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PERSPECTIVES IN ORNITHOLOGY

THE NEED TO QUANTIFY ECOSYSTEM SERVICES PROVIDED BY BIRDS

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WHAT ARE BIRDS worth—what is their actual dollar value to human society? To most of us in the ornithological community, birds are invaluable. But in these times we need more specific rationales to convince policy makers and business leaders to include bird conservation in land-use and development decisions. Over the past two decades, awareness of our dependence on a variety of ecosystem services (natural ecological processes that benefit human society) and of their importance and prevalence has progressed toward the goal of making conservation a mainstream value (Ehrlich and Kennedy 2005, Perrings et al. 2010, Rands et al. 2010, Sodhi and Ehrlich 2010). Building strategies for the protection of ecosystem services into conservation and land-use planning is essentially the promotion of human survival, although many policy makers misinterpret conservation efforts as luxury. Several previous reviews have identified ecosystem services that benefit human society (Costanza et al. 1997, Daily 1997, Pimentel et al. 1997, Sekercioglu 2010). The challenge, however, is to calculate the value of ecosystem services in meaningful and relevant ways that can be used to justify the protection of ecosystem services in land-use recommendations and policy decisions (Daily et al. 2000, 2009). As the case studies below illustrate, recent work on the ecosystem services provided by birds has made good progress toward this goal, but much remains to be done. Our objectives here are to describe the ecosystem services provided by birds, highlight recent steps toward quantifying those services, and, finally, suggest directions for future research. Overall, we emphasize that global efforts to conserve bird populations and sustain avian biodiversity also preserve the diverse ecosystem services provided by birds, thus contributing to human well-being.

DEFINITIONS AND BACKGROUND

Ecosystem services are divided into four categories (Millenium Ecosystem Assessment 2003). Provisioning services refer to natural products that are directly used by humans for food, clothing, medicines, tools, or other uses. Cultural services provide recreational opportunities, inspiration for art and music, and spiritual value. Regulating services include pest control and carcass removal. Supporting services, such as pollination, seed dispersal, water purification, and nutrient cycling, provide processes essential for ecological communities and agricultural ecosystems.

The Millennium Ecosystem Assessment's description of ecosystem services (Millenium Ecosystem Assessment 2003) is widely cited, but considerable debate continues on what constitutes an ecosystem service and how each should be quantified (Boyd 2007, Boyd and Banzhaf 2007, Matero and Saastamoinen 2007, Nijkamp et al. 2008, Bartelmus 2010, Farley and Costanza 2010, Kontogianni et al. 2010, Norgaard 2010, Wainger et al. 2010). The main issues include

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how to value nonmarket services, how to avoid double counting a process and its end product, and how to incorporate ecosystem valuation into policy and land-use decisions. We do not advocate any particular method of valuation here, but we argue that a consistent methodology for calculating units of ecosystem services is needed (as with any system of weights and measures; Boyd 2007).

OVERVIEW OF ECOSYSTEM SERVICES PROVIDED BY BIRDS

Birds are the best-known class of vertebrate animals, occur worldwide in nearly all habitats, and provide many services (Sekercioglu 2006a, b; Whelan et al. 2008). Thus, they are an ideal group to examine for ecosystem service valuation. Yet, surprisingly, little ornithological research has been done in an ecosystem-services context. Much ecosystem-services work has been focused on watersheds and insect pollination, perhaps because market value can readily be assigned to both fresh drinking water and agricultural crops that require pollination (Kremen et al. 2007, Brenner et al. 2010). Similarly, economic aspects of some cultural and provisioning services such as bird watching and hunting have been quantified (Sekercioglu 2002, LaRouche 2003, Leonard 2008, Carver 2009). Other historical and cultural aspects of birds have been reviewed and quantified in a general way (Diamond and Filion 1987, Podulka et al. 2004, Mynott 2009). Most of the important ecological roles that birds fill, however, involve supporting and regulating services, such as insect pest control and seed dispersal, and these types of services are the most difficult to quantify (Farber et al. 2006; Sekercioglu 2006a, b; Whelan et al. 2008, 2010). As we describe below, many of the most important ecosystem services that birds provide result from their foraging behavior. Through their foraging, birds act as mobile links that transfer energy both within and among ecosystems, and thus contribute to ecosystem function and resilience (Lundberg and Moberg 2003). We know that birds are important ecologically; the challenge is to quantify that importance in terms that are currently meaningful to humans.

Pest control.—The regulating and supporting services provided by birds result mostly from foraging (i.e., consuming and processing resources; Table 1). The prime example is insectivory, which can provide the ecosystem service of pest control. More than 50% of bird species are predominantly insectivorous, and nearly 75% eat invertebrates at least occasionally (Sekercioglu 2006b; Table 1). The beneficial role of birds in consuming arthropods, and especially their responses to and influence on insect outbreaks (e.g., spruce budworms [*Choristoneura* spp.], cicadas [*Magicicada* spp.], and Mormon Crickets [*Anabrus simplex*]), is well documented (U.S. Biological Survey reports, summarized by Whelan et al. 2008). Furthermore, numerous studies in both natural and agricultural habitats show not only that birds reduce herbivorous insect populations, but also that plants respond with higher growth rates or crop yields (see Whelan et al. 2008: Table 1), a classic "trophic cascade" (Terborgh and Estes 2010). To cite an anecdotal example, the 1958 extermination campaign in China against the Eurasian Tree Sparrow (*Passer montanus*) ultimately contributed to insect pest outbreaks rather than rice yield increases, demonstrating indirectly that the sparrows' control of insects benefited the crop (Suyin 1959, Becker 1996).

Other trophic cascades that involve birds potentially benefit agriculture, but they have seldom been studied. For example, although many raptors (both hawks and owls) consume rodents, we know of no study that has examined this predator–prey interaction from the perspective of economic value or trophic cascades. A few studies have directly assessed birds of prey as agricultural rodent-control agents, and the results are somewhat ambiguous. Wood and Fee (2003) reviewed measures to control rats in Malaysian agroecosystems, including deployment of nest boxes to raise populations of Barn Owls (*Tyto alba*). They concluded that the evidence was inconsistent and that the effect of owls warrants further investigation. Kay et al. (1994) reported that perches placed around soybean fields in Australia increased the number of diurnal raptors around and over the fields, which in turn decreased House Mouse (*Mus musculus*) population growth rate and maximum population density in the fields. Perches placed 100 m apart were more effective than those placed 200 m apart. Other studies demonstrated that providing artificial perches attracts various birds of prey, including American Kestrels (*Falco sparverius*), which also suggests that this method may enhance or concentrate foraging in potentially beneficial ways (Wolff et al. 1999, Sheffield et al. 2001). Clearly, more research is needed on the potential for birds of prey to drive trophic cascades in natural and agricultural ecosystems.

The role of granivorous birds in control of agricultural weeds is essentially unknown, but one example is suggestive. In New Zealand, a granivorous bird introduced for aesthetic reasons, the European Goldfinch (*Carduelis carduelis*), destroyed 10× more seeds of the aggressive pasture weed *Carduus nutans* than a weevil (Curculionidae: *Rhinocyllus conicus*) that was introduced to provide biological control of *C. nutans* (Kelly and McCallum 1990). In fact, the 32% of seed destroyed by goldfinches at that site compares favorably to the highest well-documented seed losses attributed to *R. conicus* (30–40%) at sites where the insect provided effective biological control (Kelly and McCallum 1995). While it is likely that most species of avian granivores are beneficial in agroecosystems, especially because most species also eat considerable quantities of invertebrates during the breeding season, the most prominent studies of granivores are those on birds as agricultural pests (Weatherhead et al. 1982, Elliott and Lenton 1989, Dolbeer 1990, Basili and Temple 1999, Avery et al. 2001, Blackwell and Dolbeer 2001, McWilliam and Cheke 2004, Cirne and Lopez-Iborra 2005, Hagy et al. 2008). Future research should examine more fully the costs and benefits of avian granivory in agricultural settings.

Bird–plant mutualisms.—The bird–plant interactions of pollination and seed dispersal have potentially large effects on ecosystems. Nearly 33% of bird species disperse seeds, primarily through fruit consumption, but also through scatter-hoarding of nuts and conifer seed crops (Vander Wall 2001, Sekercioglu 2006b). It is difficult to estimate the number of plant species dispersed by birds, because of overlap with seed-dispersing mammals and incomplete knowledge of many habitats. In the temperate zone (i.e., Europe, North America, Japan, and New Zealand), 36–55% of woody flora are fleshy-fruited (Burrows 1994). Nonwoody species are less likely to have fleshy fruit, so the average across whole floras is lower; for example, in New Zealand, fleshy fruits are found in 59% of trees (Kelly et al. 2010) and 48% of all woody species (Burrows 1994), but in only 12% of the whole flora (Lord et al. 2002). These temperate-zone totals exclude dry (lacking a fleshy covering), scatter-hoarded tree nuts and conifer seeds, which are common in the Northern Hemisphere (Tomback and Linhart 1990, Vander Wall

TABLE 1. Relative importance of dietary categories among avian orders (+ indicates primary item, – indicates less important item, blank indicates an item rarely or never eaten at family level within orders). List based on Gill and Donskar (2010). Diets from Harris (2009).

				Terrestrial		Aquatic						
Order	Families	Genera	Species	Inverts	Verts	Inverts	Verts	Carrion	Fruit	Seeds	Vegetation	Nectar
Tinamiformes	1	9	47	+	–				–	–	–	
Struthioniformes	1	1	2	–					–		+	
Rheiformes	1	2	2	–	–						+	
Casuariiformes	2	2	4	+	–			–	+	–	–	
Apterygiformes	1	1	5	+								
Galliformes	5	83	297	+					+	+	+	
Anseriformes	3	51	169	+		+				+	+	
Gaviiformes	1	1	5			–	+					
Sphenisciformes	1	6	19			+	+					
Procellariiformes	4	26	134			+	+	–				
Podicipediformes	1	6	21			+	+					
Phoenicopteriformes	1	3	6			+						
Phaethontiformes	1	1	3			+	+					
Ciconiiformes	1	6	19			+	+	+				
Pelecaniformes	5	35	111	–	–	+	+	–			–	
Suliformes	4	8	55			+	+	–				
Accipitriformes	4	72	260	+	+		+	+	–			
Falconiformes	1	11	65	–	+			–				
Otidiformes	1	11	27	+							+	
Mesitornithiformes	1	2	3	+					–	–		
Cariamiformes	1	2	2	+	+					–		
Eurypygiformes	2	2	2	+	–	–	+					
Gruiformes	6	42	162	–	–	+	–		–		+	
Charadriiformes	19	94	379	+	–	+	+	–	–	+	–	
Pteroclidiformes	1	2	16	–						+		
Columbiformes	1	42	321	–					+	+		
Psittaciformes	3	86	373	–					+	+	–	–
Opisthocomiformes	1	1	1						–		+	
Musophagiformes	1	6	23	–					+		–	
Cuculiformes	1	32	146	+	–				–			
Strigiformes	2	27	220	–	+		–					
Caprimulgiformes	4	21	117	+	–				+			
Apodiformes	4	128	454	+								+
Coliiformes	1	2	6						+		+	
Trogoniformes	1	7	42	+					+			
Leptosomiformes	1	1	1	+	–							
Coraciiformes	6	35	157	+	–	+	+		–			
Bucerotiformes	4	17	73	+	–			–	+	–	–	
Piciformes	9	67	431	+	–				+	–		
Passeriformes	120	1278	6237	+	–	–		–	+	+	–	+

2001). Also, the tropics hold most plant species diversity, and tropical floras are disproportionately woody and fleshy-fruited (Howe and Smallwood 1982, Willson et al. 1989, Fleming 1991). Thus, probably 30–50% of all plant species have vertebrate-dispersed fruit (80,000–140,000 species). Certainly, many tens of thousands of plant species benefit from bird dispersal in terms of gene flow, colonization of open sites, escape from predators, directed dispersal to favorable sites, or enhanced germination (Vander Wall and Balda 1981, Howe and Smallwood 1982, Johnson and Webb 1989, Tomback and Linhart 1990, Jordano 2000, Tomback 2005).

Birds disperse the seeds of many woody plant species with direct value to humans for timber, medicine, food, or other uses; yet the dependence of these plants on birds for dispersal and the anthropogenic influences on the seed-dispersal pathways are in many cases poorly understood. The great declines in abundance of large frugivorous birds and mammals have resulted directly or indirectly from human activities, and some have been extirpated from regions or have become extinct (Cordeiro and Howe 2003, Sekercioglu et al. 2004, Peres and Palacios 2007, Terborgh et al. 2008). Large-seeded plants are most at risk because they require large-bodied dispersers, which are more vulnerable to anthropogenic effects (Hansen and Galetti 2009, McKinney et al. 2009). As a result, the number of relatively large-seeded plants with few or no dispersers is now rising, especially on islands, which have lower

diversity and less ecological redundancy than continental areas (e.g., Kelly et al. 2010). Lower densities of frugivores may disperse a smaller fraction of the fruit crop, which can result in fewer seedlings or in seedlings being more concentrated under the parent plants (Cordeiro and Howe 2003, Terborgh et al. 2008, Cordeiro et al. 2009, Sethi and Howe 2009, Sharam et al. 2009, Chimera and Drake 2010). These effects generally result in changes in plant community composition rather than the local extirpation of plant species (Wright and Duber 2001; Cordeiro and Howe 2003; Muller-Landau 2007; Wright et al. 2007a, b; McKinney et al. 2009; Sharam et al. 2009). It is unknown how these changes will affect plant populations, or even entire forest communities, that are important to humans. More experimental work is needed to determine the ecological processes involved and their outcomes.

Fewer bird and plant species are involved in bird-pollination mutualisms (~900 bird species and ~5% of regional floras; Stiles 1985, Nabhan and Buchmann 1997), but recent evidence suggests that bird-pollination failure still poses important risks. The relationships tend to be more specialized than with seed dispersal, and the outcome of a failed mutualism is unambiguously negative (failure to produce seed; Kelly et al. 2004). For some plants in New Zealand, insects were regarded as effective substitutes for missing birds, but data do not support this belief (Kelly et al. 1996, Robertson et al. 2005), even for some temperate-zone plant species with apparently insect-adapted flowers (Anderson 2003). As with seed dispersal, plant extinction may not follow loss of pollinators, but we have few good measures of such effects, especially in cases where birds have declined rather than become extinct. One recent study provides a cautionary example: Anderson et al. (2011) showed a terrestrial trophic cascade in New Zealand whereby mammalian carnivores reduced densities of pollinating birds, resulting in an 84% reduction in seed output of the bird-pollinated shrub *Rhabdothamnus solandri* and a 55% reduction in shrub regeneration. The authors stress that gradual plant declines might frequently pass unrecorded. Where comparisons have been made within a single region, bird-pollinated plants seem to be more pollen limited than dispersal limited; thus, the effects of mutualism breakdown may be greater and faster-acting for bird-pollination than for seed-dispersal systems (Kelly et al. 2004, 2010). However, where pollination is primarily by insects, seed dispersal is probably the mutualism more at risk (Corlett 2007).

Scavenging and nutrient cycling.—The ecological importance of scavenging birds is often underappreciated. Despite the common assumption that decomposers (i.e., microbes and insects) are primarily responsible for recycling carrion biomass, DeVault et al. (2003) demonstrated that vultures and other vertebrate scavengers usually consume most available carcasses in terrestrial ecosystems. Although vultures are one of the most recognizable types of birds to non-ornithologists, this familiarity is often not accompanied by appreciation of the services they provide. By scavenging, vultures and other carnivorous vertebrates contribute to waste removal, disease regulation, and nutrient cycling (Houston 1979, DeVault et al. 2003).

In addition to vultures, many other bird species scavenge animal carcasses at least occasionally, including raptors, seabirds, gulls, herons, rails, shorebirds, woodpeckers, and passerines (DeVault et al. 2003). Seabirds, in particular, are accomplished scavengers, often feeding on fishery discards (Hill and Wassenberg 1990, 2000; Wassenberg and Hill 1990; Jennings and Kaiser 1998). Among passerines, corvids—especially American Crows (*Corvus brachyrhynchos*) and Common Ravens (*C. corax*)—are the most conspicuous scavengers (DeVault et al. 2003). More research is needed on the ecological consequences of obligate and facultative scavenging, particularly on how these processes are affected by contemporary human activities such as transportation (Dean and Milton 2003, Antworth et al. 2005) and commercial fisheries (Britton and Morton 1994), which make many dead animals and byproducts available for scavengers.

Birds contribute to nutrient cycling in all habitats, but most impressively where aquatic birds nest colonially on islands (Polis and Hurd 1996, Anderson and Polis 1999). Seabirds often nest in dense colonies both in coastal areas and on islands where they process large amounts of food in small areas. In this manner, seabirds transport nutrients from the aquatic zone to the terrestrial zone. Such large inputs of phosphate-rich guano can influence the structure and composition of plant communities (Ellis 2005). Conversely, removal of nesting birds after introduction of a predator fundamentally alters the plant community (Croll et al. 2005, Bellingham et al. 2010).

Birds as ecosystem engineers.—Ecosystem engineering is the one supporting service provided by birds that does not result from foraging but involves construction of nests that are later used by many other organisms. Nests vary greatly in building materials, structure, complexity, size, longevity, and usefulness to other organisms. Examples include excavated cavities or burrows, cup nests, platform nests, mud nests, and domed nests (see Ehrlich et al. 1988). Open-cup and domed nests, the most common nest types (Collias and Collias 1984, Collias 1997), are often taken over by small mammals (Gates and Gates 1975), overwintering spiders (Otzen and Schaefer 1980), and bumble bees (Dame et al. 2002). Many animals, including insects like beetles and social wasps, rodents, lizards, snakes, frogs, and even other bird species, use the domed ground nests of tropical ovenbirds (Furnariidae; Remsen 2003). Woodpecker cavities are used by other birds and by many other animal species, including mammals, amphibians, and arthropods (Conner et al. 1997, Neubig and Smallwood 1999, Monterrubio-Rico and Escalante-Pliego 2006). Nest burrows are excavated by many bird taxa, including penguins, seabirds, alcids, parrots, owls, kingfishers, and passerines. These nests alter soil properties and thus affect nutrient cycling (see above), and, like woodpecker cavities, they are used by many other taxa, including birds, snakes, mammals, and amphibians (Casas-Criville and Valera 2005).

Summary: Indirect services.—Birds are highly mobile, occur globally, fill many ecological roles, and respond rapidly to environmental change. As described in the overview above, bird activities provide links within and between ecosystems and can have large effects on other species. The ecosystem services that birds provide are largely indirect and support or enhance other services. For example, insectivory, pollination, seed dispersal, and nutrient cycling benefit plants that then produce oxygen, food, lumber, medicine, flood and erosion control, aesthetics, recreation, and other benefits for human society. Birds may act as density-dependent consumers that exert strong top-down effects on food webs, which can result in prey population regulation, pest control, and corresponding changes in plant communities. Therefore, in

the context of ecosystem services, population decline among birds may lead to changes that cascade through ecosystems and cause subsequent declines in benefits to humans.

Because the services are usually indirect, neither birds nor their services are generally included in ecosystem-valuation models. Therefore, birds are only indirect beneficiaries of any conservation actions advocated by economic models. This approach implies an indicator-species model of conservation in which a limited subset of species or other environmental indicators are the basis for conservation planning and land-use decisions. Such indirect benefits may be sufficient for bird conservation in some cases, but to date, the indicator-species model has had inconsistent success in predicting abundance and diversity of other species (Roberge et al. 2008, Larsen et al. 2009, Cushman et al. 2010). Data that enable valuation of bird services will improve the models of ecosystem valuation and increase bird-conservation efforts as well as the benefits to humans. At the same time, efforts to establish valuation will promote additional research on many fundamental and important ecological questions.

Quantifying Ecosystem Services

The overall goal of determining the value of ecosystem services can be divided into three components. First is the need to describe and quantify the services themselves at local and regional levels. The goal of describing ecosystem services is largely accomplished (Sekercioglu 2006a, b; Whelan et al. 2008), and we know considerable natural-history details that are relevant to many ecosystem services. But we need more detail at local levels from a variety of sites to make global comparisons; in this way we can minimize the problems associated with "benefit transfer" (i.e., assuming that value estimates from one site are equivalent to those at a similar habitat elsewhere; Farber et al. 2006, Plummer 2009, Eigenbrod et al. 2010). Data from multiple sites will also allow an assessment of the extent and sources of variation in ecosystem services. Understanding the variation in services among sites will lead to more robust estimates of the value of ecosystem services and more effective conservation plans.

Second, we need methods to quantify the direct or indirect values of ecosystem services provided, and to test these methods with case studies. Finally, we need to combine the information from multiple ecosystem services to form a metric or model of values to assess how ecosystem services can be maximized under different land-use scenarios or policy changes. We need this type of modeling approach because a given service (e.g., seed dispersal) will not be protected successfully by itself, but rather as part of a comprehensive conservation strategy. Several models incorporating some ecological input have been developed (Daily and Matson 2008, Ranganathan et al. 2008, Daily et al. 2009, Nelson et al. 2009).

Most of the supporting and regulating ecosystem services are not traded in traditional markets, and in that sense they are public goods with approximately the same cost (usually "free") and value to all users. However, the value of some public ecosystem services or resources may decline with level of use. For example, intensive birdwatching at a given site may disturb the birds to the point that they leave or alter their behavior, thus rendering the resource unavailable or less worthwhile for additional viewers (Blumstein et al. 2005). As public goods, ecosystem services are susceptible to "externalities," such as uncompensated side effects from other users of a common resource. For example, extensive habitat modification by one landowner may negatively affect pollination or pest control for an adjacent landowner. An additional complication is that the economic value in environmental markets that are driven by regulations (e.g., those mandated by the Clean Water Act and Endangered Species Act) is not determined by production functions or the value to the end users, as in traditional markets. Instead, regulators set the value. For all of these reasons, market failure (i.e., the failure of market value to reflect full social cost), is more often the rule than the exception for ecosystem services. These problems raise fundamental concerns about the ability of neoclassical economic theory to adequately address environmental issues (Hall et al. 2000, Lux 2003, Nadeau 2010), and in that sense ecosystem valuation is a step toward bridging the divide between economics and natural sciences.

A variety of methods have been used in valuation of ecosystem services (Farber et al. 2002, 2006). Here, we briefly review the methods that are useful for quantifying services provided by birds. All of these methods are conventional in that the output is an economic value and therefore represents the "marginal value" people are willing to pay for an item or service. Non-monetary valuation methods such as ranking or stakeholder analysis have promise for community-level decisions, but they have not yet been applied to the services discussed here.

The value of birds in pest control can be estimated as the costs avoided by using birds instead of pesticides. These valuations have been determined for bats (Cleveland et al. 2006) and insects (Losey and Vaughan 2006). Data necessary for this estimate include first the monetary loss (e.g., reduced crop yields) from herbivory under current conditions, and then, based on diet and natural history of both insects and insectivores, an estimate of the additional loss that would occur with no birds present. Assuming that pesticides could accomplish the pest-control function of birds and would yield the same crop levels in the absence of birds, the cost of that amount of pesticides is the avoided cost and an estimate of the value of avian pest control. Note that this method works well for agricultural crops or timber species for which we have both market values and natural-history data (e.g., Takekawa and Garton 1984), but not for most wild plants (e.g., Sharam et al. 2009). Also note that this is short-term costing, assuming no evolutionary responses of the pests to the pesticides, whereas experience has shown that pests rapidly evolve resistance to pesticides (Gassmann et al. 2009, Bourguet et al. 2010) but have not yet managed to do so to birds because birds also evolve.

An alternative, but one that still requires some estimate of the market value of an end product, is production valuation in which value is assigned on the basis of the economic outcome that results from changes in services. For example, the value of scatter-hoarding of seeds by corvids could be based on the reforestation value of the species they disperse (see case study below). Similarly, replacement costs reflect the value of replacing or recreating a missing ecosystem service. The Biosphere 2 experiment, which created an artificial habitable system and cost ~$9 million per human inhabitant per year, took this to an extreme (Avise 1994).

Finally, through surveys or polls, preference-based approaches can yield contingent values that are essentially the

willingness to pay for an ecosystem service (Bowker and Stoll 1988). Contingent values, along with travel and equipment costs, are used to estimate the economic impact of tourism and other recreational uses. For example, birdwatchers in the United States spend more than $30 billion annually for travel and equipment (LaRouche 2003, Carver 2009) and would be willing to spend $35 to $134 per day for birdwatching opportunities (LaRouche 2003).

Case Studies

Coffee pest control in Jamaica.—Shade-coffee farms can be high-quality habitats for insectivorous birds, especially migratory generalist species that do not rely on intact understory vegetation (Tejeda-Cruz and Sutherland 2004, Johnson et al. 2006). Bird foraging within farms is concentrated in the shade trees that grow over the coffee shrubs (Wunderle and Latta 2000). The coffee shrubs are naturally chemically defended and comparatively poor in insect abundance (Lepelley 1973, Greenberg et al. 2000). Nonetheless, many birds also forage, to some degree, on insects on the coffee shrubs (Wunderle and Latta 2000). Bird exclosure experiments have confirmed that bird foraging reduces overall insect biomass on coffee shrubs in Guatemala (Greenberg et al. 2000), Mexico (Philpott et al. 2004), Panama (Van Bael et al. 2008), Puerto Rico (Borkhataria et al. 2006), and Jamaica (Johnson et al. 2009). The Coffee Berry Borer (*Hypothenemus hampei*) is the world's most damaging insect pest of coffee (Damon 2000). Recent experiments in Jamaica indicate that birds reduce pest populations, increase saleable fruit, and boost farm income (Kellermann et al. 2008, Johnson et al. 2010). Calculations of the benefits provided were obtained by documenting pest infestation levels in the presence and absence of bird foraging (via exclosures) and translating higher saleable crop yields in the presence of birds into a dollar figure using crop market prices. Birds boosted farm income by $75 ha^{-1} $year^{-1}$ on high-elevation farms (Kellermann et al. 2008) and by $310 ha^{-1} $year^{-1}$ on a mid-elevation farm (Johnson et al. 2010; here and below, figures are in U.S. dollars).

As agents of ecosystem services, birds are notably mobile and capable of utilizing multiple habitats. Therefore, the delivery of ecosystem services by birds in some cases may depend strongly on habitat configuration and landscape composition. To harness economic forces for conservation of birds and their habitats in agricultural landscapes, ornithologists must not only document the economic value of the ecosystem services provided by birds, but also clarify bird movements and relationships among agricultural lands and surrounding natural habitats. Several models are available for projecting ecosystem services over a changing landscape, such as InVEST (Daily et al. 2009) and individual-based models (Grimm and Railsback 2005). Ongoing radiotelemetry studies have shown that an important coffee pest predator, the Black-throated Blue Warbler (*Dendroica caerulescens*), commutes from diurnal foraging territories within coffee habitat to nocturnal roosting sites within natural forests (Jirinec et al. 2011) and establishes foraging territories close to farm edges and patches of uncultivated vegetation within farms (B. R. Campos and M. D. Johnson unpubl. data). These results establish links between the provisioning of an economically valuable ecosystem service and natural vegetation both within and outside coffee farms. By linking bird movements to maps of landscapes and estimates of pest-control services, a spatially explicit individual-based model can simulate how changes in landscape composition can affect the delivery of pest-control services (M. D. Johnson and S. F. Railsback unpubl. data). This approach could be used by conservation planners to estimate the economic value of forested habitats within agricultural landscapes, and to provide economic estimates of ecosystem services under proposed land-use scenarios.

Swedish oaks.—The replacement costs for the seed-dispersal services of Eurasian Jays (*Garrulus glandarius*) in Stockholm National Urban Park were estimated by Hougner et al. (2006). The National Urban Park of Stockholm features one of the largest oak forests in Sweden. The Swedes recognize oaks as keystone species that support unique communities of insects, lichens, mosses, and fungi, as well as nesting birds and bats (Hougner et al. 2006). In the National Urban Park of Stockholm, many of the oaks (*Quercus robur* and *Q. petrea*) are more than 500 years old. Nearly 85% of the oaks in the park most likely result from acorn dispersal, primarily by Eurasian Jays. Given that an epidemic of lethal oak disease is spreading across Europe and that most of the oaks in the park are currently healthy, Hougner et al. (2006) argued that the natural seed-dispersal services of the jays will be especially important for maintaining healthy forests through natural local seed-dispersal over time. The authors calculated the replacement value of one pair of territorial jays, using two approaches: the cost of manually planting acorns and the cost of planting sapling oaks. They used data from several references to quantify acorn dispersal by Eurasian Jays and the number of sapling oaks that arise from jay dispersal each year, estimating germination and survival rates. Having computed the costs of manual reforestation, the authors concluded that the minimum replacement value of a pair of Eurasian Jays was about $4,035 (conversion from SEK, based on 2005 values) if acorns are seeded, and about $22,560 if saplings are planted. Given the area occupied by oak forest in the Park, these jays represent a value of $2,115 to $9,450 per ha for forest regeneration.

Nutcrackers and pines.—A similar example is the economic value of scatter-hoarding (caching) seeds of Whitebark Pine (*Pinus albicaulis*) by Clark's Nutcrackers (Corvidae: *Nucifraga columbiana*). The cones of Whitebark Pine do not open, so this conifer obligately depends on nutcrackers for dispersal (Tomback 1978, 2001; Hutchins and Lanner 1982). Pine squirrels (*Tamiasciurus* spp.) are important conifer-seed predators and compete with nutcrackers for Whitebark Pine seeds, but they contribute little or no seed dispersal (Siepielski and Benkman 2008, McKinney et al. 2009). *Cronartium ribicola*, an invasive fungal pathogen that causes white pine blister rust, and regional outbreaks of native pine beetles have produced precipitous declines in Whitebark Pine nearly rangewide; this pine is currently being evaluated for federal listing as a threatened or endangered species (Tomback and Achuff 2010). The U.S. Forest Service has undertaken restoration programs that involve the planting of putative pathogen-resistant seedlings, grown from seeds harvested from screened parent trees (e.g., Schwandt et al. 2010, Tomback and Achuff 2010). The cost of these restoration efforts essentially represents the valuation of natural seed-dispersal activities throughout the range of the pine.

On the basis of figures obtained from two U.S. national forests, D. F. Tomback (unpubl. data) calculated the costs of planting upper subalpine terrain with a typical density of Whitebark Pine

seedlings (440 ha^{-1}). Ironically, a large part of the cost of obtaining seeds requires that trees be climbed and cones caged in early summer to prevent nutcrackers from depleting the seeds and squirrels from cutting down cones, and then climbed again in September to harvest the cones. These costs were reduced by assuming that adequate numbers of seeds for a 1-ha planting could be harvested from only one tree, although restoration efforts would actually require more genetic diversity. Other expenses, such as materials, travel, and the cost of protecting trees each year from pine beetles were excluded, whereas the costs of growing seedlings, planting seedlings, and administrative oversight were included.

Replacing nutcracker seed-dispersal services costs the U.S. Forest Service a minimum of $2,190 ha^{-1} in two national forests. Whereas this seedling planting could be accomplished within one field season, D. F. Tomback (unpubl. data) used a study of postfire regeneration after the 1988 Yellowstone fires to estimate the average number of new seedlings per year that germinated per hectare from natural seed caches (Tomback et al. 2001). She concluded that it would take a minimum of 5 to 6 years in the Yellowstone area for nutcrackers to produce 440 Whitebark Pine seedlings per hectare. Although this is slower, spreading regeneration over several years may yield benefits by spreading risks over time (e.g., reducing risks of failure in a dry season, higher genetic diversity by including parents seeding in different years). However, given that the nutcrackers would spread both pathogen-resistant and susceptible genotypes, establishing 440 healthy trees per hectare under current conditions by way of nutcrackers would take additional time.

Vulture decline in South Asia.—The consequences of the recent catastrophic decline of vultures (three *Gyps* spp.) in South Asia because of toxic livestock chemicals vividly demonstrate the vital role that vultures play in ecosystems (Pain et al. 2003, Green et al. 2004, Oaks et al. 2004). In the near absence of vultures, cattle carcasses remained on the landscape for longer periods and were available to other scavengers. As a result, populations of feral dogs and other human-commensal facultative scavengers increased, and diseases spread to humans and domestic livestock. Markandya et al. (2008) estimated that human health costs attributable to population crashes of vultures in India totaled $34 billion over the years 1993–2006. Additional cultural costs to the Parsi sects, which rely on vultures for corpse cleansing, totaled $1.6 million (Markandya et al. 2008).

RESEARCH NEEDS

The overview of selected ecosystem services and case studies discussed above point to some very specific research needs that are outlined below. More generally, we lack basic information on all the ways that birds could contribute to ecosystem services that ultimately benefit humans. Although we know in general the types of ecosystem services that birds provide, we often lack sufficient details of bird behavior and ecology to formulate models of ecosystem valuation in a broader framework relevant to human well-being.

In addition to the more specific research subjects noted below, a topic that has received relatively little attention in the ecosystem-services literature is the economic costs of some bird activity. For example, some birds may be crop pests (Elliott and Lenton 1989, Dolbeer 1990, Basili and Temple 1999), disperse weed seeds (Williams 2006), damage property or livestock (Lowney 1999, Harding et al. 2007), or generate noise and droppings in residential areas (Gorenzel and Salmon 1995). Some research regarding birds as agricultural pests has shown that perceived damage can be greater than actual damage (Basili and Temple 1999) or that the damage can be minimized with appropriate management (Dolbeer 1990). Crop pests also have beneficial effects, such as insectivory (Dolbeer 1990), and research on potential pest species needs to examine all the ecological roles that a bird fills in order to evaluate the economic costs and benefits. Although a few bird species cause economic damage, at the ecosystem level the services provided by birds are overwhelmingly positive (Sekercioglu 2006a, Whelan et al. 2008). More generally, payments for ecosystem services (PES) are receiving increased attention in natural-resource management practice and theory (e.g., Pagiola 2008, Farley and Costanza 2010, Sommerville et al. 2010), and the recognition of ecosystem disservices (McCauley 2006) is also becoming more formalized (Lyytimaki et al. 2008, Dunn 2010, Power 2010). Very little of that work, however, has been focused on organismal delivery of services and costs (but see Nelson 2009), and it is important for ornithologists to contribute to this line of research in the future.

Pest control.—The key aspect of pest control in need of further study is the extent to which trophic cascades have measurable economic benefits in terms of increased plant growth or agricultural production. We know that top-down effects of bird foraging are widespread, but most studies are still restricted to two trophic levels: birds and their prey. More experiments involving all three trophic levels (e.g., Marquis and Whelan 1994, Mols and Visser 2002, Johnson et al. 2010) are needed, especially in agroecosystems. Similarly, Fayt et al. (2005) concluded that woodpeckers can regulate populations of insect pests of northern temperate conifer forests, but no studies have explicitly examined the economic benefits to the timber industry of this interaction. Research examining the consequences of bird consumption of pests (arthropod or rodent) for either crop yield or plant demographics would be extremely useful if conducted within multiple agricultural ecosystems to determine generality and variability. This is a prime example of an area of research where repetition aimed at establishing the generality of research, rather than aimed at "being first" or "novel," needs to be encouraged by funding agencies. Another aspect of pest control that avian ecologists (and funding agencies) should be poised to exploit is centered on unfortunate natural "experiments" like avian population declines in eastern North America from West Nile virus (LaDeau et al. 2007). Research on potential consequences (e.g., increases in human diseases carried by insects) of those population declines on ecosystem function and provision of ecosystem services would be very useful and instructive.

Other useful avenues for research involve determining the feasibility and effectiveness of habitat manipulations that boost either populations of key avian pest consumers (e.g., deploying nest boxes) or their effectiveness as pest consumers (e.g., providing perches for foraging). These sorts of manipulations should be a standard component of any integrated pest management (IPM) plan. Additionally, we need cost–benefit analyses of the effectiveness of such manipulations, at least in agroecosystems, and cost–benefit comparisons of bird control versus chemical control mechanisms with large externalities (i.e., pesticides). Moreover, studies that examine the effectiveness of such manipulations must incorporate

effects from the framework of "landscapes of fear" (Laundré et al. 2001). For example, perches may alter the behavior of small rodents through their increased fear, thus restricting their foraging, even if rodent population size does not decline markedly.

A few studies have suggested that avian granivores exert weed control, but these studies need to examine the effects on an agricultural crop or other plants. Exclosure experiments are needed to carefully document birds' seed consumption in a variety of contexts, from natural communities to agroecosystems to restoration projects. In areas where birds are considered pests (e.g., Basili and Temple 1999), careful documentation of trophic function would be useful—birds may, for example, consume seeds of crops, but may compensate via consumption of pest insects.

Dispersal and pollination.—The key remaining questions about dispersal and pollination are largely very hard to answer. We need more information on the mechanisms (preferably from manipulative experiments) over the whole life cycle of the plants. Unresolved topics include (1) how various factors, including frugivores (birds and mammals), seed predators, pathogens, habitat fragmentation, and plant competitors, interact to determine plant reproductive success; (2) how widespread density- and distance-dependent seed and seedling mortality effects are (so-called Janzen-Connell effects), both in the tropics and in the temperate zone (Packer and Clay 2000), because these greatly increase dependence on dispersers; (3) the level of change in dispersal services and its impacts at the plant community level following hunting, habitat fragmentation, disturbance such as fire, or other anthropogenic change; (4) the extent of seed limitation, which determines whether pollination limitation matters (Kelly et al. 2007); and (5) more studies to determine whether the unexpected importance of bird pollination to plants with flowers that are apparently suited to insect pollination in temperate New Zealand (Kelly et al. 2010) applies in other areas.

Birds disperse seeds of native and non-native plant species and in some areas play a role in the spread of invasive plants (Sallabanks 1992, Vila and Dantonio 1998, Renne et al. 2002, Cordeiro et al. 2004, Gosper et al. 2005, Bartuszevige and Gorchov 2006, Milton et al. 2007, Underhill and Hofmeyr 2007). Such dispersal is not necessarily detrimental—the non-native plant species themselves may provide ecosystem services, such as erosion control or aesthetics. The question becomes whether the benefits of seed dispersal outweigh their detrimental effects. The situation is complicated further when non-native plants are dispersed by non-native birds such as European Starlings (*Sturnus vulgaris*) in North America and European Blackbirds (*Turdus merula*) in New Zealand (Williams 2006). More work is needed on dispersal of non-native plant species in an ecosystem-services framework. As with other ecological processes, if we understand the specifics we will be better able to develop realistic valuation models.

Scavengers.—Unfortunately, the value provided by ecosystem services is most apparent after their loss. The catastrophic ecological and human-health ramifications created by the recent collapse of vulture populations in India (Markandya et al. 2008) have revealed the importance of ecosystem services provided by carrion-feeding birds. It is clear that in some areas proper ecosystem function is dependent, in part, on scavenging birds. Even so, the cycling of carrion biomass, whether by scavenging or decomposition, is a complex process governed by an intense competition for carcasses among vertebrates, insects, fungi, and microbes (DeVault et al. 2003, 2004; Selva et al. 2005; Selva and Fortuna 2007; Parmenter and MacMahon 2009). Habitat type, climate, carcass type, composition of the vertebrate community, and other biotic and abiotic factors all influence competition for carrion (DeVault et al. 2003). In some situations, the competitive balance for carrion is shifted naturally away from birds, toward insects and microbes (e.g., DeVault et al. 2004) or facultative mammalian scavengers (e.g., Putman 1983). Future research aimed at identifying the conditions under which various taxa consume carrion would be beneficial. Such work would help elucidate vital links between ecosystem health and the population status of various vertebrates, such as the vulture–cattle carrion system in India. Future investigations into the scavenging ecology of birds would also improve our understanding of disease ecology (Jennelle et al. 2009), nutrient transport across ecosystem types (Polis et al. 2004), and the distribution of predators and their prey (Cortes-Avizanda et al. 2009a, b).

CONCLUSIONS

Birds provide many ecosystem services, which by and large are invisible and underappreciated. Several sudden losses of such services (e.g., carrion scavenging in India, pest control in China when sparrows were locally exterminated, forest plant pollination in New Zealand) provide a sense of the negative consequences should such services be lost. We suggest that ecosystem services be better studied and valued properly to ensure that humans continue to receive the benefits, and that birds continue to provide them. The case studies presented here show promising lines of research, but much work remains to be done. Despite the huge role of birds as insectivores, very little research has been done on insectivory in an ecosystem-services context (pest control), and most of what has been done is on pest control in coffee plantations. Similarly, the ecosystem service of seed dispersal has been quantified only for seed-caching corvids. Dispersal of woody plants by terrestrial frugivores and dispersal of aquatic plants by waterfowl have not been addressed. We are not aware of any ecosystem-services valuation research on the role of birds in nutrient cycling or as ecosystem engineers. Further research to better understand the economic value of birds will enable better policy and restoration practices, promote and justify bird conservation efforts, and ultimately demonstrate the vital connections among human well-being, intact ecosystems, and the preservation of avian biodiversity.

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