaning rate is also determined independently by weather (Karels & Boonstra 2000). Similarly, endangered San Joaquin kit foxes in California respond to both density (high density both caps territorial breeders and increases juvenile mortality) and rainfall (rain affects vegetation, which in turn affects small mammals, whose numbers can drive fox reproductive rate; White & Garrott 1999, Dennis & Otten 2000). For applied population biology the important point is to recognize that density can at times negatively affect vital rates, and the resulting population growth rate.

LITERATURE

Density-Dependence

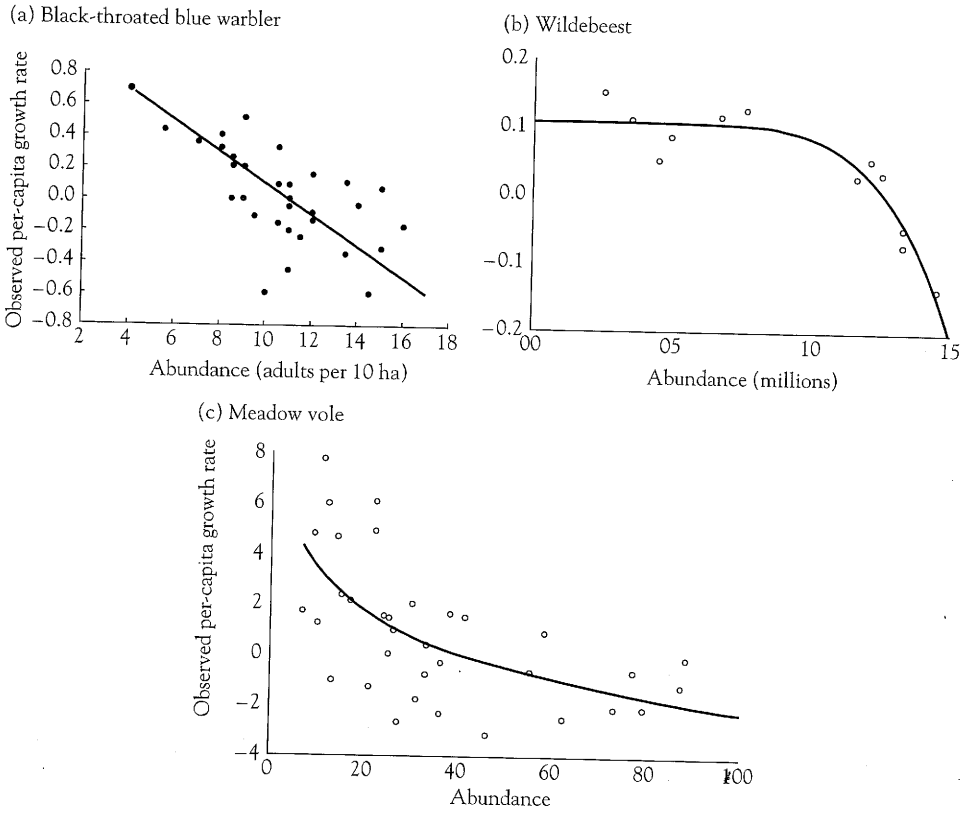


Fig. 6.1 Some examples of negative density dependence in wildlife populations. Observed per-capita population growth rate measured from time series of abundances $[\ln(N_t/N_{t-1})]$ is plotted against abundance. (a) Black-throated blue warblers (modified from Rodenhouse et al. 2003; reproduced by permission of The Royal Society); (b) wildebeest (from Turchin 1999 after Sinclair 1996; reproduced by permission of Oikos); (c) meadow vole (from Turchin 1999; reproduced by permission of Oikos). Notice that all sorts of linear and nonlinear responses of population growth to density are possible.

Positive density dependence

Of course, interactions among members of a population are not always negative. An increase in vital rates or population growth as density increases (or a decrease as density decreases) is referred to as positive density dependence[2]. The ecologist W.C. Allee was the first person to give comprehensive attention to the existence and

[2]Sometimes you will see positive density dependence referred to as **inverse density dependence**, where inverse is used because it is the opposite of traditional (negative) density dependence. In the fisheries literature this form of density dependence is often called **depensation**. I'll stick with positive density dependence: survival, reproduction, and population growth are positively related to density.

implications of positive density dependence (Allee 1931), so the phenomenon is often referred to as an **Allee effect** (for reviews see Courchamp et al. 1999, Stephens & Sunderland 1999). Box 6.1 shows a detailed example.

Some of the most important instances of positive density dependence occur when a population becomes very small, teetering on the brink of extinction[3]. In these cases,

Box 6.1 Multiple Allee effects in African wild dogs

There are fewer than 5000 African wild dogs remaining, and their persistence may be affected by Allee effects (Creel & Creel 2002). Larger pack sizes increase the likelihood of a successful kill in a given hunt, with heavier prey killed, shorter chases, and more meat per dog. Increasing pack size also confers benefits in predator defense. Larger packs can better defend their kills against spotted hyenas, and can more successfully counter attacks from other wild dog packs. Larger packs can also more easily defend their pups from predation.

The increased food acquisition and defense leads to a positive relationship between pack size and the number of offspring born and raised. Nonbreeders guard pups and feed them regurgitated meat. As pups grow older, nonbreeders continue to guard the carcass as pups eat. Through these mechanisms, packs with 10 or more adults raised three times as many yearlings compared to packs with nine or fewer adults (with 10.4 compared with 3.4 pups surviving 1 year, respectively). Packs with fewer than five adults are unable to raise pups (Creel & Creel 2002).

Of course, the benefits of increasing pack size evaporate at larger numbers as negative density dependence kicks in, with factors such as reproductive suppression at large pack size. Thus African wild dogs are an excellent example of positive density dependence at low numbers and negative density dependence at higher numbers.

A group of African wild dogs attacking a young wildebeest. Photograph by Scott Creel.

[3]Although some include as Allee effects both demographic stochasticity and inbreeding depression, I consider these elsewhere (see Chapters 5 and 9). These processes do depress population growth at low numbers, and therefore lead to the same outcome as Allee effects (Lande et al. 2003), but they can be modeled and managed separately from Allee effects (Chapter 12).

Table 6.1 Some possible mechanisms that lead to positive density dependence (Allee effects) in wild populations (Creel & Creel 2002).

Mechanism	Example
Minimizing predation	
Increased predator detection and defense	Survival rates in Dwarf mongoose in Kenya increase with group size because vigilance behavior by guards decreases predator attacks; the guards also defend against ground predators (Rasa 1989).
Greater confusion for predator	The confusion effect causes largemouth bass to take longer to capture silvery minnows as minnow school size increases (Landeau & Terborgh 1986).
Decreased probability of individual capture	Predator swamping: per-capita nest mortality is reduced in larger black brant colonies because predator numbers are overwhelmed (Raveling 1989).
Foraging advantages	
Access to foods	Small colonies of blind mole-rats are more likely to fail because they are unable to rapidly extend burrow systems to obtain food during the brief time period when the soil is moist and easily worked (Jarvis et al. 1998).
Increased resource detection	After being reduced in numbers by hunters and habitat alteration, a cause of further decline in passenger pigeons may have been that small flocks were compromised in their ability to find their patchy and sporadic food sources (e.g. acorns and nuts; Reed 1999).
Cooperative resource defense	Larger groups of coyotes are better able to defend carcasses against intruder coyotes (Bekoff & Wells 1986).
Mating and caring for young	
Finding mates	Glanville fritillary butterflies less likely to locate mates and successfully reproduce in small populations (Kuussaari et al. 1998).
Caring for young	The number of young fledged per nest increases with group size in white-fronted bee eaters because helpers reduce starvation of nestlings by provisioning food; helpers also assist in nest excavation, nest defense, and egg incubation (Emlen 1990).
Conditioning of environment	
Temperature tolerance	Bobwhite quail in large coveys standing in a circle with their tails towards the center of the circle are better able to survive extreme low temperatures (Allee et al. 1949).

extinction risk is exacerbated because individuals in small populations or groups are compromised for some or all of the following reasons (Table 6.1): (i) detection, confusion, or avoidance of predators, or the dilution of per-capita predation risk; (ii) foraging ability; (iii) mating and caring for young; or (iv) conditioning of the environment.

Positive density dependence can also affect dynamics in large populations. A spectacular illustration occurs in mormon crickets, which form migratory bands 16 km long and several kilometers wide packed with crickets; mortality within the group is nearly zero, while animals outside the group have high mortality (Sword et al. 2005). In invasive or pest populations, positive density dependence can affect how outbreaks occur and whether a pest will spread (Taylor & Hastings 2005). For example, after first being released in the New York City area about 1940, house finches spread relatively slowly at first, then abruptly accelerated their population growth and range expansion across eastern North America, consistent with crossing an Allee-effect threshold (Veit & Lewis 1996).

Overall, positive density dependence is probably widespread, especially in critically small wildlife populations (Liermann & Hilborn 2001). The most likely scenario for the majority of wildlife populations is that both positive and negative density dependence occur at different densities.

The logistic: one simple model of negative density-dependent population growth

Having considered some biological mechanisms that cause populations to exhibit negative and positive density dependence, we are ready to capture the effects of these processes on population growth. In the exponential growth model (Chapter 5), birth and death rates are unaffected by densities. Thus, for populations growing exponentially the change in numbers is described by

$$dN/dt = rN \tag{6.1}$$

Exponential growth under this continuous time model indicates that at any time the population change equals the number of individuals (N) at that instant multiplied by r, the instantaneous growth rate per capita.

In contrast, with density dependence, population growth is not constant as population size changes over time. In particular, reproduction and/or survival changes with density, leading to potential changes in population growth. Figure 6.2 shows just a few ways that density dependence could change per-capita mortality (1 − survival) and/or reproduction. The point at which per-capita mortality and reproduction are equal, so that the population just replaces itself and $\lambda = 1$ ($r = 0$), is called the **carrying capacity** (denoted by K). The carrying capacity is considered to be an **equilibrium** because if density is greater than K then mortality exceeds reproduction and the population will decrease to K; if it is less than K then reproduction exceeds mortality and the

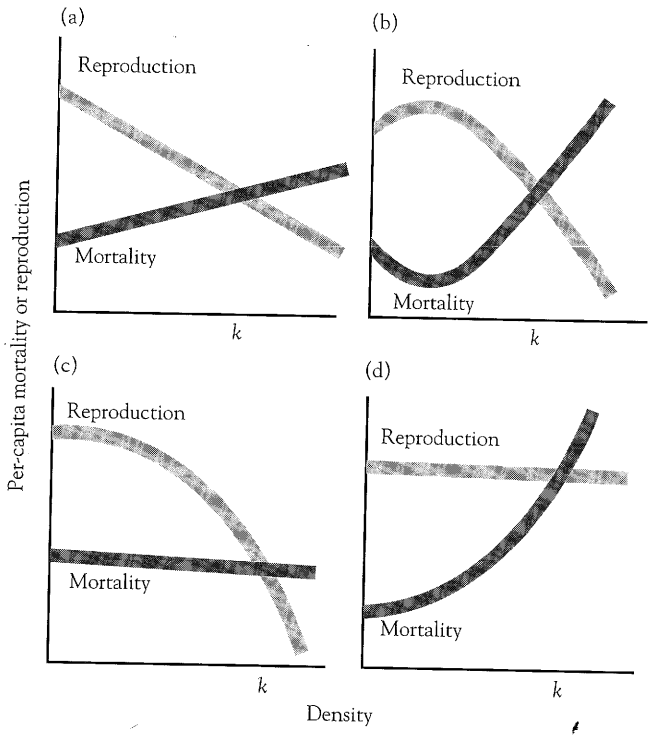


Fig. 6.2 Four possible ways that density dependence could affect per-capita mortality and reproduction rates. All graphs show only negative density dependence except (b), which at low density shows a small range of positive density dependence. The bands embrace the uncertainty and changes in the relationships. The region where the bands cross represents the carrying capacity (K), where births and deaths are equal.

population increases towards K[4]. Notice in Fig. 6.2 that the vital rates are drawn as bands (not lines), so that the carrying capacity (where mortality balances reproduction) is a zone, not a single number. The bands reflect inevitable uncertainty in both the density-dependence relationship and in vital rates and abundance over time, so carrying capacity becomes a range of abundances, not some exact number. Another important point conveyed by Fig. 6.2 is that one could draw an infinite number of ways in which density dependence could change vital rates.

As per-capita reproduction and mortality change with density, the realized per-capita growth of the population [$\ln(N_{t+1}/N_t)$] becomes a function of both the instantaneous growth rate per capita of the exponential model (r; often called the **intrinsic growth rate**) and of the way that the r value is affected by density. In a simple population model, the r gets multiplied by a term that dampens (or increases) it by an

[4]Don't fall into the trap of thinking of carrying capacity as the maximum population size observed. For many reasons (including stochastic fluctuations) a population could, at times, exceed or be less than K.

amount depending on the size of the population and the form that density dependence takes. The form of the relationship between density and realized per-capita growth rate $[\ln(N_t/N_{t-1})]$ could be linear or it could be a curve. The absolute simplest model is for negative density dependence to impose a linear decrease in realized per-capita growth rate as abundance increases. At very low abundance, realized per-capita growth rate is equal to r, the intrinsic rate under exponential growth. But as density increases, the realized per-capita growth rate declines in a steady, linear fashion. This is a **logistic growth model** (Fig. 6.3).

The logistic growth model, plotting abundance over time (Fig. 6.3b), has the characteristic S shape that we know and love from ecology classes. Notice too that the population size asymptotes at K, the carrying capacity. In other words, at K the population is stationary, neither increasing nor decreasing.

We can put the logistic curve of Fig. 6.3(b) into a continuous-time formula by simply modifying the exponential growth equation (eqn. 6.1) to dampen the expression of r as abundance increases:

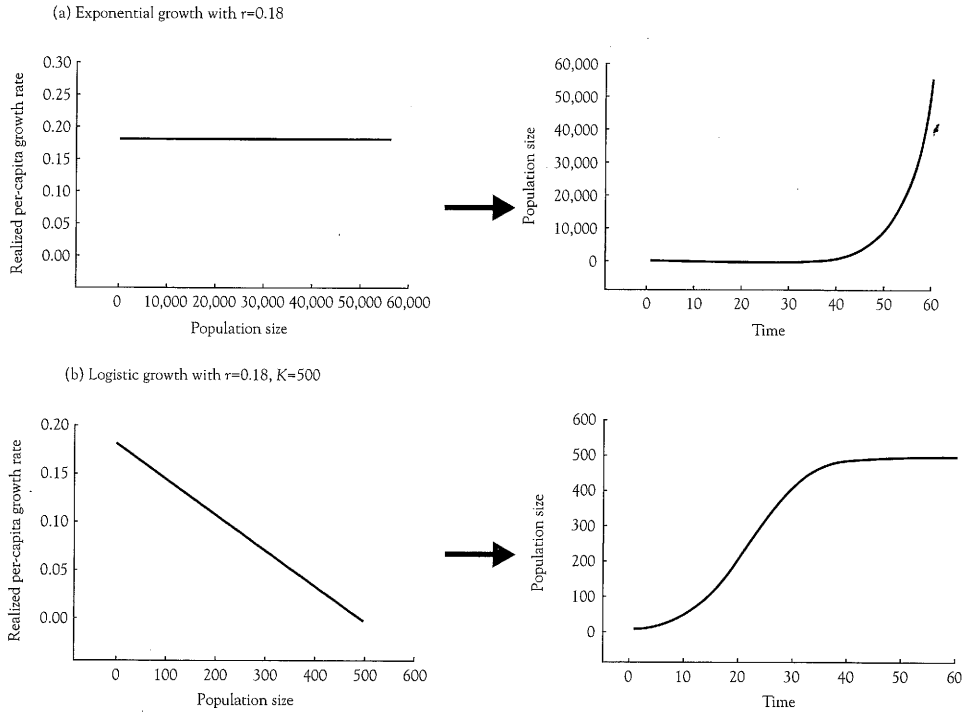


Fig. 6.3 The contrast between exponential and logistic growth. (a) Exponential growth. The realized per-capita population growth rate measured from a time series ($\ln[N_{t+1}/N_t]$) is equal to the intrinsic exponential growth rate (r), no matter what the population size is. This lack of density dependence leads to exponential growth of the population over time. (b) Logistic growth. With a linear decline in realized per-capita population growth rate as the population size increases, the population increases exponentially at first, then slows its growth as it approaches carrying capacity.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{6.2}$$

To dissect this equation, notice that the rN part is just exponential growth (eqn. 6.1). The rest of the equation $(1-N/K)$ decrements population growth as density increases[5]: when abundance is very small relative to carrying capacity (small N compared to K), the part in parentheses is basically one and population change (dN/dt) is nearly exponential. When N equals K, the part in parentheses is zero so dN/dt is zero (no change in population). When N is greater than K the population declines.

From eqn. 6.2 we can derive another way of writing the per-capita growth rate:

$$\frac{dN}{dt} * \frac{1}{N} = r\left(1 - \frac{N}{K}\right) \tag{6.3}$$

The translation in words is again that per-capita population growth declines linearly as N goes from zero to K.

A topic of major interest in applied ecology, especially for thinking about harvest regulations, is the **recruitment** of new individuals or **yield** of the population. In practical terms, this is the net number of new individuals in a population over a unit of time; in terms of modeling it is characterized by dN/dt. For logistic growth, recruitment is maximized when the population is one-half the size of the carrying capacity (Fig. 6.4): at low abundance growth is essentially exponential, unhampered by negative density dependence, but the small numbers of breeders means that few individuals are born (dN/dt is small). Near K, dN/dt is also small, even though the population size is large, because negative density dependence is really dampening the per-capita growth rate of all the individuals. Another way to see that dN/dt is maximized at intermediate population sizes is to notice that in the S shape of the logistic growth curve (Fig. 6.4b) the tipping, or inflection, point – the steepest point of population increase – occurs at $0.5K$. In harvested populations, the high point of dN/dt is often described as the population size at which the **maximum sustained yield** could be taken; we'll put some serious cautions around this interpretation in Chapter 14.

The logistic equation can also be expressed in discrete time (May 1974) as:

$$N_{t+1} = N_t e^{\left(r\left[1-\left(\frac{N_t}{K}\right)\right]\right)} \tag{6.4}$$

The discrete time form of the equation introduces a time step, such that dynamics of the population at one time step are a function of abundance at the previous time (for example, the previous year). This time lag is realistic for many populations because reproduction or survival in one year often depends on conditions the previous year.

[5]The parenthetical part of eqn. 6.2 is derived from $\frac{K-N}{K} = \left(\frac{K}{K} - \frac{N}{K}\right) = \left(1 - \frac{N}{K}\right)$.

(a)

Recruitment or $\frac{dN}{dt}$

(b)

600
500
400
300
200
100
0

Population size

Fig. 6.4 (a) P
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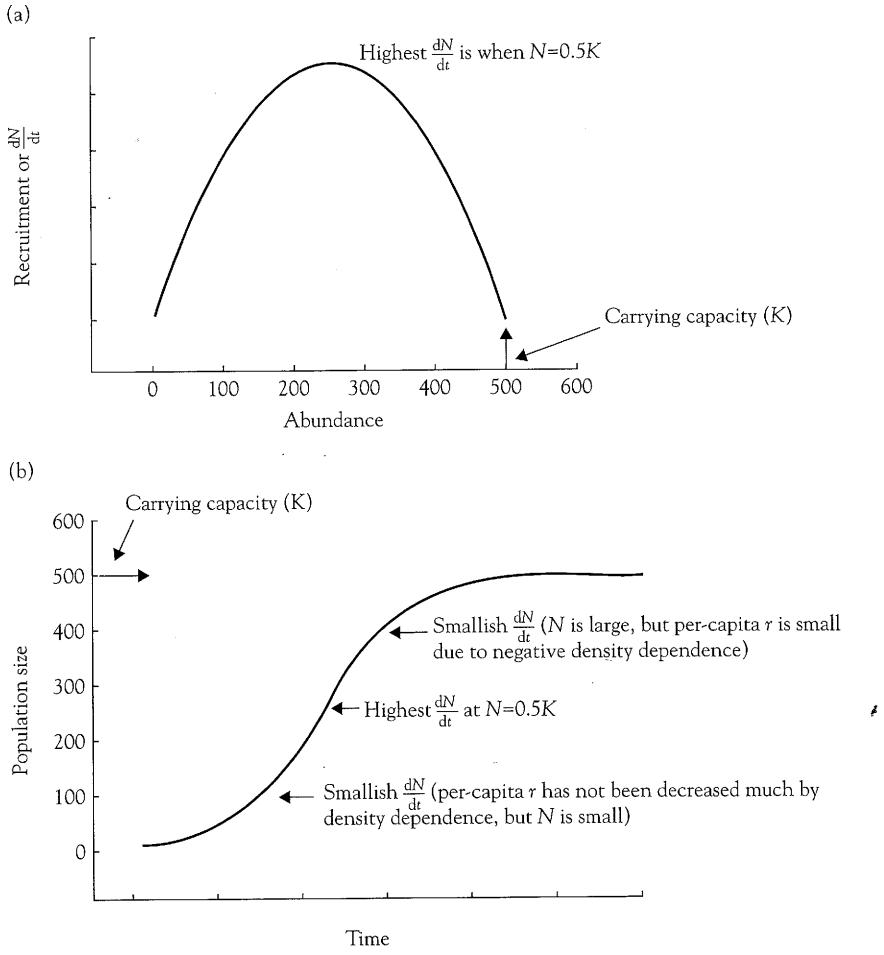


Fig. 6.4 (a) Population production or recruitment (dN/dt) for a population growing with logistic growth and a carrying capacity (K) of 500. Recruitment under logistic growth is maximized when the population is at 0.5K. (b) The basis for the recruitment in (a), demonstrating how recruitment changes as the population increases in numbers over time.

For example, winter starvation in feral Soay sheep and red grouse depends on population size the previous summer (Caughley & Sinclair 1994).

I'll say again that logistic growth is just one simple way of describing density dependence (actually, of negative density dependence only). Do not think of the logistic function as the only density-dependence function. The linear decline in per-capita growth rate with density as modeled by logistic growth (Fig. 6.3b) is not a biological law, or even necessarily general; in fact, a majority of species probably exhibit nonlinear density dependence, with their per-capita population growth rate declining relatively rapidly as population size increases from low density, then flattening out as carrying capacity is approached (Sibly et al. 2005); thus the relationship on the left-hand side of Fig. 6.3(b) would be concave. A variety of

alternative equations exist to model concave (or even convex) relationships for density dependence, with the most widely used being the **theta-logistic**[6]. Also, simple **ceiling models** allow population growth to be exponential up to a ceiling that cannot be exceeded (applicable to cases where space is limited, as for birds that nest in tree hollows, or bison on the National Bison Range in western Montana where managers cull the herd each year to maintain a population below the expected carrying capacity). In Chapters 12 and 14 we will see how different forms of density dependence can affect extinction probability and harvest models. For now, the important point is that logistic growth shows us the consequences of density operating on populations, a useful contribution as long as we do not confuse the logistic with a law of population growth (Box 6.2).

Given the many biological reasons why small populations may exhibit positive density dependence, where per-capita growth rate increases with population density, it is useful to see how population growth would be affected if we add positive density dependence to the logistic equation[7]. If a population experienced this combination of

Box 6.2 The logistic equation captures one form of density dependence but is not a universal law

Although the use of an S-shaped logistic curve to capture negative density-dependent population growth goes back to at least 1838, Raymond Pearl became the hardcore marketing man for the logistic curve around 1920. Working with experimental populations of fruit flies, Pearl noticed that he could fit a very nice S-shaped logistic curve to describe the population growth trend of the flies over time. So far so good: he had a solid experimental demonstration of a form of density dependence. But the problem was that Pearl leapt from this observation to an intense campaign to argue that the logistic represented a law of population growth that all populations must follow. Unfortunately, Pearl's campaign haunts us still, as many people think only of logistic growth when they consider density dependence (see Kingsland 1985).

The strength of the logistic growth model is that it simplifies the messy dynamics of real populations; knowing how a population deviates from it is useful for refining initial assumptions so as to better understand how populations will change over time. However, while logistic growth is a mathematically simple and useful way to describe one form of negative density dependence, it really is just one way that density dependence may manifest itself in wild populations. Or, to state it more eloquently, we can turn to the words of Alfred Lotka, one of many who tried to put the brakes on Pearl's enthusiasm for logistic growth. Lotka argued that the logistic equation should merely serve as a catalyst for us to ask what mechanisms are affecting population dynamics: "An empirical formula is therefore not so much the solution of a problem as the challenge to such a solution. It is a point of interrogation, an animated question mark" (Lotka 1925 quoted by Kingsland 1985:85).

[6]The theta logistic model is a simple generalization of eqn. 6.4: $N_{t+1} = N_t e^{\left(r\left[1-\left(\frac{N_t}{K}\right)^{\theta}\right]\right)}$.

[7]For example, Courchamp et al. (1999) modified the logistic growth equation so that per-capita growth rate becomes negative below some threshold A: $\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)\left(\frac{N}{A}-1\right)$.

negative (logistic growth) and positive (Allee effect) density dependence, it would decline to extinction below the Allee-effect threshold A and increase if it were between A and K (Fig. 6.5). In fact, it may be very common in nature for populations to experience both positive and negative density dependence at different times and population sizes (Burgman et al. 1993). Whenever density dependence affects per-capita growth rate in any way other than that assumed by logistic growth (a linear decline from zero to K), both the carrying capacity and the way the growth rate changes with density will vary. To emphasize this point, if you modeled a population using logistic growth, with a linear density-dependence function (Fig. 6.3b, left-hand panel), you would be assuming that the population would do well at very small population sizes. However, if the population actually experienced positive density dependence at low densities, it could decline to extinction below a threshold (as in Fig. 6.5, where populations of less than 25 decline toward extinction).

Density-dependent population growth will be influenced by stochasticity due to small numbers or environmental perturbations (see Chapter 5). As we saw for exponential growth, the expected population size under stochastic growth is lower than without stochasticity (Burgman et al. 1993:79–85). If the carrying capacity fluctuates, the average value of N will always be less than the average value of K,

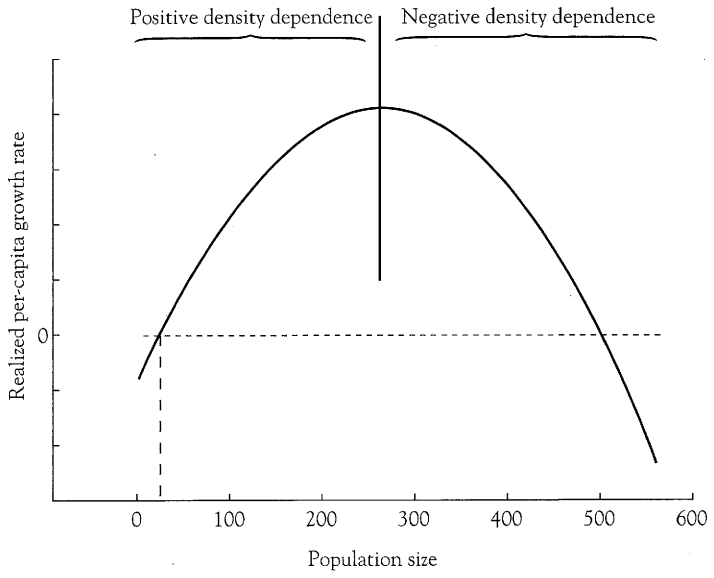


Fig. 6.5 The effect of positive and negative density dependence on the realized per-capita population growth rate [$\ln(N_t/N_{t-1})$]. Carrying capacity is 500 and r is 0.18, as in Fig. 6.3(b), but a positive density-dependence term (Allee effect) is added to the logistic model. When the population is below 25 it will decline to extinction, and positive density dependence dominates until the population size exceeds 250. When the population is above 500 it will decline until it reaches 500. Between 25 and 500 it will increase towards 500. Don't confuse this with Fig. 6.4(a); although they have similar-shaped curves they have different axes and cover different ideas.

because under logistic growth a population above K declines at a faster rate than a population increasing from a corresponding level below K (Gotelli 2001:38). For example, use eqn. 6.2 to calculate the change for a population with $r=0.1$, $K=500$, and $N=400$, compared to a population with the same r and K values but $N=600$.

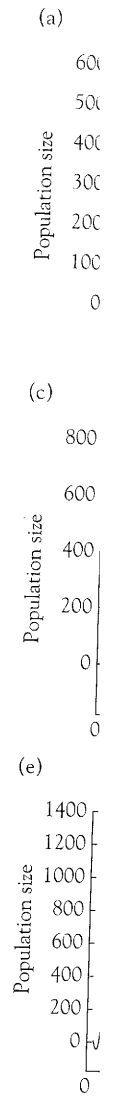
Some counterintuitive dynamics: limit cycles and chaos

In 1974 Robert May reported a wild observation: populations growing according to the discrete logistic growth equation (eqn. 6.4), with absolutely no stochasticity, could show dynamics that bounce, or cycle, or become entirely unpredictable (Fig. 6.6). When r is less than 1.0, population growth follows a smooth, monotonic increase to carrying capacity, following the standard S-shaped curve discussed above. When r is between 1.0 and 2.0 logistic growth shows **damped oscillations**, so that the population overshoots K, then undershoots it by a lesser amount, and so on until it settles back down to the equilibrium. Between $2.0<r<2.69$, the population will show **stable limit cycles**: dynamics are still regular and predictable, with a repeated succession of valleys and peaks. So, things are getting interesting already: the logistic equation is leading to cycles created purely by the amount of population growth in discrete time (where population size next year depends on population size this year). If r increases more, so $r>2.69$, you get **chaos** (Fig. 6.6e,f).

What is chaos? For practical purposes, chaos is distinguished by dynamics that are highly sensitive to initial conditions. Notice in Fig. 6.6(e,f) that the two populations are identical except for starting sizes of 10 animals in Fig. 6.6(e) and 11 animals in Fig. 6.6(f). The populations differ by only one individual initially, but by time step 40 they are vastly different (988 compared with 201 animals). Although the fluctuations generated under chaotic dynamics are unpredictable, they are different from random or stochastic fluctuations. One difference is that there is a structure to the unpredictable fluctuations under chaos (see Fig. 6.6e,f), with bursts of short-term cycles interspersed with stretches of irregular and erratic population sizes. Chaos is also distinguished from environmental stochasticity because if you start with exactly the same initial conditions, you will get exactly the same population trajectories every time (try it for yourself using eqn. 6.4 and an r value of, say, 2.8).

So, chaos is different from stochasticity. But the sensitivity to initial conditions reverberates into dynamics that over the long term are unpredictable and seemingly random. Thus if chaos is operating, you will not be able to predict future population dynamics, and a chaotic time series will appear as if it is fluctuating stochastically. Therefore, chaotic dynamics can drive apparently random fluctuations, even in an absolutely constant environment, and can exacerbate fluctuations when occurring in tandem with stochasticity (Hastings et al. 1993, Perry et al. 2000).

Nonlinear dynamics including stable limit cycles and chaos are profound in population biology first because they show that simple deterministic models can produce



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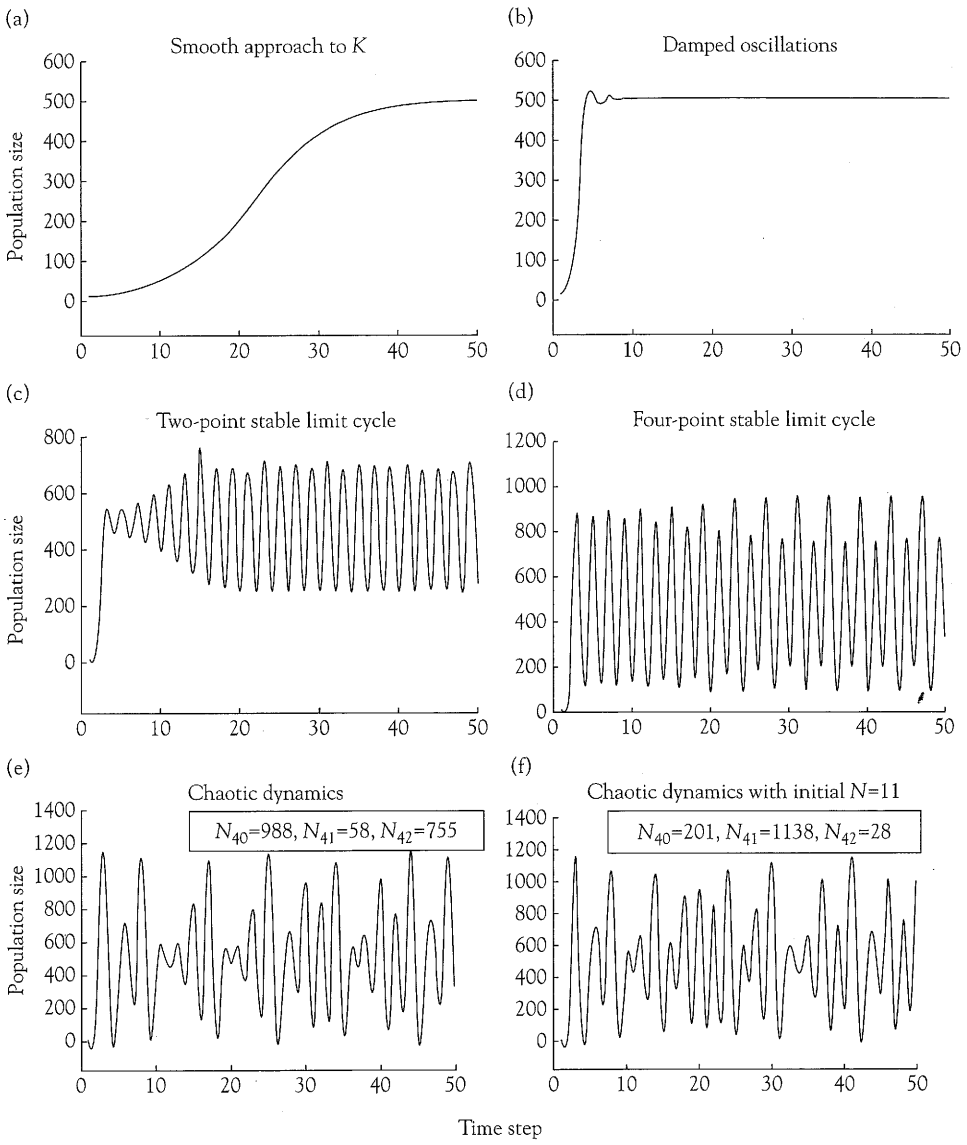

Fig. 6.6 Wild dynamics in population size over time that come from deterministic discrete logistic growth (eqn. 6.4) with a K value of 500 and an initial N value of 10. (a) r=0.18: a steady S-shaped curve flattens at K. (b) r=1.5: damped oscillations, overshooting then undershooting but settling down at K. (c) r=2.2: stable limit cycles of two points (two steps between each repeated high or low). (d) r=2.6: stable limit cycles of four points. (e) r=2.9: chaotic dynamics with starting N=10. (f) Chaotic dynamics with the same conditions as in (e) except initial N=11 to show the sensitivity to initial conditions. Although (e) and (f) may look similar at a quick glance, notice that abundances are actually vastly different.

what looks like environmentally induced cycles or random dynamics. Second, very subtle differences in starting conditions (say, in terms of initial population size) can have huge effects on the future population size. Third, chaotic dynamics abandon the concept of a traditional equilibrium density.

All of which brings us to the question of how often we need to know about this stuff in applied wildlife population ecology. First, for chaos to manifest through the single-species logistic growth equation, a time lag must be present. Time lags are quite common in most vertebrate populations. There can be time delays in the recovery of a resource (say, overbrowsed vegetation), in gestation time, or in behavior or physiology of individuals, producing a lagged response between change in resources and change in vital rates and population growth (e.g. Turchin 1999). An implicit time lag of one step is included in the discrete form of the logistic growth model, which is why May (1974) was able to use this simple equation to demonstrate the potential for chaos in biological populations.

Nevertheless, you may be disturbed by another necessary condition for chaos to occur via discrete logistic growth. Specifically, you may be astonished that I am taking time to worry about what happens when $r > 2.69$. After all, a wildlife population increasing with an r of 2.7 would have a $\lambda = e^r = 14.9$, meaning that it increases by 14-fold each time step!

In fact, if chaotic dynamics could only occur under the conditions specified by Robert May's groundbreaking work (discrete logistic growth with $r > 2.69$), such a complaint would be correct. But it turns out that many nonlinear processes affecting population growth could theoretically lead to chaotic dynamics, with or without discrete time (time lags) and with single or multiple species interacting (Hastings et al. 1993), at growth rates considerably lower than 2.69 in the discrete logistic model. Therefore, although almost no real wildlife population would have a growth rate high enough to drive chaotic dynamics using the simple May model, other ecological conditions could lead to nonlinear dynamics, and potentially chaos, in real populations.

The study of chaotic dynamics is blossoming in ecology, and current evidence indicates that chaotic dynamics could occur in real wildlife populations (Box 6.3). However, chaotic dynamics are certainly not lurking everywhere, and in fact traditional stochastic fluctuations probably explain much more of the noise in real ecological systems than do chaotic dynamics (Lande et al. 2003). Knowing how nonlinear dynamics and chaos might manifest in wildlife populations will help you understand the implications if future work demonstrates a wide occurrence of chaotic dynamics in field populations.

Summary

Density of conspecifics is a ubiquitous driver of vital rates for wildlife populations, with implications ranging from management of endangered species to harvest strategy assessment. Sometimes, density is really just a surrogate for proximate factors such as food availability, parasite burden, predation, or other variables that influence vital

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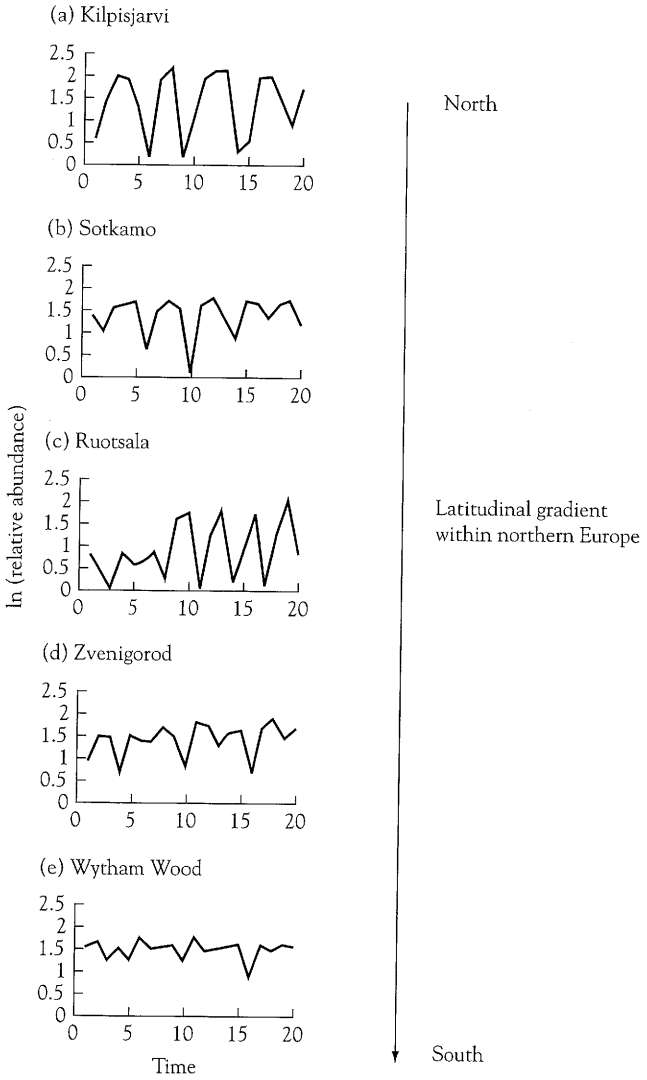
Box 6.3 Chaotic dynamics in northern small mammals

Fluctuations in small mammal populations have been studied intensively for more than 100 years. In northern Europe, fluctuations in voles (*Clethrionomys* spp. and *Microtus* spp.) range from low-amplitude, noncyclic to high-amplitude, cyclic (periods of 4–5 years) and even chaotic dynamics, roughly following a south–north latitude gradient (Turchin & Hanski 1997; see figure). The dynamics of these species have been explained by an intensive linking of field data to quantitative population models. The models are based on logistic growth and include the effects of predator and prey on each other. Specialist predators (especially weasels) exhibit a delayed numerical response (see Chapter 8) to



Population fluctuations of voles on a north–south gradient in northern Europe. Modified from Turchin and Hanski (1997). Reproduced by permission of the University of Chicago Press.

(*Continued*)

Box 6.3 Continued

changes in prey, creating a time-lagged density dependence in the voles. In the southern regions of northern Europe, generalist predators such as foxes and nomadic specialists such as short-eared owls dampen cycles because these predators are less dependent on local vole numbers. In contrast, a diminution of generalist predators in the northern region causes vole numbers to be much more closely coupled to the dynamics of the specialist predators. As a result, voles in the more northern regions show multi-annual, high-amplitude oscillations. Statistical analyses of the time series indicate that, in some cases, these oscillations are chaotic.

rates (Turchin 1999, Krebs 2003). Whether we consider density per se or the underlying outcomes of changing density, the effects on vital rates can change population growth rate for better or worse.

Negative density dependence increases vital rates (and population growth rate) as density decreases; thus declining small populations will become less likely to go extinct while growing larger populations will have reduced growth rates. On the other hand, positive density dependence – where smaller populations experience compromised predator avoidance, forage efficiency, or mating or caring for young – acts against small declining populations and in favor of large growing populations.

A common way to model negative density dependence is as a logistic growth function, whereby realized per-capita growth rate declines linearly with increasing density and becomes zero at the carrying capacity. As a distillation of complexity, logistic growth has been useful, for example making the strong graphic point that recruitment into a population is maximized when the population is held at half the carrying capacity, where a moderate number of individuals are breeding while incurring only moderate deleterious effects of density. The logistic model has also motivated study into how density dependence – potentially coupled with other factors that cause nonlinear relationships between density and population growth – can lead to stable limit cycles or even chaos, where dynamics become extraordinarily sensitive to initial conditions and fluctuations appear wildly random.

As useful as density dependence can be to understanding, modeling, and managing populations, we must be careful to embrace the uncertainty of how density dependence operates, acknowledging that it does not happen at all times and places and that the form and strength vary across time, space, and vital rates. Assuming only a simple logistic growth model for managing harvest or predicting extinction ignores the fact that other forms of negative density dependence, or positive density dependence, would lead to very different predictions. Ideally, we should use field data to quantify both the form and strength of density-dependence relationships for any particular population (Burgman et al. 1993, McCallum 2000, Turchin 2003). When data are insufficient to clearly demonstrate how density dependence acts, management implications can be explored using a number of different scenarios that might include exponential growth (no density dependence), and different forms of both negative and positive density dependence.

Further reading

Burgman, M.A., Ferson, S., and Akçakaya, H.R. (1993) *Risk Assessment in Conservation Biology.* Chapman and Hall, London. A practical and well-written book with useful applications of density-dependence concepts.

Gleick, J. (1987) *Chaos: Making a New Science.* Viking Penguin Books, New York. A compelling portrayal of chaotic dynamics in ecology and elsewhere.

7

Accounting for age- and sex-specific differences: population-projection models

> *For what is man? First, a child, soft-boned, unable to support itself on its rubbery legs, befouled with its excrement, that howls and laughs by turns, cries for the moon but hushes when it gets its mother's teat; a sleeper, eater, guzzler, howler, laugher, idiot, and a chewer of its toe; a little tender thing all blubbered with its spit, a reacher into fires, a beloved fool.*
>
> **Thomas Wolfe (1942:432), *You Can't Go Home Again***

> *If you can't generalize from data there's nothing else you can do with it either. A science without generalization is no science at all. Imagine someone telling Einstein, 'You can't say "$E=mc^2$." It's too general, too reductionist. We just want the facts of physics, not all this high-flown theory. Cuckoo.'*
>
> **Robert Pirsig (1992), *Lila***

Introduction

Bull elk, cowbird eggs, frog larvae, mother wallabies, turtle hatchlings. Often wildlife ecologists care about particular parts of a population as much as they do the population as a whole. Whether the applied goal is to harvest, recover, reduce, or reintroduce wildlife populations, one cannot long avoid the dynamics of particular ages, stages, and sexes. The last two chapters have described a foundation for how to predict and describe changes in wildlife populations, but thus far dynamics have been described by a single term (λ or r) applied to the total population size (N). In this chapter I will explore how particular groups of individuals, and their birth and death rates, affect population growth and the likely numbers of individuals of different classes.

Here is a story to transition us, adding the wrinkles of age and sex structure (Coulson et al. 2001). Soay sheep studied on the island of Hirta, off the coast of Scotland, fluctuate dramatically, more than expected based on weather or density dependence alone. Why? In large part because survival of lambs and older males is heavily influenced by winter weather, whereas yearlings and prime-aged females are

most affected by rainfall at the end of winter. Meanwhile, negative density dependence affects lambs and older females more than prime-aged adults or yearlings. In turn, the changing proportions of different sex and age classes caused by weather and density dependence cascades into effects on population growth (see also Box 9.3). Not all sheep are equal (Gaillard et al. 2001). Counting the sheep as equivalent, ignoring age and sex, would tell us very little about how ecological stresses affect population fluctuations or population growth.

For humans and a few other species, age can be tracked as a meaningful descriptor of an individual. However, vital rates in wild populations often depend on developmental, morphological, or even behavioral stages more than calendar age. Consider, for example, larval forms and adults in amphibians, fish of different sizes, or big trees and saplings. Furthermore, different stages can often be distinguished more easily in the field than age classes can, and management often centers more on recognizable stages than on ages (e.g. ungulate males of different sizes or antler-development stages). The predominance of stage structure means that throughout this chapter (and the book), I will refer to **stage** instead of repeating age or stage.

In basic ecology classes, age or stage structure is typically covered using life tables. Although life tables are important for basic ecological understanding, most of the applied things that life tables can tell us about wildlife population dynamics (e.g. estimates of λ, stage structure, and reproductive value) can be better estimated using matrix-projection models[1]. Thus I will skip life tables and focus on less well known yet more versatile and practical tools for understanding how structure affects wildlife population dynamics.

Specifically, the aim of this chapter is to describe the wonders of matrix-projection models for understanding wildlife populations. If the thought of matrix math makes you nervous, think of a population-projection matrix as merely a box to help keep straight the bookkeeping of birth and survival, a mathematical representation of biological processes. That's it, really. Lots of bells and whistles can be added to matrix projections, but at their heart they are less intimidating than they may look. So let's look at what a matrix is, then we will quickly come back to the surface to gulp the air of application to wildlife population biology.

Anatomy of a population-projection matrix

Throughout the chapter, I will use as a tangible example the common frog, a species found throughout much of Europe. The projection matrix, **M**, is a square of k columns and k rows, where k is the total number of stage classes (Fig. 7.1). Each element (or cell) of the matrix contains a value that is used to project stage-specific reproduction or survival forward one time step. A time step can be anything:

[1]For good overviews linking life tables to matrix models, see Noon and Sauer (1992) and Case (2000).

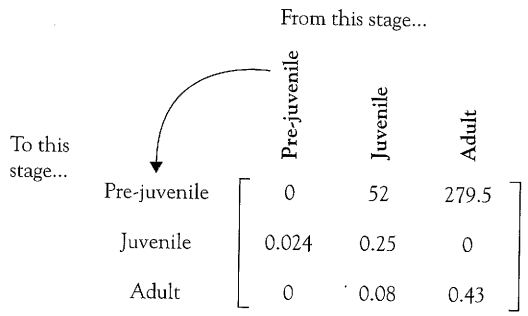


Fig. 7.1 Anatomy of a female-based projection matrix, using as an example the common frog (Biek et al. 2002; see also Box 4.8). This species has three stages: pre-juvenile (first year, consisting of the embryo, tadpole, and overwintering metamorph), juvenile (next 2 years), and adult. The projection interval, or time step, for this matrix is 1 year. The first row represents reproduction from each stage to the next year. The diagonal (e.g. $a_{2,2}=0.25$ and $a_{3,3}=0.43$; see text for an explanation of this notation) represents the proportion of individuals in a stage that will survive and still be in the same stage next year, while the subdiagonal (just below the diagonal; e.g. $a_{2,1}=0.024$ and $a_{3,2}=0.08$) represents the proportion surviving and advancing to the next stage next year.

for a yeast, the relevant time step of life and death might be an hour; for small mammals, it might be a month. For logistical and biological reasons, however, the most common time step for wildlife studies is a year, so throughout the book I will often use the terms year or annual as shorthand for the more general time step.

The elements of a matrix are described with subscripts that tell what row and column they are in (with the row first and the column second); for example, element $a_{2,1}$ is the element in row 2 and column 1. A handy way to decipher the biological meaning of any matrix element is to label the rows and columns of the matrix with the consecutive stages of your organism. Each element gives the transition – one time step later – from whatever column the number is in to whatever row the number is in. Another way to say the same thing is that $a_{i,j}$ represents the number of individuals contributed on average by each individual in class j at the current time step to class i at the next time step. For the common frog in Fig. 7.1, element $a_{2,1}$ is 0.024, meaning that on average 0.024 (or 2.4%) of the pre-juvenile frogs in the population survive to become juveniles the next year.

Notice in Fig. 7.1 that animals can remain in some stages for multiple time steps (for example 0.25 of the juveniles can remain as juveniles and 0.43 of the adults as adults). In a stage-based matrix, otherwise known as a **Lefkovitch matrix** (Lefkovitch 1965), transitions from any stage to any other stage can be accommodated. Stage-based matrices are more versatile than the original **Leslie matrix** (Leslie 1945), whereby vital rates depend on ages that are identifiable, and where the span of each age is the same as the length of the time step. In a Leslie matrix, an individual can only survive and transition to the next age, or die, so everything below the first row and not on the sub-

diagonal of the matrix must be zero. For practical purposes the distinction between Leslie and Lefkovitch matrices is only important to help you understand the terms in published papers.

With this brief lesson in projection-matrix anatomy, a few biological generalizations should become clear. First, each element of the top row of the matrix represents the reproductive contribution of each stage to the next time step. Second, the survival of individuals of any stage to the next time step (e.g. annual survival) can be determined from any matrix by adding up all the values for that column, excepting the first row[2]. For example, for the frogs in Fig. 7.1, annual survival of juveniles would equal 0.33, the sum of the proportion of juveniles that survive as juveniles (0.25) plus the proportion that survive and become adults (0.08). Third, the rates in the matrix must correspond to the stages you are interested in projecting. In particular, where the sexes have different survival rates, or where reproduction is known for females only, the vital rates are often female-based. In other cases, male-based models are most appropriate, as you will see for the red-cockaded woodpeckers in case study 1, below; two-sex matrix models are also possible, and you will see an example for ungulates in Chapter 14. The important thing is to be clear about which sexes are included in the projection, and how.

How timing of sampling affects the matrix

Because we are discussing applied population biology, let's think more about how to link the model to the field data, particularly to observable stages and to the timing of the surveys that produced counts of animals and estimates of vital rates (Fig. 7.2). Because each element of the top row contains the reproductive contribution of class j to the first stage class in the next time step, the top-row elements contain not only stage-specific fecundity (m_j), but also a term to advance the newborns to the next time step[3]. What does that mean? Well, newborns have to survive to be counted, or mothers counted last year have to survive to successfully bear their babies next year. So reproduction to the next time step depends on two terms: fecundity (m) and survival (P).

Exactly what we put into the elements of the top row depends on the kind of data collected. Suppose we were interested in projecting population growth for American bison, a species where most young are born at nearly the same time. For simplicity, assume all calves are born on May 31, and consider only the female portion of the population. If

[2]When building a matrix from field-collected vital rates, one of many decisions is how to partition annual survival into the appropriate elements in a stage-based model. Crouse et al. (1987) give a nice, simple approach to partitioning survival into matrix elements for a stage-based model.

[3]Remember, **fecundity** (or m_j) refers to the average number of offspring an individual in stage j produces in a year (see Chapter 4); if you are familiar with life tables, then m_j is the same as the m_x or b_x. I use **reproduction to next time step** for the top-row matrix elements that include both the fecundity and survival terms needed to project the fecundity to the next time step; this is often called **fertility** by human demographers, but fertility has different meanings in the ecological literature so I will avoid the term here.

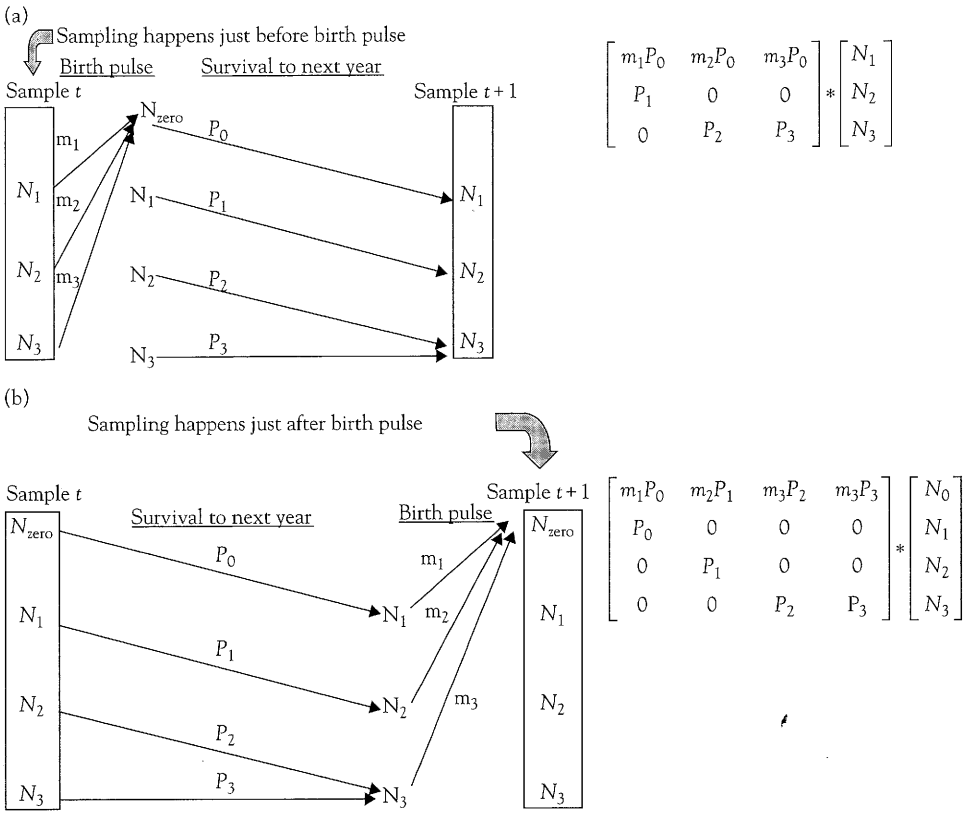


Fig. 7.2 General schematics of the birth and death processes captured when the sampling is either (a) before the birth pulse or (b) after the birth pulse. The animals sampled at times t and $t+1$ are boxed, with N_j representing number of individuals in each stage class j. This example assumes that animals stay in each stage for only one time step, except that those in the last stage can survive and remain in that stage for multiple time steps. Fecundity for each age class (m_j) represents the average number of offspring born to each individual of N_j. The probability of survival through one time step is represented by P_j. To the right of each schematic is the resulting projection matrix and population-size vector. In (a), note that newborns (N_0) are not seen until they have survived through their first year (P_0) to be counted as N_1 at the next sample interval; likewise, individuals in age class 1 (N_1) are just about to become 2 years old, and so on. The next batch of N_0 individuals are born just after sampling. In (b), note that there is an extra column and row in the post-birth-pulse matrix (compared to the case of the pre-birth pulse) because post-birth sampling occurs just after reproduction, making N_0 recognizable as its own class.

we sampled on May 30 (just before the birth pulse), then the youngest age class counted would be the calves born last May 31 that had lived to be counted just as they are about to become 1 year old. The reproductive contribution for each stage class, then, must include not only stage-specific fecundity (m_j; the average number of female calves born per year per female in stage j) but also the probability of newborns surviving to be counted at the end of their first year (call this P_0). Now, what if instead of sampling on

May 30 we sample on June 1, the day after the birth pulse? In this case we would sample newborns. We would know exactly how many female calves were born per female, but some of the mothers alive last year would have died during the year (remember again that the goal is to project the population forward through time). Thus the reproductive-contribution elements of the top row would include stage-specific fecundity (m_j) as well as survival of mothers in that stage to have the newborns (P_j).

People who spend a lot of time messing with population-projection matrices often denote as F_j each element of the top row, where each element is this composite of fecundity and survival of either the mothers or the newborns. Thus each element of the top row of the matrix represents the reproductive contribution to the next time step under either

- pre-birth-pulse sampling, $F_j = m_j P_0$, or
- post-birth-pulse sampling, $F_j = m_j P_j$.

So **post-birth** models have an extra stage class, because the newborns are recognizable as their own class (they were born just before sampling), whereas with **pre-birth**-pulse sampling we do not see newborns until they become class N_1 (as in Fig. 7.2a). I've been a little excruciating in detailing these two model types because it turns out to be a confusing topic in many ecology textbooks and published papers. If the accounting is kept straight, though, the two approaches give exactly the same population growth rate. And the strict pre- versus post-birth-pulse sampling can be relaxed to account for varying periods between the birth pulse and the sampling, or even to allow for continuous breeding (see Further reading). The development of the matrix for the common frog is shown in Fig. 7.3.

Projecting a matrix through time

How to project the matrix

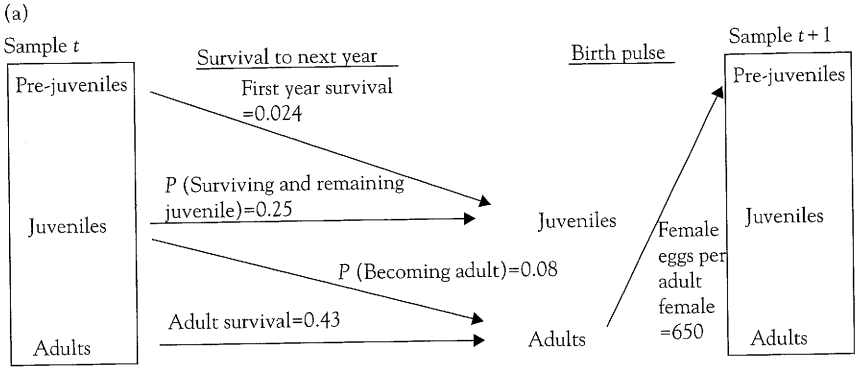
Once the matrix model is filled with vital rates, it can be projected through time. The advantage of a matrix approach over the nonstructured models of the previous two chapters is that it keeps track of not just the total population size but also the numbers in each stage. In matrix terms, we will project through time the population-size vector. A vector is a skinny matrix of one column and k rows that contains the number of individuals in each of the k stages. To determine the population-size vector next year $[\mathbf{n}(t+1)]$, multiply the matrix $\mathbf{M}$ of vital rates by the vector of individuals at time t, $\mathbf{n}(t)$:

$$\mathbf{n}(t+1) = \mathbf{M} * \mathbf{n}(t) \qquad (7.1)$$

By convention, matrices and vectors are shown in bold.

How do you multiply a matrix by a vector? Go across each row of the matrix, multiplying each element j by the same element of the vector (Fig. 7.4). Add up the products for one row to obtain the total number of individuals in that element of the vector. Again, if the math intimidates you, take a breath and realize that the projection

(a)



(b)

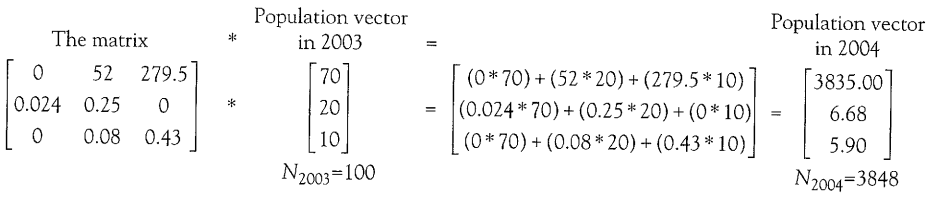
$$\begin{bmatrix} 0 & P(\text{Juvenile becoming adult} * \text{eggs/adult}) & P(\text{Adult survival} * \text{eggs/adult}) \\ P(\text{First year survival}) & P(\text{Remaining juvenile}) & 0 \\ 0 & P(\text{Juvenile becoming adult}) & P(\text{adult survival}) \end{bmatrix}$$

Fig. 7.3 A real-life example of a female-based post-birth-pulse matrix model for the common frog (Fig. 7.1). Female eggs per adult female refers to fecundity (see Box 4.8). (a) A diagramatic representation of the model; (b) the matrix (try plugging in the values and make sure you get the matrix in Fig. 7.1). Note that the matrix shows reproduction for juveniles (row 1, column 2) as well as adults (row 1, column 3) because a portion of the juveniles transition during the time step to become adults, at which point they reproduce. In general, for post-birth-pulse models for iteroparous species with n reproductive stages there should be $(n+1)$ non-zero elements in row 1.

of a matrix makes biological sense. The number of individuals in the first stage (newborns) next year comes from the reproductive contribution of each stage to the next time step (the top row of the matrix) multiplied by the number of individuals in each stage (the population vector). Likewise, the number of individuals advancing to a different stage or staying in the stage at the next time step are the product of survival (or other possible transitions below the first row) and the number of individuals in that stage.

Stable stage distribution and reproductive value

Matrix-projection methods can start with any number of individuals in different stages, and keep track of the relative number in each stage as well as population growth over time. This feature makes an important tool for many applications, ranging from tracking the possible growth of a translocated population to predicting what



Repeat multiplying the matrix by the current vector to get

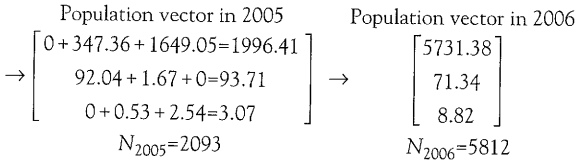


Fig. 7.4 An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size (N) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

might happen to certain stages during harvest. Although you can start with whatever number of individuals you want in each stage class, if vital rates stay relatively constant over time the population will converge on a population growth rate and stage distribution that is characteristic for that particular matrix. As a demonstration, Fig. 7.5 shows the projections for frogs from Fig. 7.4 for 14 years from the initial vector in 2003. By 2017 the population growth rate per year has become constant (λ=1.46; calculated by N_{t+1}/N_t). Also, the proportion of individuals in each class is constant, with about 98% of the population being pre-juveniles [e.g. (306,931/313,490) * 100=98%], 1.9% juveniles, and 0.2% adults (for practice, calculate the age distribution for the year 2016 from the information in Fig. 7.5). This constant proportion of individuals in each stage class is known as the **stable age distribution** (SAD) or, more generally, the **stable stage distribution** (SSD). Nearly any population matrix – whether it represents a declining, increasing, or stationary population – will converge on a constant population growth and SSD if the vital rates making up the matrix stay relatively constant[4]. (The time to SSD depends on factors such as the initial age structure and the characteristics of the matrix itself, but should be achieved within 20 time steps or so for most vertebrate populations.) The population growth rate at SSD, and the SSD itself, are characteristic of the matrix, and are independent of the initial age distribution.

Although the SSD and λ_{SSD} are independent of initial stage distribution, the distribution of animals across stages influences both the time to reach SSD and the population abundance in the future. Consider population growth curves for our frogs again,

[4]There are matrices that will not converge to an SSD, including matrices that have only a single non-zero element in the first row, which can lead to stable oscillations (Leslie 1945, Caswell 2001).

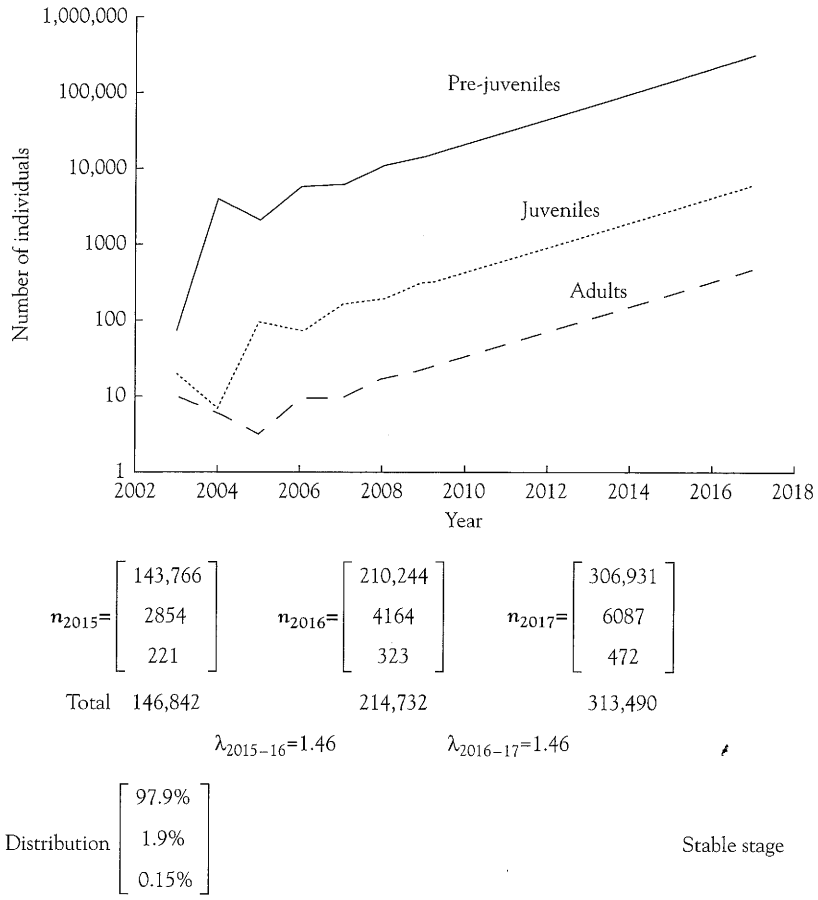


Fig. 7.5 Convergence to a SSD for the common frogs considered in previous figures. Population numbers over 14 years (from 2003 to 2017) are shown by stage class. The number of frogs is plotted on a logarithmic scale to accommodate the huge numbers of pre-juveniles, and because at SSD the trajectories become linear. Below the graph are the vectors (**n**), total population sizes, and geometric growth rates (λ) for the final 3 years. When the population reaches SSD, both the population growth rate (λ) and the proportion of individuals in each stage remain constant.

this time plotting total population size for 14 years with populations of 100 frogs that are seeded with all of one stage: 100 pre-juveniles, 100 juveniles, or 100 adults (Fig. 7.6). Even though all three populations start with the same initial number of frogs and the same constant set of vital rates, and after 14 years have all achieved the same growth rate at SSD, the numbers of frogs at time step 14 are vastly different for the three populations. Why? Because all stage classes are not created equal in their contribution to population growth, a phenomenon quantified by the concept of **reproductive value**. In Fig. 7.6 you can see that a population founded with 100 frogs, all adults, would reach a size of 2,125,660 frogs in 14 years, in contrast to the 477,171 individuals in the juvenile-seeded population and 7,843 in the population begun with 100 pre-juveniles. By convention, reproductive value is scaled relative to that of the first age

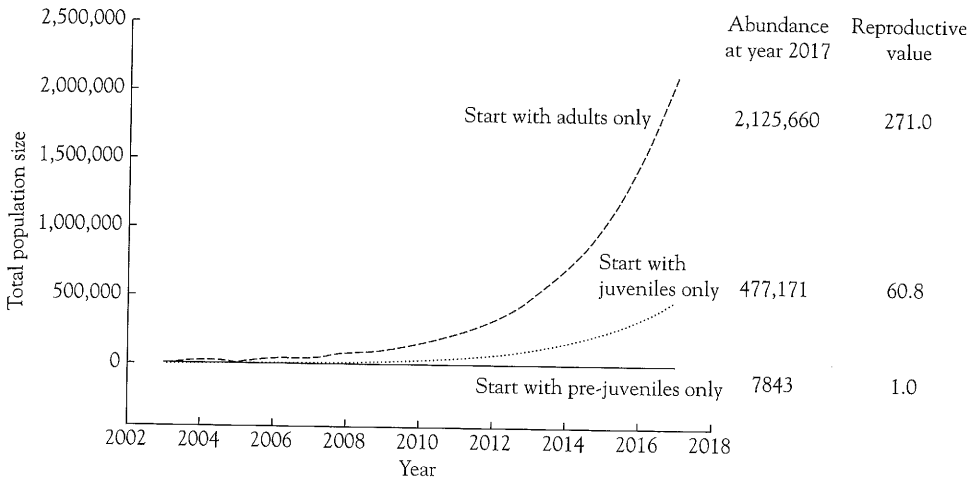


Fig. 7.6 A demonstration of reproductive value by projecting common frog population size beginning with 100 adults, 100 juveniles, or 100 pre-juveniles, with the constant vital-rate matrix from Fig. 7.1. Although the initial abundance, the projection matrix, and eventual population growth rate and SSD are identical in each case, the initial stage distribution causes bounce in population growth early on, and leads to drastic differences in abundance. Reproductive value is typically scaled relative to the first age class. The right side of the graph shows how reproductive value can be calculated based on relative abundances at SSD, dividing each abundance by that of the population begun with the first age class. (I used abundances in year 2017, after 14 years had passed, but you could use abundances any time after SSD was achieved.)

class. Therefore, for the frogs, adults have a reproductive value of 271.0, and juveniles of 60.8, compared to the reproductive value of 1.0 for pre-juveniles (Fig. 7.6).

Because the reproductive value quantifies how much each stage acts as a seed for future population growth (Caswell 1989:67), it has immense yet under-appreciated applications in wildlife population biology. Reproductive value is not a synonym for fecundity, or reproduction in the top row of the matrix. Rather, it takes into account reproductive output at that stage, as well as future reproduction, the likelihood to survive to those stages, and the population growth rate. In other words, reproductive value is a weighted average of present and future reproduction, accounting for population growth rate, that provides us with a practical way to assess contribution of different stages to future population growth (see Lanciani 1998, Case 2000).

So, here's what we've got so far on projecting matrices: Because all stages are not equal in their effects on population growth – that is, they have different reproductive values – the initial age distribution affects future abundance and the time required to reach SSD[5]. It also causes the population size to bounce around early on (as the age

[5]Look back at Fig. 1.3, showing how population momentum would cause the global human population size to increase even if women had only replacement numbers of children. The momentum is caused by an age structure leading to lots of babies even though modified vital rates would lead one to expect stationary population growth.

Box 7.1 How to calculate reproductive value, SSD, and the expected population growth at SSD

Because any constant population-projection matrix attains a constant SSD and λ, with each stage having a characteristic reproductive value, these are called **asymptotic matrix properties**. In the text I showed an approach to calculating each of the asymptotic matrix properties. For SSD and λ, project any initial population vector out by a number of times, say 100 time steps, and then calculate at time step 100 the proportion of individuals in each stage and the growth rate ($\lambda = N_{100}/N_{99}$). For reproductive value, you could use the seeding method (as in the frog example in Fig. 7.6).

Although these projection-based approaches are perfectly legitimate, intuitively transparent, and pretty easy to accomplish with simple multiplication that could be done, for example, in a Microsoft Excel spreadsheet, there are more elegant approaches to calculating the asymptotic matrix properties. For example, the **dominant eigenvalue** of the matrix, calculated using matrix math, equals λ, and its associated **right eigenvector** equals the SSD vector. Likewise, the **left eigenvector** of the dominant eigenvalue gives the vector of reproductive values.

distribution settles down to a SSD), and this is in the absence of any demographic or environmental stochasticity. However, the SSD and corresponding growth rate are a function of the matrix values and not the initial age distribution, so a population of any composition will eventually reach SSD and its associated λ as long as the matrix rates are relatively constant. Various ways to estimate reproductive value, SSD, and its associated λ value are described in Box 7.1.

For wildlife population management the implications of these population dynamics properties are profound. First, a set of vital rates represented as a projection matrix, coupled with a count of animals by stage class, provides insights into the inherent growth rate to be expected and the proportion of individuals eventually expected in each stage class over time. Second, the effect of age distribution means that a newly reintroduced population can be wildly erratic in its population growth – even without any stochasticity occurring – if the initial composition of the population is far from the expected SSD. Third, the reproductive value itself conveys the consequences of losing individuals of certain stages through harvest, or gaining them through translocations.

Before leaving this discussion on projecting matrix models through time, I should emphasize that I have only talked about density-independent matrix models. Density dependence can be added to matrix models (see the Further reading section of this chapter). I have also limited the discussion so far to the case where vital rates in the matrix are constant through time. Next I will briefly show how random variation (demographic and environmental stochasticity) can be incorporated into matrix projections.

Adding stochasticity to a matrix model

Although asymptotic properties such as the reproductive value, SSD, and population growth at SSD are useful, they are based on vital rates in the matrix being constant, or nearly so. But we know that vital rates are seldom constant for any length of time. And as we saw in Chapter 5, stochasticity has important implications, including the fact that it will decrease the likely future growth of a population compared with that expected from λ at the SSD[6].

Fortunately, computers make it quite easy to project a stage-structured model incorporating both environmental and demographic stochasticity (Chapter 5), assuming you have a specified starting population vector, and estimated means and variances for vital rates. To incorporate environmental stochasticity over time for a population, the computer builds a new matrix each time step, where each element in the matrix is chosen from a set of random numbers with a specified mean and process variance. The distribution of random numbers may be from a uniform distribution (all values equally likely to be chosen between a high and low value) or – more usually – from a distribution with central tendency, such as lognormal, normal, or beta (see Morris & Doak 2002). An alternate approach randomly picks one of several vital rates measured in the field (or even entire matrices of vital rates from field data; Bierzychudek 1982, Akçakaya 2000). Box 7.2 gives an example of environmental stochasticity in action for a population projection for the red-legged frog.

Demographic stochasticity in survival can be modeled to capture the real-world phenomenon whereby animals live or die as whole animals and not as fractions (Chapter 5). A common way to model demographic stochasticity in survival using the computer is to determine the fate of each individual in a stage based on the mean survival rate. Specifically, for each individual the computer picks a random number between 0 and 1; if the random number is less than the mean survival probability (also between 0 and 1) then the animal lives, if not, it dies. For example, suppose that your population vector has six yearlings, and the mean survival probability for yearlings is 0.8. Without demographic stochasticity, the expected number of subadults next time step is $(0.8 * 6 = 4.8)$. With demographic stochasticity, the computer might pick the following six random numbers: 0.32, 0.89, 0.51, 0.11, 0.94, 0.70. Thus, four of the animals would live, but two would die (the second and fifth). At small numbers the proportion of survivors can deviate greatly from that expected from the mean survival rate, just as a small number of coin tosses can lead to a big deviation from 50:50 heads/tails (see Chapter 5).

Sensitivity analysis

As we have seen, all stage classes are not created equal in their management importance, their effects on population growth, or in their relative abundance. Similarly, it

[6]Specifically, stochasticity will decrease population growth by an amount depending on which rate varies, how much it varies, and the sensitivity of λ to changes in that rate (Morris & Doak 2002:239). We will look at how to quantify sensitivity in the next section.

Box 7.2 An example of how to model environmental stochasticity, based on a population-projection matrix for red-legged frogs (*Rana aurora*)

Notice that this is a different frog species than the one discussed previously in this chapter. Data come from Biek et al. (2002).

Step 1: here is the matrix of vital rates.

$$\begin{bmatrix} 0 & \begin{pmatrix}\text{Probability of juvenile becoming adult * probability of laying * } \textbf{clutch size}\end{pmatrix} & \begin{pmatrix}\textbf{Adult survival * probability of laying * clutch size}\end{pmatrix} \\ \begin{pmatrix}\text{Embryo survival * larval survival * metamorph survival}\end{pmatrix} & \begin{pmatrix}\text{Probability of remaining a juvenile}\end{pmatrix} & 0 \\ 0 & \begin{pmatrix}\text{Probability of juvenile becoming adult}\end{pmatrix} & \begin{pmatrix}\textbf{Adult survival}\end{pmatrix} \end{bmatrix}$$

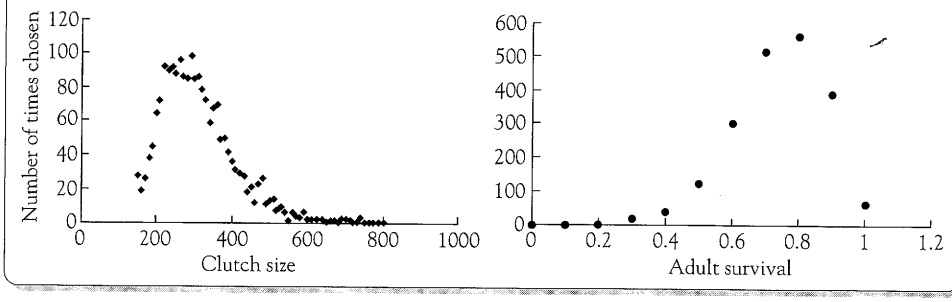
Step 2: environmental stochasticity for the two emboldened vital rates (clutch size and adult survival) is as follows.

	Clutch size	**Adult survival**
Mean	303	0.69
SD	95	0.13
Distribution for random numbers	Lognormal	Beta

Step 3: for five time steps, the vital rates chosen randomly from the specified distributions might, for example, be as follows.

Time step	**Clutch size**	**Adult survival**
1	287.6	0.66
2	326.8	0.71
3	252.0	0.93
4	382.9	0.55
5	251.9	0.60

Step 4: the distribution of vital rates chosen many times would look like the graphs below.



should not be surprising to learn that the vital rates themselves also vary widely in their effects on population growth and structure: all vital rates are not created equal. Intuition alone is insufficient to predict how changes in individual life-history components will affect population growth. Although one commonly hears conclusions like "forest fragmentation affects adult survival" or "acid rain affects clutch size," such statements do not indicate how the expected changes in vital rates affect population growth.

This simple demographic fact – that different vital rates do not have equal impacts on population growth rate – has been known for a long time (e.g. Cole 1954). But it was Hal Caswell's book on *Matrix Population Models* (1989), arriving on the heels of unprecedented access to desktop computers, that irrevocably convinced ecologists of the importance of a formal framework evaluating the effects of changes in vital rates. Sensitivity analysis provides that framework in the form of analytical and simulation-based tools to evaluate how past or future changes in life-history attributes or demographic vital rates affect population growth or persistence.

One of the earliest and most influential uses of sensitivity analysis in animal population biology targeted loggerhead sea turtles, which had been declining in the Atlantic by 3–5% per year for a long time. On the east coast of the USA enormous public sentiment built up concerning mortality of the eggs on the beach and the tiny (and adorable) hatchlings that were killed by predators, crushed by vehicles, and disoriented by lights as they tried to make their way from the nest to the ocean. Therefore, management focused on what seemed to be the obvious solution: increasing the survival of eggs and hatchlings. But in 1987 Deborah Crouse and colleagues published a sensitivity analysis that showed that even large increases in egg or hatchling survival would do little to reverse the population decline: the key was to increase survival of young adults in the ocean. It turned out that roughly 50% of loggerhead mortality in the Atlantic was due to young adult turtles becoming entangled in shrimp nets. The paper by Crouse et al. (1987) was key to the development of legislation requiring turtle-excluder devices to be installed by shrimpers (Crowder et al. 1994). In this case, sensitivity analysis of a matrix-projection model showed that intuition focusing on eggs and hatchlings alone to recover the species was wrong, and that a different management action would be much more beneficial and efficient for recovery.

Three main approaches are used by applied wildlife population ecologists to conduct sensitivity analyses (see Mills & Lindberg 2002 for more details). I will give a brief overview of these approaches, followed by a peek into the range of questions that can be answered with sensitivity analysis of matrix population models.

How to do a sensitivity analysis

Manual perturbation

The most basic approach to sensitivity analysis is to manually perturb, or change, the input to a population model and observe how the change affects the output[7].

[7]Output could be population growth rate, or it could be probabilities of quasi-extinction (see Chapter 14).

For example, one could ask how the deterministic population growth rate (λ) of a matrix model changes when adult survival is increased by 10% compared with an increase in fecundity. Management options can be explored by comparing the expected effects on population growth or persistence when each option changes certain vital rates by any pre-determined amount. The approach is infinitely flexible; sensitivity analysis via manual perturbations is not limited to investigating the importance of vital rates alone, but rather can explore a range of factors including density dependence, inbreeding depression, and movement among populations (Chapter 12). Also, manual-perturbation sensitivity analysis can incorporate different age or stage structures, quantifying the effect of age structure on population growth.

Analytical sensitivity and elasticity analysis

You have learned that different age classes may have very different relative abundances at SSD, and different effects on future population size (i.e. different reproductive values). Therefore, a vital rate for a certain age class will influence λ more if there are proportionately more of that age class (larger SSD) and if each individual of that age class has a larger impact (bigger reproductive value). Analytical **sensitivities** and **elasticities** elegantly combine the reproductive value of an age class with its expected SSD to evaluate how infinitesimal changes in individual vital rates will affect λ. Specifically, sensitivity for a vital rate that makes up matrix element $a_{i,j}$ (remember this is the matrix element in row i and column j) is a function of the reproductive value of the age class (v_i) and the SSD (w_j)[8]:

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\left(\sum_{k=1}^{\text{Last stage class}} v_k w_k \right)} \qquad (7.2)$$

A larger reproductive value (v_i) or SSD (w_j) leads to a larger sensitivity. Notice that sensitivity is a partial derivative, defined as the infinitesimal absolute change in population growth rate given an infinitesimal absolute change in a vital rate or matrix element, while all other vital rates are held constant. As an alternative to the calculus in eqn. 7.2, you can also estimate sensitivity by making a tiny manual change to the vital rate of interest, and quantify how λ at SSD changes before and after the perturbation. For example, increase the element $a_{i,j}$ by 0.01, leaving everything else unchanged, and estimate λ before and after, as follows.

[8]If you prefer to think about equations graphically, consider that as a partial derivative, the sensitivity of matrix element $a_{i,j}$ equals the slope of the tangent to the curve relating population growth rate to the matrix element, evaluated at the mean element.

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\lambda_{a_{i,j}+0.02} - \lambda_{\text{original}}}{0.01} \tag{7.3}$$

So, for the red-legged frogs in Box 7.2, analytical sensitivity would quantify how a tiny change in juvenile survival (say, from 0.69 to 0.70) would affect population growth compared with the same tiny change in another vital rate, such as clutch size (from 303 to 303.01). Although this may be useful for some applications, you can see immediately that from a practical perspective we have a scaling problem; the same absolute change of 0.01 in the mean of these two rates is very different for survival (a 1.4% change) compared with clutch size (a 0.003% change). That's where elasticity becomes useful. Elasticity is sensitivity's cousin, a metric that rescales the sensitivity to account for the magnitude of the vital rate. Thus elasticities are **proportional sensitivities** that describe the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate[9]:

$$\text{Elasticity of matrix element } a_{i,j} = (\text{sensitivity of } a_{i,j}) * \frac{a_{i,j}}{\lambda} \tag{7.4}$$

When matrix elements are composed of more than one vital rate (e.g. where each element of the top row of a projection matrix contains both reproduction and survival components), or when a particular vital rate shows up in more than one matrix element, component sensitivities and elasticities can be calculated for each vital rate that appears in one or more matrix elements. Although the analytical formula for component sensitivities requires chain-rule differentiation for each $a_{i,j}$ that contains a particular vital rate x, in many cases the procedure is pretty simple[10].

As a proportional measure of sensitivity, analytical elasticities are more widely used in applied population biology than sensitivities. Elasticities can be added together to predict the joint effect of changes in multiple rates (assuming the changes in vital rates and λ are linearly related). Elasticities of all matrix elements sum to one; elasticities of component vital rates do not add up to one but can still be ranked. Based on analysis of measured vital rates from hundreds of studies of different bird and mammal species, predictable patterns link life-history traits to the relative elasticities of different vital rates (Box 7.3).

[9]Analogous to sensitivity, elasticity is the slope of the tangent to the curve relating proportional changes in λ to proportional change in matrix elements.

[10]Assuming that each matrix element is a simple linear combination of different vital rates, here is a simple translation of the chain rule to calculate sensitivity for a vital rate x that is a component of more than one matrix element, where each element containing x has sensitivity $s_{i,j}$.

$$\sum_{1}^{\text{Elements containing } x} [(s_{i,j}) * (\text{product of components other t}$$

You can also use eqn. 7.3 to tweak a component vital rate and calculate sensitivity. Either way, the elasticity of vital rate $x = (\text{component sensitivity of vital rate } x) * \left(\frac{x}{\lambda}\right)$.

Box 7.3 How might we predict which vital rates will have highest elasticities for a wildlife species?

Although the best way to assess elasticity of a vital rate is to conduct analysis on a complete set of field-derived vital rates for a particular population, it is useful to know that some coarse generalizations can support general principles. For example, species with early maturation and large litters tend to have elasticities that are higher for reproduction (litter size and offspring survival) and lower for adult survival; conversely, in species with late maturation, fewer offspring, and higher survival rates, population growth is affected more by adult survival than by reproduction (Heppell et al. 2000, Sæther & Bakke 2000, Oli & Dobson 2003). Survival of all stages will tend to have higher elasticities than reproductive output for most taxa with lifespans longer than a year (Crone 2001). The implication is that "in any sharp change of population growth rate for a long-lived species, one should first suspect a change in adult survival" (Lebreton & Clobert 1991:108).

Although these life-history general principles give us first-cut insights into which rates will have the highest elasticities, that does not mean that those rates are most important. Remember, vital rates with low elasticities but that change a large amount could actually affect the growth rate more than rates with high elasticities but that change little.

Analytical sensitivities and elasticities are easily applied, comparable across studies, and can be calculated from a single population matrix constructed from average or even best-guess vital rates. However, we should keep in mind their fundamental assumptions (Mills et al. 1999, 2001). First, they are asymptotic, relying on the population being at SSD (although this assumption can be relaxed; see Fox & Gurevitch 2000, Grant & Benton 2000, Caswell 2001). Second – and perhaps most importantly – analytical sensitivities and elasticities by themselves say nothing about how much vital rates change in nature or under management.

A classic case in point (Gaillard et al. 1998, Raithel et al. 2006) is that for ungulates in general, adult survival would be expected to have the highest elasticity by far. However, juvenile survival will be much more variable than adult survival, because juveniles are less buffered against density-dependent influences or environmental factors such as predation, bad weather, and so on. The fact that juvenile survival may easily vary from 0.1 to 0.7, whereas adult survival will tend to be much less variable, means that the rate with relatively low elasticity that changes a lot (e.g. juvenile survival) may affect population growth more than a rate with high elasticity that doesn't vary much (e.g. adult survival). Elasticities based on a mean matrix cannot capture how much a vital rate, and therefore population growth, can change in nature or under management.

An extension of analytical sensitivity and elasticity analysis, called **life-table-response experiments** (or LTREs for short), does explicitly account for variation with an analytical equation (Caswell 2001). For practical purposes, changes simulated on the computer are a more versatile way to the same end, so I will discuss such an approach next.

Life-stage simulation analysis

Wisdom and Mills (1997) developed a simulation-based approach to sensitivity analysis that might be considered a hybrid of the manual perturbation and analytical sensitivity/elasticity-based methods. The approach is called **life-stage simulation analysis** (LSA; Wisdom et al. 2000)[11] because it uses simulations to evaluate the impact of changes in different vital rates on elasticity rankings and λ. For the purposes of conservation decision-making, the user obtains (from the field if possible) both means and variances for vital rates. The variance should be based on process variance, uninflated by sample variance (Mills & Lindberg 2002). For projecting what might happen in the future, you can couple information from the past with specified changes in means and variances that are considered biologically, politically, and logistically possible under management in the future[12]. Correlations among vital rates are specified, if possible, as are the distribution functions for each vital rate (i.e. uniform, lognormal, beta, etc.). A computer program constructs many matrices with each rate in each matrix drawn from the specified distributions. Population growth rate is calculated for the matrix (usually asymptotic λ at SSD, although stochastic λ could also be calculated).

Output metrics in LSA include elasticity-based measures (e.g. the proportion of replicates where the vital rates shift rankings of elasticities, or the differences in elasticity values whenever the rankings of elasticities change across the replicates; Wisdom et al. 2000), as well as other metrics that avoid elasticity entirely. For example, one LSA output could be the percentage of replicates having positive population growth under different scenarios (Fig. 7.7).

Another way that LSA has commonly been used to evaluate the importance of vital rates for management is to regress λ on each vital rate as all rates change simultaneously (including the vital rate of interest) in 1000 or so simulated matrices (e.g. Wisdom & Mills 1997, Crooks et al. 1998, Cross & Beissinger 2001). The coefficient of determination (R^2) represents proportion of the variation in population growth rate that is explained by environmental variation in that vital rate, with all other vital rates varying simultaneously. When all main effects and interactions are included, the R^2 values sum to one. When λ is a linear function of the vital rates, the slope of the line equals the analytical sensitivity and R^2 is a function of both the slope (i.e. analytical sensitivity) and the proportionate variation in that vital rate, adjusted for covariance among vital rates. The same relationships hold for elasticity if the regression is done on log-transformed data (Brault & Caswell 1993, Horvitz et al. 1997). Therefore, the

[11]Morris & Doak (2002:344–8) refer to this approach as a "simulation-based sensitivity analysis."

[12]I avoid use of the terms prospective and retrospective sensitivity analysis (Caswell 2001) because these terms have been used to imply that the inclusion of variation in a sensitivity analysis prohibits one from asking what might occur under future management. When conducting a sensitivity analysis of potential management scenarios, it seems more constructive to simply make explicit whether or not variation is included, the origin of the estimates of both variation and mean rates, and the rationale for potential future changes in vital rates (Mills et al. 2001, Wisdom et al. 2000, Mills & Lindberg 2002).

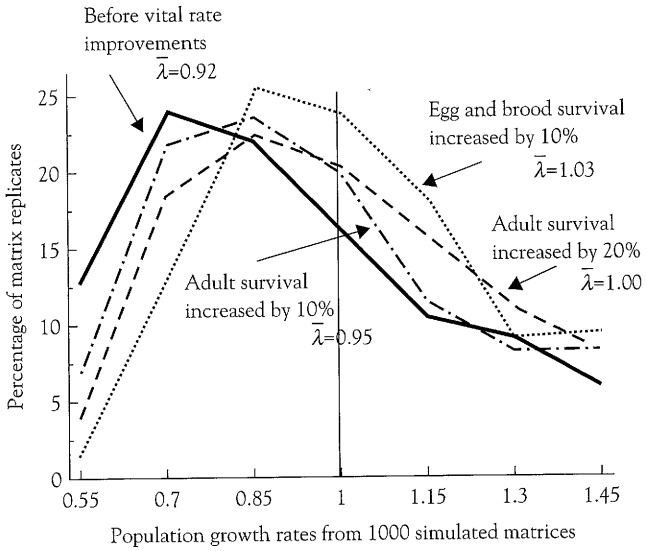


Fig. 7.7 An example of one form of LSA output for greater prairie-chickens, a species whose populations are declining, scattered, and potentially vulnerable to extirpation (see Wisdom & Mills 1997). The potential consequences to expected population growth (λ), for different potential management strategies are derived from simulations of mean (and variances) of vital rates using a LSA. The expected distribution of λ in 1000 simulated matrix projections before vital-rate improvements is shown by the solid line; dashed and dotted lines show how the distribution of expected growth rates change as particular vital rates are improved by increasing their means by specified amounts (and decreasing their variation by 20%). $\bar{\lambda}$ gives the mean of the λ for that distribution. Increasing by 10% the average survival during part of the first year (egg and brood survival) gives the biggest increase in the expected population growth (dotted line). Increasing by 10% the average adult survival gives much less improvement (dotted/dashed line). To get about the same increase in population growth as the 10% increase in first-year survival, average adult survival would need to be increased by 20% (dashed line). Modified from Wisdom et al. (2000). Reproduced with permission of the ESA.

simulation-based LSA R^2 can be compared with analytical life-table-response experiment approaches, in that both account for infinitesimal effects (e.g. elasticity) as well as the range in variation of different rates (Wisdom et al. 2000). However, LSA is more flexible than life-table-response experiments because any sort of change can be simulated, and a variety of output metrics are possible.

Case studies

To end the chapter, I will consider four case studies that used the application of matrix projections and sensitivity analysis to inform management, often in nonintuitive ways.

Case study 1: what are the best management actions to recover an endangered species?

Red-cockaded woodpeckers are an endangered species endemic to mature pine forests of the southeastern USA. They are cooperative breeders, with males staying on natal territories as nonbreeding helpers to the breeding pair for up to 11 years before inheriting natal territories or dispersing. How should managers decide which management strategies are most likely to increase the population growth of this endangered species? Detailed field studies provided critical insights into vital rates, behavior, and potential effects of management actions (Walters 1991), which could then be extended with population models exploring how population growth and persistence could be most efficiently increased through management.

Selina Heppell and colleagues (1994) used an innovative matrix-modeling approach based on male red-cockaded woodpeckers and using behavioral transitions associated with helping in addition to the usual size or age transitions (Fig. 7.8a). For example, fecundity in the top row was defined as the number of fledglings produced by individuals that survived the year and were helpers or breeders in that time step. Four management techniques with specific predicted effects on one or more vital rates were evaluated using the manual-perturbation approach coupled with elasticity analysis. Each of these actions targeted specific vital rates, thereby affecting one or more elements $a_{i,j}$ of the matrix in Fig. 7.8(a). The management options were as follows.

1. Remove invaders: remove cavity invaders such as flying squirrels and other woodpecker species that inhabit red-cockaded woodpecker nest cavities, increasing woodpecker fecundity (all elements of top row).
2. Female translocation: capture and relocate female red-cockaded woodpecker fledglings to solitary male territories, causing more solitary males to become breeders (increase $a_{6,4}$ and $a_{1,4}$).
3. Cavities in occupied territories: drill cavities in existing territories, increasing the fecundity of breeders (increasing all of the top row) and the probability that fledglings become helpers ($a_{2,1}$) while decreasing the chance that fledglings become breeders ($a_{5,1}$).
4. Cavities in unoccupied territories: increase new territories by drilling artificial cavities in unused yet suitable habitat and by reducing hardwood understory. This action should increase both fledgling-to-breeder and helper-to-breeder transitions (top row, and $a_{5,1}$ and $a_{6,2}$) while decreasing fledgling mortality (all of first column).

What would be the predicted relative effect of these management actions? Creating new territories through cavity construction in unoccupied territories (management option 4) had the biggest benefit (Fig. 7.8b) through its effects on two vital rates with relatively high elasticity (fledgling-to-breeder and helper-to-breeder transitions). Removing cavity invaders and placing more cavities in unoccupied territories were also potentially reasonable approaches, whereas female translocation (option 2) seems a waste of money. Importantly, Fig. 7.8 also underscores a recurring theme: the best strategy ultimately depends on how much rates could be changed. For example, a 25% change by removing invaders (option 1) would increase red-cockaded woodpeckers more than a smaller (10%) change via the best strategy of installing cavities in unoccupied territories.

(a)

Transition	From fledglings	From helpers	From floaters	From solitary males	From 1-year-old breeders	From ≥2-year-old breeders
Fledglings produced	0.080	0.266	0.324	0.275	0.486	0.522
To helpers	0.294	0.494	0.000	0.000	0.000	0.000
To floaters	0.031	0.000	0.000	0.000	0.000	0.000
To solitary males	0.043	0.020	0.172	0.216	0.000	0.000
To 1-year-old breeders	0.074	0.000	0.000	0.000	0.000	0.000
To ≥2-year-old breeders	0.000	0.257	0.483	0.410	0.725	0.800

(b)

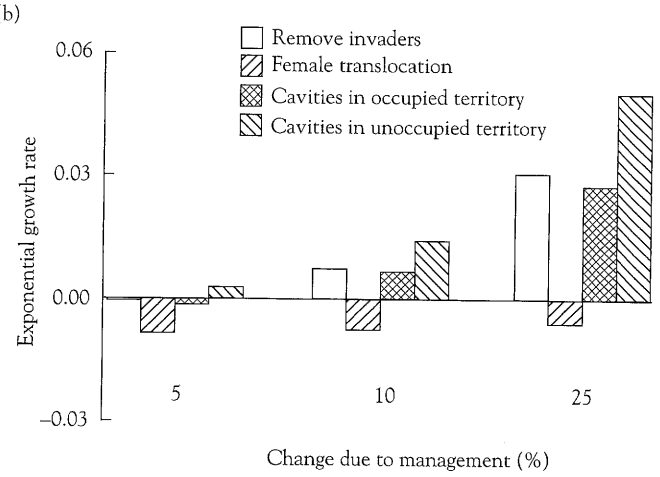


Fig. 7.8 Male-based population-projection modeling to inform management of the endangered red-cockaded woodpecker (from Heppell et al. 1994; reproduced by permission of The Wildlife Society). (a) The stage-based matrix model; (b) expected growth rates expected following implementation of the four management alternatives, each of which was expected to influence different vital rates.

A critical part of red-cockaded woodpecker life history not incorporated into this model is the spatial structure among multiple groups. Because helper males do not disperse far to fill a breeding vacancy, the new territories established with cavities need to be close to currently occupied territories. Although matrix models can be built to incorporate multiple populations with specified movement among them, individual-based models provide an alternative framework to matrix models for population projections. Using an individual-based model that was also spatially explicit, Walters et al. (2002) extended the findings of Heppell et al. (1994) to conclude that new artificial cavity sites need to be aggregated, or clumped near current territories, emphasizing not only density but also spatial distribution of the managed cavities; even quite small local populations could be supported if the territory groups were aggregated. Importantly, these recommendations about cavity establishment – born of a union of excellent field work coupled with thoughtful population modeling – have been incorporated into the new federal recovery plan for red-cockaded woodpeckers (US Fish and Wildlife Service 2003).

Case study 2: what are the most efficient management actions to reduce a pest population?

Brown-headed cowbirds are a nest parasite native to the short-grass Great Plains of North America. Although scattered populations may have been present historically throughout much of North America (Morrison & Hahn 2002), their numbers and distribution increased with landscape fragmentation associated with European settlement and agriculture during the 19th and 20th centuries. Because cowbirds exist at high densities in many agricultural areas, and each female can lay up to 40 eggs per season in the nests of other species, cowbirds can reduce nest success of their passerine hosts. To reduce the effects of cowbirds on native and threatened species, land managers have implemented control efforts since at least the early 1970s. For example, trapping efforts in Texas have removed 3000–5000 female cowbirds per year, and in Michigan control programs to protect Kirtland's warblers have removed 3000 or more cowbirds and eggs each year (Kelly & DeCapita 1982). Given limited funds, is the most efficient way to decrease cowbird population growth to remove eggs, to remove adults on the breeding or wintering range, or some other action?

Citta and Mills (1999) used both analytical sensitivity analysis and LSA to examine the consequences of cowbird control efforts. The LSA scatterplots of the variation in λ explained by each vital rate in 1000 simulated cowbird matrices indicate that egg survival alone explains a preponderance (61%) of the variation in λ (Fig. 7.9a). By contrast, fecundity and survival of other stages all explain less than 15% of variation in λ (Fig. 7.9b–f). Why? It turns out that the proportional infinitesimal effect of each rate (i.e. analytical elasticity) is equal for egg, nestling, and yearling survival, but egg survival probably varies a lot more (see the range on the x axis in Fig. 7.9) and so has a greater opportunity to affect λ. Thus LSA captured the fact that both elasticity – the infinitesimal effect – and the variation in a rate determine the merit of altering certain vital rates.

So, the next question is how easy it would be to change egg survival, which is normally highly variable. Killing certain stages (adults or eggs) may be more or less palatable to the public, and more or less feasible under field conditions, both of which affect how much a rate can be changed. At SSD, 92% of the cowbirds would be eggs, so that in a population of 5000 cowbirds you would have to destroy more than 400 eggs to change survival enough to cause λ to be less than 1.0; to remove that many eggs would involve intense effort, making it not only expensive but also prone to disrupting the host species that are innocently caring for the cowbird's eggs (Citta & Mills 1999).

The conclusion of the modeling was that management-induced changes in neither fecundity nor egg survival alone would easily affect population growth. Likewise, adult survival on the breeding grounds would have to be reduced by a lot to cause λ to decline, an option limited by the compensation that occurs via replacement by floaters and immigrants; reducing survival on wintering grounds is logistically daunting. Thus, although local cowbird reductions can successfully protect sensitive host species on a local scale (Rothstein & Cook 2000), the sensitivity analysis clarified that easy fixes in the form of removals of one stage would not reduce long-term population growth of the parasitic pest. Instead, multiple vital rates would have to be hammered simultaneously, probably by managing land use across a landscape.

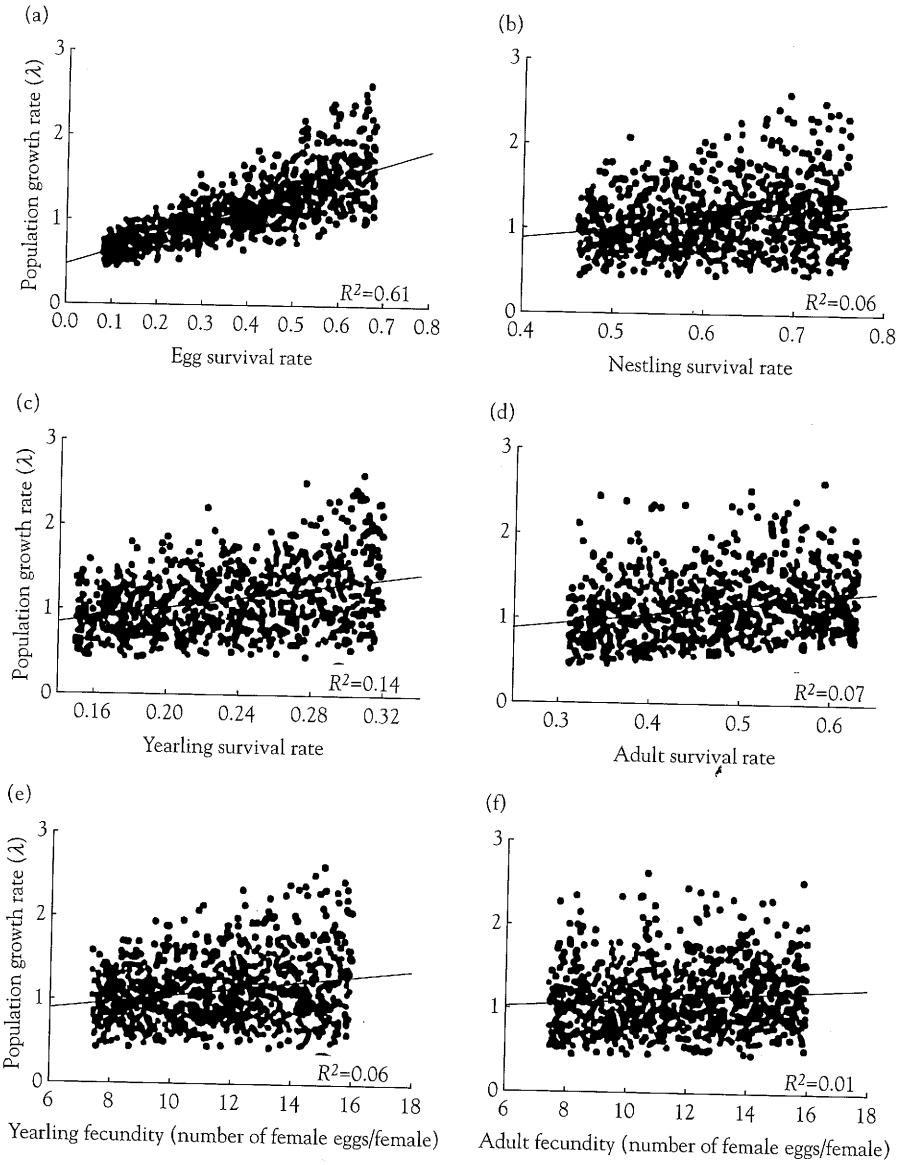


Fig. 7.9 An LSA-based approach to evaluating the relative importance of different vital rates to population growth in brown-headed cowbirds. The R^2 value describes the proportion of variation in λ explained by variation in a vital rate, based on 1000 simulated matrices where vital rates were chosen from the range of variation determined from published studies. Notice that egg survival alone accounts for 61% of the variation in λ. From Citta & Mills (1999)

Case study 3: how should a harvested species be managed?

Migratory waterfowl have been intensively studied and managed, to both protect populations and provide compatible hunting opportunities. In the USA about $50 million in migratory bird conservation funds (primarily funded by duck stamps bought by

hunters) are dispersed each year to protect and enhance wetlands and grasslands for waterfowl habitat. Traditionally, less than 40% of these funds has been apportioned to breeding areas. An ongoing debate has centered on how much effort (and money) should be dedicated to protection and enhancement of habitats on breeding areas (especially wetlands and nesting habitat) compared with non-breeding areas (especially wetlands for migratory and wintering waterfowl).

Hoekman et al. (2002) used LSA to assess the effects of management and environmental variation on population growth of the North American mid-continent mallard population, considering both the infinitesimal effect of each vital rate, and the observed variation in each. The LSA indicated that vital rates on breeding grounds (hen survival during the breeding season, clutch size and nest success, and survival of ducklings) collectively explained about 84% of the variation in λ, compared to only 9% explained by nonbreeding survival on migration and wintering areas[13] (Fig. 7.10).

The finding that the contribution to duck population growth of nonbreeding survival is dwarfed by vital rates on breeding grounds has profoundly influenced waterfowl management. An expert panel assembled in 2004 by the US Fish and Wildlife Service came to a striking science-based conclusion based largely on the sensitivity analysis: given that variation in vital rates on breeding grounds explains the vast majority of the variation in λ for mid-continent mallards, and given the general absence of strong differences in the ability to change vital rates on breeding compared with nonbreeding areas through habitat management, the panel recommended that approximately 90% of the waterfowl conservation funds should go to breeding areas (Cox et al. 2004). This suggestion has been elevated to the top levels of the US Fish and Wildlife Service, and although politics will certainly play a role, it appears likely that proportionately more management funding will shift to the breeding grounds. Simultaneously, current adaptive harvest management for waterfowl (see Chapter 14) is recognizing the need to incorporate breeding-area processes to optimize harvest management. Thus, a matrix population model has distilled a nonintuitive insight (that breeding-ground dynamics drive population growth) that is changing the trajectory of waterfowl funding and management. These results have also been useful in reassessing research priorities, with increased funding directed toward sources of variation in nest and duckling survival.

Case study 4: what research is needed to understand global amphibian declines?

Beginning around 1990, researchers from around the world sounded an alarm that amphibian numbers seemed to be declining. The call to action came from monitoring studies, and for the last decade or so the question has been how the declines would best be reversed. Work on a variety of species has shown how various vital rates might be affected by ultraviolet radiation, pH, disease, habitat destruction, or other factors. But there has been a missing link between the data showing declines and the data

[13]The final 7% can be thought of as statistical noise, accounted for by interactions among rates and the nonlinear response of λ to the changes in vital rates.

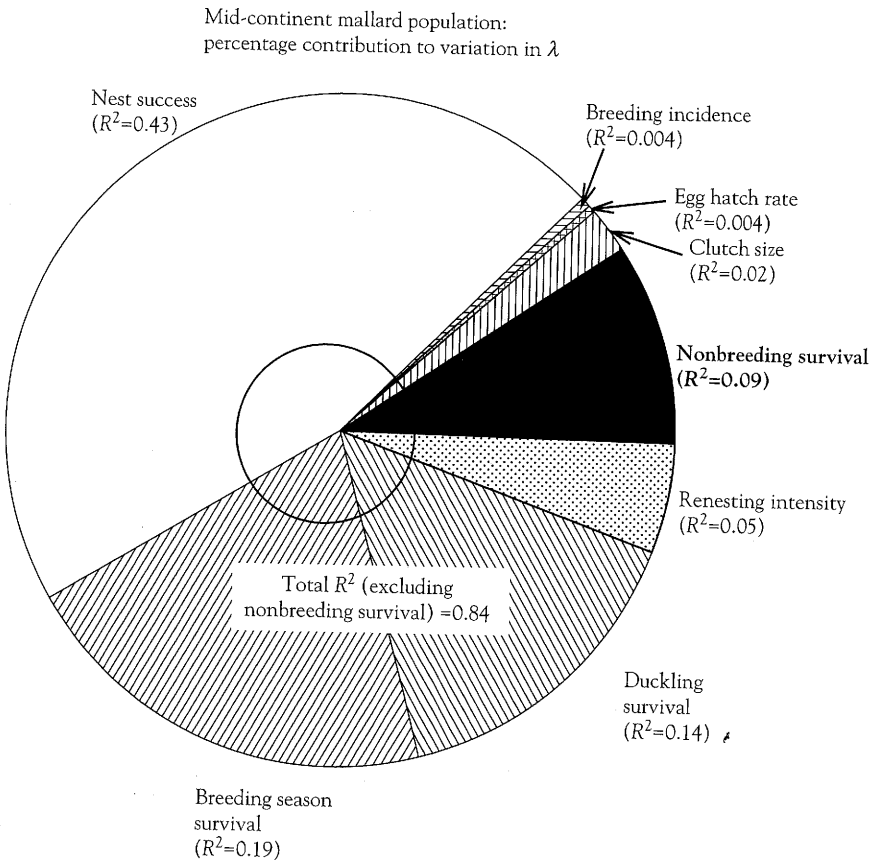


Fig. 7.10 Results of an LSA analysis for female mid-continent mallards in North America (Hoekman et al. 2002). Each pie slice shows the proportion of variance in population growth rate explained by that vital rate in 1000 simulations of vital rates drawn from field studies. In other words, the plot shows the R^2 from regression plots of vital rates against population growth determined as in the cowbird example (Fig. 7.9). Approximately 84% of the variation in population growth rate is expected to arise from breeding-ground vital rates. The 7% not accounted for in the pie can be thought of as statistical noise, accounted for by interactions among the rates and the nonlinear responses of population growth to the changes in vital rates.

showing that vital rates have changed by certain amounts: would those changes in vital rates be likely to cause the observed declines?

Biek et al. (2002) conducted sensitivity analysis for three potentially declining amphibian species for which there were reasonable vital-rate estimates and purported mechanisms driving reduced vital rates: western toads, red-legged frogs, and common frogs (the latter two species formed the basis for the matrix examples in this chapter). In all three species, post-metamorph survival (juvenile or adult) had the highest elasticity, indicating that λ was most likely to be decreased by a given reduction in these rates compared with others (such as embryonic or larval survival) that have been the target of most experimental studies. Manual perturbation and LSA enriched the

conclusions by reinforcing (as in other case studies) that if rates with low elasticities vary a lot, then they can affect λ even more than rates with higher elasticities.

Summary

Understanding the effects of age or stage structure on population processes is critical for wildlife population ecologists, both because different stages are important to management decision-making (e.g. bull elk compared with fawns, or turtle eggs compared with ocean-going juveniles) and because structure affects population growth. Matrix population models are certainly not the only way to account for population structure, but they are popular due to their relative simplicity and straightforward links to vital rates measured in the field.

The fact that different stages are not equal in their influence on population growth means that a saavy population ecologist will quantify the reproductive values of each stage to help inform translocations, harvest strategies, or control of pest species. If vital rates remain relatively constant over time, a population will achieve a SSD and a population growth rate characteristic of those vital rates.

Because both reproductive values and proportions in the population will differ between stages, survival and reproduction in different stages do not have the same effects on population growth. In other words, just as different stages are not equal in their effects on population growth, neither are vital rates equal. The broad and important field of sensitivity analysis seeks to quantify the relative importance of different vital rates and the expected efficacy of different management actions on population growth or persistence. Analytical sensitivity and elasticity show how much an infinitesimal change in each vital rate might affect population growth. As useful as this insight is, remember that the amount that a rate can change in nature or under management will also affect how important a vital rate is to population growth.

The two sensitivity analysis methods that do the best job of specifically and intuitively incorporating a specified range of variation in vital rates include manual perturbations and LSA. Manual perturbations of vital rates can contrast specific predictions from management actions that are expected to have specific effect, an approach that identified useful steps for managers to take in the recovery of red-cockaded woodpeckers. LSA can simulate many possible matrices from user-specified means and variances. Its output can be variable, including assessment of the stability of elasticity rankings across variation in vital rates as well as direct insight into how changes in certain rates are expected to affect population growth. Management of pest species (e.g. cowbirds), harvested species (e.g. mallards), and other species of concern (e.g. declining amphibians) would be more efficiently directed using LSA to evaluate the effects of management scenarios on expected population growth rate.

I will end with an apt metaphor borrowed from Ron Reynolds of the US Fish and Wildlife Service. A good general always goes into battle with a thoughtful focus on achieving the most with the resources at hand; troops are not scattered randomly across the battlefield or positioned according to political whims. Likewise, a good

wildlife manager should use the insights from population-projection models and sensitivity analysis to see how proposed actions could ripple through to affect population growth in ways that are not obvious, revealing which actions will be a waste of time and money and which would be cost-effective. Population-projection models frame the biological context to help win the management battle.

Further reading

Caswell, H. (1989/2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 1st and 2nd edns. Sinauer Associates, Sunderland, MA. The single most important reference for the mathematics of matrix models.

Noon, B.R. and Sauer, J.R. (1992) Population models for passerine birds: structure, parameterization, and analysis. In: *Wildlife 2001: Populations* (eds. D.C. McCullough and R.H. Barrett), pp. 441–64. Elsevier Applied Science, London. Although specifically focused on birds, this is one of the most readable and practical discussions of building and analyzing matrix populations.