CHAPTER 14

Population biology to guide sustainable harvest

Aldo Leopold was a hunter who I am sure abjured freeze-dried vegetables and extrusion burgers. His conscience was clean because his hunting was part of a larger husbandry in which the life of the country was enhanced by his own work. He knew that game populations are not bothered by hunting until they are already too precarious and that precarious game populations should not be hunted. Grizzlies should not be hunted, for instance. The enemy of game is clean farming and sinful chemicals, as well as the useless alteration of watersheds by promoter cretins and the insidious dizards of land development.

Thomas McGuane (1997:168), The heart of the game

To go fishing with your father: that is an ancient and elemental proposition, and if not as overwhelming as sex or death or the secret lives of animals, still there are legendary shadows about it entrancing to a boy twelve years old.

Fred Chappell (1987:150), I Am One of You Forever: A Novel

INTRODUCTION

Whales, lions, foxes, deer, kangaroos, ducks, turtles, quail: all are harvested wildlife species. Wildlife harvest has been practiced and regulated – to varying extents – for nearly the full history of human civilization (Chapter 1). Hunting will continue because it can provide commercial profit, food for subsistence, control of invasive species, and a profound philosophical connection between people and the hunted animal. Harvests can be sustainable, yet can also contribute to species’ decline and extinction.

In the past, most wildlife harvest strategies were based on hunches and trial and error with little connection between population-biology principles, data, and harvest regulations. Such casual methodologies may be acceptable or even appropriate where hunting pressure is not intense, so that errors in harvest strategy have little impact on population dynamics. However, for harvests with a strong commercial interest (including both classic fisheries examples as well as some game animals, especially those harvested for trophies), there will often be pressure to push the harvest beyond where casual management will suffice. In fact, even for many relatively nonintense sport harvests, intuition or trial and error alone may be dangerous when habitat fragmentation or other stressors make overharvest more likely.

In short, population biology is an essential part of sustainable harvest management. The entire battery of knowledge and techniques discussed in this book can be brought to bear on harvest strategies for subsistence, sport, or profit, or to decrease population size of exotic or pest populations. In this chapter I will first explore how to determine whether hunting is likely to affect either the demographic (abundance and growth rate) or evolutionary trajectory for a harvested population. From this foundation, I will next describe models to determine sustainable harvest levels, starting first without age or stage structure, then proceeding to
Box 14.1 Genetic tools and poaching

Many of the forensic tools mentioned in Chapter 3 and elsewhere have some of their most important applications in helping law-enforcement agents identify poachers. Matches of DNA profiles can definitively connect a crime scene (say, the gut pile of a poached deer) to an individual poacher (say, a piece of venison in someone’s freezer). The assignment test may be used to determine the birthplace or origin of a poached individual, facilitating both detection of illegal harvest and trade routes (Manel et al. 2002). For example, African elephants are being decimated, in large part due to the illegal trade in ivory. Where exactly do poachers operate and how do they move ivory out of Africa? A range-wide database of genotype frequencies based on both tissues and noninvasively sampled feces allows the geographic origin to be determined from seized elephant tusks (Wasser et al. 2004). In fact, even the threat of prosecution based on the assignment test can lead to confessions: for example, an assignment test indicated that an unusually large 5.5 kg salmon originated not from the location of a fishing contest in Finland but rather from a nearby area that supplied fish markets; when confronted with this genetic evidence the fisherman confessed to buying the salmon at a local fish shop and sneaking it into the competition (Primmer et al. 2000).

more complex approaches using demographic information. Because waterfowl management stands out as a shining example where population biology has intersected with and influenced harvest management, I will specifically address the adaptive harvest-management approaches applied in the waterfowl world. Finally, I will end with a mention of the special case of harvesting overabundant or pest wildlife.

EFFECTS OF HUNTING ON POPULATION DYNAMICS

In Chapter 8 I emphasized three primary factors determining whether a predator was likely to control the numbers of its prey: (a) predation rate (a function of predator numerical and functional response); (b) whether the mortality due to predation is compensatory or additive; and (c) which age, stage, or sex of prey is killed. Hunting by humans is of course a form of predation, so we can use that same framework to ask how each of these factors might affect population dynamics for a particular harvest scenario.

Harvest level: numerical and functional responses of hunters

The number of hunters in any season (numerical response) and how many animals each hunter kills (functional response) collectively determine the total number of animals killed by hunters. Laws and regulations are (we hope) a primary determinant of numerical and functional responses, because the number of hunters and the number of animals taken per hunter are affected by bag limits, season lengths, special licenses, and hunting zones. Other factors like weather and hunter interest, which can in turn be affected by economics and politics, can also be nearly as important.

Less obvious factors affecting the numerical and functional response of hunters on a hunted population are poaching, crippling losses, and incidental take. Poaching losses can be extreme where enforcement is weak and species have high commercial value (Chapter 11). Box 14.1 describes how genetic tools can help reduce poaching.

Crippling losses include animals that must be accounted for as killed because they are mortally wounded but not found by the hunter. For example, crippling loss in northern bobwhite quail may be as much as 50% of the retrieved harvest (Connelly et al. 2012).

Incidental take, called by-catch in fisheries, refers to animals of one species taken accidentally in the process of harvesting another species (Chapter 11). It is easy to imagine how this happens when a net is drawn through the ocean for, say, shrimp, and other species such as sea turtles get caught and killed in the net. Incidental harvest can also occur in terrestrial harvests, as in Serengeti National Park in Tanzania, where game-meat hunting using snares has led to sub-
stansial harvest of nontarget carnivores, including 11% of the spotted hyena population during 1991 (Hofer et al. 1996).

Is hunting mortality additive or compensatory?

As noted in Chapters 7 and 8, mortality via predation (or human harvesters) might be compensated for via increases in survival, reproduction, or immigration, thereby ameliorating the effects of predation or harvest mortality on population growth. On the other hand, predator or harvest mortality could be additive, causing survival and population growth to decline.

Consider for the moment compensation operating on survival rates (Nichols et al. 1984, Williams et al. 2002), extending in the context of harvest the framework of equation (8.2) in the predation chapter. We will even use the same symbols, except now $H$ represents mortality due to the annual predation rate by hunters. As with predation, we will call $S_0$ the annual survival rate in the absence of hunting and $S_a$ the realized annual survival in the presence of hunting.

If hunting mortality were completely compensatory, an increase in hunting mortality ($H$) prompts an equivalent decrease in nonharvest mortality, so realized annual survival is the same as the background annual survival rate in the absence of hunting ($S_0$):

\[
S_A = S_0
\]

At the opposite extreme, if hunting mortality were totally additive, then harvest mortality and nonharvest mortality are independent competing risks. Animals have to survive the hunting season with probability $(1 - H)$ and they must survive everything else ($S_0$). Combining these two probabilities gives

\[
S_A = S_0 (1 - H) = S_0 - S_0 H
\]

(14.2)

(The same as equation 8.2).

We can generalize the relationship between annual survival ($S_A$) and harvest mortality by adding a slope coefficient, $\beta$, to equation (14.2):

\[
S_A = S_0 (1 - \beta H)
\]

(14.3)

The slope coefficient tells us how harvest mortality changes annual survival (Fig. 14.1). A slope of $\beta = 1$ implies additive mortality. A slope $\beta > 1$ implies superadditivity, whereby harvest causes cascading mortality, perhaps by disrupting social structure, by causing survivors to escape to poorer quality habitats, or from crippling losses.

In contrast, a slope of $\beta = 0$ in equation (14.3) implies complete compensation (compare with equation 14.1). As noted in Chapter 8, harvest mortality can only be fully compensatory if it does not exceed

1 Although we assume that hunting mortality ($H$) and nonhunting mortality ($1 - S_0$) occur at separate times, this adequately captures additivity in more realistic situations where nonhunting mortality also occurs during the hunting season (Nichols et al. 1984:537–40, Sandercock et al. 2011).
other nonpredation-related mortality sources (i.e. when \( H \leq (1 - S_0) \)). (This threshold is indicated with a T in Fig. 14.1.) Therefore, even under complete compensation, harvest must become additive at high harvest levels.\(^2\) A practical result of the limit for complete compensation at \( H = (1 - S_0) \) is that species with low background survival (\( S_0 \) approaching 0) will have more capacity for compensating harvest mortality because they have more alternate mortality that can be replaced by harvest. In general, we can expect that species characterized with “live fast, die young” type life histories (often smaller species) will be able to sustain relatively high hunting rates with compensation so that survival is unaffected; on the other hand, species characterized by longer life times (high yearly survival) and low reproductive rates will be less able to compensate for hunting mortality (Leopold 1933, Cardillo et al. 2005).

**Overcompensation**, where harvest increases survival, occurs when \( \beta < 0 \). For example, if harvest occurs sequentially with other mortality factors, harvest may release survivors from negative density dependence and cause survival to be higher than it was without hunting (Boyce et al. 1999).

Between complete additivity and complete compensation (\( 0 < \beta < 1 \)) harvest may be **partially compensatory** (Fig. 14.1c). In this case, survival decreases by a less-than-additive amount when harvest is between 0 and \((1 - S_0)\). As a tangible example, a careful study of hunting mortality based on 206 radiocollared willow ptarmigan monitored for 3 years showed partial compensation when \( H < 15\% \), and additive mortality thereafter (Sandercock et al. 2011). In fact, the plot of survival versus rate in this study closely resembled Fig. 14.1(c).

So far we have only been considering how harvest mortality might or might not affect survival rates. However, as throughout the book, we are reminded that survival is only one vital rate affecting population growth. Because \( \lambda \) is a function of age-specific survival and reproduction – and movement among populations – harvest mortality also can be compensated for through changes in these other vital rates. This means that even if harvest mortality has totally additive effects causing adult survival to decline linearly as harvest increases, \( \lambda \) may remain unaffected – or even increase due to compensatory or overcompensatory reproduction, immigration, or survival in other age classes.

Coyotes exhibit spectacular compensation of harvest mortality by increasing multiple vital rates: heavy exploitation of adults leads to increased litter sizes of surviving females, increased reproduction in yearlings, higher juvenile survival, and higher immigration into the population, all of which frustrate efforts to reduce local coyote populations (Knowlton et al. 1999). Similarly, upland game birds such as bobwhite quail can compensate mortality due to sport hunting by increasing reproduction (Roseberry & Klimstra 1984). As an example of adjusted movement rates among populations affecting harvest compensation, hunting mortality on ruffed grouse in Wisconsin became increasingly more additive as immigration from adjacent areas with lower hunting mortality became restricted by habitat fragmentation, thereby exposing the heavily harvested populations to decline (Small et al. 1991; see also Labonté et al. 1998 for moose). The phenomenon of spatial compensation of mortalities in harvested populations by animals from nearby reserves underlies the spatial harvest control method of harvest management whereby some areas closed to harvest serve as sources to replenish numbers in harvested areas (McCullough 1996). Box 14.2 gives an example for foxes in Argentina.

Of course the fact that \( \lambda \) depends on multiple vital rates also means that hunting effects on reproduction or other rates can cause the harvest to have superadditive effects, driving \( \lambda \) lower than expected from harvest effects on survival alone. A compelling example of this may be found in colonial prairie dogs (Box 14.3).

In short, the degree to which hunting mortality can be compensated by other mortality, or by reproduction or movement, is species- and context-specific. For most species the question is not *if* harvest is compensatory but rather *how much*. What is the threshold where survival from other sources can no longer compensate for harvest mortality and what other vital rates might increase to prevent additive harvest mortality from translating into a decreased population growth rate? For example, compensation is variable in ungulates, where current levels of sport harvest range from being mostly compensatory (e.g. deer in Ontario, Canada; Giles & Findlay 2004) to superadditive (e.g. elk in the northern Yellowstone region; Vucetich et al. 2005). Harvest mortality in feld populations is generally con-

\(^2\)Whenever harvest is additive above a threshold \( T \) of complete compensation (which can be at most \( 1 - S_0 \)), survival above that threshold is (Williams et al. 2002:228) \( S_A = S_0(1 - H)/(1 - T) \).
Box 14.2 Spatial compensation supports a hunted fox in Argentina

Culpeo foxes (*Pseudalopex culpaeus*) are hunted intensively in Argentinean Patagonia both for their fur and because they prey on sheep. Cattle ranches, however, often ban fox hunting because foxes are thought to control numbers of European hares (*Lepus europaeus*) that compete with livestock for forage. This landscape mosaic of hunted and unhunted sites was studied using radiotelemetry, analysis of carcasses, and matrix models (Novaro et al. 2005). The hunting mortality was not compensated for through changes in survival or reproduction. However, population growth was maintained on the hunted sites via dispersal of animals from the unhunted sites. Population modeling implied that the foxes were likely to be sustained as long as the unhunted sources comprised >30% of the landscape mosaic.

Box 14.3 Superadditive effects of harvest on prairie dogs

Although compensation may ameliorate mortality losses in a harvested species, behavioral and physiological responses to the perceived predation risk may lead to superadditivity of harvest mortality on population growth. Black-tailed prairie dogs are colonial animals whose concentrated numbers attract their main predator, human hunters (historically >2 million prairie dogs/year were killed by recreational shooters from three western US states). The prairie dogs’ colonial social structure can be disrupted by heavy harvest, and limits their ability to compensate harvest mortality by moving away from the disturbance. In a well-replicated experiment with five control colonies and five shooting treatments (approximately a 25% reduction in abundance), multiple factors caused both survival and reproduction to decline on shooting treatments (Pauli & Buskirk 2007). Body condition of adults declined and juveniles exhibited elevated stress hormones. Shooting increased alert behavior at the expense of foraging: also, because survivors had to be hyper-alert and flee underground when a shot was fired, cooperative vigilance against predators was compromised. Reproductive output plunged on the shooting treatment because high mortality reduced the ability to find mates. Overall, the synergistic effects on survival and reproduction resulted in superadditive effects of heavy recreational shooting on prairie dog population growth.

sidered to be noncompensatory for survival or reproductive rates, but with strong potential for spatial compensation (e.g., Cooley et al. 2009 for cougar).

If nothing is known about compensation, the most cautious approach would assume none, and set harvest models as if the harvest mortality were completely additive. Next we will consider how the effect of harvest depends on which individuals are harvested.