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# Applications of Reproductive Biology to Bird Conservation and Population Management

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## 11.1 INTRODUCTION

Population management encompasses a wide variety of activities, ranging from species conservation and recovery, to the control of pests and invasive species, to the sustainable harvest of wild populations. In all cases, however, the fundamental goal is to manipulate demographic processes so as to influence a population's trajectory to meet some specific objective. At its most basic, this means altering the number of juveniles that are recruited into the breeding population or changing the rate at which breeders are lost from the population. In this chapter we focus on the first of these processes and provide an overview of the ways in which an understanding of reproductive biology can be used to increase the number of recruits.

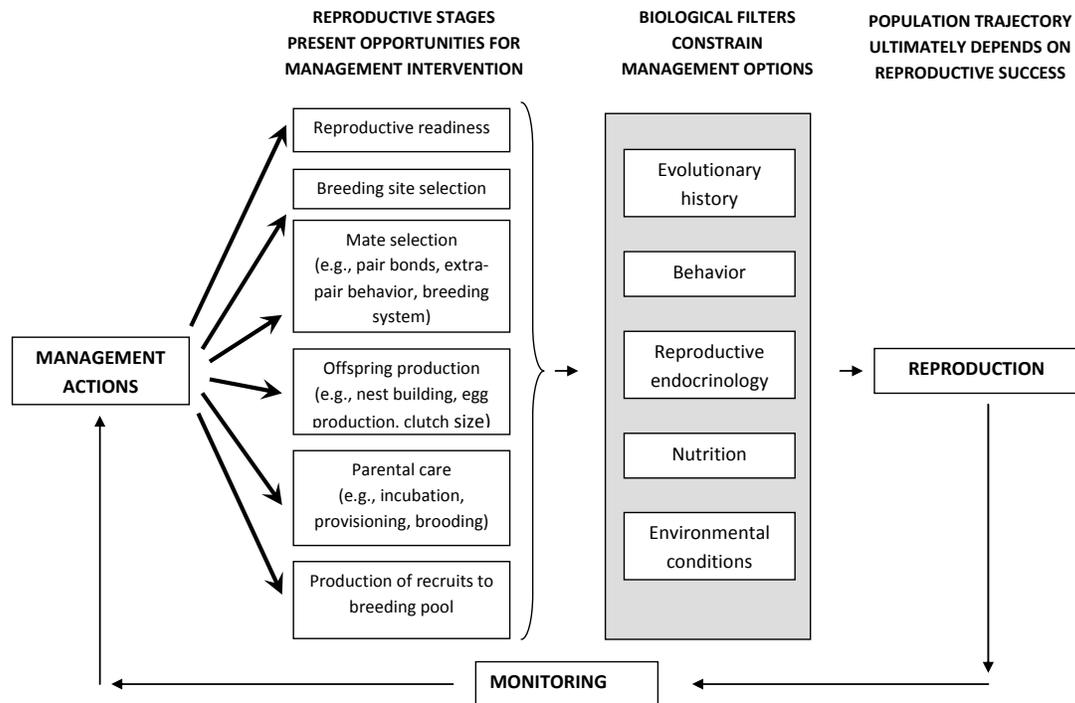
Although the specific goals of population management can be extremely different – e.g., to increase the production and survival of young in the conservation arena, or to decrease or eliminate them in the field of pest control – the underlying biological system available for manipulation is the same. In order to reproduce, birds must come into reproductive condition, find a suitable breeding area, select individuals with which to mate, produce large complex eggs that require substantial parental care, and, for most species, care of the young (Fig. 11.1). If birds can accomplish each of these steps successfully, there will be a pool of new individuals that become the next generation. Population management involves manipulating these stages to influence the direction of population change over time (Williams *et al.* 2001).

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**Fig. 11.1.** Diagram of the relationships between the reproductive stages available for management manipulation and the biological constraints on management alternatives. In order to reproduce, birds must come into reproductive condition, find a suitable breeding area, select individuals with which to mate, produce large complex eggs that require substantial parental care, and, for most species, then take care of the young. Collectively, these processes determine the reproductive rate, which in turn influences population size and trajectory. This trajectory, and how management actions affect it, are tracked through monitoring.

Humans have been managing bird populations for millennia (Wood-Gush 1971; Sossinka 1982; Kear 1990). In combination with selective breeding, the development of husbandry techniques has allowed considerable increases in productivity of domesticated species (Korver and van Arendonk 1988; Gillespie 2004). These methods take advantage of knowledge about reproductive endocrinology, nutrition, genetics, and animal behavior to increase the rates at which eggs are produced and offspring mature. The production of more individuals in wild species has received parallel attention from managers who are intent on finding ways to increase the number of birds that can be harvested from a population for human use (Kear 1990; Kadlec and Smith 1992). In this context, the focus has been more on creating or enhancing habitat, to provide more opportunities for breeding and on reducing non-human sources of mortality (Payne 1992; Baldassarree and Bolen 1994), than on directly manipulating reproductive systems *per se*.

More recently, there has been a shift from a focus on food production and other direct benefits to humans to one that also emphasizes species conservation. One-eighth of the world's bird species are considered to be at risk of

extinction during the twenty-first century (BirdLife International 2004) and projections suggest that this number will continue to rise in the foreseeable future (Butchart *et al.* 2004). Habitat loss, fragmentation, and degradation are the primary causes of bird species endangerment, affecting at least 70% of threatened bird species (Wilcove *et al.* 1998; Owens and Bennett 2000; Li and Wilcove 2005). Overkill – caused by such things as over-harvest, depredation by exotic species, and disease – and habitat alteration by invasive species also affect large numbers of species (Collar *et al.* 1994; Wilcove *et al.* 1998; Owens and Bennett 2000; Gamarra *et al.* 2005; Keane *et al.* 2005; Li and Wilcove 2005). Climate change is expected to further exacerbate and complicate all of these issues by altering habitat distributions and changing the physiological constraints on where particular species can live (Walther *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003, 2005). Consequently, many more bird species may face extinction as a result of human impacts on global climate (Böhning-Gaese and Lemoine 2004; Thomas *et al.* 2004; Visser *et al.* 2004).

Causes of endangerment, and the effectiveness of techniques designed to recover populations, differ among species with different characteristics. For instance, species that are large bodied and have long generation times are more likely to be threatened by overkill, either through direct human persecution or the impact of introduced predators (Owens and Bennett 2000). These same species are also often slow to recover from population declines because of low reproductive rates and large-scale habitat needs. In contrast, species that have small body sizes and that are habitat specialists are more likely to be threatened by habitat loss (Owens and Bennett 2000) but may respond quickly to management. Some species also exhibit characteristic behaviors that increase extinction risk (Reed 1999). The links between the life history characteristics of species and endangerment create a direct connection between phylogeny and extinction risk. For example, families such as the Psittacidae (parrots) and Diomedidae (albatrosses) contain disproportionately high numbers of rare and endangered species (Beissinger and Snyder 1992; Bennett and Owens 1997; Butchart *et al.* 2004).

Simultaneous with this interest in enhancing the size or productivity of bird populations to meet societal goals, humans have also invested considerable energy in finding ways to reduce the population size of species considered to be pests. Again, the historical focus has been on species that directly impact humans, for example through crop depredation (Ward 1979; Decker and Avery 1990; Linz *et al.* 1996; Jones *et al.* 2000). Increasingly, though, population control is becoming an important issue in conservation biology too, for instance where introduced birds create problems for native species (Smith *et al.* 2005) or where native populations of one species have increased to the detriment of another (e.g., Wanless *et al.* 1996; Coates and Delehanty 2004).

Reproductive biology, clearly, is central to the processes that underlie population management, and has important roles to play both in identifying

management problems and finding solutions. Much of this book, then, relates at least indirectly to the issues discussed in this chapter, and other chapters provide detailed discussions of many areas of reproductive biology that could be used to better manage bird populations. Here, our goal is to illustrate the connections between this wealth of basic knowledge and specific management activities that are used to address applied questions. In such a small space, we can only begin to scratch the surface of this topic. Consequently, we provide only a brief summary of each step in the sequence of events that leads to successful breeding (Fig. 11.1), focusing on specific examples in which knowledge of reproductive biology has been used by managers. No doubt there are other connections that have, or could, be made, and it is our hope that this chapter will encourage further collaboration between biologists studying the details of reproductive biology and those that study population management.

## 11.2 REPRODUCTIVE READINESS

Avian reproduction is shaped by a mixture of evolutionary innovation related to the fundamental features that collectively characterize the order, and the constraints imposed by their reptilian (theropod) past (Prum 2002). With their high metabolic rate, birds have achieved extraordinary physiological capabilities, such as long-distance continuous flight, but are constrained by their high energetic needs (Blem 2000). Because normal maintenance activities are so costly, successful reproduction can occur only when birds can acquire sufficient energy, nutrients and minerals in excess of their high basic requirements. This situation is exacerbated because birds produce large, energy-rich eggs that require incubation and because their young have high metabolic needs of their own and must be fed frequently after hatching. The production of external eggs that need constant attention further constrains birds to breed only when there are adequate resources for them to remain resident in an area for long enough to raise their young. These conditions put additional limits on species that are migratory or that rely on ephemeral food supplies. Reproduction is constrained yet further to times when birds are not diverting excess energy and nutrients to other activities, such as feather molt (e.g., Moreno *et al.* 2001). Laysan albatross (*Phoebastria immutabilis*) and Black-footed albatross (*P. nigripes*), for example, replace only 20-90% of their wing flight feathers each year, and it has been suggested that molt patterns in large birds such as these might result from a tradeoff with reproductive constraints (Edwards and Rohwer 2005). This tradeoff, however, is apparently not present in some large species (e.g., White ibis *Eudocimus albus* Heath *et al.* 2003). Given the many constraints they face, most wild birds breed seasonally in a manner timed to take advantage of abundant food resources.

While it is essential for a bird to be fertile during times of resource abundance, it is costly for birds to maintain functional reproductive tracts during times when breeding cannot succeed because of environmental (food,

weather, etc.) or other (molt, migration) constraints (Clark and Wilson 1981; Gill 1995). A fully developed reproductive tract also has a large mass (Lake 1981; Blackburn and Evans 1986; Proctor and Lynch 1993), which would add unnecessarily to the cost of flight during the nonbreeding season. Because of these costs, most wild birds severely diminish the size, mass, and functionality of the reproductive system during the nonbreeding season (regression) and regrow a functioning reproductive system at the onset of each breeding season (recrudescence). Temperate and high latitude birds have especially distinct breeding seasons, but cyclical reproduction is also characteristic of tropical and desert species, although in these environments some species cycle more than once each year or have a less sharply demarcated breeding season (Wingfield and Farner 1993, Johnson 2000).

From a management perspective, understanding the timing of regression and recrudescence is important because it determines when reproduction is possible and when certain reproductive behaviors are most likely to occur. In the wild, this timing is not something over which managers are likely to have control. Nonetheless, understanding when birds come into reproductive condition and when resources necessary for breeding are available, can be helpful in determining when and what management activities are most appropriate. For example, population monitoring might be most effective at times when birds are displaying and most obvious to human observers (e.g., Aspury and Gibson 2004; Becker and Agreda 2005; see section 23.7). Such information is especially important for groups that have not been well studied, perhaps especially in tropical areas where reproductive activities are less well synchronized across species (Johnson 2000).

Undoubtedly, the single most common management action used to help birds reach reproductive readiness is to provide and protect habitats that support prebreeding nutritional needs. For instance, the United States government purchases shallow ephemeral wetlands and manages them for seed-producing wetland vegetation and high invertebrate productivity in order to provide a good food supply for pre-breeding waterfowl. Maintaining a good diet at this time of year translates directly into improved body condition (Heitmeyer and Fredrickson 1990), which in turn is related to higher reproductive success (MacCluskie and Sedinger 2000).

Prebreeding nutrition has been especially well studied in waterfowl, but it is also gaining attention in other avian management systems. In western North America, for example, loss or alteration of the forb (i.e., non-woody, non-grass herbaceous plants) component of grass/shrubland ecosystems is thought to reduce female fecundity in some game birds. Female Greater sage-grouse (*Centrocercus urophasianus*), for example, shift from a diet high in sagebrush *Artemisia* spp. leaves to a diet high in forbs during the prelaying period of early spring, the only time of year in which sagebrush is not the major component of their diet (Barnett and Crawford 1994). Hence, adjusting agricultural grazing regimens to promote forb availability might provide a mechanism for increasing female fecundity in this species. Experiments on

captive Mountain quail (*Oreortyx pictus*) indicate that female fecundity can be manipulated directly by altering the nutritional value of the bird's food. In particular, the addition of certain plant nutrients to the diet of pre-breeding females leads to an earlier onset of gonadal recrudescence, a higher rate of egg-laying, and greater overall egg production (Delehanty 1997).

Not all nutritional intervention is intended to promote reproduction, and dietary manipulations have been proposed as a means of inducing temporary infertility in birds as an avian control method (Cook *et al.* 1996). The avian egg is characterized by a lipid- and nutrient-rich yolk that progressively "feeds" the embryo through the incubation period (Chapter 12). This process relies in part on the integrity of the semi-permeable vitelline membrane that surrounds the yolk. Permeability of this membrane depends on which lipids the female consumed during egg production, and consumption of particular lipids (e.g. conjugated linoleic acid) causes females to produce eggs that have overly permeable yolk membranes and are consequently not viable (Cook *et al.* 1996; Aydin and Cook 2004).

Another way of altering the conditions in which birds live, is to change the social environment. The importance of social facilitation (initiation or stimulation through conspecific interactions) to breeding is apparent in breeding site selection, with many species preferentially settling near conspecifics (Reed *et al.* 1999; see Section 24.3). Once a breeding site has been selected, social interactions also appear to facilitate mating and reproduction in many bird species, particularly in colonial species (Darling 1938; Orians 1966; Kress 1983). Hypothetically, then, the social environment of breeders might be manipulated to increase reproductive readiness or to facilitate reproductive output (discussed by Reed 2002, 2004). Manipulating cues to increase reproductive activities in small populations could stimulate reproductive behavior and ultimately increase population growth. For example, Pickering and Duverge (1992) stimulated pre-reproductive displays in a captive Lesser flamingos, (*Phoenicopterus minor*) flock by putting up mirrors to give the appearance of more individuals. Artificial stimulation of this type also might be effective in wild settings, as shown by O'Connell-Rodwell *et al.* (2004) who combined visual and vocal displays (decoys, playback, artificial nests) to stimulate nesting behavior in a reintroduced population of Caribbean Greater flamingos (*P. ruber ruber*) that had not yet bred (Fig. 11.2A). Broadcasting the sounds of lekking birds (both vocalizations and other mechanically produced sounds) and placement of taxidermy mounts of adults are both regular features of prairie grouse restoration and are intended to provide social stimulation to grouse being released into potential breeding habitat (Coates and Delehanty (in press)).

In captivity, options for manipulating the reproductive system are more numerous than in the wild, and can range from directly altering the bird's physical and social environment to changing its physiological state. Manipulations in captivity could include something as simple as changing photoperiod (e.g., Smulders 2002) or supplementing diet. For example, the

breeding cycle of the King penguin (*Aptenodytes patagonicus*) can be shortened in captivity through supplemental feeding to increase chick growth (Jouventin and Mauget 1996). In other cases, more direct manipulation of the breeding cycle may be possible. For instance, although the use of endocrine therapy to bring captive individuals of rare species into breeding condition is in its infancy, Wingfield *et al.* (2000) have described how endocrine problems in captive settings could be investigated and possibly ameliorated in their study of Japanese Crested ibis (*Nipponia nippon*), a critically endangered species in which many captive individuals had abnormal gonadotropin and sex steroid production. They point out that work on Japanese quail (*Coturnix japonica*) has shown that hormone therapy can correct problems with gonadal maturation, egg laying, and production of offspring, and these methods might be refined for use in other species. For now, however, approaches such as these are likely to be quite invasive and costly to implement, and realistically can be applied only to a relatively small number of individuals in situations where a species is in particularly dire straits.

The 1980s and 1990s saw substantial progress in understanding the reproductive endocrinology of birds which, in turn, has led to recent experimentation of endocrine manipulation to both promote and inhibit avian reproduction. This emerging field so far has focused largely on the control of pest species through the use of contraceptives, usually administered using food bait as a carrier (Dell'Omo and Palmery 2002; Johnston *et al.* 2003). For example, 20,25-diazacholesterol, a compound that appears to inhibit steroid formation by blocking the creation of cholesterol, itself a steroid precursor, may be an effective avian contraceptive (Johnston *et al.* 2003). An urban population of Rock pigeons (*Columba livia*) allowed to forage on corn bait treated with the endocrine disruptor Ornisteril, declined by 24% over a 3-year period (Dobeic 2003). The administration of nicarbazin, for which elevated levels in prelaying females results in egg infertility, is also being developed to control Canada goose (*Branta canadensis*) populations (Johnston 2003). Most of the research in this field to date has been done on captive birds, such as Japanese quail (e.g., Yoder *et al.* 2004) or domestic Chicken (*Gallus domesticus*) (Johnston *et al.* 2002), but recent work has also addressed waterfowl species, such as Canada geese and Mallards (*Anas platyrhynchos*), that can be pests in urban settings (e.g., Yoder *et al.* 2005). The obvious concern with application of these methods to wild species, particularly when contraceptive chemicals are delivered through feed, is the potential harmful effects on non-target species.

### 11.3 BREEDING SITE SELECTION

The nature of a bird's breeding site is a primary determinant of the success or failure of its attempts to reproduce (Howard 1920; Lack 1966; Wiens 1976). The minimum function of breeding sites for all bird species is to provide a place to lay and hatch eggs. Even for the megapodes or "brush turkeys"

(Megapodiidae) of Australasia, the only avian group that does not provide post-hatching parental care, the "nests" are maintained by breeding males during the breeding season (Jones *et al.* 1995b). For most species, breeding sites are used for a variety of activities, such as attracting mates, providing foraging habitat, nesting, and raising young.

If one knows the habitat features that are used for breeding site selection, they can, in principle, be manipulated to alter population size. This is done most extensively for hunted waterfowl and other game birds, where habitat creation and restoration has been practiced for centuries with the goal of increasing species harvest (Payne 1992; Baldassarre and Bolen 1994). For example, altering water availability in arid and semi-arid environments is a common manipulation of the physical environment employed by wildlife managers to effect change in reproductive output. Despite their mobility, which facilitates seeking out water sources, desert birds can face substantial water stress due to the absence of locally available water (Dawson and Bartholomew 1968) and can be excluded from otherwise suitable habitat if sufficient water is not available. This effect is magnified by the relatively low mobility of chicks. In response, the placement of self-filling wildlife watering devices known as "guzzlers" has become a common management practice in arid regions (Delehanty *et al.* 2004). These devices are placed throughout potential breeding habitats to passively collect seasonal precipitation (usually winter rain or snow) into storage tanks that birds can access the following summer. Growing juvenile Mountain quail in western North America can exhibit remarkably high fidelity to these artificial water sources during periods of substantial water stress (Delehanty *et al.* 2004), suggesting that the benefits extend throughout the reproductive cycle.

Habitat creation and restoration also have become central tools in the conservation of endangered species and are particularly important because habitat loss and degradation affect the majority of the world's threatened bird species (Owens and Bennett 2000). Habitat manipulation clearly can take many forms, but might be as simple as providing platforms or artificial ledges for nesting (e.g., Northern bald ibis *Geronticus eremita*, Hirsch 1977, Osprey *Pandion haliaetus*, van Daele and van Daele 1982, respectively). A frequent approach is to provide nest boxes, which has helped to increase the number of available nest sites in a wide variety of cavity-nesting species, ranging from waterfowl (Kadlec and Smith 1992; Bellrose and Holm 1994) (Fig. 11.2B), to raptors (Korpimaeki 1985; Wheeler 1992), to passerines (Willner *et al.* 1983; Minot and Perrins 1986). Similarly, the creation of nest cavities in trees has become an important tool in the recovery of Red-cockaded woodpecker (*Picoides borealis*) populations in the southeastern United States. This endangered species is unusual because it lives in fire-maintained pine savannah, where it makes cavities only in live trees and is limited by the availability of mature pines (*Pinus* spp.) (Jackson 1994). Copeyon and her colleagues solved the technical problem of drilling nest cavities in live trees without causing them to fill with sap, and showed that birds rapidly

occupied newly created nest sites (Copeyon 1990; Copeyon *et al.* 1991). More recently, simpler methods using artificial cavities for this species have come into use (Saenz *et al.* 2001). Identifying and refining artificial breeding site features to better attract and house target species can be an important area of conservation research (e.g., Lalas *et al.* 1999; Stamp *et al.* 2002).

Within a suite of suitable habitat patches, it is sometimes also possible to manipulate where birds settle. This might be done because of a desire to attract individuals to newly restored sites (Ward and Schlossberg 2004), to sites that are protected (Podolsky 1990; Kress 1997), or to draw birds away from so-called ecological traps where reproduction is low or mortality is high (Kokko and Sutherland 2001). Not only can nest site features be manipulated, but one also can alter other cues used during breeding site selection (Reed 2004). In particular, conspecifics frequently provide cues to the suitability of habitat, and affect settlement decisions by prospective breeders (Stamps 1988, 1991; reviewed by Reed *et al.* 1999). Decoys fashioned to resemble the target species or sound recordings of colonies have been used to induce colonial seabirds to establish new breeding colonies (e.g., Kress 1978, 1983, 1997; Kress and Nettleship 1988) and to attract wading birds to foraging sites (Crozier and Gawlik 2003). Potential cues of breeding site quality using decoys have been further refined in the Laysan albatross, where decoys of chicks and of adults in courtship poses were displayed (Podolsky 1990). Similarly, Sarrazin *et al.* (1996) used white paint to simulate the appearance of feces on cliff faces at sites once used for conspecific breeding in order to attract Eurasian griffons (*Gyps fulvus*).

Birds might also respond to cues from other species through heterospecific attraction. For instance, some beach-nesting shorebirds frequently nest in association with colonial seabirds (e.g., Burger 1987; Alleng and Whyte-Alleng 1993; Warnock *et al.* 2002). Such behaviors are coming under greater scrutiny in a wider variety of bird species (e.g., Mönkkönen and Forsman 2002) and eventually could lead to more sophisticated tools for manipulating the behavior of species in ways that provide management benefits.

Breeding site selection might also be manipulated to draw species that are perceived to be a nuisance away from areas where they are causing problems. For instance, Caspian terns (*Sterna caspia*) became a problem to salmon (*Oncorhynchus* spp.) restoration efforts along the Columbia River in the western U.S.A. following a major shift in nest site selection, and rapid population increase, associated with the creation of sand islands from deposited dredge material (Roby *et al.* 1998; Suryan *et al.* 2004). Collis *et al.* (2001, 2002) found that juvenile salmon migrating from their hatching grounds to the ocean made up over 70% of the terns' diet in parts of the river. Using bioenergetic models, they estimated that a colony of over 9,000 pairs took over 8 million and 12 million salmon in two years, respectively, representing approximately 15% of the juvenile salmonid population reaching that part of the river (Roby *et al.* 2003). Caspian terns were successfully relocated to a site where they would have less impact on salmon populations

by creating nesting habitat at the new site, using social attraction techniques (decoys and sound playback), and predator control, while simultaneously discouraging terns from nesting at the old sites by planting vegetation and erecting fencing, wiring, and streamers (Roby *et al.* 2002). The colony completely shifted breeding sites within three years, and the proportion of the birds' diet made up of salmon dropped to less than half compared to its previous breeding site.

There are, of course, limits to the degree to which a species' breeding site selection can be manipulated. A species' evolutionary history, for instance, often constrains nest site selection, even when certain choices seem maladaptive in the context of modern human activities. Certain taxonomic groups, for example the Anseriformes, Galliformes, and Charadriiformes, are dominated by species that nest directly on the ground, and, at least among passerines, ground-nesting species suffer greater depredation than do species that nest in trees (Terborgh 1989). Many species, even habitat generalists, are relatively inflexible in the types of nest sites they will use. Exceptions occur, but they are usually not species that are a focus of management attention, simply because generalists typically are not a focus of conservation concern. One class of exceptions includes rare species that are able to occupy novel habitats that inadvertently mimic their natural habitat. Peregrine falcons (*Falco peregrinus*) for instance typically nest on cliff faces, but in parts of their range where this habitat does not occur, they sometimes nest on power line towers or high-rise buildings (White *et al.* 2002). In other cases, it might be possible to encourage greater use of rarely occupied nest sites. Common moorhens (*Gallinula chloropus*), for example, usually nest in dense emergent marsh vegetation but individuals occasionally nest in trees or in artificial nest boxes (Bannor and Kiviat 2004). Recognizing this potential flexibility, elevated, enclosed nest sites are now being used in an attempt to protect nests from terrestrial predators in the endangered Hawaiian moorhen (*G. c. sandvicensis*; Reed *et al.* personal observation).

Breeding site creation is not always a simple matter of recreating a breeding structure and placing it in a suitable habitat and the technique should be used with care. For example, Wood ducks (*Aix sponsa*) are obligate cavity nesters, and there is a long history of providing nest boxes as a management tool (Fig. 11.2B; Bellrose and Holm 1994). Wood ducks also are conspecific brood parasites, however, and high parasitism rates can cause abnormally large clutches that cannot be effectively incubated and in which eggs frequently get damaged. At high population densities, reproductive success can be reduced sufficiently to cause populations to crash (Haramis and Thompson 1985; Eadie *et al.* 1998). Semel *et al.* (1988) and Semel and Sherman (1995) found that the location of Wood duck boxes affects the rate of brood parasitism, with higher parasitism rates when boxes are placed in the open and at high densities. These results suggest that hiding nest boxes, and spacing them widely, can reduce parasitism rates and thus increase the effectiveness of the management.

## 11.4 MATE SELECTION

Mate quality, and the number of individuals with which a bird is able to reproduce, are important determinants of fitness, and birds exhibit sophisticated mate selection behaviors (see Chapters 1-7). Cues used to assess mate quality differ among species but often are associated with body size, body condition (e.g., stored fat), singing rate, or traits displayed in the plumage or skin (e.g., Olson and Owens 1998; Hill 2002; Chapters 1,2,3,5,6). Displayed traits can either provide direct or indirect information about individual quality. In some species, plumage cues can be obvious, such as the large, elaborate tails of Indian peafowl (*Pavo cristatus*) and other species (Darwin 1871; Loyau *et al.* 2005). Recent research, however, has also shown that some important cues have been overlooked; for example, because they are visible only in the ultraviolet spectrum, which is not directly perceived by humans (e.g., Andersson *et al.* 1998; Hunt *et al.* 1999; see also Chapter 1).

Although mate selection is largely studied in the context of its effects on individual fitness, an understanding of the decisions made when a bird chooses which individuals it will copulate with can potentially provide opportunities to manipulate mating patterns in order to achieve some management goal (Reed 2002). For example, mate availability in some rare species could be increased either (a) by translocating individuals (e.g., Kakapo *Strigops habroptilus*, Triggs *et al.* 1989; Po`ouli *Melamprosops phaeosoma*, Groombridge *et al.* 2004, although the attempt for this species failed), (b) by attracting individuals to a new site via decoys or playback (see sections 11.2 and 11.3), or (c) by increasing the amount of a limiting resource (see Red-cockaded woodpecker example in section 11.3). Within very small populations, where there can be concern about inbreeding depression, one theoretically could decrease the loss of genetic variability by altering mate selection patterns (Blumstein 1998; Reed 2002). For instance, one could limit the number of matings between close relatives or decrease the variance among individuals in the number of young they produce (Crow and Kimura 1970). To achieve these results, one would have to physically interfere with mating decisions, by limiting which individuals are able to breed together or by changing the apparent quality of some individuals in order to alter copulation patterns. In captive populations, genealogies can be generated from studbook records in order to determine which individuals should be allowed to mate with each other to achieve genetic conservation. For example, one important aspect of the Guam rail (*Gallirallus owstoni*) captive breeding program was to minimize the loss of genetic variability from the small captive population, prior to reintroduction of the species to the wild. This was done by determining kin structure using molecular markers and analyzing alternative pairing scenarios (Haig *et al.* 1994; Haig and Ballou 1995). In the wild, genealogical information is less likely to be available (though see Blackwell *et al.* 1995), and directing mating patterns is much more difficult to achieve than in captivity. Ecologists, however, have influenced mate selection in many

experiments designed to test basic questions about animal behavior by altering the appearance of individuals (Andersson 1982; Burley 1986; Witte and Curio 1999; Safran *et al.* 2005), and this approach could theoretically be used in extreme situations where a species' persistence was in jeopardy.

If mate selection is based on territory quality or external cues related to individual quality, this further opens the possibility of manipulating mate selection. For example, bower birds have specialized structures designed to attract mates, and some structures are adorned with bright objects (Diamond 1986). Borgia (1985) found that removing most of the decorations at the bowers of Satin bowerbirds (*Ptilonorhynchus violaceus*) reduced mating success. Some such manipulations, however, might result in increased intra-sexual competition with no concomitant increase in mating success, as Madden (1992) found when he manipulated display items of Spotted bowerbirds (*Chlamydera maculata*).

It has been predicted that species with polygynous mating patterns would be less vulnerable to extinction than are species with monogamous mating systems, particularly when population sizes are small (Legendre *et al.* 1999; Møller and Legendre 2001). This is due in part to Allee effects that cause population growth rates to decline as populations get smaller. Random variation can cause small populations to have skewed sex ratios, and a shortage of males in a polygynous system is predicted to be less likely to limit reproduction by females (Courchamp *et al.* 1999). Species that are socially monogamous, however, do not appear to be at more risk of extinction than are polygamous species (Morrow and Pitcher 2003), nor are they less likely to become established following introduction or translocation (Bessa-Gomes *et al.* 2003; see also McLain *et al.* 1995, 1999). Moreover, females in some socially monogamous species apparently overcome a shortage of males by engaging in extra-pair matings (Conover and Hunt 1984). Recent modeling studies show that the relationship between mating system and extinction risk are not systematic and instead depend on local population size, operational sex ratio, and the details of density-dependent feedback on vital rates (Bessa-Gomes *et al.* 2004; Sæther *et al.* 2004). Consequently, mating system *per se* does not appear to identify particularly extinction prone or resilient species.

## 11.5 PRODUCTION OF OFFSPRING

Once a breeding site and mate have been selected, birds must build nests and produce eggs. Knowledge about reproductive biology can be valuable to managers both because it can help to identify situations where the natural reproductive capacity of a population is compromised and because it can provide insights into the ways in which the rate of offspring production can be altered to meet management goals. Understanding the phylogenetic constraints that species face is also important because they might influence the range of options available to managers. For instance, if clutch size is fixed certain management techniques may not be plausible.

Various studies of environmental contaminants illustrate the way in which an understanding of reproductive biology can help to better address a management problem. Well known research on the declines of predatory birds lead to the discovery that pesticides such as dichlorodiphenyltrichloroethane (DDT) can alter the structure of eggshells, making them more vulnerable to premature cracking and resulting in reduced production of young (Hickey and Anderson 1968; Ratcliffe 1970). Similarly, more recent work has shown that nest building behavior in Tree swallows (*Tachycineta bicolor*) differs between area with high levels of polychlorinated biphenyl (PCB) contaminants and control areas. These differences result in lower quality nests that are less likely to fledge young in the contaminated area (McCarty and Secord 1999).

Once sources of nest failure have been identified, methods for removing the problem can be developed. In the case of environmental contaminants, this can be done through legislative means or through environmental clean-up activities. In other situations more direct management might provide a means by which the production of young can be increased. For instance, several endangered species in North America are thought to have benefited from the control of Brown-headed cowbird (*Molothrus ater*) populations (Eckrich *et al.* 1999; Whitfield *et al.* 1999). Sometimes, however, management activities designed to enhance productivity prove not to be as successful as they are perhaps assumed to be, as indicated by a meta-analysis of studies that have investigated the impact of predator control on bird populations (Côté and Sutherland 1997).

Increasing reproductive success at this stage of reproduction, however, is often costly and can require the use of quite invasive methods. Logistical challenges and idiosyncratic differences among species often also require extensive trial-and-error to develop effective methods. Consequently, this general approach to management is used in relatively few species and is usually considered a last resort in the conservation of rare species. In cases where alternative management strategies have failed or are not available, however, a common method of increasing the offspring production rate is to remove eggs from nesting birds and take them into captivity where they can either be incubated artificially or by a foster parent of another species (e.g., Fyfe *et al.* 1977). This general approach has three variants. First, eggs can be removed from the nest of a species that normally cannot rear all of the young that normally hatch. Second, eggs can be removed sequentially from a partially complete clutch, so that the female lays more eggs than normal in order to obtain a complete clutch. Finally, entire clutches are sometimes removed to induce the bird to lay a replacement clutch. An example of this approach comes from the Mauritius kestrel (*Falco punctatus*) population recovery program (Jones *et al.* 1995a). Here, researchers (a) removed eggs as they were laid to increase total egg production, and (b) removed entire clutches of eggs, causing females to lay replacement clutches (referred to as double-clutching). Researchers found that the second approach was more effective at

increasing egg production in this species. In principle, removed eggs or clutches can be transferred among nests in both wild and captive settings. Before employing this method, however, it is critical to understand the biology of the target species sufficiently well to ensure that additional eggs will be laid, and that the management activities will not simply result in nest abandonment. Clutch size reduction, for instance, can lead to nest abandonment in some species (e.g., Wilson's phalarope *Phalaropus tricolor*, Delehanty and Oring 1993), and the likelihood of abandonment can be affected by the severity of the clutch reduction (e.g., Mallard, Ackerman and Eadie 2003). Consequently, it is important to know when best to remove eggs in order to ensure that relaying occurs and that abandonment does not happen.

Another labor-intensive approach to increasing reproductive output that could be used in captive-breeding settings is artificial insemination. Although artificial insemination has been used mostly in domestic species (Perry 1968), there are notable uses in non-domestic bird species such as falcons (Gee 1995), semi-domestic species such as Emus (*Dromaius novaehollandiae*) (Malecki and Martin 2004), and captive wild birds (Jones and Nicolich 2001). Semen has been gathered from birds via natural copulation with dummies or some other receptacle (Berry 1972; Boyd 1978) and by massaging the cloacal protuberance (or phallus, in species that have one) of a captured male (Gee 1983); electroejaculation techniques conducted under anesthesia are available, but are not commonly used for wild species (Gee 1995). Females subsequently are inseminated with a device that, preferably, achieves deep vaginal (rather than cloacal) semen placement (Gee 1995). Artificial insemination has been used successfully for some wild bird species, such as Golden eagle (*Aquila chrysaetos*), Peregrine falcon (Blanco *et al.* 2002), and Aleutian Cackling goose (*Branta hutchinsii leucopareia*; Gee and Sexton 1990). Collecting viable sperm, storage, and insemination can cause problems, however and methods need to be developed for each species (e.g., Penfold *et al.* 2001). Because the methods are time intensive, sperm collection and insemination can result in injury, and sperm storage is temporary (e.g., Saint Jalme *et al.* 2003), artificial insemination should be viewed as a last resort in species' conservation efforts, and would most often be done as part of a captive breeding program (Hutchins *et al.* 1995, Saint Jalme 2002).

Theoretically cloning also could be used to create new embryos for rare species, and therefore increase reproductive output (Lanza *et al.* 2000; DeSalle and Amato 2004). Cloning methods, however, are in the early stages of development and birds have not been a primary research focus. Although cloning might attract public attention because of its "science fiction" quality, we do not foresee a future where cloning plays a significant role in species conservation, except as a last resort for highly endangered species. Even in these cases, it is likely to be difficult to create populations with sufficient genetic variability to be viable over the long term (e.g., Loi *et al.* 2001; Ryder 2002; Gómez *et al.* 2004). Although the preservation of genetic material

suitable for future cloning efforts may be a worthwhile activity, in the near term it is probably more important to direct resources towards preventing species from becoming highly endangered in the first place (DeSalle and Amato 2004).

Manipulations designed to increase reproductive output are effective only within the context of (or are limited by) species-specific behaviors. For example, cross-fostering and double-clutching using surrogates could exacerbate inbreeding in small populations if inbreeding avoidance is learned via early familiarity. That is, if inbreeding avoidance is a consequence of not mating with brood mates, then splitting clutches for rearing could prevent sibling recognition. Conversely, if unrelated individuals are raised together they might be unwilling to mate once they are adults. Early learning also can affect species recognition in ways that influence the selection of appropriate mates once maturity is reached (Reed 2004). An example of this arose when Whooping cranes (*Grus americana*) that came from eggs that were cross-fostered into a Sandhill crane (*G. canadensis*) nest courted members of their foster species, rather than their own (Mahan and Simmers 1992).

Complex technological or manipulative solutions to the problem of increasing the production of young in captive settings may not, however, always be necessary. For instance, a study of captive Humboldt penguins (*Spheniscus humboldti*) that correlated husbandry conditions with measures of reproductive success using data from many different zoo collections, produced a number of simple recommendations for improving the reproductive success in captive populations that could be implemented simply by changing the conditions in which birds were kept (Blay and Côté 2001).

The converse of the problem of enhancing reproduction for species of concern is to reduce reproductive success of birds considered to be pest species. The most common approach has been to destroy eggs, through procedures such as oiling or puncturing (e.g., Lewis and Malecki 1984; Blackwell *et al.* 2002). These methods are preferred to egg removal or crushing because they prevent obvious clutch loss, which increases the chance that the parents will continue to incubate the dead eggs rather than produce a new clutch. An alternative is to prevent egg laying through the use of chemical contraception (e.g., Hurley and Johnston 2002; Dobeic 2003; Johnston *et al.* 2003; section 23.2). This approach has not been used extensively for any type of wildlife but its limited use on White-tailed deer (*Odocoileus virginianus*; Rutberg *et al.* 2004) and other mammals suggests to us that it is not likely to be a promising avenue for the control of most avian pests (see also Barlow 2000).

## 11.6 PARENTAL CARE

For the production of young to influence population dynamics, it must result in the recruitment of birds to the breeding population. In almost all birds, this requires some level of post-hatching care. The type and extent of care,

however, varies greatly among species and understanding the requirements of a particular species can provide important management insights. For species with altricial young that are completely helpless, parents must provide all basic maintenance activities, such as providing their young with food and protecting them from the elements and predators. For species with precocial young that can get around on their own and find their own food, parents still provide considerable protection by brooding, by warning against and distracting predators, and by guiding the young to safe areas. In some species, parental care also involves the transmission of complex behavioral information. For example, geese and other species usually migrate in family groups, suggesting that young learn migration routes from their parents.

Understanding both the amount and type of parental care needed by a species is especially important when breeding endangered species in captivity, both for biological and logistical reasons (Hutchins *et al.* 1995). When rare species are bred in captivity, surrogate parents are often used to raise the young. This method leaves the actual parents free to produce additional clutches (see section 23.5). For this approach to work, however, it is critical that the foster chicks be raised appropriately.

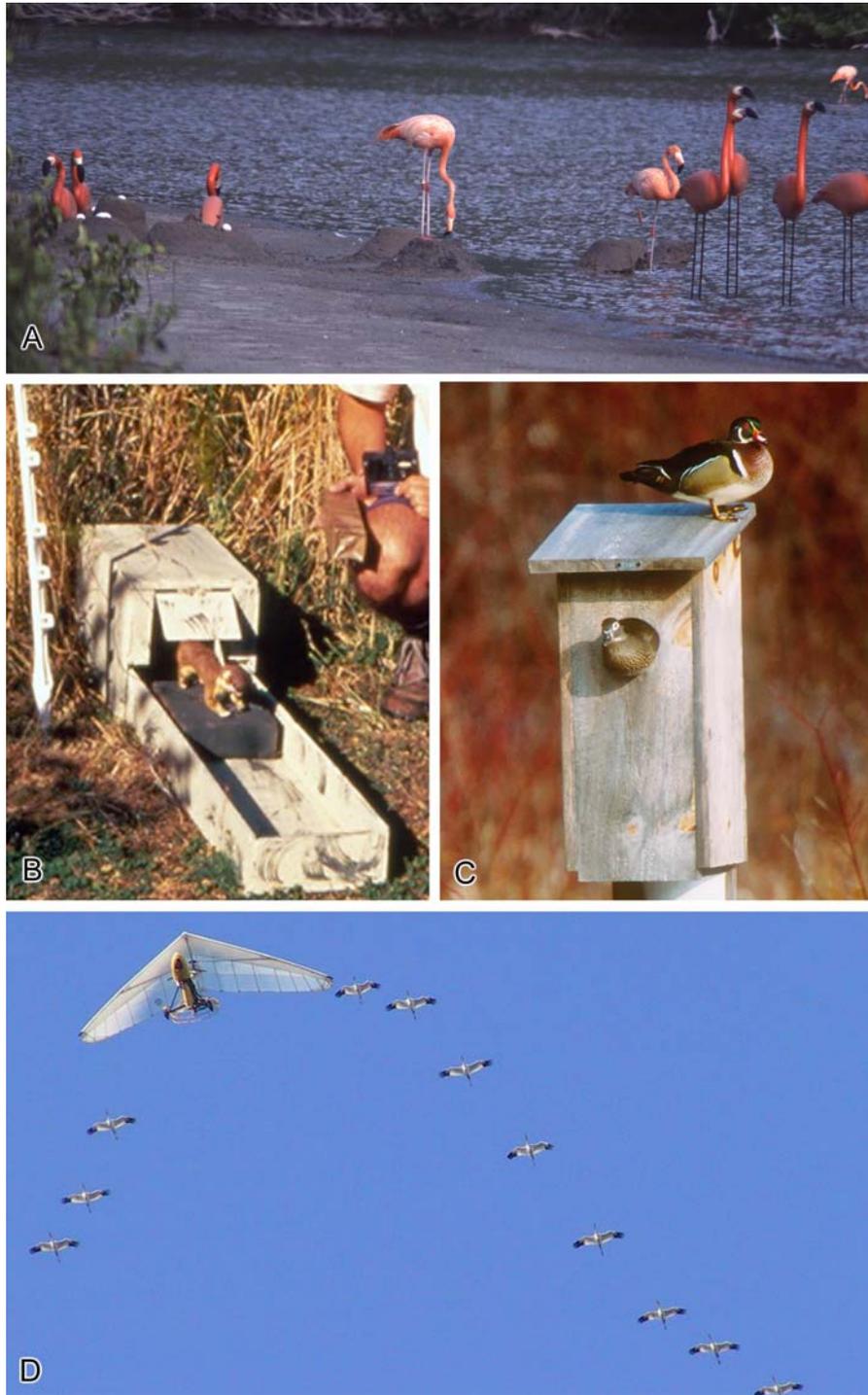
Foster parents are sometimes birds of another, usually closely related, species. For instance, Madagascar turtle-doves (*Streptopelia picturata*) have been used to raise endangered Pink pigeons (*Columba mayeri*) from Mauritius (McKelvey 1976; Bruning 1989). For some species, however, the use of foster parents from another species can cause unanticipated problems (see section 23.5), and for others there might not be appropriate surrogate parents available. This could be a particular problem where extensive cultural learning is important. Consequently, humans sometimes take on the parental role. This situation also raises concerns that young birds might learn inappropriate behaviors from the humans that raise them and that they might fail to learn key behaviors that are important for survival in the wild. Hand-reared individuals, for example, are often tamer and less aware of potential threats than are their wild counterparts, and this can result in high mortality when they are released into the wild (Hutchins *et al.* 1995). Studies of captive parrots, for example, have shown that hand-reared birds have lower reproductive success than individuals raised by their parents (Myers *et al.* 1988) and that hand-reared birds do not survive well when introduced into the wild (Wiley *et al.* 1992).

If captive breeding is to be attempted, understanding the mechanism by which imprinting occurs can be extremely helpful in designing effective husbandry techniques. For instance, initial attempts to hand rear Andean condors (*Vultur gryphus*) resulted in the offspring imprinting on their human keepers, but this problem was alleviated by minimizing contact between birds and humans and the use of condor-like hand puppets to feed the chicks (Bruning 1983). Understanding the timing of imprinting also can be helpful, as it allows one to identify periods when extreme measures are most critical (Hutchins *et al.* 1995).

Appropriate predator recognition and response behaviors are also learned by some species from their parents, and therefore birds reared in captivity sometimes must be taught the appropriate cues and responses. For example, passive and active models of predators have been used to investigate the responses of endangered species, such as the Takahe (*Porphyrio mantelli*; Bunin and Jamieson 1996) and New Zealand robin (*Petroica australis*; McLean *et al.* 1999), to predators, and can be used to train them to recognize predators and respond appropriately (I. Jamieson, personal communication). Takahe, for example, were tested by exposing them to a stuffed Stoat (*Mustela erminea*), which was placed on a box that covered a small remote control car, such that the box hid the wheels (Fig. 11.2C). The stoat could then 'emerge' from the cover of a larger box hidden in vegetation, as desired by a human observing from some distance away. In initial tests, a young Takahe that had been raised by foster-parents of a species with a well developed defensive response to stoats exhibited more appropriate anti-predator behaviors than did a control Takahe that had been raised by its true parents (Bunin and Jamieson 1996).

Captive breeding has created both problems and opportunities for managers. Conservation efforts for Whooping cranes, for example, have emphasized captive breeding as a mechanism for increasing population size. In order to successfully introduce the captive-bred cranes into the wild population, however, it is necessary to teach them where they should migrate. Because these birds do not have wild parents who can teach them, managers have developed innovative training methods, which have involved imprinting the youngsters so that they follow ultralight aircraft and then using the aircraft to lead them to wintering grounds (Fig. 11.2D). This approach also has been used in Sweden to reintroduce Bean goose (*Anser fabalis*) and Lesser white-fronted goose (*A. erythropus*) populations (Morner 1986). Although the use of ultralight aircraft, and other motorized vehicles, was developed to solve a problem caused by the complexity of a species' biology, the solution has created new opportunities for conserving species. The use of motorized vehicles to teach migration routes to young birds, for example, now makes it possible to manipulate migratory pathways and create populations in new places (Ellis *et al.* 2003).

Overall, however, captive breeding is a logistically difficult and typically expensive endeavor (Snyder *et al.* 1996). Understanding the biological requirements of parental care, therefore, can help managers not only to ensure that it is done well but also to decide whether it should be attempted in the first place. Because species differ in the amount and type of parental care they need, they also differ in their suitability for captive breeding. Altricial young that need to be fed frequently, for instance, generally require far more work than do precocial young that can feed themselves. Consequently, species with altricial young may be logistically easier to raise in captivity than species with precocial young, and it is not surprising that most domesticated species are highly precocial (although this relationship is confounded by the fact that domesticated species also tend to be relatively large, which makes them more



**Fig. 11.2.** A. Wooden flamingos and eggs (in artificial mud nests) alongside living Caribbean Greater flamingos (*Phoeniconais ruber ruber*). B. Male (top) and female (emerging) Wood ducks (*Aix sponsa*) using an artificial nest box. C. Stuffed Stoat

*Fig. 11.2 Contd. ....*

suitable for meat production). On the other hand, many species with precocial young are also large and take a relatively long time to reach maturity, meaning that parental care might require a longer-term investment than for smaller species with altricial young (e.g., compare cranes to passerines). Similarly, some species with altricial young are easier to raise than others. For instance, species that are insectivorous and need feeding multiple times an hour require a much greater time investment than do altricial carnivores, which can be fed less frequently and more easily.

Despite the extensive opportunities to manipulate parental behavior in captivity, there probably are limited options to make equivalent manipulations in wild populations. Opportunities to directly manipulate incubation and brooding behaviors, or predator defense, seem unlikely. Food provisioning, however, could indirectly influence all of these things by decreasing the amount of time parents need to be away from a nest, decreasing the amount of time a chick or fledgling is exposed to predators, and improving body condition for both adults and young (e.g., Dewey and Kennedy 2001). Some food provisioning experiments, however, have found that supplemental feeding of chicks had no effect on offspring condition or fledging success (e.g., Leach's storm-petrel *Oceanodroma leucorhoa*, Takahashi *et al.* 1999; House wren *Troglodytes aedon*, Styrsky *et al.* 2000), again pointing to the need to understand the idiosyncratic differences that arise in different situations. Food provisioning might benefit chicks and adults in other ways as well. There is evidence from captive-bred birds that increased activity and energy expenditure during reproduction can decrease antibody responsiveness (Deerenberg *et al.* 1997), which suggests that there could be health benefits if reproductive effort were reduced, e.g., through supplemental feeding. Supplemental feeding also has been associated with reduced chronic stress (as measured by baseline and stress-induced corticosterone levels) in male Song sparrows (*Melospiza melodia*) with chicks (Clinchy *et al.* 2004); chronic stress can lead to decreased reproduction and death in some circumstances (Wingfield *et al.* 1996).

In wild populations, pollutants can interfere with parental care, and therefore measuring parental behavior might function as a biological indicator of some environmental contaminants (Døving 1991; Cohn and MacPhail 1996; Kulig *et al.* 1996; Reed 2004). Grue *et al.* (1982), for example, found that European starlings (*Sturnus vulgaris*) exposed to an organophosphate insecticide (dicrotophos) exhibited reduced attentiveness to their offspring.

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*Fig. 11.2 Contd. .... (Mustela erminea) used to investigate the response of captive-bred Takahes (Porphyrio mantelli) to predators. D. Whooping cranes (Grus americana) following an ultralight airplane to learn a new migration route. Photographs courtesy of: A, Timothy Rodwell, Stanford University; B, Paul Fusco, Connecticut Department of Environmental Protection; C, Ian Jamieson, University of Otago; D, Operation Migration.*

A single oral dose of the pesticide resulted in females making fewer trips to feed their young and increased the amount of time that the mothers spent away from their nests. As a result, nestlings lost weight. European starlings also reduced food provisioning to chicks when exposed to PCBs, resulting in decreased chick survival (Arenal *et al.* 2004). Interference of parental behavior due to chemical exposure, with subsequent effects on chick survival, has been documented for other species as well, including Ringed turtle-doves (*Streptopelia risoria*; Peakall and Peakall 1973), Tree swallows (Bishop *et al.* 2000), and Common loons (*Gavia immer*; Nocera and Taylor 1998). Using these behaviors as bioindicators would require an adequate database of “normal” behaviors against which to compare observed behaviors, which may limit the utility of the approach (Kulig *et al.* 1996; Peakall 1996). In cases where there is a high risk of contamination, however, aberrant parental behaviors might provide an inexpensive means of determining whether more detailed study is warranted.

## 11.7 MONITORING

Throughout this chapter we have focused on ways in which reproductive biology can be used to manipulate population sizes. A separate, extremely important, component of population management involves monitoring population size in order to assess when management is necessary and whether management actions are successful. Because much monitoring occurs during the breeding season, many methods require a basic understanding of reproductive biology in order to maximize their effectiveness. For instance, many survey protocols are designed to count the number of singing birds, which requires an understanding of when singing activity is likely to peak, both seasonally and during the daily cycle (Ralph and Scott 1981; Bibby *et al.* 1992). Other surveys are designed to monitor the number of nests or young produced, and thus must be designed with a knowledge of the basic breeding biology of the target species in mind.

In some cases, understanding breeding behavior might be especially useful in designing an appropriate monitoring program. For example, species are often easiest to count when they are aggregated into a small area, and so identifying situations where birds gather in groups as part of their reproductive activities can be useful. This approach is particularly helpful when the locations where aggregations occur are predictable from year to year. Monitoring colonial species, such as seabirds and herons, consequently often occurs at nesting colonies (e.g., Dyer *et al.* 2005), and lekking species, such as bustards and various grouse, are often monitored at traditional display sites (e.g., Lane and Alonso 2001).

Situations also arise where an understanding of a species' reproductive behavior can be useful in designing methods that improve upon passive counting. For instance, some species are difficult to survey because they are cryptic, live in dense vegetation, or are largely nocturnal. Such species often communicate largely through sound and their presence and abundance can

be effectively determined using playback surveys in which vocalizations are broadcast and the responses counted (e.g., Conway and Gibbs 2005). For any of these methods to be useful, however, they must be based on a detailed understanding of the reproductive biology of the target species. For instance, singing rates in some species decline after a male has found a mate (Gibbs and Wenny 1993; Tyler and Green 1996), meaning that high levels of singing in an area could indicate the presence of high numbers of unpaired males – which, in an apparent paradox, could be a sign of poor habitat conditions (McGregor *et al.* 2000).

## 11.8 CONCLUSIONS

We have organized this chapter around the biological processes that collectively constitute reproduction (Fig. 11.1), rather than around the work that occurs in particular sub-disciplines or on specific conceptual ideas. The reason for this organization is to emphasize that effective management requires that one intervene with the breeding cycle wherever an intervention is most likely to achieve a desired goal. Recognizing where interventions will be most useful in order to meet a specific goal, therefore, requires both a broad base of information about all aspects of a species' biology as well as detailed knowledge of the precise mechanisms involved in different areas of reproductive biology. Consequently, there are many potential ways in which specialists collaborating with applied ecologists can contribute to the discovery of novel solutions to management questions.

The ultimate goal of most population management is to effect change in a population's size. In many cases, perhaps most, this is done indirectly by manipulating the breeding habitat in which a species occurs. Directly manipulating the reproductive biology of individuals is generally more of a logistical challenge, simply because it becomes difficult to apply specific treatments to large numbers of birds. This reason is probably why approaches, such as the development of contraceptive methods for species that are considered pests, have not been successfully applied at large scales in wild populations. Many aspects of reproductive biology, therefore, may be most relevant in conservation settings where populations are already small and the number of birds involved is logistically manageable. Many potential interventions, however, are also very intrusive and can be expensive to implement. Consequently, the possible benefits of activities such as cross-fostering and captive breeding should be weighed against the risks of interfering with populations that are already in a precarious situation and against the benefits that can be gained by directing money towards other activities such as habitat improvement.

Overall, though, there are clearly a wide range of opportunities to apply basic research on the reproductive biology of birds to the general problem of altering rates at which young birds are recruited into a population. When set in the context of other demographic processes, this information can be used to address many diverse questions in applied avian ecology.

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