PART I

BACKGROUND TO APPLIED POPULATION BIOLOGY

CHAPTER 1

The big picture: human population dynamics meet applied population biology

The metabolic rate of history is too fast for us to observe it. It's as if, attending to the day-long life cycle of a single mayfly, we lose sight of the species and its fate. At the same time, the metabolic rate of geology is too slow for us to perceive it, so that, from birth to death, it seems to us who are caught in the beat of our own individual human hearts that everything happening on this planet is what happens to us, personally, privately, secretly. We can stand at night on a high, cold plain and look out toward the scrabbled, snow-covered mountains in the west, the same in a suburb of Denver as outside a village in Baluchistan in Pakistan, and even though beneath our feet continent-sized chunks of earth grind inexorably against one another, go on driving one or the other continent down so as to rise up and over it, as if desiring to replace it on the map, we poke with our tongue for a piece of meat caught between two back teeth and think of sarcastic remarks we should have made to our brother-in-law at dinner.

Russell Banks (1985:36–7), *Continental Drift*

Experience with game has shown, however, that a determination to conserve, even when supported by public sentiment, protective legislation, and a few public reservations or parks, is an insufficient conservation program. Notwithstanding these safeguards, non-game wild life is year by year being decimated in numbers and restricted in distribution by the identical economic trends – such as clean farming, close grazing, and drainage – which are decimating and restricting game. The fact that game is legally shot while other wild life is only illegally shot in no [way] alters the deadly truth of the principle that it cannot nest in a cornstalk.

Aldo Leopold (1933:404), *Game Management*

INTRODUCTION

Should Texas panthers be brought in to breed with Florida panthers? What factors are most likely to explain global amphibian declines, and what is the most efficient path to reverse the decline? Do wolves reduce the numbers of elk available for hunters? What factors affect harvest regulations for waterfowl? Was the introduction of foxes to Australia likely to have driven native prey species to extinction, and how best to decrease the numbers of the exotic predator? These are just a few samples of the sort of real-world questions that can be informed by knowledge of applied population biology.

To set the stage for this book, consider some of the key words in the title. **Population** has many meanings, but for now let us consider the term in a broad sense, referring to a collection of individuals of a species in a defined area; the individuals in a population may or may not breed with other groups of that species in other places. A similar definition traces back to Cole (1957:2) who defined a population as "a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate,

Conservation of Wildlife Populations: Demography, Genetics, and Management, Second Edition. L. Scott Mills.

a sex ratio, and an age structure in describing the properties of the unit." The advantage of such vague yet practical definitions is that they allow discussion of both single and multiple populations, with and without gene flow and demographic influence from other populations.

Next, some thoughts are provided on the term **wildlife**. Although about 1.5 million species have been described on Earth, vertebrates comprise only about 3% of the total and terrestrial vertebrates less than 2%. Yet policy, public opinion, and ecological research still deal disproportionately with vertebrates, particularly birds and mammals (Leader-Williams & Dublin 2000, Clark & May 2002). Certainly, harvest management outside of fisheries and forestry centers mostly on terrestrial vertebrates.

However, the term wildlife means considerably more than merely terrestrial game (harvested) species. Even Aldo Leopold's classic book *Game Management* (Leopold 1933) made clear that harvested species should be considered a narrow segment of "wild life" (two words). Recognition of "The little things that run the world" (Wilson 1987) has emphasized the importance of small creatures – especially insects – to ecosystem structure and function, and, of course, Leopold (1953) reminded us more than 50 years ago that "To keep every cog and wheel is the first precaution of intelligent tinkering," an admonition that our focus should be on all the parts. Happily, it seems that now, more than ever, people value the conservation of all species (Czech et al. 1998). Reflecting these philosophies, US federal wildlife law in its broadest sense recognizes all nonhuman and nondomesticated animals (plants occupy a different conceptual status in law; Bean & Rowland 1997). Recent texts with wildlife in the title have considered all free-ranging undomesticated animals, and in some cases plants (e.g. Moulton & Sanderson 1997, Krausman 2002, Bolen & Robinson 2003). This perspective has historical precedent: the first issue of the *Journal of Wildlife Management* (1937) stated that wildlife management actions "...along sound biological lines are also part of the greater movement for conservation of our entire native fauna and flora."

This book will embrace a broad view of wildlife, because most concepts in population biology can be applied to all taxa. However, several core ecological, genetic, and life-history phenomena are idiosyncratic to plants, insects, or fish (e.g. seed banks, larval instars, anadromous breeding, self-fertilization, etc.), and so would require detailed treatment to understand population biology in detail for those taxa. For one book to effectively convey applications for species that are – at this point in human civilization – most prominent in the public eye, the majority of examples and case studies in this book will focus on the subset of wildlife consisting of amphibians, reptiles, birds, mammals (and fish to a much lesser extent).

Finally, some thoughts on the word **management**. This term is a pejorative in the minds of some, conjuring up images of manipulation and arrogance. It is certainly true that, in most cases, humans and human actions are ultimately what is managed, not the animals themselves. For others, the inclusion of management in the same book title with **conservation** is repetitive. Nevertheless, I have included management in the title because it is convenient shorthand for applied outcomes of population biology, ranging from measuring and interpreting trends to setting harvest limits, to evaluating viability of endangered species, and to determining the effects of predation on prey populations.

The overall influence of a species – any species – on its community and ecosystem is a function of its local density, its geographic range, and the per-capita impact of each member of the population. Virtually every problem related to wildlife conservation can be traced at least in part to human population growth – in terms of absolute numbers and distribution – as well as the per-capita impact of humans as strong interactors on the global stage (Channell & Lomolino 2000, Pletscher & Schwartz 2000). In the spirit of acknowledging that managing wildlife populations is really a matter of managing anthropogenic factors, the following section considers human population ecology, both emphasizing the role that humans play in affecting other species and conveying several principles to be elaborated on throughout the book.

POPULATION ECOLOGY OF HUMANS

Human population growth

Humans have experienced remarkably positive, often exponential growth (see Chapter 5) for thousands of years, resulting in enormous abundances. However, human population growth has not been constant. Let us start about 12,000 years ago, some 30,000 years after the evolution of indisputably modern humans

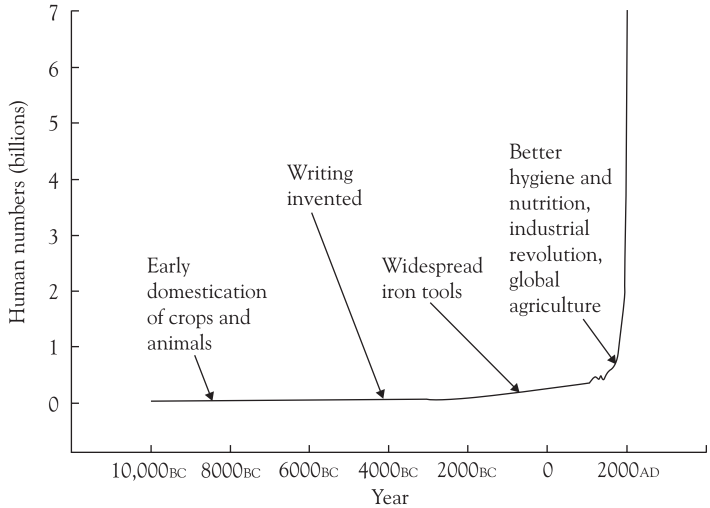

Fig. 1.1 Human population growth from 10,000 BC to the present day. The dip in the 14th century represents deaths due to bubonic plague. Data from the US Census Bureau, International Database.

and just after the last major ice age had ended. Humans were beginning village life in some parts of the world and had recently spread into and through the Americas. Plant and animal domestication would begin in one or two thousand years (Diamond 1999). At this point, somewhere between 1 and 10 million humans existed worldwide. It took about 10,000 years – until roughly 1 AD – to increase to about a quarter of a billion (Fig. 1.1). Thus, our population growth has historically been low, with increases of a tiny fraction of a percent per year.[1] This relatively low growth rate continued over the next 1600 years, with some noticeable setbacks such as the outbreaks of Black Death (bubonic plague) that killed one-quarter of the people in Europe between 1346 and 1352.

Between 1650 and 1850, growth of human numbers began to rocket (Fig. 1.1), following development of global agriculture, the initiation of the Industrial Revolution in western Europe, and improved nutrition and hygiene across much of the world. By the late 1960s, the Earth held about 3.6 billion humans. At that point the rate of increase of our species had just passed its peak of 2.2% per year (Fig. 1.2). Think about it: it took 10,000 years to increase by a quarter of a billion, but by 1968 our numbers were increasing by that much every 4 years.

What about now? The global population growth rate has declined since the late 1960s (Fig. 1.2). However, current growth is still positive, and multiplying this growth by the ever-larger numbers of our current population size results in enormous increases in abundance. In 2012 human numbers passed the 7 billion mark (Box 1.1). At current rates of growth and population size (2012) we are adding about 75 million people per year to the planet. That is a little over 200,000 additional people per day, or about 8500 net new people – subtracting deaths from births – added to Earth during a 1-hour lecture.

What next? Humans cannot escape the factors that constrain the numbers of all species. Resources (physical, chemical, biological, technical, institutional) cannot be without limit on the planet, so no species can increase indefinitely (see Chapter 7). Pinpointing where this population limit is – or when or how we will reach it – is highly uncertain, but some predict that our numbers will stabilize around 10 billion by the end of the 21st century (Lutz et al. 2001, Bongaarts 2009).

Population biology can help elucidate how changes in certain human vital rates, such as the number of offspring per mother, age at first reproduction, or survival at different ages, will influence population

[1] See Diamond (1999) for a fascinating treatise on how local biological diversity and environment have historically caused great variation in the growth of human populations around the world.

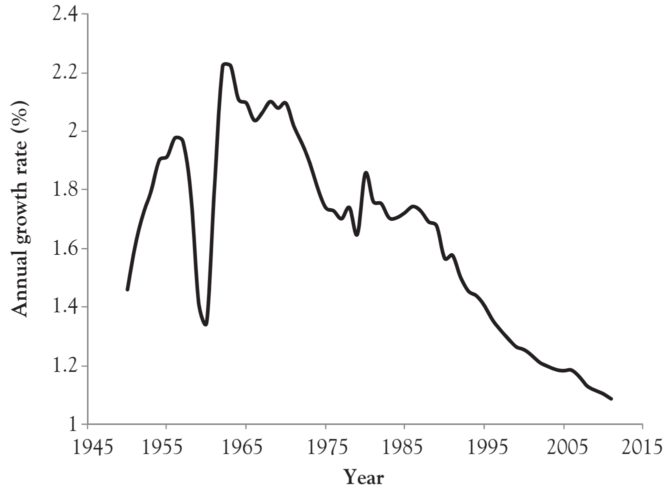

Fig. 1.2 Global human population growth rate (presented as the percentage change per year) since 1950. Data from the US Census Bureau, International Database (http://www.census.gov/ipc/www/idb/worldpopinfo.php). The dip in the global population growth rate 1959–61 was due to the Great Leap Forward in China, which resulted in over 20 million premature deaths from famine in a 2-year period (Becker 1996).

Box 1.1 Grasping the meaning of billions of people

A billion is a hard number to fathom. First, count the zeros. A billion is 1000 million, otherwise written as 1,000,000,000, or in scientific notation as 10^9. (In some European countries this number is the **milliard**, with **billion** referring not to a thousand million but rather to a million million, adding three more zeros; Cohen 1995.)

So how much is 7 billion people? If you traveled 7 billion miles around the equator you would circle the earth almost 300,000 times. If you lived 7 billion seconds you would live for 222 years. If you spaced 7 billion people 38 cm apart in a straight line, they would go from the Earth to the moon and back seven times – a lot of people.

change. For humans as for wildlife, these effects are not necessarily intuitive. The historical increase in the human growth rate, for example, occurred as much or more from increased survival as from increases in the number of children per female. Less obviously, population growth can also be strongly affected by the age when reproduction begins. Bongaarts (1994) provides a striking example for humans: the world population could be decreased by 0.6 billion over 100 years if the mean age of childbearing increased by 2.5 years and by 1.2 billion if the mean age increased by 5 years.[2] An increase in average childbearing age could occur as a by-product of education, because when girls and women stay in school longer they tend to get married later and delay childbearing. Overall, women with a

[2]The current mean age of first reproduction varies a lot by country and region, but tends to be in the mid-20s, with the Netherlands having the oldest mothers at first birth, at 29 years (Beets 1999).

high level of education have their first child about 5 years later than those with low education (Bongaarts 1994, Beets 1999).

The distribution of individuals across different ages also interacts with vital rates and population growth. In more developed regions of the world, increased survival and declines in fertility prior to 1950 have increased the percentage of the population older than 65, from 8% in 1950 to 15% in 1990 to 19% in 2010 (US Census Bureau data). Because women generally outlive men (for reasons discussed in Chapter 4), a shift to older age classes also shifted to a higher proportion of women.

Age structure also creates what is known as **population momentum**, which can cause population growth to be very different from what we would expect if birth and death rates were at levels that should lead to a stationary (not increasing, not decreasing) population. For humans, even if reproduction dropped from the current average of 2.5 offspring per female to below replacement (about 1.4 children per female), our numbers would still increase by about a billion between now and 2050, largely due to population momentum (Fig. 1.3); in short, the cohort of youngsters characteristic of the increasing population would be reproductive for decades, inflating population

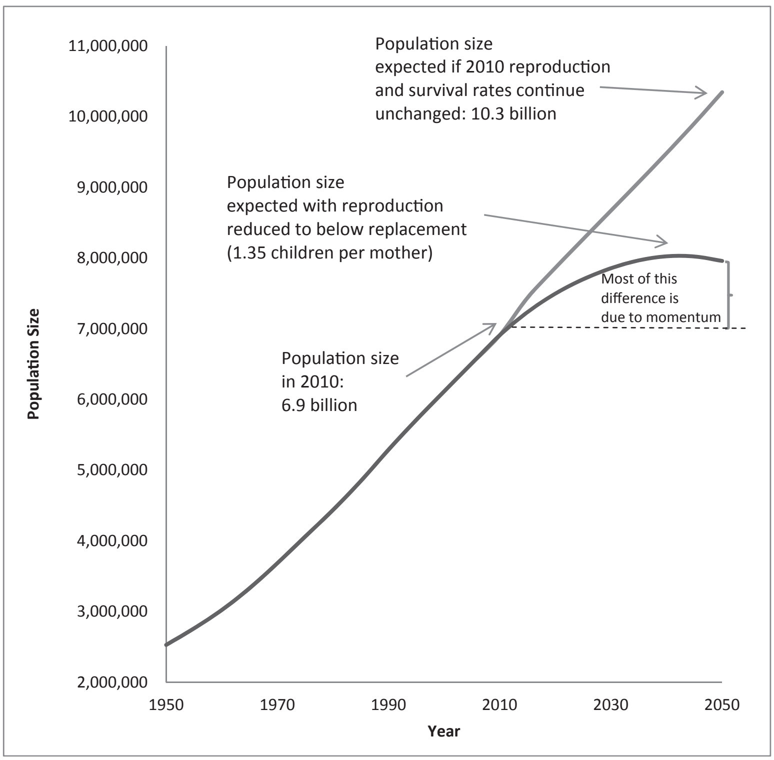

Fig. 1.3 Population momentum due to age structure in humans (using global data from the 2008 Revision of the "World Population Prospects", United Nations Population Estimates and Projections Section: Note: 2011 projections are available as this book goes to press). The dotted line shows a hypothetical flat trajectory remaining stationary at the nearly 7 billion people present in 2010. The top solid line shows what human population growth would look like under "no change"; that is, if fertility and mortality stays the same as it is now (2005–10). The lower line shows the projected growth under an assumption where, starting in 2010, mortality decreases slightly over time as life expectancy for humans increases, but where fertility is decreased in a big way, to about 1.35 children per woman. Although the draconian decrease in fertility causes population growth to become stationary or negative by 2050, our numbers would still be a billion or so more than now, due mostly to population momentum caused by the current population having a high proportion of younger females with a greater reproductive value.

growth until the age distribution adjusts to the smaller proportion of young, childbearing individuals expected at a stable age distribution (Chapter 6 explains this idea in detail). Conversely, population momentum could cause declining endangered species to continue to decline for some time, even after management has increased birth or survival rates to replacement levels.

Human impacts on wildlife through effects other than population size

Obviously, human numbers affect other species. However, the overall influence of any species on its community and ecosystem is a function not just of numbers but also of per-capita (or per-individual) interactions. Human use of inanimate energy (wood, oil, etc.) has grown from the energy equivalent of each person in the world keeping two light bulbs (40-watt) burning continuously through the year in 1860 to each person burning 52 bulbs continuously in 1990 (Cohen 1995). Extraction and use of this energy has profoundly affected the global environment and other species (Chapter 11).

The distribution and social grouping of humans has also changed. In 1880 only about 2% of people lived in cities with more than 20,000 people; by 1995 about 45% lived in cities and more than 17% of all people lived in cities larger than 750,000 (Cohen 1995:13). Humans have also shifted the number of people per household, going from 3.2 to 2.5 per household in more developed nations and from 5.1 to 4.4 in less developed countries over the last 30 years (Keilman 2003). Fewer people per household means more houses and more resource use per person. For example, as China goes from 3.5 people/house in 2000 to a projected 2.7 by the year 2015, 126 million new households will be added, even if China's population size remains constant (that is more new households in China over 15 years than the total current number of US households; Diamond 2005). Of course, the **footprint** humans have on other species also involves complex interactions with cultural norms, wealth distribution, and per-capita consumption rates. In short, humans are strong interactors (Chapter 13) whose impact on other species comes from both raw numbers and distribution as well as the large per-capita influences each individual human has on other species.

EXTINCTION RATES OF OTHER SPECIES

As the human population has climbed, the extinction rate of other species has increased as well; indeed, humans began causing extinctions about 45,000 years ago (Brook & Bowman 2004). Next we will consider how many species are on Earth and how current extinction rates compare to the background over geologic time.

Number of species on Earth: described and not yet described

My discussion of the number of species on Earth will focus on eukaryotic species, excluding bacteria and viruses. I am ignoring the domain of bacteria – those wondrous organisms that have been on Earth for more than 3.5 billion years; who metabolize sulfur in deep-sea trenches to make carbohydrates without sunlight; who thrive in boiling mud, in steam vents, and 4 km deep in the Earth at temperatures exceeding 100 °C; who fill our mouths in numbers averaging 4 billion bacteria per mouthful (between brushings!); and who comprise nearly 90 trillion of the 100 trillion cells that make up an individual human[3] – because bacterial population dynamics and life histories are fundamentally different than those of vertebrates (even more so for viruses, those important pseudo-life forms that can persist but not replicate outside the cells they infect).

About 1.5 million species of nonbacterial eukaryotes have been described (Fig. 1.4). Although more animal species have been described than any of the other three eukaryotic kingdoms (protoctista, plants, fungi), vertebrates make up only a small slice (3%) of the life-on-Earth pie. Excluding fish, the more-or-less terrestrial vertebrates (mammals, birds, amphibians, and reptiles) collectively amount to less than 2% (approximately 30,000) of described species.[4] By contrast, beetles rule the world in species numbers: with 300,000 described species, one out of five species on Earth is a beetle! More than 85% of all recorded species are terrestrial, although aquatic systems have a greater

[3] For good overviews of these and other astonishing feats of bacteria see Rothschild and Mancinelli (2001) and Buckman (2003).

[4] Approximate numbers of species: mammals (5500), birds (10,000), amphibians (5800), reptiles (8200).

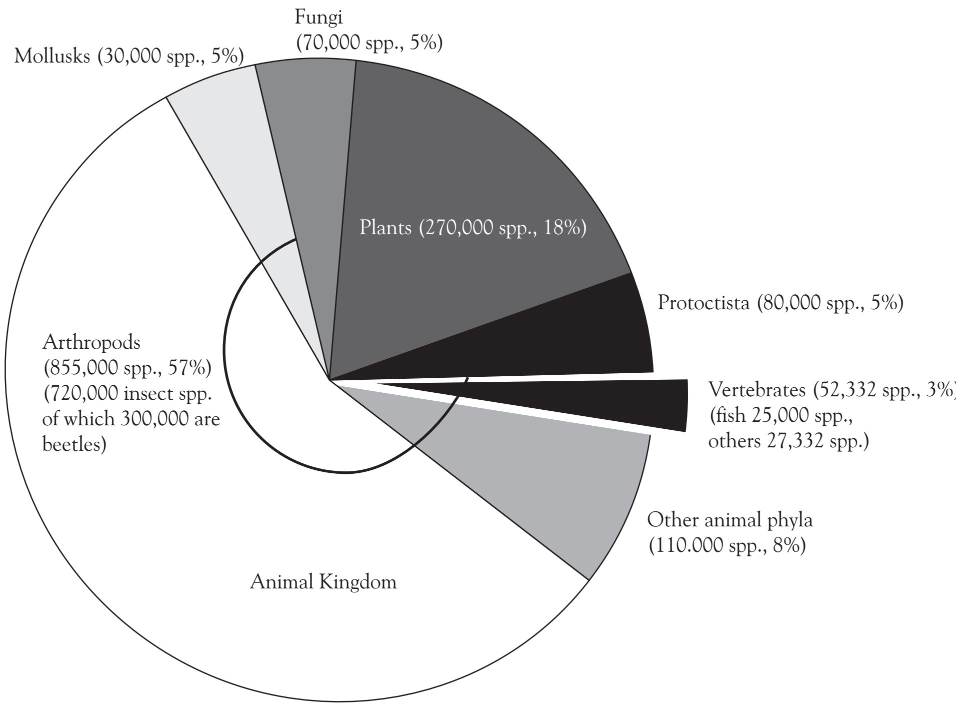

Fig. 1.4 Composition of the 1.5 million described eukaryotic species on Earth. Three of the four kingdoms (protoctista, plants, fungi) are each represented by one pie slice. The fourth kingdom – animals – include 37 phyla encompassed by the looping line at the center of the pie; three of the 37 animal phyla are distinguished (mollusks, arthropods, vertebrates), with vertebrates shown in the exploded slice. Although the total count of eukaryotic species comes to slightly more than 1.5 million, uncertainties warrant rounding to this figure. Data sources include Groombridge and Jenkins (2002), Hoffmann et al. (2010), and May (1997).

variety. For example, 32 of the 33 multicellular animal phyla are found in the sea (21 are exclusively marine), with only 12 on land (only one exclusively; May 1994). On land, biodiversity is certainly not distributed evenly. For example, species richness overall is highest in equatorial regions and the Earth's neotropical zone in Central and South America holds more vertebrate species than any other biogeographic realm. Another **biodiversity hotspot** can be found in the tiny Himalayan country of Bhutan (Tempa et al., 2012), where a 74 km^2 study area (<1/100th of the size of the Yellowstone National Park) contains 16% of the world's cat species (including the Bengal tiger on the cover of this book, captured by a remote camera trap in Bhutan's Royal Manas Park).

Without a doubt, only a fraction of the species on Earth has been described (Box 1.2). Therefore, if 1.5 million species have been described, how many are there really? The plausible range for numbers of eukaryotic species on Earth is 5–50 million species, with the best guess somewhere around 9 million (Groombridge & Jenkins 2002, Mora et al. 2011). We are left with the disconcerting realization that only 10% or so of the species that exist on Earth have been described.

Historic versus current rates of extinction

Just as every human dies, every species goes extinct. The big concern is not so much that it will happen, but rather whether the *rate* of death or extinction is higher than what we would expect from the past. Although the trend over geologic time has been one of increasing

Box 1.2 Erwin's estimate of the number of tropical arthropod species on Earth

Although there have been many different approaches to estimating the number of existing species on Earth, one of the most creative and high profile of these was by Terry Erwin (1982), who used an insecticide fogger to kill beetles in 19 trees of *Luehea seemannii* in tropical rainforests of Panama. Erwin estimated that the dead beetles comprised 1200 species, with 163 species depending strongly on this one tree species (high host specificity). Extending the 163 host-specific beetle species to an estimated 50,000 other tropical tree species led to an estimated 8.1 million tropical-canopy beetle species. Assuming that 40% of arthropod species are beetles leads to an extrapolated 20 million canopy arthropod species. Finally, assuming next that the canopy fauna is twice as rich as the fauna of the forest floor adds another 10 million noncanopy arthropods, leading to a richness estimate for tropical arthropods of 30 million species. Hamilton et al. (2010) refined Erwin's approach and embraced uncertainty in the estimates to come up with about 2.5 to 4 million tropical arthropods. This was much fewer than Erwin's, but still implies that about 70% of the Earth's arthropods have not yet been described.

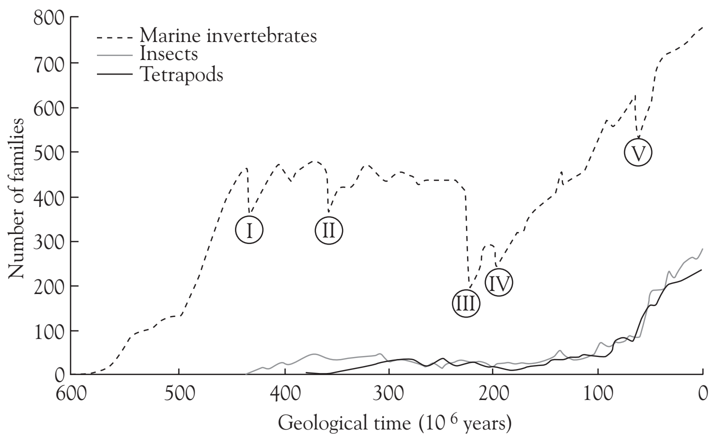

Fig. 1.5 Historical extinctions and increasing diversity. The increase in biodiversity (animal family diversity) over time has been punctuated by occasional mass extinctions. The top line represents marine invertebrates, the second line insects, and the bottom line tetrapods (amphibians, reptiles, birds, and mammals); to maintain clarity fish are not shown, but their line tracks almost directly atop the tetrapods. Families are used instead of species because the fossil record is more complete at the family level. The five classic mass-extinction events are indicated with roman numerals: (I) late Ordovician (440 million years ago); (II) late Devonian (365 million years ago); (III) late Permian (250 million years ago); (IV) late Triassic (205 million years ago); (V) late Cretaceous (66 million years ago). Modified from Groombridge and Jenkins (2002). Reproduced by permission, The Regents of the University of California.

species richness (Fig. 1.5), the species currently on Earth represent less than 2% of all species that have ever lived over the past 3 billion years. (The parallel with human life and death holds here as well; although far more humans exist on Earth than ever before, the humans currently on Earth represent less than about 6% of all those who ever lived; Haub 2002.) Given that species have always "died" over geologic time, we can use the fossil record to determine the background rate of extinction. In other words, what is the average species lifespan, from origination to extinction, over the last 600 million years since the explosive diversification of multicellular animals? Assembling estimates from many sources indicates that the average species has had a lifespan of about 1–10 million years (May et al. 1995). Superimposed on the background extinctions during geologic time are five major extinction periods (Fig. 1.5). Although uncertainty in the time span of extinction spasms makes it difficult to express mass extinction events as a rate (Jablonski 1991), the losses were massive, with some 75–95% of all species on Earth becoming extinct during each mass extinction period[5] (Fig. 1.5).

The key question is therefore how current rates of extinction compare to background extinction rates. To state it more provocatively: are humans now causing the sixth **mass extinction**, with species lifespans shortened to lengths similar to those during the five geologic mass extinctions? To answer this question, we need to estimate current extinction rates, a difficult task since we know so little about how many species exist! One approach estimates current losses of both described and undescribed species by coupling rates of deforestation in the tropics with species-area relationships, leading to a predicted 27,000 species lost per year (Wilson 1992).

A more direct and conservative approach estimates current extinction rates using only described species and documented extinctions. During the past 400 years extinctions have been recorded for about 60 mammal, 120 bird, 26 reptile and amphibian, 81 fish, 375 invertebrate, and 380 plant species (Groombridge & Jenkins 2002). Focusing on birds and mammals, which have the most reliable records from written accounts and skeletal remains, reveals 180 observed extinctions over 400 years, an average of about 0.5 extinctions per year. To make those numbers more tangible, let's name names of a few species that have gone extinct just during your lifetime (since 1988; see Hoffmann et al. 2010): the golden toad (*Incilius periglenes*) from Costa Rica; the kamao (*Myadestes myadestinus*), a Hawaiian bird; the Alaotra grebe (*Tachybaptus rufolavatus*), a Madagascaran bird; the scimitar-horned Oryx (*Oryx damnah*) persisting only in captivity; and the Yangtze River dolphin (*Lipotes vexillifer*), possibly persisting in small pockets in Central Asia, but likely not.

Is this current extinction rate higher than what would be expected based on historical species lifespan? If an historical 10-million-year lifespan per species were applied to the currently existing 15,000 described bird and mammal species, we would expect 15,000 species/10 million years = 0.0015 extinctions per year; using a 1-million-year lifespan gives an annual expectation of 0.015 extinctions per year.

Thus the current rate of extinction for birds and mammals of 0.5/year is 33–333 times greater than expected by the background extinction rate of 0.015–0.0015/year. Several other approaches produce considerably higher extinction rates, especially if they account for impending losses likely in the future if current trends continue (May et al. 1995, Pereira et al. 2010). Although uncertainty in the analysis may still spawn legitimate debate as to whether current extinction rates are yet as high as those of geological mass extinctions, absolutely no question remains that rates are considerably higher than natural background levels, and if things do not change we will indeed find ourselves presiding over a sixth mass extinction event in the near future.

So what? There are both philosophical and utilitarian reasons to care about loss of species and genetic diversity (see Chapters 9 and 12), as well as the loss in ecological services upon which other species, including humans, depend. For example, many bird species contribute strongly to ecosystem processes, including decomposition, pollination, and seed dispersal; in turn these services are valued by humans (e.g. commercial plant pollination and control of insect pests that damage plants or spread human disease). If, as predicted, by 2100 as many as one-half of bird species either go extinct or decline to the point where their ecosystem interactions are compromised, humans are likely to experience the cascading effects of an altered system (Şekercioğlu et al. 2004).

However, I do not want to end this section in despair, because the point of this book is to give you some tools that can help this situation. Indeed, conservation actions, on the whole, have had demonstrable positive success in recent years (Butchart et al. 2006, Hoffmann et al. 2010). Continued and improved conservation success will take hard work on many fronts, including policy, law, economics, sociology, and, of course, population ecology science. I hope that the

[5] Major extinction events are really just the tail of a fairly continuous distribution of extinction magnitudes distributed across geologic history (Groombridge & Jenkins 2002).

stuff here, in this book, can be one piece of what you need to act on to help save the world.

HUMANS AND SUSTAINABLE HARVEST

Obviously, not all species are negatively affected by all human activities. In fact, quite a number of species have reached historically high numbers and are considered pests or overabundant. Certainly, humans have harvested a great many species without negative effects.

The study of the effects of harvest on wildlife populations and the regulation of harvest probably have deeper roots than any other topic in applied ecology. Early recorded history includes Egyptian hunting records tracing back to about 2500 BC (Leopold 1933, Gilbert & Dodds 2001). Graeme Caughley (1985) noted that under Genghis Khan (13th century) the Mongols "conserved wildlife much better than they did people," for example by restricting hunting to the 4 months of winter and allowing some animals to escape hunting drives.

Despite the long history of harvest regulation, many cases exist of overharvest by humans. Most of the US colonies had established closed seasons on some species by the mid-1700s, although the first hunting licenses were not required until 1864 (in New York) and the first bag limits implemented by about 1878 (when Iowa limited the prairie chicken harvest to 25 birds per hunter per day; Connelly et al. 2012). There was little connection between these early laws and enforcement, or between the laws and expected population response. By the late 1800s extinctions due to overharvest loomed for species ranging from passenger pigeons to beaver to bison. Leopold (1933:17) attributed these disasters to an American viewpoint – in rebellion against the European philosophy of wildlife harvest that was perceived to benefit only the wealthy – whereby game laws "were essentially a device for dividing up a dwindling treasure which nature, rather than man, had produced."

Implementation of science-based, enforced harvest laws in the US began with President Theodore Roosevelt. In a passage that typifies his views, Roosevelt wrote in 1903 (Morris 2002:221):

> Every man who appreciates the majesty and beauty of the wilderness and of wild life, should strike hands with the far-sighted men who wish to preserve our material resources, in the effort to keep our forests and our game-beasts, game-birds, and game-fish – indeed, all the living creatures of prairie and woodland and seashore – from wanton destruction. Above all, we should recognize that the effort toward this end is essentially a democratic movement. . . . But this end can only be achieved by wise laws and by a resolute enforcement of the laws.

Sportsmen-naturalists such as Roosevelt, dedicated to hunting and fishing, led the movement in the US to preserve nongame species as well as game species. By the late 1870s these individuals called for preserves to protect against forest decimation and denounced market hunting for food and for fashionable hats adorned with bird feathers. Thus in the late 1800s individuals committed to sport hunting and conservation led the charge to conserve wildlife, "in spite of the utter indifference of a nation seemingly obsessed with economic development" (Reiger 2001:88).

One can point to a number of success stories over the last century where knowledge of population biology has been linked to enforced regulations, leading to sustainably harvested populations (see Chapter 14). For example, wood ducks and sharp-tailed grouse were nearly wiped out by overharvest in the early 1900s, but are now successfully and sustainably harvested in the US (Bolen & Robinson 2003). Equally striking has been the recovery of white-tailed deer in North America: overhunting and habitat destruction reduced numbers to less than 500,000 by the late 1800s, but by the 1980s – following widespread initiation and enforcement of hunting regulations (as well as habitat change) – deer numbers had increased 100-fold or more.

In Australia, large kangaroos have been harvested by humans for more than 20,000 years (Grigg & Pople 2001). At least 66 million kangaroos were harvested in the 1980s in the state of Queensland alone (Calaby & Grigg 1989) and 1–3 million continue to be harvested annually from about 40% of mainland Australia, even as they increase to higher densities than before the arrival of Europeans. In large part the increase is due to tree clearing for agriculture, implementation of watering points for introduced stock, and control of dingo, but clearly credit also goes to a well-managed harvest. The kangaroo is a national symbol for Australia, and so the animals have high conservation status and generate money as tourist attractions. However, their range overlaps with sheep, making them pests in the eyes of the sheep industry. The resolution to this tension between conflicting desires for conservation and extermination may be linked to the commercial value of kangaroos. Leather from kangaroo hide is arguably superior to that of cattle and the high-quality meat has growing potential on the world market. Thus the conflict between the sheep industry – who would like to vastly decrease or eliminate kangaroos as pests – and conservation may be partially resolved by a truly sustainable harvest. An expansion of the meat market, coupled with the market value of the skin, may give landholders an incentive to reduce sheep numbers and maintain kangaroo numbers as a harvested species, while still providing the draw of live animals for tourists. This vision has been referred to as "sheep replacement therapy for rangelands" (Grigg & Pople 2001).

In the same way that declining or small wildlife populations can be better managed based on population biology principles, harvest management is most sound on a scientific footing. Human removal of individuals via harvest is analogous in many ways to the effects that predators have on their prey populations. Insights into how hunting or predation affects the prey species depends, for example, on how many of which ages or sex are killed and how much the mortality is added on to other factors that cause death to the prey (see Chapters 8 and 14). Determination of vital rates, monitoring of populations, and incorporation of ecological understanding are all part of harvest management.

THE BIG PICTURE

Harvested species and species in decline are driven by similar ecological processes, and the history of hunting parallels and overlaps conservation of nonharvested species. Thus conservation of harvested species is inseparably related to conservation of nonharvested species. Ecology, conservation biology, and wildlife biology have merged and intertwined to contribute to the use of biological knowledge, data, and models to help us understand and manage interactions between humans and other species. Today's wildlife population ecologist must also master knowledge of experimental design (see Chapter 2) and genetic tools (see Chapters 3 and 9). In short, my attempt in writing this book is to combine demography and genetics, theory and practice, and to apply slices from the conceptual basis of population biology to problems of wildlife conservation.

FURTHER READING

Cohen, J.E. (1995) *How Many People Can the Earth Support?* W.W. Norton & Co., New York. Although the current numbers are now a bit out of date, this remains a careful compendium of human population growth and its consequences.

Groombridge, B. and Jenkins, M.D. (2002) *World Atlas of Biodiversity*. UNEP World Conservation Monitoring Centre, University of California Press, Berkeley, CA. A complete reference addressing biodiversity status, with lots of great graphics.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Burchart, S.H., et al. (2010) The impact of conservation on the status of the world's vertebrates. *Science* **330**, 1503–9. A good recent update with descriptions of both promise and pitfalls for conservation.

Leopold, A. (1933) *Game Management*. Charles Scribner's Sons, New York. Leopold's insights are as timely now as they were 80 years ago; the book also provides an excellent history of harvest management.