

Ecological Significance of Bird Populations

People worldwide are rapidly degrading ecosystems, especially in the tropics, leading to a massive reduction in biodiversity (Laurance & Bierregaard 1997; Vitousek *et al.* 1997; Pimm & Raven 2000; Dirzo & Raven 2003). This is best-documented in the extinctions and population declines of hundreds of bird species (Bennett & Owens 1997; Anon. 2006b, 2004d; Sekercioglu *et al.* 2004). The accelerating extinctions of species (Anon. 2006c) comprise the tip of the iceberg of global wildlife declines (Hughes *et al.* 1997; Jackson *et al.* 2001; Ceballos & Ehrlich 2002; Gaston *et al.* 2003) that threaten to disrupt vital ecosystem processes and services (Redford 1992). Ecologically, declines and extinctions of distinct populations are as important as the losses of species (Chapin *et al.* 1998). Reductions in the numbers of individuals in important functional groups are likely to extensively diminish ecosystem processes and services (Figure 1) such as decomposition, pest control, pollination, and seed dispersal (Redford 1992; N. Myers 1996; Daily 1997). Besides the outright loss of ecological actors, changes in the proportions of species in various functional groups may result in the disassembly of ecological communities (Gonzalez & Chaneton 2002).

Currently, 21.5% of bird species are considered “extinction-prone” (Figure 2), a category that includes species that are extinct (1.4%), threatened (12.1%) or near threatened (8.0%) with extinction (Anon. 2006c). Birds are integral to many ecosystem processes, even soil formation (Heine & Speir 1989), and many species provide key ecosystem services, such as pollination and seed dispersal (Table 1). Ongoing reductions in bird abundance (Gaston *et al.* 2003) and species richness (Anon. 2004d) are likely to have far-reaching ecological consequences (Sekercioglu *et al.* 2004), with diverse societal impacts ranging from the spread of disease and loss of agricultural pest control to plant extinctions and trophic cascades. Rapid losses of bird species (Figure 3) may cause substantial reductions in certain ecosystem processes before we have time to study and understand the underlying mechanisms. Fortunately, birds are the best known class of organisms (Anon. 2004d), and their conservation status has been assessed multiple times (Anon. 2006c). Various studies on frugivorous, nectarivorous, and insectivorous birds have established their significance in the dynamics of diverse natural and human-dominated ecosystems (Stiles 1978, 1985; Proctor *et al.* 1996; Westcott & Graham 2000; Mols & Visser 2002; Croll *et al.* 2005). Although field studies on birds’ ecological effects have been mostly non-experimental and focused on a small subset of species (Feinsinger *et al.* 1982; Robertson *et al.* 1999; Rathcke 2000; Bleher & Bohning-Gaese 2001; Loiselle & Blake 2002), research on birds’ ecological functions and services is growing and becoming more experimental (Abramsky *et al.* 2002; Mols & Visser 2002; Croll *et al.* 2005). Although precise understanding of the ecological consequences of bird population losses will be impossible to achieve, there is a pressing need to assess avian ecosystem services and estimate the potential ecological effects of differential extinctions in various functional groups.

Given birds’ ecological significance and the extensive literature on avian ecology and conservation, the time is ripe for a synthesis of the avian contributions to ecosystems. Part of my objective here is to draw attention to the ecological and societal implications of bird declines and extinctions. The factors that make bird species susceptible to extinction have been superbly reviewed by Collar (1997) in the pages of HBW, so I will only address the consequences of avian declines rather than examine the causes of avian extinctions. The inspiration for this review has come from our study on the ecosystem consequences of bird declines (Sekercioglu *et al.* 2004), based on an analysis of a database encompassing the conservation status, distribution, and basic ecology of all extant and historically extinct bird species. The creation of the database itself was inspired by the detailed species accounts in the *Handbook of the Birds of the World*. It is my pleasure and honor to complete this circle.

Functional group	Ecological process	Ecosystem service and economical benefits	Negative consequences of loss of functional group
Frugivores	Seed dispersal (Snow 1981; Howe & Smallwood 1982; Stiles 1985; Howe & Miriti 2000, 2004)	Removal of seeds from the parent tree (Greenberg <i>et al.</i> 1995; Ávila <i>et al.</i> 1996; Sun <i>et al.</i> 1997; Wenny & Levey 1998); escape from herbivores and seed predators (Janzen 1970; Connell 1971; Howe 1993a); improved germination (Murphy <i>et al.</i> 1993; Meyer & Witmer 1998); increased economical yield (Hammond <i>et al.</i> 1996; Hutchins <i>et al.</i> 1996; Narang <i>et al.</i> 2000; Yumoto 2000); increased gene flow (Howe <i>et al.</i> 1985; Hamrick <i>et al.</i> 1993; Gibson & Wheelwright 1995); recolonization and restoration of disturbed ecosystems (Robinson & Handel 1993; Tucker & Murphy 1997; Wilkinson 1997; Galindo-González <i>et al.</i> 2000; Hjerpe <i>et al.</i> 2001)	Disruption of dispersal mutualisms (Stocker & Irvine 1983; Clark <i>et al.</i> 2001; Meehan <i>et al.</i> 2002); reduced seed removal (Cordeiro & Howe 2003); clumping of seeds under parent tree (Bleher & Bohning-Gaese 2001); increased seed predation (Howe 1993a); reduced recruitment (Cordeiro & Howe 2001, 2003); reduced gene flow (Shapcott 1999; Pacheco & Simonetti 2000) and germination (Compton <i>et al.</i> 1996; Peres & van Roosmalen 1996; Meyer & Witmer 1998); reduction (Santos & Tellería 1994; Santos <i>et al.</i> 1999) or extinction (Bond 1994; Hamann & Curio 1999; Loiselle & Blake 1999; da Silva & Tabarelli 2000) of dependent species
Nectarivores	Pollination (Stiles 1978, 1985; Proctor <i>et al.</i> 1996)	Outbreeding of dependent (Keighery 1980; Ford 1985; Proctor <i>et al.</i> 1996) and/or economically important species (Nabhan & Buchmann 1997; Narang <i>et al.</i> 2000)	Pollinator limitation (Nabhan & Buchmann 1997; Murphy & Kelly 2001); inbreeding and reduced fruit yield (Feinsinger <i>et al.</i> 1982; Robertson <i>et al.</i> 1999; Cox & Elmqvist 2000; Paton 2000; Rathcke 2000; Montgomery <i>et al.</i> 2001); evolutionary consequences (Stiles 1978; Thompson 1996; Nabhan & Buchmann 1997); extinction (Bond 1994; Sakai <i>et al.</i> 2002)
Insectivores	Predation on invertebrates (Mols & Visser 2002)	Control of insect populations (Crawford & Jennings 1989; Marquis & Whelan 1994; Kirk <i>et al.</i> 1996; Greenberg <i>et al.</i> 2000; Jantti <i>et al.</i> 2001; Mols & Visser 2002; Van Bael <i>et al.</i> 2003); reduced plant damage (Sipura 1999; Greenberg <i>et al.</i> 2000; Sanz 2001); alternative to pesticides (Dolbeer 1990; Naylor & Ehrlich 1997; Mourato <i>et al.</i> 2000)	Loss of natural pest control (Dolbeer 1990; Naylor & Ehrlich 1997); insect pest outbreaks (Crawford & Jennings 1989; Kirk <i>et al.</i> 1996; Quammen 1997); crop losses (Greenberg <i>et al.</i> 2000); trophic cascades (Terborgh <i>et al.</i> 2001)
Raptors	Predation on vertebrates (Parrish <i>et al.</i> 2001; Brown & Kotler 2004)	Regulation of rodent populations (Korpimäki & Norrdahl 1991; Ims & Andreassen 2000); secondary dispersal (Nogales <i>et al.</i> 2002)	Rodent pest outbreaks (Korpimäki & Norrdahl 1998); trophic cascades (Crooks & Soule 1999; Terborgh <i>et al.</i> 2001; Dunne <i>et al.</i> 2002); indirect effects (Sih <i>et al.</i> 1985; Parrish <i>et al.</i> 2001)
Scavengers	Consumption of carrion (Houston 1994)	Removal of carcasses (Pain <i>et al.</i> 2003; Prakash <i>et al.</i> 2003); leading other scavengers to carcasses (Houston 1994); nutrient recycling; sanitation (Pain <i>et al.</i> 2003; Prakash <i>et al.</i> 2003)	Slower decomposition (Houston 1994); increases in carcasses (Pain <i>et al.</i> 2003; Prakash <i>et al.</i> 2003); increases in undesirable species (Pain <i>et al.</i> 2003; Prakash <i>et al.</i> 2003); disease outbreaks (Pain <i>et al.</i> 2003; Prakash <i>et al.</i> 2003); changes in cultural practices (Parry-Jones 2001; Pain <i>et al.</i> 2003)
Piscivores	Predation on fishes and invertebrates Production of guano (Croll <i>et al.</i> 2005)	Controlling unwanted species (Wootton 1995); nutrient deposition around rookeries (Powell <i>et al.</i> 1991; Anderson & Polis 1999; Hawke <i>et al.</i> 1999; Palomo <i>et al.</i> 1999; Sánchez-Piñero & Polis 2000; Croll <i>et al.</i> 2005); soil formation in polar environments (Heine & Speir 1989); indicators of fish stocks (Crawford & Shelton 1978); environmental monitors (Gilbertson <i>et al.</i> 1987)	Loss of guano and associated nutrients (Oliver & Legovic 1988; Croll <i>et al.</i> 2005); impoverishment of plant communities (Oliver & Schoenberg 1989; Croll <i>et al.</i> 2005); trophic cascades (Wootton 1995; Williams <i>et al.</i> 2002; Croll <i>et al.</i> 2005); ecosystem shifts (Croll <i>et al.</i> 2005); loss of socio-economic resources (Haynes-Sutton 1987) and environmental monitors (Gilbertson <i>et al.</i> 1987);
All species	Miscellaneous	Environmental monitoring (Eriksson 1987; Bryce <i>et al.</i> 2002); ecosystem engineering (Sekercioglu 2006); indirect effects (Izhaki & Safriel 1989; Dean <i>et al.</i> 1990; Loiselle 1990; Paine <i>et al.</i> 1990; Wootton 1994a; Milton <i>et al.</i> 1998; Murakami & Nakano 2002; Nogales <i>et al.</i> 2002); birdwatching tourism (Jacquemot & Filion 1987; Sekercioglu 2002c; Bouton & Frederick 2003); reduction of agricultural residue (Bird <i>et al.</i> 2000); cultural and economic uses (Diamond 1987b)	Losses of socio-economic resources (Filion 1987; Sekercioglu 2002c) and environmental monitors (Peakall & Boyd 1987); unpredictable consequences (Wootton 1994a)

Table 1 Ecological and economical contributions of avian functional groups. Modified from Sekercioglu, C.H., Daily, G.C. & Ehrlich, P.R. (2004). Ecosystem consequences of bird declines. Proc. Natl. Acad. Sci. U. S. A. **101**: 18042-18047. Copyright (2004) National Academy of Sciences, USA.

Conceptual Issues

Diversity and ecosystem function

The role of biodiversity in ecosystem function is a current and active field of inquiry (Chapin *et al.* 2000; Loreau *et al.* 2001; Tilman *et al.* 2001; Hooper *et al.* 2005; France & Duffy 2006). Since it is usually difficult to isolate and quantify the significance of any one factor, there is ongoing disagreement over the relative contributions of biomass (Schwartz *et al.* 2000), diversity (Chapin *et al.* 1997), dominance (Smith *et al.* 2004),

functional richness (Naeem & Wright 2003), and keystone species (Power *et al.* 1996). Nevertheless, we are becoming increasingly aware of the importance of each, and the diversity and spatio-temporal variability of natural systems mean that any of these elements can be significant in different contexts (Ives & Cardinale 2004). Although it makes intuitive sense that the species that dominate in number and/or biomass are more likely to be important for ecosystem function (Raffaelli 2004; Smith *et al.* 2004), in some cases even rare species can have a role, for example, in increasing invasion resistance (Lyons & Schwartz 2001). In tropical communities there are many rare and specialized bird species (Terborgh 1974), the removal of which may increase invasibility to generalist taxa and have unpredictable impacts that may further damage already impoverished communities.

In contrast to dominant species, by definition a keystone species is one that has an ecosystem impact that is disproportionately large in relation to its abundance (Power *et al.* 1996; Hooper *et al.* 2005). Many large frugivores (Stocker & Irvine 1983) and top predators (Terborgh *et al.* 2001) can be considered keystones. There is a growing literature on keystone species (Davic 2003), but identifying keystone species in advance has been difficult (Power *et al.* 1996). Species that are not thought as “typical” keystones can turn out to be so, even in more ways than one (Daily *et al.* 1993). It is hard to predict the importance and “replaceability” of individual species without detailed studies, but since we are increasingly faced with the ecosystem consequences of accelerating biodiversity loss (Redford 1992), an improved ability to predict and protect keystones may help alleviate some of these consequences.

An indisputable role of species richness comes in the guise of the “sampling effect” (Wardle 1999), i.e. the more species that are present in a community, the higher the probability of having a species that will have a significant ecological impact. This is particularly important when there is a major perturbation to the system. With more species present, there is a higher probability of a formerly “insignificant” species being able to respond to this disturbance and maintain ecosystem function (Ives & Cardinale 2004), thereby increasing “resilience” (Elmqvist *et al.* 2003). The “insurance hypothesis” is an analogous way to think about this phenomenon (Yachi & Loreau 1999). Yachi & Loreau (1999) showed that in a fluctuating environment, species richness can insure against a decline in ecosystem functioning by both buffering (reducing the temporal variance of productivity) and by enhancing ecosystem performance (increasing the mean of productivity). Even though in many communities only a few species have strong effects, the weak effects of many species can add up to a substantial stabilizing effect and “weak” effects over broad scales can be strong at the local level (Berlow 1999). In other studies, communities with higher species richness of functional groups had reduced probabilities of cascading extinctions following the removal of a species (Borrvall *et al.* 2000). Such communities also retained higher portions of species following extinction events (Ebenman *et al.* 2004). Thus, increased species richness can insure against sudden change, which is now a global phenomenon (Parmesan & Yohe 2003; Root *et al.* 2003).



Equivalence (a.k.a. redundancy)

Declines in bird species that are important for a particular ecosystem process/service may not necessarily mean a decline in that process/service if the populations of other functionally equivalent species increase in response (May 1974; Walker 1992). Compensatory growth (May 1974) may ensure that an ecosystem function will not suffer drastically from the extinctions of species, as long as one or few dominant species fulfilling that function do not go extinct. However, assuming that most species are superfluous is risky (Ehrlich & Ehrlich 1981; Ehrlich & Walker 1998). Even though a few species may make up most of the biomass of most functional groups (Walker *et al.* 1999), this does not mean that other species are unnecessary. Species may act like the rivets in an airplane wing, the loss of each unnoticed until a catastrophic threshold is passed (Ehrlich & Ehrlich 1981). After all, the very fact that these different species exist suggests that they are more adapted to different conditions than the dominant species (Ghilarov 2000). Indeed, an important contribution of biodiversity to ecosystem resilience is by increasing the efficiency of resource use (Chapin *et al.* 1997). Hutchinson (1957) formalized this concept by envisioning that each species’ niche occupies a hyper-volume that is unique, which means that no other species’ function can be exactly equivalent.

Empirical research has also shown that many bird species, such as Southern Cassowary (*Casuaris casuaris*) (Stocker & Irvine 1983) or Three-wattled Bellbird (*Procnias tricarunculata*) (Wenny & Levey 1998), have irreplaceable roles in ecosystems. Even generalist species may not be replaceable (Cordeiro & Howe 2003). The fact that large and highly specialized species are more likely to go extinct (Anon. 2004d;

Sekercioglu *et al.* 2004) reduces the probability of other bird species taking the place of, for example, specialized seed dispersers threatened with extinction, such as cassowaries, bellbirds, or turacos (Sun *et al.* 1997). Besides the decrease in the numbers of individual birds (Gaston *et al.* 2003), a quarter of all European (Heath *et al.* 2000) and North American (Sauer *et al.* 2003) bird species have significantly declined in the past three decades and, globally, 78% of threatened bird species have continuously diminishing populations. Such widespread declines mean that the losses of sensitive species are not, overall, being compensated by increases in other bird species.

Due to the differing niches of related species, if a species goes extinct, the presence of more species in a functional group increases the probability that another species will adapt to the new conditions. This may compensate for the loss of a species, and ensure the continuity of the ecological process (Walker 1995; Wellnitz & Poff 2001). Given the lack of information and the reality of rapid ecological change around the world, our focus should be on preserving as many species as possible to increase ecosystem reliability (Naeem & Li 1997) and to insure ecosystems against the deleterious effects of rapid global change (Ehrlich & Walker 1998). Unfortunately, many ecological studies necessarily focus on one section of an environmental gradient and often treat environmental variation as “noise” rather than as an integral feature of ecosystems (Wellnitz & Poff 2001). However, environmental variation is critical to understanding species’ equivalence since functional equivalence is context-dependent and the functional role of a species may change significantly with changing environmental conditions (Wellnitz & Poff 2001). In addition to the significance of context-dependency in species’ equivalence, the difficulty of gathering enough information about most species makes it impractical, if not impossible, for ecologists to be able to measure the equivalence of species with confidence (Ives & Cardinale 2004). Therefore, we are unlikely to accurately predict the consequences of the removal of a species from an ecosystem.

Avian transport of plant genetic material provides a good case study of equivalence. Plants often seem to compensate for high risk in one aspect of reproductive mutualism by reducing risk in another (Bond 1994). For example, a plant species with high pollinator or disperser specificity may make up for this risk by not being highly dependent on pollination, dispersal, or even seeds. Particularly in temperate ecosystems, unstable weather conditions seem to have resulted in various compensatory mechanisms, likely to make up for the reduced activity of mutualists under unfavorable conditions. On the other hand, a plant’s dependence on mutualisms with animals increases with decreasing seasonality. Consequently, avian dispersers and pollinators for some plant communities, including Cape fynbos and tropical lowland humid forest, have low equivalence, resulting in a high risk of plant extinctions from lost mutualisms (Bond 1994). Although local and global extinctions of some avian pollinators and dispersers do not seem to have resulted in plant extinctions yet (Bond 1994), given the short history of the detailed studies of mutualisms and the limited extent of our knowledge of aseasonal ecosystems where such extinctions are most likely, we may only be observing the survivors of many unrecorded extinctions.

Body size

Large and highly mobile bird species are often important mobile links (Lundberg & Moberg 2003), top consumers, and keystones (Raffaelli 2004). These species are relatively few and have small populations in relation to the avifauna in general. The very factors that make them particularly valuable to ecosystems also make these birds vulnerable to human impact. Bigger species, with correspondingly more ecological influence, are much more likely to be hunted for their meat. Birds with bigger home ranges, since they sample larger areas, are likely to encounter more threats. Furthermore, large species’ life histories, characterized by long life spans, small clutch sizes, infrequent breeding, and low population densities (e.g. albatrosses), also mean that they are far more sensitive to adult mortality, from which they may never recover. That people are selectively doing more damage to the very bird species that often contribute most to ecosystem function means that ecosystem consequences of avian declines and extinctions are likely to be more severe than suggested by random models of extinction (Zavaleta & Hulvey 2004).

Birds as Mobile Links

From an ecosystem functional perspective, birds are mobile links (Gilbert 1980; Lundberg & Moberg 2003) that are crucial for maintaining ecosystem function,



Figure 1. Examples of the four main types of avian mobile links (Lundberg & Moberg 2003) and potential consequences of the lack of their services. Drawings are based on the cited references. (a) Genetic linkers. Loss of Philippine seed dispersers, such as Palawan Hornbills (*Anthracoceros marcei*), can result in most seeds being deposited under the parent tree and being consumed by seed predators (Hamann & Curio 1999). (b) Resource linkers. Introduced foxes eliminating Aleutian seabirds, such as Tufted Puffins (*Fratercula cirrhata*), can lead to reduced nutrient deposition triggering a shift from grassland to maritime tundra (Croll *et al.* 2005). (c) Trophic process linkers. Disappearance of scavenging Indian Long-billed Vultures (*Gyps indicus*) can cause increases in the numbers of rotting carcasses and of attending mammalian scavengers (Prakash *et al.* 2003). (d) Trophic and non-trophic process linkers. Reduced numbers of Three-toed Woodpeckers (*Picoides tridactylus*) in forest fragments can cause increases in spruce bark beetles (Fayt *et al.* 2005) and decreases in nesting holes used by other species (Daily *et al.* 1993). In addition to habitat loss that affects all avian functional groups, large frugivores are highly susceptible to exploitation, bycatch mortality and introduced species threaten seabirds, woodpeckers decline as a result of fragmentation, and vultures are particularly sensitive to chemicals.

Illustration by Darryl Wheye/birds.stanford.edu. Reprinted from Sekercioglu, C. H. (2006), Increasing awareness of avian ecological function, *Trends in Ecology & Evolution*, Volume 21 (8), copyright (2006), with permission from Elsevier.

memory, and resilience (Nyström & Folke 2001). The three main types of mobile links, namely genetic, process, and resource linkers (Lundberg & Moberg 2003), encompass all major avian ecological functions (Figure 1). Seed dispersing frugivores (Figures 1a, 4) and pollinating nectarivores (Figure 5) are genetic linkers that carry genetic material to habitat suitable for regeneration or from an individual plant to another plant, respectively. Trophic process linkers are grazers (Figure 6), such as geese (Maron *et al.* 2006), and predatory birds, such as antbirds (Figure 7) and eagles (Figure 8), that influence the populations of plant, invertebrate, and vertebrate prey and often provide natural pest control (Mols & Visser 2002). Scavenging birds, such as vultures (Figures 1c, 9), are crucial process linkers that hasten the decomposition of potentially disease-carrying carcasses (Prakash *et al.* 2003). Piscivorous (fish-eating) birds (Figures 1b, 10) provide good examples of resource linkers that transport nutrients from water to land in their droppings and often contribute significant resources to island ecosystems (Anderson & Polis 1999). Woodpeckers (Figure 1d) act both as trophic process linkers and as physical process linkers or “ecosystem engineers” (Jones *et al.* 1994). Many woodpeckers and other bird species (Figure 11) engineer ecosystems by building nest holes used by a variety of other species (Daily *et al.* 1993).

Although mobile link categories are not mutually exclusive (e.g. seabirds are both process linkers as predators of fish and resource linkers as transporters of nutrients from sea to land in their guano), I shall focus on the most significant function of each group and will conclude with an overview of other services, such as environmental monitoring, provided by all birds.

Seed dispersal

Darwin (1859) was one of the first people to realize that birds are “highly effective agents in the transportation of seeds” (Figure 1a). Indeed, seed dispersal may well be the most important avian ecosystem service. This is especially true in the tropics where avian seed dispersal may have led to the emergence of angiosperm dominance (Regal 1977; Tiffney & Mazer 1995) and is arguably key to the maintenance of extraordinary plant diversity (Janzen 1970; Connell 1971; Stiles 1985; Schupp *et al.* 2002; Terborgh *et al.* 2002). Vertebrates are the main seed vectors for angiosperms (Regal 1977; Tiffney & Mazer 1995), particularly woody plants (Howe & Smallwood 1982; Levey *et al.* 1994; Jordano 2000). Increased seasonality in the temperate zone and consequent fluctuations in fruit and frugivore numbers make animal seed dispersal less reliable than in the tropics (Snow 1981), where vertebrate seed dispersers are especially important (Howe & Smallwood 1982; Stiles 1985) and the majority of taxa in many plant families are dispersed by birds (Hilty 1980; Snow 1981; Stiles 1985; Renner 1989; Willson & Crome 1989; Hamann & Curio 1999; Ganesh & Davidar 2001; Shanahan *et al.* 2001).

Seed dispersal is thought to benefit plants in three major ways (Howe & Smallwood 1982):

- 1) Escape from density-dependent mortality caused by pathogens, seed predators, competitors, and herbivores, also known as the Janzen-Connell escape hypothesis.
- 2) Chance colonization of favorable but unpredictable sites via wide dissemination of seeds.
- 3) Directed dispersal to specific sites that are particularly favorable for establishment and survival.

Seed passage through animals may also increase germination likelihood (Traveset & Verdú 2002) as a result of gut passage breaking seed dormancy (Noble 1975) or reducing seed infestation (Webber & Woodrow 2004), but most seeds do not require gut passage for germination and this mechanism is not considered to be a major advantage of dispersal (Howe & Smallwood 1982). After outlining the main advantages, I discuss the evolutionary, ecological, and conservation implications of avian seed dispersal, as well as its limitations.

Advantages of seed dispersal

The most important contribution of seed dispersers to plant survival is by reducing the density-dependent mortality of seeds and seedlings (Janzen 1970; Connell 1971; Howe 1989; Loiselle 1990; Harms *et al.* 2000) and by enabling escape from seed predators (Janzen 1970), herbivores (Connell 1971), competitors (Nathan & Muller-Landau 2000), and pathogens (Antonovics & Levin 1980; Packer & Clay 2000). A recent

Neotropical study (Terborgh *et al.* 2002) has shown the importance of negative density-dependent recruitment in increasing plant diversity from saplings to adults. In a detailed study of the seeds, saplings, and adults of trees in a 2.25 ha plot at Cocha Cashu, Peru, of over five hundred seeds that fell on one m² of forest floor in a given year, only four survived to become saplings (Terborgh *et al.* 2002). Over 95% of saplings originated from dispersed seeds and the probability of a seed >75 m away from the parent tree becoming a sapling was roughly five orders of magnitude higher than a seed under the parent tree. This confirms the importance of escape from localized enemies in greatly enhancing survival away from the parent tree. In this study, seed dispersal was particularly important for rare tree species, which contributed substantially to the high diversity observed and many of which would disappear if seed dispersal were reduced (Dirzo & Miranda 1991).

Complementary to these results that show the importance of even modest seed dispersal distances, radio-tracking of small (13 g), relatively non-mobile, and frugivorous Ochre-bellied Flycatchers (*Mionectes oleaginous*) in Costa Rican lowland forest revealed median dispersal distances of 42 to 56 m for six plant species (Westcott & Graham 2000). This indicates that even small, atypical avian frugivores can provide significant seed dispersal away from the parent tree. Even though dispersal may not always provide an escape from mortality and competition (Mack *et al.* 1999) and may even be disadvantageous at times (Silander 1978), its advantages are often considerable.

In addition to its “top-down” role by enabling escape from seed predators, seed dispersal can also provide a “bottom-up” advantage to seeds by increasing the probability that seeds will colonize a site with favorable germination conditions, be they light, nutrients, temperature, humidity, or some type of required disturbance (Howe & Miriti 2004). The advantage of increased colonization potential is likely to accrue more to plants with small, abundant, and highly vagile seeds that favor open, disturbed conditions and can grow rapidly. These “weedy colonists”, such as *Cecropia* spp., contrast with large-seeded and persistent “climax” species that cannot disperse as readily, but are better competitors as a result of their greater reserves (Kennedy *et al.* 2004), and usually replace colonizing species with the passage of time. The reality is often more complex, however. For example, poplars and sequoias are persistent species with colonist seeds (Howe & Smallwood 1982). Time scales of community persistence vary greatly, and plant communities are constantly, if slowly, in flux. It is therefore impossible to speak of truly unchanging “climax” communities and seed dispersal contributes a lot to this dynamism (Howe & Smallwood 1982).

Birds can eliminate the dispersal disadvantage of large-seeded species and a recent seed dispersal model showed that long-distance dispersal may be more regular than we thought (Clark *et al.* 1999). Jays and nutcrackers have been documented to carry acorns up to 20 km at a time (Vander Wall & Balda 1977; Bossema 1979 in Howe & Smallwood 1982), and thanks to avian dispersal, large-seeded trees have followed glaciers north significantly faster than one would expect (Howe & Smallwood 1982). On the other hand, scattered dispersal of many-seeded fruits, in addition to increasing the chances of small seeds encountering favorable physiological conditions, can also enhance germination success (Barnea *et al.* 1992). Nonetheless, it is the large-seeded species with low vagility that benefit most from avian seed dispersal, which seems to be crucial to maintaining the diversity of relatively stable tropical communities.

Avian dispersal is often considered “random” from the plant’s perspective in that, besides the advantage of being deposited away from the parent tree, seed dispersal is not thought to be directed towards sites where plant survival probability is high. However, directed dispersal may not be rare (Wenny 2001), and may be particularly common in regenerating and arid areas (Wenny 2001). In such areas, the few available trees both attract birds and provide a favorable microclimate to seedlings. Bird droppings fertilize the soil and gut passage may increase seed germination probability and speed (Trecu & Tamba 1997). Three-wattled Bellbirds (*Procnias tricarunculata*) in Costa Rica exemplify this phenomenon. In contrast to four other native avian dispersers, bellbirds dispersed seeds >40 m from the parent tree, under song perches in canopy gaps where recruitment success was significantly higher due to a reduction in fungus-induced mortality (Wenny & Levey 1998). Similarly, in New Guinea, Dwarf Cassowaries (*Casuarius bennetti*) preferentially dispersed the seeds of *Aglaia aff. flavida* uphill from the parent tree (Mack 1995). The absence of Dwarf Cassowaries, which are heavily hunted (Stattersfield & Capper 2000), would lead to downhill dispersal resulting in smaller and fragmented populations of this plant (Mack 1995). In some cases, however, directed dispersal may also favor the expansion of introduced species (Dean & Milton 2000). In contrast to various models assuming non-directional seed dispersal, field data indicate that there may be marked directionality, which increases dispersal efficacy, but which could be a disadvantage when habitat size is reduced (Wagner *et al.*

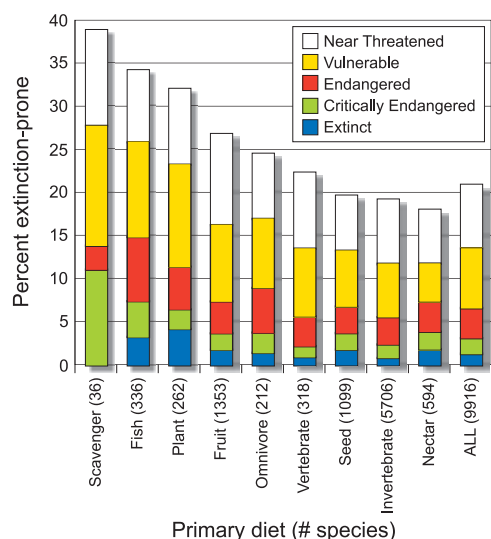


Figure 2
Distribution of extinction-prone species based on primary diet. Number of species in each group is in parentheses. If omnivores are reclassified based on first diet choice, percentages do not change except for scavengers (32%).

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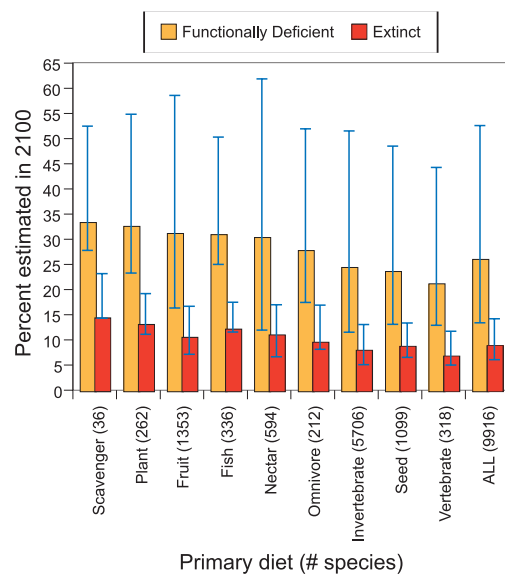


Figure 3
Predicted percentages of extinct and functionally deficient bird species for 2100 based on an intermediate extinction scenario. For details, see Sekercioglu et al. 2004. Threatened and extinct species are considered functionally deficient. "Error bars", not used in a conventional sense, indicate the averages of 10,000 simulations of scenarios 1 (best-case) and 3 (worst-case).

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2004). All the same, directed dispersal can provide significant advantages, especially in human-dominated ecosystems where restoration is critical (Wenny 2001).

A little-mentioned but potentially crucial service of frugivorous birds is that the removal of fruit pulp can significantly reduce the risk of bacterial and fungal infections that can kill the seeds before they germinate (Howe & Vandekerckhove 1981; Jackson *et al.* 1988, and others in Witmer & Cheke 1991). In fact, this might have been the most important contribution of the extinct Dodo (*Raphus cucullatus*) to the germination of the Tambalacoque tree (*Sideroxylon grandiflorum*, previously *Calvaria major* (Sapotaceae); Witmer & Cheke 1991). The famous story of the Tambalacoque tree now being on the verge of extinction since its seeds had to pass through Dodos to germinate (Temple 1977) has been shown to be more complicated (Witmer & Cheke 1991). Unabraded seeds of this tree still germinate and there are living trees less than 300 years old, indicating that this is not an example of obligate mutualism (Witmer & Cheke 1991). Nevertheless, Dodos were doubtlessly crucial as one of the few frugivores on Mauritius who could clean and disperse the large seeds of the Tambalacoque tree and a thorough cleaning of the fruit pulp by frugivorous birds may be the key to successful germination in many plant species (Howe & Vandekerckhove 1981; Jackson *et al.* 1988).

Dispersal "syndromes" and seed "predators"

There has been considerable research describing "dispersal syndromes", which are co-occurring fruit character complexes, such as color, size, and protection, that are thought to differ between bird, mammal and wind dispersed fruits (Janson 1983; Knight & Siegfried 1983). However, as our knowledge of seed dispersal expands, we are realizing that the boundaries between bird/mammal/wind dispersal syndromes (Gautier-Hion *et al.* 1985; Fischer & Chapman 1993; Jordano 1995; Tamboia *et al.* 1996; Pizo 2002) and even the divisions between seed dispersers and predators (Hulme 1998) may be more fluid than previously thought.

Detailed field studies (Gautier-Hion *et al.* 1985; Tamboia *et al.* 1996; Pizo 2002) and comparative analyses that correct for phylogeny (Fischer & Chapman 1993; Jordano 1995) found no evidence for clear-cut bird versus mammal dispersal syndromes, with the exception of "rodent fruits" (Gautier-Hion *et al.* 1985; Pizo 2002) and large fruits that are mainly mammal-dispersed (Janson 1983; Mack 1993; Jordano 1995; Pizo 2002). Most birds cannot swallow fruits >2 cm in diameter (Wheelwright 1985), although they can disperse small seeds from the large fruits they peck on (Debussche & Isenmann 1989; Pizo 2002). In fact, the relative scarcity of large seed dispersers in the Neotropics seems to have limited the evolution of large-seeded plants there (Mack 1993). Insect and nectar eating birds can also consume and disperse seeds (Stanley & Lill 2002a), and secondary seed dispersal by predatory birds can be important (Stiles 2000; Nogales *et al.* 2002), particularly in insular ecosystems with few dispersers (Grant *et al.* 1975). Many water birds, such as ducks (Figuerola & Green 2002), geese (Willson *et al.* 1997), gulls (Nogales *et al.* 2001; Calvino-Cancela 2004), and waders (Figuerola & Green 2002), can disperse seeds, especially in open habitats with low songbird diversity (Willson *et al.* 1997). Furthermore, many water birds cover long distances and may facilitate plant colonization of oceanic islands (Nogales *et al.* 2001). This dispersal can be both internal and external (through adhesion) and over evolutionary time scales, can significantly increase the species richness of island floras (Price & Wagner 2004). Indeed, even species thought to be wind-dispersed, may experience substantial bird dispersal, especially at larger spatial scales (Vander Wall 1992). The consequences of such dispersal, such as multi-genet tree clusters, occur in sufficient frequency to affect plant population structure and mating patterns (Torick *et al.* 1996).

Although there has often been a strict division between seed predators and seed dispersers, it is likely that seed dispersal and seed predation by bird species occur on a continuum. Some bird species traditionally considered seed dispersers may actually digest some of the seeds they consume (Traveset & Verdú 2002) whereas some "seed predators" disperse viable seeds via caching or defecation (Hulme 2002).

Specialization, redundancy, and complementarity

Even though earlier overviews of avian seed dispersal emphasized specificity and tight coevolution (McKey 1975), starting in the 1980's (Howe & Smallwood 1982; Wheelwright & Orians 1982; Howe 1984; Estrada 1986) there has been an increasing realization that, with the possible exception of large-seeded species and large frugivores

(Stocker & Irvine 1983; Hamann & Curio 1999), plants do not depend on a single species and diffuse coevolution is more widespread (Jordano 1987b). Thus, a black-or-white view of disperser specificity is unwarranted, especially since we have limited knowledge of dispersal systems in the tropics (Howe 1993b), where most species are and where we would expect the tightest coevolution to occur.

Nevertheless, there are various examples of tight relationships (Reid 1991; Beehler & Dumbacher 1996; Loiselle & Blake 2002) and specialized dispersers can provide higher quality services (Murphy *et al.* 1993). In the Costa Rican cloud forest of Monteverde, Murray (1988) found that only half of the bird species that consumed the seeds of three gap-dependent plant species dispersed the seeds in a viable condition. By combining radio-tracking data with seed passage rates, Murray calculated that these medium-sized species, namely Prong-billed Barbets (*Semnornis frantzii*), Black-faced Solitaires (*Myadestes melanops*), and Black-and-yellow Silky-flycatchers (*Phainoptila melanoxantha*), not only deposited most consumed seeds away from the parent plant, but also dispersed some seeds more than half a kilometer, increasing plant reproductive success 16-36 times. Also in Costa Rica, of the five bird species consuming the seeds of *Ocotea endresiana* (Lauraceae), only Three-wattled Bellbirds dispersed the majority of seeds >25 m away from the parent tree, and to gap sites where seedling recruitment was higher (Wenny 2000). On the Barro Colorado island of Panama, Black-mandibled Toucans (*Ramphastos ambiguus*) are three to 30 times better dispersal agents of *Virola nobilis* than other birds, including the larger Crested Guans (*Penelope purpurascens*) (Howe 1993a).

Fruit consumption may not equal effective seed dispersal, and even legitimate and closely-related seed dispersers are not necessarily equivalent. A good example of non-equivalence comes from a study of three turaco species in Rwanda (Sun *et al.* 1997). These large birds were observed to disperse a majority (>80%) of the seeds up to 304 m away from the parent tree. However, each species was best at a different aspect of seed dispersal. Ruwenzori Turacos (*Ruwenzorornis johnstoni*), which spent the shortest time in feeding trees, dispersed the highest percentage of seeds away from the parent tree, Black-billed Turacos (*Tauraco schuetti*) deposited the seeds most evenly, whereas Great Blue Turacos (*Corythaeloa cristata*), due to their large size, long flights, and extended gut retention time, dispersed seeds the farthest. Thus, these related species' seed dispersal patterns were complementary, not redundant.

Clearly, declines in frugivorous birds will affect some plant taxa more than others. In his influential review of tropical frugivorous birds and their food plants, Snow (1981) pointed out that many specialist frugivores target larger (up to 40 mm × 70 mm) and highly nutritive (up to 67% fat) fruits concentrated in the families Lauraceae, Bursaraceae, and Palmae. He suggested that these families may have coevolved with avian frugivores and therefore will be heavily impacted by the declines in the populations of their dispersers. Since frugivorous birds are often less common in the forest interior (Armesto *et al.* 2001), even some small-seeded forest understory shrubs adapted for dispersal by unspecialized frugivores (Snow 1981), as exemplified by the *Miconia* (Melastomataceae) species of Costa Rica, may be dispersal limited and more vulnerable to the extinctions of their dispersers (Loiselle & Blake 1999).

Mistletoes provide a good example of a keystone taxon highly dependent on avian seed dispersers, which likely contributed to mistletoes' diversification (Restrepo *et al.* 2002). Mistletoes, due to their hemiparasitic growth that buffers variation in resources, have extended phenologies, few defenses, high-quality nectar and fruits, and act as keystone resources, providing food for at least 97 vertebrate families and nesting sites for at least 50 (Watson 2001). There are marked differences between frugivores in their efficiency of the deposition of mistletoe seeds in required "safe sites" with favorable germination conditions. The viscosity of mistletoe seeds induces certain frugivores to deposit seeds in safe sites, but deters many others (Reid 1991). Therefore, mistletoes depend on a small subset of frugivorous birds, some of which, such as mistletoebirds and euphonias, need mistletoes in return. Mistletoes may require frequent seed establishment and removal of exocarps by seed dispersers, and consequently, population reduction of an avian seed disperser may limit mistletoe population size and/or distribution (Ladley & Kelly 1996). Mistletoes seem to be particularly important keystone resources in the forests of Australia (Watson 2002) and New Zealand (Ladley & Kelly 1996). Reductions in seed dispersers may have contributed to the decline of mistletoes in Australian forest fragments (Norton *et al.* 1995) and to the extinction of *Trilepidea adamsii* endemic to New Zealand (Norton 1991). Conversely, experimental reductions in mistletoe density in two similar Australian woodland remnants resulted in a significant decrease in mistletoe-feeding and woodland-dependent bird species (Watson 2002), emphasizing the mistletoe-bird co-dependence.

Some ecologically and economically important tree species, such as mahoganies, also depend on a few specialized avian dispersers, as exemplified by the dispersal of

two Papuan mahogany (Meliaceae) species by birds of paradise (Beehler & Dumbacher 1996). Moreover, the recruitments of two African mahogany species, *Entandrophragma utile* and *Khaya anthotheca*, were shown to be significantly limited by seed dispersal (Makana & Thomas 2004).

Large seeds



Figure 4.
Resplendent Quetzal (*Pharomachrus mocinno*), seed-dispersing genetic linker.

San Gerardo de Dota, Costa Rica.
Cagan H. Sekercioglu.

Having large seeds poses an evolutionary dilemma for many plants. On the one hand, large seed size can increase establishment success by providing more reserves to seedlings (Kennedy *et al.* 2004), by decreasing seed predation (Mack 1998; Ceballos *et al.* 2002; Jones *et al.* 2003), and by increasing survival (Tonioli *et al.* 2001), emergence rates (Tonioli *et al.* 2001), growth rates (Hegde *et al.* 1991; Sousa *et al.* 2003), and resprouting after herbivory (Green & Juniper 2004). The importance of large avian frugivores (Figure 4) for tropical primary forests is further emphasized by the larger seeds which characterize shade-tolerant, late successional, larger tropical tree species that predominate in terms of basal area, at least in Peruvian lowland forests (Foster & Janson 1985; Silman 1996).

On the other hand, most birds cannot swallow fruits larger than a few centimeters in diameter (Levey 1987; Pizo 2002) and dispersal efficiency of seeds declines with seed size (Levey 1987; Hegde *et al.* 1991). Therefore, large-seeded plants provide good examples (Green 1993; Corlett 1998; Hamann & Curio 1999; Kitamura *et al.* 2002) of taxa that are dependent on relatively few large frugivores (Meehan *et al.* 2002; Kitamura *et al.* 2004), whose sizes make them vulnerable (Kattan *et al.* 1994), and whose demise may lead to plant recruitment bottlenecks (Peres & van Roosmalen 2002) and extinctions (da Silva & Tabarelli 2000). For example, mid- to late-successional tree species in the Philippines have specialized dispersal syndromes, and are mostly dispersed by hornbills and fruit pigeons, many of which are highly threatened (Hamann & Curio 1999). Consequently, the elimination of large avian seed dispersers from tropical forests may have significant long-term consequences for tree species composition and forest structure (Figure 1a).

Large tropical frugivores have declined in many parts of the globe, and have disappeared from some areas, particularly many islands in the Pacific (Pimm *et al.* 1995; McConkey & Drake 2002; Meehan *et al.* 2002). On these islands, the extinctions of hundreds of bird species (Pimm *et al.* 2006) have already stressed ecosystems, and the introductions of rodent seed predators (*Rattus* spp.) have made seed dispersers even more important than in the past (McConkey *et al.* 2003). Introduced avian frugivores, such as silvereyes (*Zosterops* spp.), can be inefficient even for plant species with large fruits containing many small seeds, since they can avoid ingesting seeds (Stanley & Lill 2002b). Disappearances of large frugivorous birds can also have economic consequences since many timber tree species have significantly larger seeds than non-timber species (Hammond *et al.* 1996). In addition, the elimination of many large, seed-dispersing mammals from tropical areas (Redford 1992; Laurance *et al.* 2000; Peres & van Roosmalen 2002) may mean that large tropical avian seed dispersers are becoming increasingly important (Holbrook & Smith 2000), although some research suggests that the two groups may not be able to compensate for each other (Clark *et al.* 2001).

Importance of long-distance dispersal

Home range size increases with body size (Jetz *et al.* 2004) and even non-migrating large avian frugivores can roam over extensive areas (Kinnaird 1998; Holbrook & Smith 2000; Holbrook *et al.* 2002). Individual *Ceratogymna* hornbills in the Central African Republic have been documented to occupy home ranges of 4472 ha (Holbrook & Smith 2000) and to make long-distance movements up to 290 km (Holbrook *et al.* 2002). Calculations of seed shadows indicate that these species can disperse roughly 80% of seeds more than 500 m from the parent tree and up to 3.5 km (Black-casqued Hornbill (*C. atrata*) or 6.9 km (Brown-cheeked Hornbill (*C. cylindricus*)). However, introductions of non-native species can turn this valuable service into a problem. In the Usambara Mountains of Tanzania, Silvery-cheeked Hornbills (*Ceratogymna brevis*) are effective long-distance (up to four km) dispersers of the exotic *Maesopsis eminii* (Rhamnaceae) (Cordeiro *et al.* 2004), and significantly contribute to the rapid invasion of this West African species that is also dispersed by *Ceratogymna* hornbills in its native habitat (Holbrook & Smith 2000).

Nevertheless, long-distance seed dispersal by birds is mostly beneficial and modeling has also confirmed the importance of rare long-distance seed dispersal events in increasing the diversity of forest stands (Malanson & Armstrong 1996). Many “wind-

dispersed" species may be dispersed by birds at larger spatial scales, with important consequences for colonizing distant areas (Vander Wall 1992). In fact, birds, including seabirds (Nogales *et al.* 2001) and owls (Grant *et al.* 1975), play major roles in the plant colonization of islands (Whittaker & Turner 1994; Willson & Traveset 2000). Particularly seabirds not only visit and colonize barren islands, but can also jumpstart ecosystem buildup by simultaneously transferring nutrients and dispersing seeds, exemplified by gulls on the newly-formed island of Surtsey (Magnusson & Magnusson 2000). Endemic, bird-dispersed angiosperms on Hawaii exhibit significantly higher species richness than the taxa with other dispersal regimes (Price & Wagner 2004). Some migrant birds can carry seeds for more than 200 hours (Proctor 1968), although there may be a trade-off between longer retention time and establishment success (Murphy *et al.* 1993).

Relatively rare events of long-distance dispersal can have high evolutionary significance (Raven & Axelrod 1974; Regal 1977; Cain *et al.* 2000; Nathan 2005), but the role of avian seed dispersal over evolutionary time frames is underappreciated, due to the difficulty of designing studies with the appropriate perspective. Bird dispersal has led to higher speciation rates of tropical understory plants with small, fleshy fruits (Smith 2001) and in Europe, species richness of avian dispersers is four times more important for plant species richness than the influence of other environmental factors (Márquez *et al.* 2004). Increased taxonomic diversity of birds compared to mammals may have even given rise to the higher richness of bird-dispersed plant species (Fleming *et al.* 1993).

Reductions in seed dispersing birds

Currently, over a quarter of frugivorous bird species are extinction-prone (Figure 2), significantly above the global average (Sekercioglu *et al.* 2004). Given the importance of seed dispersal for maintaining plant biodiversity, reductions in frugivorous birds can have major ecological consequences. In the Gunung Palung rain forest of Indonesia, a combination of field research and modeling showed that the loss of animal seed dispersers would reduce local seedling species richness by 60% (Webb & Peart 2001). A bird species does not need to be endangered or extinct for its ecosystem services to decline. Many relatively common birds, such as the Eurasian Jay (*Garrulus glandarius*), provide crucial seed dispersal services (Mosandl & Kleinert 1998). The recent population declines of such formerly common species will result in reduced services (Hughes *et al.* 1997). In fact, avian vegetation preferences may result in dispersal limitation even in areas with healthy frugivore populations. An analysis of wild olive (*Olea europaea* var. *sylvestris*) seed shadows created by frugivorous birds revealed that most seed rain occurred under well-preserved dense scrubland, suggesting that a reduction in scrub density will diminish seed dispersal (Alcántara *et al.* 2000), possibly creating a positive feedback loop. Although both birds and bats are important for tropical forest regeneration (Galindo-González *et al.* 2000), birds are thought to disperse a wider range of plant forms (Whittaker & Turner 1994) and bat seed dispersal is unlikely to make up for the losses of avian seed dispersers.

Consequences of the reductions in avian seed dispersers can be especially dramatic on oceanic islands, which are more vulnerable to disturbance and to introduced species, and where alternative seed dispersers may be non-existent (Traveset 2002). For example, reduced species richness of avian frugivores in Madagascar with respect to South Africa has resulted in clumped tree distribution, reduced seed dispersal (8% vs. 71%), greater benefit of seed dispersal (6 times vs. 80 times), and reduced average distance to nearest conspecific (0.9 m vs. 21 m) for *Commiphora harveyi* (Bleher & Bohning-Gaese 2001). Most forest tree species in New Caledonia are thought to be bird-dispersed, and the long-term fate of large-seeded species is in the balance, since their remaining principal disperser, the endemic New Caledonian Imperial Pigeon (*Ducula goliath*) is in decline (Carpenter *et al.* 2003). In the past millennium, humans and introduced vertebrates have eliminated over 1000 bird species from the Pacific islands (Pimm *et al.* 2006) and the decline in the species richness of Polynesian Columbidae is likely to have affected intra-island seed dispersal (Steadman 1997a). Such declines in avian seed dispersers of Pacific islands (Murphy & Kelly 2001; Meehan *et al.* 2002) may lead to declines or even extinctions of dependent plant species (da Silva & Tabarelli 2000), further impoverishing oceanic island ecosystems.

Effects of fragmentation

Since many frugivorous birds range widely to track highly variable fruit resources, forest areas below a certain size may not have enough fruiting trees to support some

wide-ranging species (Price 2004), especially in the tropics. As a result, frugivorous birds, particularly large species, often decline in forest fragments (Kattan *et al.* 1994; Santos & Tellería 1994; Renjifo 1999). These declines can exacerbate the manifold effects of fragmentation (Laurance & Bierregaard 1997) and result in regional plant extinctions (da Silva & Tabarelli 2000). In Spain, *Juniperus thurifera* declined in fragmented forest as a result of a nine-fold increase in rodent seed predators (*Apodemus sylvaticus*) coupled with a five-fold decrease in thrushes (*Turdus* spp.), whose seed dispersal services could not be replicated in fragments by less effective mammalian seed dispersers (Santos & Tellería 1994). In Australia, most avian providers of highest quantity and quality of dispersal, including of large seeds, had reduced abundance outside extensive forest (Moran *et al.* 2004). In central Amazonia, seedling establishment of *Heliconia acuminata* was 1.5-6 times higher in continuous forest than in 1 ha or 10 ha fragments (Bruna 2002). In Tanzania's East Usambara Mountains, Cordeiro & Howe (2001) showed that reductions in the numbers of frugivorous birds and primates in small forest fragments resulted in a three-fold decrease in the recruitment of the seedlings and juveniles of 31 animal-dispersed tree species, compared to no reductions in the recruitment of wind and gravity-dispersed species. Furthermore, recruitment was 40 times lower for ten of the animal-dispersed species that were endemic to the area. Even generalist avian frugivores can decline significantly in fragments (Cordeiro & Howe 2003), and combined with limited frugivore movement between fragments (Githiru *et al.* 2002; Hewitt & Kellman 2002), this can result in severe reductions in seed dispersal. Avian seed dispersal in forest fragments may significantly favor introduced species over native ones (Montaldo 2000), further modifying natural communities.

The increased mobility of avian seed dispersers with respect to mammals, as well as birds' higher capacity to travel through human-dominated rural landscapes (Jensch & Ellenberg 1999; Holbrook & Smith 2000; Graham 2001) can enable better gene flow between increasingly fragmented plant populations (Jordano & Godoy 2000). In fragmented ecosystems, particularly in the tropics, many specialized bird species can not leave forest fragments (Sekercioglu *et al.* 2002) and avian seed dispersal declines rapidly away from forests (da Silva *et al.* 1996). In such areas, even modest efforts like planting native trees to act as stepping stones (Fischer & Lindenmayer 2002) or changing the geometry of clearings (da Silva *et al.* 1996) can significantly improve seed dispersal, increase connectivity of bird and plant populations, facilitate recolonization, and may help encounter the genetic effects of reduced pollination caused by fragmentation (Bacles *et al.* 2004). These trees can also help sustain populations of some resilient native frugivores (Luck & Daily 2003), such as African Pied Hornbills (*Tockus fasciatus*) in Ivory Coast. These birds, as the only large seed dispersers crossing open areas and moving between forest fragments, transport seeds up to 3.5 km away and facilitate the regeneration of and genetic exchange between fragmented forest plant populations (Jensch & Ellenberg 1999).

Role of avian seed dispersal in regeneration and restoration

Avian seed dispersal affects vegetation succession (Debussche & Isenmann 1994), is vital for plant colonization and regeneration in naturally (Shiels & Walker 2003; Nishi & Tsuyuzaki 2004) and artificially (Robinson & Handel 1993; Wunderle 1997; Lwanga 2003) disturbed areas, and can reduce the cost of restoring degraded lands (Robinson & Handel 1993). In Europe, avian seed dispersal has enabled the rapid postglacial expansion of glossy buckthorn (*Frangula alnus*) (Hampe 2003) and has established regular gene flow between its populations. In North America, whitebark pine (*Pinus albicaulis*) has quickly increased its postglacial range as a result of dispersal by Clark's Nutcrackers (*Nucifraga columbiana*) (Richardson *et al.* 2002). In Norway, seed dispersal and establishment was critical for the colonization of regenerating woodland by the native wood anemone (*Anemone nemorosa*) (Brunet & von Oheimb 1998), and data from a mixed plantation of native tree species planted in a Panamanian exotic grassland suggest that birds, which generally visited large trees, may have been fundamental facilitators of seedling recruitment (Jones *et al.* 2004). In tropical secondary habitats, as few as two trees may contribute most of the genes to a founding population and an intact seed disperser community is essential to restore genetic diversity to old-growth levels (Sezen *et al.* 2005). Avian seed dispersal can also have an important economic role in promoting natural regeneration in commercial plantations (Hutchins *et al.* 1996; Narang *et al.* 2000).

In Brazilian Atlantic montane forest plots ranging from five-year-old regeneration to old growth, Tabarelli & Peres (2002) found a positive correlation between forest age and the number of woody plant species with larger seeds and those with seeds dispersed by

vertebrates, indicating the long-term significance of avian seed dispersal in this critically threatened hotspot. In the Philippines, where dozens of highly threatened endemic bird species reside (Stattersfield & Capper 2000), birds dispersed more forest seed species and individuals than bats into successional vegetation, although this was limited to 40 m from the forest edge and the distance declined with increasing seed mass (Ingle 2003). Numbers of seed dispersing birds and consequent seed dispersal are many times higher in windbreaks (Harvey 2000) and isolated “perch” trees (McClanahan & Wolfe 1993; Debussche & Isenmann 1994; Toh *et al.* 1999; Carriere *et al.* 2002). These arboreal remnants also provide increased soil moisture (Verdú & García-Fayos 1996), longer water retention (Verdú & García-Fayos 1996), and higher nutrient availability (Toh *et al.* 1999), creating favorable microenvironments for seed germination and establishment. Planting and maintaining windbreaks, riparian strips, and perch trees will likely increase avian seed dispersal of native plants in deforested landscapes (Lwanga 2003). Nevertheless, in some cases, dispersal of forest species may be limited (Duncan & Chapman 2002), and plant regeneration may be highly restricted due to competition with grasses (Holl *et al.* 2000; Duncan & Chapman 2002), harsh physical conditions (McClanahan & Wolfe 1993), and seed predation by rodents (McClanahan & Wolfe 1993).

Summary

Currently, over a quarter of all frugivorous bird species are near threatened, threatened, or extinct (Figure 2). Avian seed dispersal is complex and variable, and changes in the populations of frugivorous birds will result in equally varied and often unpredictable changes in plant communities. The extent to which remaining species may compensate for disperser losses is unknown. Extinctions of seed dispersing birds are likely to reduce heterogeneity (Traveset *et al.* 2001) and species richness (Tabarelli & Peres 2002) of plant communities. As is the case with bird declines in general, the effects of seed dispersal will not be uniform and will be particularly felt in certain tropical taxa, such as Lauraceae, Burseraceae, and Sapotaceae, that have large seeds with few large avian dispersers. These large frugivorous birds are significantly more threatened than average, which can have significant consequences for tropical forest communities with many shade-tolerant, late successional, and dominant tree species with large seeds (Foster & Janson 1985). Large birds can disperse seeds dozens if not hundreds of kilometers away (Holbrook *et al.* 2002). Since it is relatively rare and difficult to observe, the importance of long-distance dispersal by birds, especially over evolutionary time scales, has been underappreciated. Long-distance dispersal is now thought to be crucial (Cain *et al.* 2000; Nathan 2005), especially over geological time scales during which some plant species have been calculated to exhibit colonization distances 20 times higher than would be possible without vertebrate seed dispersers (Cain *et al.* 2000). In this era of rapid climate change, long-distance seed dispersal by birds is becoming a necessity for more and more plant species, but this ecosystem service may be rapidly eroding in parallel with bird populations, especially of large species. As the dispersers of large seeds disappear, small-seeded, vagile species, already better colonizers that are more adapted to disturbed, rapidly changing environments (Howe & Smallwood 1982; Foster & Janson 1985), will have fewer competitors in deforested areas, and will establish themselves “by default” (Terborgh *et al.* 2002). Furthermore, avian seed dispersers can contribute to the spread of such invasive species with generalized dispersal mechanisms (Renne *et al.* 2002). Therefore, biotic homogenization via the replacement of specialist birds with generalist birds may contribute to increases in invasive plants. Losses of frugivorous birds will have significant implications for the ecology of forests and may result in the domination of many areas by short-lived pioneer species, with long-term effects cascading through the community.



Maybe...tentar verificar o quão longe as aves dispersam as seeds...mas

Pollination

Even though the vast majority of pollination is done by insects (Proctor *et al.* 1996), over 900 bird species (Nabhan & Buchmann 1997) pollinate about 500 of the 13,500 genera of vascular plant species (Renner 2005), concentrated in the families Bromeliaceae, Ericaceae, Fabaceae, Gesneriaceae, Heliconiaceae, Loranthaceae, Myrtaceae, Proteaceae, and about 20 others (Proctor *et al.* 1996). Flower-visiting has been recorded from approximately 2000 species (Herrera & Pellmyr 2002) in 50 bird families, in all biogeographic regions except Antarctica and most of the Palearctic. With the exception of Australia (Ford *et al.* 1979), the majority of avian pollination by far takes place in the tropics, and is mostly limited to hummingbirds, bananaquits, sunbirds, sugarbirds (Figure 5), honeyeaters, honeycreepers, lorikeets, and white-eyes (Proctor *et al.* 1996).



Figure 5.
Cape Sugarbird (*Promerops cafer*),
pollinating genetic linker.

Cape Town, South Africa.
Cagan H. Sekercioglu.

Explanations for the evolution of nectarivory in birds discuss birds “discovering” nectar while seeking other resources such as water, insects, fruit, flowers, or sap, but given birds’ intelligence and the wide availability of energy-rich nectar sources, there may be no need for an explanation (Dafni 1992). All nectarivores do include some invertebrates in their diet to meet their protein needs (Schuchmann 1999), especially during the breeding season (Stiles & Skutch 1989), and some of the first birds that fed on flower-visiting insects must have developed a taste for nectar rather quickly. In fact, avian pollinators visit six of the eight main flower blossom types, the exceptions being the dish and trap types (Dafni 1992). Stiles (1981) and Schuchmann (1999) provide detailed overviews of hummingbird pollination, and Proctor *et al.* (1996) do the same for birds in general, so here I will not elaborate on the evolutionary, mechanistic, physiological, and taxonomical details of avian pollination.

Quality of avian pollination

Since bird pollination requires large amounts of nectar, it is energetically expensive for plants. This has led to the evolution of floral strategies such as the bonanza-blank pattern where a small proportion of the flowers of a species may contain abundant nectar while the rest contain none, forcing hummingbirds to visit and cross-pollinate many flowers (Feinsinger 1978). Even though the greater energetic needs of birds mean increased nectar production, the same needs also force individual birds to visit up to thousands of flowers in one day (Proctor *et al.* 1996), increasing the gene flow between flowers. Individual hummingbirds have often been recorded to travel more than a kilometer during a single morning’s foraging and some species, such as the near threatened Saw-billed Hermit (*Ramphodon naevius*) in Brazil, can pollinate more than 20 flower species in the course of a year (Sazima *et al.* 1995). It is an underappreciated advantage of bird pollination that birds, especially trap lining species, with their good spatial memory and multi-year lifespans, provide higher quality pollination services than insects, particularly to self-incompatible flowers with patchy distributions (Schuchmann 1999).

Prevalence in ecosystems

In contrast to seed dispersal, however, birds pollinate a relatively small percentage of plant species, even in the western hemisphere where over 330 species of hummingbirds, the most specialized of avian pollinators, reside. For example, in five diverse ecosystems in Costa Rica, 6% to 10% of bird species feed on nectar, as opposed to 22% to 37% of the avifauna being frugivorous (Stiles 1985). In parallel, while 39% to 77% of shrub and tree species at these sites are bird dispersed, only 2.1% to 3.4% are bird pollinated (Stiles 1985). Most species that rely on hummingbird pollination are perennial herbs with limited nectar because the highly territorial nature of hummingbirds means that they often occupy and remain at a tree with abundant nectar, largely limiting cross-pollination between trees (Schuchmann 1999). As a result, about 1% of Costa Rican trees are bird pollinated, as opposed to 6% to 10% of epiphytes (such as bromeliads), with shrubs and terrestrial herbs having percentages in between (Stiles 1985). Bromeliaceae also seems to be the most important plant family for hummingbirds in the Brazilian Atlantic forest, where members of this family comprise a third of bird-pollinated species (Buzato *et al.* 2000).

The dominant avian pollinators in Brazilian (Buzato *et al.* 2000) and Costa Rican (Stiles 1985) lowland forests are the hermit hummingbirds (subfamily Phaethornineae), which are mostly replaced by non-hermit hummingbirds (Trochilineae) with increasing elevation (Stiles 1985). Endothermic hummingbirds, unlike ectothermic insects, do not need warm and sunny weather to be active, and as such, are more reliable pollinators (Schuchmann 1999), especially under the foggy, rainy, and chilly conditions that characterize many mid- to high-elevation tropical habitats. In fact, despite their small sizes and high metabolisms, hummingbirds can be surprisingly common in the high mountains of the Andes (Schuchmann 1999). The Ecuadorian Hillstar (*Oreotrochilus chimborazo*) is found as high as 5200 m (Heynen 1999). At this elevation, in order to survive through the night when the temperature often dips below freezing, this species goes into torpor, all but shutting down its metabolism, like many other hummingbirds that deal with cold weather.

Researchers in Colombia (Linhart *et al.* 1987), Mexico (Cruden 1972), and New Guinea (Stevens 1976) have shown the rising importance of bird pollination with increasing precipitation and elevation and decreasing temperatures (Stiles 1985). In fact, the 450 species in the tribe Vaccinieae, most of which are found in Neotropical

cloud forests, are almost entirely pollinated by hummingbirds (Luteyn 2002). Hummingbird pollination is particularly important for many of the 800+ Neotropical species of the Ericaceae family, most of which are found in the highlands (Luteyn 2002). As with seed dispersal (Gentry 1982), bird pollination is the least important in dry, windy ecosystems, such as tropical dry forests (Stiles 1985), where hummingbird pollination is rather limited and icterids are probably the most important of avian pollinators (Stiles 1985). In fact, these birds may be the most significant of pollinators among all Neotropical songbirds (Cruden & Toledo 1977) since social passerines such as orioles, given their sizes and numbers, cannot rely on a single tree like hummingbirds and provide more effective cross-pollination as they travel from tree to tree.

Hermits and exhibitionists

The major taxonomical division in hummingbirds, between hermits (Phaethornithinae) and “exhibitionists” (Trochilinae) parallel important ecological divisions (Proctor *et al.* 1996) that are soon noticed even by birdwatchers visiting a Neotropical forest for the first time. As quantified in detail by Snow & Snow (1972) in Trinidad, the drab-colored hermits are almost exclusively found in the forest understory. With their long, decurved beaks, reaching an extreme in sicklebills (genus *Eutoxeres*), these birds specialize in shade-tolerant herbs with prominent flowers, particularly in the order Scitimanieae (Stiles 1981), well exemplified by heliconias (Heliconiaceae). These understory plants produce limited nectar, which discourages territorial defense and encourages “trap lining” (Proctor *et al.* 1996). This forces birds to visit many flowers of the same species, facilitating longer pollination distances and increasing outbreeding. Hermits are among the more specialized of hummingbirds and particularly in lowland forest habitats, they are the most important avian pollinators. Their specialized bills and high-reward trap lining strategy make hermits highly effective pollinators (Schuchmann 1999).

Many species of the more colorful “exhibitionist” hummingbirds, however, are found in more open habitats, where flowers often produce more nectar. This results in increased territoriality, which reduces the pollen dispersal distance and the quality of the pollination service (Proctor *et al.* 1996). In Costa Rica, Stiles (1981) has observed three main divisions among these typical hummingbirds, based on increasing bill size and body mass. The largest, exemplified by Violet Sabrewings (*Campylopterus hemileucurus*), weigh up to 12 grams, possess decurved bills over 30 mm, and are the most specialized, resembling hermits in their habits. The smallest species, on the other hand, have short, sharp bills, often feed on insect-pollinated flowers and frequently steal nectar, a behavior that is highly correlated with short bill length (Proctor *et al.* 1996).

Bill length and nectar robbing

After all, avian pollinators do not aim to serve plants. These birds are in search of energy-rich nectar and if they can get to it without getting any sticky pollen on themselves, all the better. As a result, the quality of an avian pollinator is often correlated with its bill length. Birds with longer, more decurved bills are more likely to be “legitimate” pollinators and they make it possible for plants to have deep, thick corollas inaccessible to most insects and nectar-robbers whereas shorter-billed species are more generalist feeders that visit many species. Some of the shortest billed hummingbird species, such as the thornbills (genus *Chalcostigma*) and Fiery-tailed Aowlbill (*Avocettula recurvirostris*), as well as passerine flowerpiercers (genus *Diglossa*), are mainly nectar robbers, using their sharp bills to pierce flower corollas and consume nectar without providing any pollination in return.

Among all nectarivorous bird taxa, there are frequent examples of nectar robbing, a behavior that might, actually, have created the evolutionary pressure for some flowers to switch from insect to bird pollination (Sargent 1918) and may have led to the increased frequency of bird pollination in Australia (Ford 1985). Some plants probably adapted to nectarivorous birds in order to increase the probability of pollination by them (Sargent 1918). Interestingly, nectar robbing may sometimes have little to no negative effect on plant fitness, and may even result in some pollination (Graves 1982; Arizmendi *et al.* 1996; Lasso & Naranjo 2003, and other references therein).

Pollination syndromes

The coevolutionary relationship between nectarivores and flowers is thought to have led to increased specialization towards certain taxa and to the evolution of ornithophily or

“pollination syndromes”, where many unrelated flower species are similar in appearance and habits (Faegri 1978; Proctor *et al.* 1996; Rodríguez-Gironés & Santamaría 2004). Some of the common characteristics of ornithophilous plant species are diurnal opening, odorlessness, year-round production of abundant nectar, larger and more robust construction than “insect flowers”, the presence of perching structures (where non-hummingbirds are involved), and vivid “parrot” colors (Faegri 1978; Schuchmann 1999).

It is well-known that many “bird flowers” are red and that hummingbirds will often inspect red objects carefully. It has been suggested that flowers in the red spectrum are inconspicuous to bees (Raven 1972) and that birds may be more sensitive to red than to other colors (Stiles 1981). The actual mechanism, however, is more subtle (Rodríguez-Gironés & Santamaría 2004). Bees do see and visit red flowers (Chittka & Waser 1997) and neither bees nor hummingbirds have inherited color preferences (Proctor *et al.* 1996). Nevertheless, bees are not good at discriminating red flowers from a green background (Chittka & Waser 1997) and are therefore at a disadvantage compared to birds. This shortcoming, combined with optimal-foraging behavior (Possingham 1992), is likely to have led to the association of birds with red flowers (Rodríguez-Gironés & Santamaría 2004). Nevertheless, such associations are often weak. The nature of plant pollination has resulted in significant generalization and dynamism (Waser *et al.* 1996), and tight linkages such as the one seen between Sword-billed Hummingbirds (*Ensifera ensifera*) and *Datura* flowers, are exceptional. As such, even between highly specialized hummingbirds and their food plants, one-to-one relationships are unknown, and coevolution is diffuse (Schuchmann 1999).

Pollinator limitation

Nevertheless, bird pollination often involves fewer species that are usually more obligate than avian seed dispersers (Kelly *et al.* 2004). Some plant species mostly depend on a single (Parra *et al.* 1993) or a few (Rathcke 2000) avian pollinator species. As a result, plants are more likely to be pollinator-limited than disperser-limited (Kelly *et al.* 2004) and a survey of pollination experiments conducted for 186 species showed that about half were pollinator-limited (Burd 1994). Compared to seed dispersal, pollination is more demanding due to the faster ripening rates and shorter lives of flowers (Kelly *et al.* 2004). In addition, the lack of seed dispersal does not necessarily reduce offspring production to zero, but the same cannot be said for the lack of pollination. Although most bird-pollinated plant species have more than one species that can pollinate them (Nabhan & Buchmann 1997), there are many flower species which require certain specialized birds for pollination. Even species that rely on common avian pollinators, such as Bananaquits (*Coereba flaveola*), can suffer significant pollination limitation if pollinator populations decline following severe disturbances such as hurricanes (Rathcke 2000). In the Neotropics alone, thousands of plant species are thought to rely solely on hummingbirds for pollination (Schuchmann 1999). In India, 17% of 93 bird-pollinated plant species were only visited by one bird species (Subramanya & Radhamani 1993). The flowers of a Javanese mistletoe only open when visited by nectarivorous birds that trigger the flowers to explode (Docters van Leeuwen 1954). Avian pollination is particularly important in the Austral, New Zealand, and Oceanic regions, where the proportions of bird-pollinated plants are higher than in other parts of the world (Ford 1985). Most of the pre-settlement avifauna of Pacific islands is already extinct (Steadman 1995; Pimm *et al.* 2006), contributing to significant avian pollinator limitation in the region (Montgomery *et al.* 2001).

Figure 6.
Cackling Goose (*Branta canadensis hutchinsii*),
grazing trophic process linker.

California, USA.
Cagan H. Sekercioglu.



Importance of bird pollination in Australia

In Australia, about 100 bird species pollinate around 1000 plant species (Ford *et al.* 1979), possibly just in western Australia alone (Keighery 1982), where at least 15% of plant species are bird pollinated (Keighery 1980). Interestingly, Australian plants may be more adapted to avian pollination in order to make up for reduced avian seed dispersal. This is supported by the fact that bird pollination is particularly common for sclerophyllous plants growing on the highly infertile soils of Australia, where bird-dispersed fruits are scarce (Willson *et al.* 1989) and where seed dispersal distances are short (Ford 1985). Furthermore, the cooler and wetter climate of Australia in the mid-Tertiary and the lack of large, social, and homeothermic bees (*Apis* and *Bombus*) from the continent also seem to have favored birds as important pollinators (Ford 1985). Since the diverse “advanced” bee community in Europe may have replaced birds as pollinators, the recent introductions of honey and bumble bees in Australia and New Zealand, in addition to facilitating the spread of many introduced plant species (Cox

& Elmqvist 2000), may also threaten nectarivorous bird communities (Ford 1985) and native insect pollinators (Kato & Kawakita 2004). Even though bees may compensate for reduced avian pollination for some species such as *Banksia ornata*, for other species such as *Callistemon rugulosus*, honeybee displacement of honeyeaters has resulted in reduced seed production (Paton 2000). Furthermore, reductions in the summer and winter feeding habitats of Australian nectarivorous birds have led to population declines, which has resulted in severe pollinator limitation of seed production for a number of bird-pollinated plants (Paton 2000).

Vulnerability of island communities

As is the case with seed dispersal, pollinator limitation is often more important in island ecosystems with fewer species, tighter linkages, and higher vulnerability to disturbance and introduced species. Declines in the pollinators of island plants (Feinsinger *et al.* 1982; Robertson *et al.* 1999; Sakai *et al.* 2002), exacerbated by numerous extinctions of island birds (Pimm *et al.* 2006), may lead to extinctions of dependent plant species. Island plant species do seem to be more vulnerable to the extinctions of their avian mutualists since many island plants have lost their ability to self-pollinate and have become completely dependent on endemic pollinators (Cox & Elmqvist 2000). For example, the island of Tobago has five species of hummingbirds as opposed to 16 on the larger island of Trinidad. For the early successional hummingbird plants of Tobago, this has meant a significant reduction in pollinator visitation rates, less specialized pollination, and increased nectar production (Feinsinger *et al.* 1982), underlining the importance of pollinator diversity for the quality and energetic cost of pollination.

A study of two New Zealand mistletoe species relying on Bellbirds (*Anthornis melanura*), both for pollination and seed dispersal, showed that these species are pollen limited but not dispersal limited, suggesting that pollination failure for New Zealand plants is at least as significant as seed dispersal failure (Kelly *et al.* 2004). Other studies (Robertson *et al.* 1999; Montgomery *et al.* 2001; Murphy & Kelly 2001) of bird-pollinated flowers in New Zealand also indicate extensive pollination limitation, with introduced mammal predators putting the greatest pressure on avian pollinator populations (Murphy & Kelly 2001). Pollination limitation due to reduced species richness of pollinators on islands like New Zealand and Madagascar (Farwig *et al.* 2004) can significantly reduce fruit sets and decrease the reproductive success of dioecous plant species. In Hawaii, for example, the extinction of the competing Hawai'i O'o (*Moho nobilis*) resulted in the I'iwi (*Vestiaria coccinea*) shifting from native lobelioid flowers to ohias, possibly contributing to the native flowers' decline (Smith *et al.* 1995).

Summary

Although it is not as common as seed dispersal by birds, avian pollination has ecological, economical, evolutionary, and conservation significance, especially in certain species-rich communities, such as tropical forest understory herbs, Australian sclerophyllous plants, and Andean cloud forest shrubs. There has been little research on the economic importance of avian pollination, but birds are thought to pollinate at least 3.5% and up to 5.4% of more than 1500 species of crop or medicinal plants, three quarters of which cannot self-pollinate (Nabhan & Buchmann 1997). Bird pollination of a number of economically important species has been demonstrated in Indomalayan (Narang *et al.* 2000) and other (Nabhan & Buchmann 1997) regions.

Reductions in avian pollinators will inevitably favor some plant species over others, as demonstrated by Bahama swamp-bush (*Pavonia bahamensis*), which experienced significant seed set reduction as a result of avian pollinator limitation following Hurricane Lili that also created sites for plant recruitment (Rathcke 2000). Such changes in population dynamics caused by species' interactions are likely to lead to modifications in community composition in the short-term, and to have evolutionary consequences for plant lineages in the long-term (Thompson 1996).

Birds are particularly important pollinators for sparsely distributed plant species with isolated populations (Ford 1985) that suffer from increased pollen limitation (Groom 2001). Both traits increase extinction likelihood, so it would be safe to say that declines in avian pollinators can have serious consequences for many rare plant species. In fact, the extinction risk of Hawaiian native plants is associated with rarity and with bird pollination (Sakai *et al.* 2002). If the extinctions of 31 species of Hawaiian Campanulaceae as a result of the disappearance of their avian pollinators (K. Wood

pers. comm. in Cox & Elmqvist 2000) is any indication, hundreds of plant species may have gone extinct on Pacific islands following extensive bird extinctions (Pimm *et al.* 2006; Steadman 1997b). Introduced Polynesian rats (*Rattus exulans*) on the Easter Island may have contributed to the extinction of the *Jubaea* palm (on which islanders depended for constructing fishing boats) by causing the extinction of its psittacid pollinator as well as by consuming *Jubaea* seeds (references in Cox & Elmqvist 2000). Even though nectarivores are currently among the least threatened of bird functional groups (Figure 2), partially due to many hummingbird species' ability to utilize open habitats, this may change in the future (Figure 3) since many of these species also have small global ranges. If the expected extinctions of nectarivorous birds do materialize, not only may we lose some of the most specialized and spectacular of bird species, but we may also be faced with the disappearances of their plant mutualists, which would have significant ecological and evolutionary repercussions.

Predation and pest control

Insectivores



Figure 7.
Ochre-breasted Antpitta
(*Grallaricula flavirostris*),
insectivorous trophic process
linker.

Wilson Botanical Garden,
Costa Rica. Cagan H. Sekercioglu.

Among all bird functional groups, insectivores have the highest species richness by far. Even among the 237 species in the family Accipitridae, known for its specialization on vertebrates, a dozen species are almost exclusively and 44 are mostly insectivorous, with roughly 100 species taking the occasional insect, especially when they swarm (Thiollay 1994). Invertebrates comprise the primary diet choice for over half of all bird species (Figure 2). More than 7400 bird species, including an extraordinary radiation of Neotropical ant-followers (Figure 7), have been recorded to feed on invertebrates (Sekercioglu 2006). Given this unequalled diversity of avian insectivores and the effects of insect herbivores on plant populations, the fundamental question regarding bird-invertebrate interactions is, do birds have significant impacts on invertebrate populations?

Population control

There are various studies that answer in the affirmative for natural (Gradwohl & Greenberg 1982; Takekawa *et al.* 1982; Holmes 1990; Marquis & Whelan 1994; Murakami & Nakano 2000; Medina & Barbosa 2002) and agricultural (Greenberg *et al.* 2000; Tremblay *et al.* 2001; Mols & Visser 2002, and references therein) ecosystems. Nevertheless, a number of studies of avian effects on insect populations found variable (Joern 1992; Mazia *et al.* 2004) or limited (Otvos 1979; Stephen *et al.* 1990) evidence of any major impact, contributing to the initial impression that birds had little control or influence over ecosystem processes (Wiens 1973). However, earlier temperate studies largely focused on the eruptions of a few economically important lepidopteran species (Otvos 1979; Holmes 1990). An increasing number of studies investigating other invertebrate taxa (Gradwohl & Greenberg 1982; Bock *et al.* 1992; Gardner & Thompson 1998), at natural densities (Holmes *et al.* 1979; Gradwohl & Greenberg 1982; Bock *et al.* 1992; Gardner & Thompson 1998), and in tropical ecosystems (Gradwohl & Greenberg 1982; Van Bael *et al.* 2003; Perfecto *et al.* 2004; Philpott *et al.* 2004) provide mounting evidence that insectivorous birds do have significant roles in controlling the populations, behavior, and evolution of their invertebrate prey (Holmes *et al.* 1979; Holmes 1990).

Overall, the majority of the studies examining the effects of bird predation on herbivorous insects have found negative effects. A review by Holmes (1990) showed that reductions in Lepidoptera populations due to temperate forest birds was mostly between 40-70% at low insect densities, 20-60% at intermediate densities, and 0-10% at high densities. The island of Guam, where the introduced brown tree snake (*Boiga irregularis*) has wiped out almost the entire insectivorous bird community (Savidge 1987; Wiles *et al.* 2003), provides an interesting test case for the roles of insectivorous birds. Although anecdotal (Quammen 1997) and indirect (Kerr 1993) evidence indicates spiders have responded significantly and rapidly to bird extinctions, unfortunately, there was not a long-term study of the populations of declining insectivorous birds and their prey on Guam. However, it would still be informative to compare these variables between Guam and nearby islands that have not been colonized by these snakes.

Variability of avian influence

One generality that seems to emerge from these studies is that these effects are temporally variable and often depend on the local population size of the invertebrate in question (Takekawa *et al.* 1982; Glen 2004). Avian predators are often unable to control the populations of invertebrates at outbreak densities (Holmes 1990; Glen 2004), although there are exceptions (Loyn *et al.* 1983; Fayt *et al.* 2005). Birds are more effective at low to moderate invertebrate population levels (Fowler *et al.* 1991). In fact, predation by Carolina Chickadees (*Poecile carolinensis*), on the leaf-mining moth *Cameraria hamadryadella* has been shown to be inversely density-dependent, complementing the density-dependent mortality caused by invertebrate intra-specific competition (Conner *et al.* 1999). Such a complementary effect may help reduce the frequency of invertebrate irruptions (Takekawa *et al.* 1982).

Some research indicates that temperate insectivorous birds are food-limited mainly in the winter (Wiens 1977; Newton 1994) and are less effective when invertebrates are abundant during spring and summer (Glen 2004). This period, however, coincides with the breeding season of most temperate songbirds, most of which need insect protein for their rapidly growing young. There is contrary evidence that these birds may in fact be more food-limited during the breeding period, and therefore have the strongest impact on invertebrate populations during this time (Holmes *et al.* 1979; Holmes 1990), at least near bird nests (Jantti *et al.* 2001). As is frequently the case in ecology, these extremes are likely to occur along a continuum, depending on the ecosystem, the season, the bird and invertebrate taxa in question, and their relative densities.

Most of the studies on bird-invertebrate interactions have taken place in the temperate zone, where seasonality increases the magnitude of population fluctuations. In the tropics, especially in forest ecosystems where many bird species are highly specialized to feed on invertebrates (Sherry 1984; del Hoyo *et al.* 2003) and where reduced seasonality may mean fewer and less severe outbreaks than in temperate systems, birds may be more significant year-around control agents, possibly contributing to the typically limited extent of tropical forest outbreaks (Van Bael *et al.* 2004). The few tropical studies provide support for the importance of insectivorous birds, both in agricultural (Greenberg *et al.* 2000; Perfecto *et al.* 2004) and forested (Gradwohl & Greenberg 1982; Van Bael *et al.* 2003) habitats. It must be noted that global climate change is expected to increase the frequency and severity of El Niño/Southern Oscillation (ENSO) events (Timmermann *et al.* 1999) and the accompanying droughts. During these periods invertebrate outbreaks may be more likely (Van Bael *et al.* 2004) and the effects of tropical insectivorous birds on herbivores greater (Mazia *et al.* 2004).

Counterintuitive effects

When considering bird-insect interactions, there is also the possibility of an *increase* in insect populations, as a result of birds feeding on predaceous insects and parasitoids (Hooks *et al.* 2003). However, Hooks *et al.* (2003) found that excluding birds did not increase spider predation of herbivorous insects. Actually, birds alone were significantly better at controlling insects and reducing plant damage than spiders alone, with 18% of plants showing extensive defoliation with only spiders versus 0% with only birds. The argument that birds may reduce the numbers of insect parasitoids (Tschantke 1992) by feeding on infected insects also needs to be considered with this in mind: various lepidopteran parasitoids only emerge from the pupal stage, thus not preventing defoliation by the caterpillars (Hooks *et al.* 2003). Parasites may actually lead to increased foliage consumption by their hosts (Coleman 1999). Since various bird species are known to select for non-parasitized individuals (Otvos 1979) and facilitate the spread of viruses, they are often complementary to other natural enemies (Takekawa *et al.* 1982 and references therein).

However, the Bell Miner (*Manorina melanophrys*) provides an unusual example of a bird species that causes infestations of an insect herbivore (Loyn *et al.* 1983). This highly territorial species mostly feeds on the nymphs, sugary exudates, and lerps (protective carbohydrate covers) of psyllid homopterans, the birds often being careful only to remove the lerps with their tongues without disturbing the nymph (Loyn *et al.* 1983). This “tending” behavior, combined with Bell Miners’ aggressive group territorial defense, can result in psyllid infestations of *Eucalyptus* trees, sometimes leading to their defoliation and death (Loyn *et al.* 1983). The same study also showed how other bird species moved in and eradicated this infestation four months after the experimental removal of Bell Miners. The aggressive expansion in Australian forest fragments of a related species, the Noisy Miner (*Manorina melanophrys*), has resulted in a simi-

lar decline in native insectivorous birds (MacNally *et al.* 2002) and may also contribute to eucalyptus dieback in forest fragments.

Interestingly, the “classic” example of the invertebrate parasite removal service provided by oxpeckers may be an example of parasitism itself (Weeks 2000). Observations of oxpeckers on various ungulates showed that not only did Red-billed Oxpeckers (*Buphagus erythrorhynchus*) not reduce tickloads on domestic cattle (*Bos taurus*), but they preferred to feed on blood from open wounds (Weeks 1999), prolonged their healing time (Weeks 2000), and even opened new wounds on captive black rhinos (McElligott *et al.* 2004).

Role of species richness

When considering the effects of insectivores on ecosystems, it may be helpful to remember that, despite extensive niche overlap among some species, each species can be considered to represent a unique combination of features in an n-dimensional hypervolume (Hutchinson 1957). Therefore, higher richness of insectivorous birds means that there will be fewer “corners” of such a hypervolume where insects can remain out of reach and cause outbreaks. Indeed, limited evidence from temperate (Floyd 1996) and tropical (Philpott *et al.* 2004) ecosystems indicates that invertebrate control by birds may be complimentary. Research in Japan has shown that two small insectivorous songbird species, Great Tits (*Parus major*) and Eurasian Nuthatches (*Sitta europaea*), reduced the densities of different insect orders (Murakami & Nakano 2000), supporting the notion that insect control services of co-existing bird species may be more complementary than redundant, although not always (Hooks *et al.* 2003).

In addition, due to the sampling effect (Huston 1997; Loreau & Hector 2001), higher species richness also increases the probability of having a species, such as the Rufous-capped Warbler (*Basileuterus rufifrons*), which is particularly effective in its ecological function, as Perfecto *et al.* (2004) observed in their study comparing insect predation in Mexican coffee farms with diverse and monodominant shade trees. The authors tested the effects of bird predation by excluding birds from diverse and monodominant shade coffee plantations. They then induced an artificial insect “outbreak” by placing lepidopteran larvae on coffee plants and increasing the larval density six-fold. Larvae removal rates were about 50% higher in the diverse shade control compared to the enclosure, whereas there was no difference between the control and enclosure plots in the monodominant plantation. The higher density of Rufous-capped Warblers in diverse shade plantations was thought to be the major cause of this difference.

Behavioral and evolutionary influences

An underappreciated impact of avian insectivores on insects (and other predators on their prey) is that, with their very presence, insectivorous birds can affect prey species’ behavior and limit their movements, as well as the damage they do to plants (Holmes 1990). The highly varied morphology and foraging behavior of tropical forest insectivores (Fitzpatrick 1981; Stiles 1985) result in significant selection pressures on tropical insects, contributing to the astounding diversity and elaboration of their camouflage (Powell 1979). Holmes (1990) convincingly argued that the evolutionary pressure on invertebrates applied by avian predation has manifested itself in the form of elaborate mimicry, aposematism, nonmimetic polymorphisms, and anti-predator behavior, as well as changes in invertebrate morphology, sex ratios, life styles, and feeding behavior. All these adaptations have significant ecological consequences for the food plants. By limiting their movements to avoid bird predation, many insects will also take longer to develop, increasing their exposure to parasitoids, disease, and predators (Holmes 1990).

Consequences for plants

In many instances, insectivorous birds do have significant behavioral, ecological, and evolutionary effects on their invertebrate prey. An equally important question is, do these behavioral changes and population reductions of insect herbivores have secondary, cascading (Schmitz *et al.* 2000) effects on the food plants (Murakami & Nakano 2000)? In some cases, bird-induced reductions in insect herbivores may not translate to reductions in plant damage (Bock *et al.* 1992). This is more likely in systems where plants have significant anti-herbivore defenses or where the herbivore community is highly diverse, both of which result in the attenuation of trophic cascades (Schmitz *et*

al. 2000). It is also critical to note the plant response variable measured, since the change in plant damage may be higher than the more meaningful measures of changes in biomass and/or reproductive output (Schmitz *et al.* 2000; Halaj & Wise 2001; Lichtenberg & Lichtenberg 2002).

Nevertheless, reviews of terrestrial trophic cascades have found that removals of predators often result in increases both in herbivores and in plant damage (Schmitz *et al.* 2000; Halaj & Wise 2001), and that the effects of vertebrate carnivores are greater than those of invertebrate carnivores (Schmitz *et al.* 2000). An experimental study by Mols & Visser (2002) showed that Great Tits (*Parus major*) reduced the numbers of caterpillars and the resulting fruit damage in apple orchards. The authors' review of the literature revealed that such reductions in plant damage caused by avian insectivory were not uncommon. There is also some indirect evidence for the importance of insectivorous birds for plant populations. By releasing volatile compounds, plants may be attracting insectivorous birds to defend against insect herbivory, exemplified by Willow Warblers (*Phylloscopus trochilus*) in Finland that preferred sawfly-damaged branches of mountain birch (*Betula pubescens czerepanovii*) to control branches (Mantyla *et al.* 2004). Invertebrate predators and parasitoids use volatile compounds to detect prey, and birds may be using olfaction and/or ultraviolet vision for the same purpose (Mantyla *et al.* 2004). This would make them more effective control agents than if they foraged randomly.

Avian control of insect herbivores and consequent reductions in plant damage can have important economical value (Takekawa *et al.* 1982; Marquis & Whelan 1994). Birds can reduce the intensity of spruce budworm (*Choristoneura fumiferana*) outbreaks and mitigate damage on spruce plantations (Crawford & Jennings 1989) at magnitudes comparable to the most effective insecticides (Takekawa *et al.* 1982). In northern Washington state, avian control of spruce budworm was calculated to be worth at least \$1473/km²/year (Takekawa & Garton 1984). Increasing insectivorous bird numbers via nest boxes is a widespread forest management tool in Europe (Takekawa *et al.* 1982), resulting in the high mortality of leaf-eating caterpillars and consequent declines in damage to economically-important species such as white oaks (*Quercus alba*) (Marquis & Whelan 1994) and Pyrenean oaks (*Quercus pyrenaica*) (Sanz 2001). Insectivorous birds have also been documented to significantly reduce insect pest damage in agricultural systems (Kirk *et al.* 1996; Greenberg *et al.* 2000; Mols & Visser 2002). The last study is particularly noteworthy since the authors found that the damage reduction translated to a significant increase in the yield of domestic apples (*Malus domestica*), from 4.7 kg to 7.8 kg of apples per tree, underlying the potential financial importance of insectivorous birds for agriculture.

Summary

Comprising by far the most diverse avian functional group, insectivorous birds are ubiquitous, abundant, and essential components of most terrestrial ecosystems. Not only do these birds often have considerable influences on the behavior, evolution, ecology, and population sizes of their invertebrate prey, they can also modify the population dynamics and even evolution of plants through indirect effects. Furthermore, as invertebrate pests develop resistance to chemicals that often eliminate invertebrate predators, as increasing numbers of farmers switch to organic agriculture, and as pesticide use is curbed by public attitudes, environmental regulations, and consumer trends (Naylor & Ehrlich 1997; Mourato *et al.* 2000; Mols & Visser 2002), insectivorous birds will increase in significance as providers of natural pest control, components of integrated pest management, and indicators of healthy agroecosystems. Therefore, it is rather disconcerting that many insectivorous birds in the USA are in decline (Sauer *et al.* 2003) and that 12%-51% of all bird species feeding on invertebrates are expected to be functionally deficient by 2100 (Figure 3). Although less threatened than the global average, insectivorous birds include far more extinction-prone species than any other group (Figure 2) and widespread declines in tropical forest insectivorous birds (Thiollay 1997; Sekercioglu 2002a, b; Sodhi *et al.* 2004), 26% of which are extinction-prone, should be a cause for concern. Extreme specializations of many insectivorous birds, especially in the tropics (Sherry 1984; del Hoyo *et al.* 2003), make it unlikely that other taxa can replace these birds' essential ecological services.

Predation and pest control

Raptors



Figure 8.
Steller's Sea-eagle (*Haliaeetus pelagicus*),
carnivorous trophic process linker.

Hokkaido, Japan.
Cagan H. Sekercioglu.

Although birds are usually not thought as important top predators (Pearson 1966; Paine & Schindler 2002), accumulating evidence suggests the contrary in some ecosystems, especially when indirect effects are considered (Parrish *et al.* 2001; Roemer *et al.* 2002). In Sweden, predation was found to be the main cause of the non-cyclicality of small rodents, with more than half of the rodents being consumed by raptors (Erlinge *et al.* 1983). Thirgood *et al.* (2000) found that the absence of predation of herbivorous Red Grouse (*Lagopus lagopus scoticus*) by Northern Harriers (*Circus cyaneus*) and Peregrine Falcons (*Falco peregrinus*) would result in a doubling of grouse density in spring and a four-fold increase in the fall. Compared to most predators, raptors are highly mobile (Figure 8), which can both increase their influence on prey populations, as when predatory birds arrive en masse to take advantage of lemming population booms in northern Alaska (Pitelka *et al.* 1955), but also decrease it, as when bird predators leave in response to declining vole populations in central California while mammalian “carnivores stay on the job” (Pearson 1966). As with insectivorous birds, raptors can also detect areas of high prey densities, sometimes by detecting rodent scent marks that are only visible under ultraviolet light (Viitala *et al.* 1995), and thus have significantly more impact than if they hunted randomly.

Ecological redundancy

In some parts of the world, such as African savanna woodlands or Neotropical humid forests, many raptor species of similar size and seemingly overlapping diets co-exist, creating the impression that some of these species may be functionally “redundant”. However, many raptor species are highly specialized and respond differently to ecological changes. The assumption that species in similar trophic positions are functionally equivalent is likely to be erroneous (Chalcraft & Reserits 2003), and an impression of ecological redundancy may often be an artifact of limited knowledge of complicated systems that exhibit significant spatio-temporal fluctuations (Jaksic *et al.* 1996). In the semidesert of Chile, for example, although some raptor species initially seemed to be ecologically “redundant”, based on diet similarity, after the first three years of research, guild structure shifted significantly, emphasizing the variable nature of raptors’ contributions to ecosystem function (Jaksic *et al.* 1996). Additionally, while in some years transient species seemed redundant, in other years they had unique trophic roles. The authors concluded that short-term ecological data on this guild would have provided misguided decisions of conservation triage.

Tropical raptors

A perusal of the literature on the effects of predation, especially avian predation, shows a significant bias towards temperate, low diversity ecosystems with open vegetation structure, particularly deserts and tundra. Not only the large majority of raptor species are found in other ecosystems, but also the influence of predation on individual species is likely to increase as one moves towards the equator and average prey population size decreases with increasing species richness. Unfortunately, due to the difficulty of studying predation (Mitani *et al.* 2001), especially in closed habitats, there are few detailed studies on the role of avian predation in shaping tropical ecosystems (Groom 1992; Robinson 1994; Mitani *et al.* 2001; Boinski *et al.* 2003), and some of the conclusions are anecdotal and speculative. Nevertheless, available evidence hints at the significance of direct and indirect effects of tropical forest raptors. For example, Robinson (1985) found that the dense clustering of Yellow-rumped Cacique (*Cacicus sela*) nests in southeastern Peru were partly driven by nest defense against Black Caracaras (*Daptrius ater*) and the cacique population fluctuated almost tenfold, mostly as a result of Great Black-hawk (*Buteogallus urubitinga*) nest predation. Raptor attacks on parrots in the same area seem to affect parrots’ foraging patterns (C. Munn, pers. comm. in Robinson 1994) and may also affect psittacid social dynamics (Munn 1986).

Predation by large forest raptors, such as eagles, may be the primary cause of death for arboreal mammals, such as sloths (Boinski *et al.* 2003) and monkeys (Mitchell *et al.* 1991; Mitani *et al.* 2001). Mitchell *et al.* (1991) found that raptor predation was the major source of mortality for the squirrel monkey species *Saimiri boliviensis* and

S. oerstedii, and primates formed 82%-88% of the prey remains under Crowned Hawk-eagle (*Stephanoaetus coronatus*) nests in Kibale National Park, Uganda (Skorupa 1989; Struhsaker & Leakey 1990; Mitani *et al.* 2001). In fact, avian predation is likely to be the main factor driving larger group size in arboreal primates (Terborgh & Janson 1986; Shultz *et al.* 2004). Increased group size increases the likelihood of noticing a raptor and reduces an individual's probability of being captured, whereas competition for resources tends to reduce group size. In addition, increased risk of avian predation results in more vigilance behavior and may reduce foraging activity in some primates (Boinski *et al.* 2003). Given the potential importance of raptors in tropical forest ecosystems, tropical avian predator-prey dynamics is a research frontier offering the possibility of novel and exciting findings.

Negative synergisms in modified ecosystems

In contrast to tropical forests, various raptor species, particularly those living in the temperate zone, have adapted to and even thrive in human-dominated landscapes (Bird *et al.* 1996). Not only some birds of prey benefit from human presence (Bird *et al.* 1996), but increases in some predaceous birds may actually endanger the populations of some threatened prey species. This is especially the case for predators that respond positively to habitat fragmentation and/or human development. Common Ravens (*Corvus corax*) in the Mojave Desert of California have high populations near human settlements and this has resulted in an increase in ravens preying on the threatened desert tortoise (*Gopherus agassizii*) (Kristan & Boarman 2003). The introduction of pigs to California's Channel Islands has resulted in a situation where a federally protected bird species, the Golden Eagle (*Aquila chrysaetos*) is threatening the existence of another protected, endemic species, the island fox (*Urocyon littoralis*). The presence of feral pigs has boosted the population of Golden Eagles that also prey on foxes. The removal of pigs, which do significant ecological damage, is impossible without the removal of the eagles since they increase their predation on foxes when the pig populations are reduced, creating a serious conservation dilemma (Roemer *et al.* 2002). This is a classic example of an island ecosystem where natural predator-prey dynamics have been upset by an introduced species. Similarly, avian nest predators can significantly reduce the breeding success of other bird species, especially in fragmented ecosystems where avian nest predation often increases (Patten & Bolger 2003). Increased nest predation in northeastern US forest fragments has had a substantial role in the decline of many migratory songbirds (Wilcove 1985).

Indirect effects

High nest predation rates may have also contributed to the extinctions of various understory bird species from Barro Colorado Island, Panama (Karr 1990), although in this system increased nest predation is likely exacerbated by *decreases* in the numbers of birds of prey such as Harpy Eagles (*Harpia harpyja*) that feed on potential nest predators like white-faced capuchin monkeys (*Cebus capucinus*) and coatimundis (*Nasua nasua*). Even though evidence for the direct effects of avian predators on prey populations is limited, data suggest that indirect effects can be equally or more important (Brown *et al.* 1988) and birds of prey can have significant indirect, counterintuitive, or even positive effects on their prey species. The importance of indirect effects, which are often hard to measure, is becoming increasingly recognized in ecology (Wootton 1994a; Parrish *et al.* 2001), and such influences may account for half or more of the ecological changes observed (Paine *et al.* 1990; Wootton 1994b; Menge 1995).

Trophic cascades

A trophic cascade is a classic example of an indirect effect where the loss of a predator such as the Harpy Eagle can result in cascading population changes in lower trophic levels, including increases in herbivory (Wootton 1995; Hamback *et al.* 2004), ecological release of mesopredators (Crooks & Soule 1999; Terborgh *et al.* 2001), and consequent declines in the abundance and diversity of plants, nesting birds, and other species. For example, sea urchin predation by Glaucous-winged Gulls (*Larus glaucescens*), American Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*) in the intertidal zone of the Pacific Northwest coast of the USA reduced sea urchins by two-fold, in turn increasing algal cover 24-fold and algal taxonomic richness six-fold (Wootton 1995). The exclusion of these birds resulted in a trophic cascade and indirectly reduced algal cover and diversity.

Even though it has been argued that terrestrial systems are unlikely to experience trophic cascades due to spatial heterogeneity, prey variability, and food web complexity (Finke & Denno 2004), increasing evidence suggests that this may not be the case (Crooks & Soule 1999; Post *et al.* 1999; Terborgh *et al.* 2001; Hamback *et al.* 2004). Trophic cascades may be dampened in strongly seasonal systems (Norrdahl *et al.* 2002), and, with few exceptions (Terborgh *et al.* 2001), most of the studies on trophic cascades have taken place in temperate systems that are strongly seasonal. This is disconcerting since most species of birds of prey live in less seasonal tropical forest ecosystems where the consequences of the losses of raptor species may be greater, especially since higher predator diversity also reduces the effects of predator cascades (Finke & Denno 2004).

Nest predation and protection

Raptors' roles in indirectly "defending" the nests of other bird species from more generalist predators are well documented (Paine *et al.* 1990; Norrdahl *et al.* 1995; Blanco & Tella 1997; Bogliani *et al.* 1999; Haemig 2001; Ueta 2001; Quinn *et al.* 2003; Halme *et al.* 2004). In Finland, Eurasian Curlews (*Numenius arquata*) preferred to breed close to the nests of Eurasian Kestrels (*Falco tinnunculus*). Even though kestrels fed on 5.5% of curlew chicks, this was lower than the rate of predation by corvids and other generalist nest predators, which the kestrels kept away (Norrdahl & Korpimäki 1995). Paine *et al.* (1990) showed that although the rebounding population of Peregrine Falcons (*Falco peregrinus*) along North American Pacific coast resulted in the population declines of Cassin's (*Ptychoramphus aleutica*) and Rhinoceros Auklets (*Cerorhinca monocerata*) via direct predation, Peregrine Falcons actually had a positive impact on other nesting seabirds such as cormorants, murrelets, and oystercatchers since falcons fed on nest-predating crows. Ironically, in the Italian Alps, the corvid Common Raven (*Corvus corax*) seems to provide protection to nesting Peregrine Falcons from an intraguild predator, the Golden Eagle (*Aquila chrysaetos*) (Sergio *et al.* 2004). However, avian predators can also increase nest predation indirectly, as ongoing studies of the same Pacific coast bird colony demonstrated (Parrish & Zador 2003). Increases in Bald Eagles (*Haliaeetus leucocephalus*), resulted in decreases in Common Murre (*Uria aalge*) populations, as a result of direct predation by eagles and eagle-induced nest abandonment leading to rises in nest predation by Glaucous-winged Gulls (*Larus glaucescens*) and Northwestern Crows (*Corvus caurinus*) (Parrish & Zador 2003). Nevertheless, the presence of avian nest predators, despite sometimes having negative effects on individual species, can increase species richness of the avian community by preventing competitive exclusion (Slagsvold 1980).

The landscape of fear

Birds of prey may affect prey populations by their very presence. By establishing a "landscape of fear" (Laundre *et al.* 2001), avian predators can have indirect effects that may be more important than these birds' direct impacts on prey populations. As is the case with insectivores and invertebrates, prey species' perceived risk of predation can significantly affect prey behavior (Sodhi *et al.* 1990), stabilize predator-prey dynamics (Ives & Dobson 1987), and lead to greater species richness via competitive coexistence (Brown *et al.* 1988). The fear of being hunted can limit the population size of a prey species by limiting its foraging behavior (Brown & Kotler 2004) and reducing its access to food (Power 1984). For example, Brown *et al.* (1988) found that three species of heteromyid rodents in Arizona spent less time in more open habitats, reduced foraging time, and left food patches sooner under the risk of owl predation. The reduction in foraging time due to the fear of predation resulted in a substantial (47% to 91%) reduction in energy intake. These rodents responded rapidly to changes in owl predation risk, and constantly adjusted their foraging levels accordingly. Moonlight increases the risk of owl predation (Kotler *et al.* 1988). Many nocturnal rodents reduce their foraging activities under moonlight (Brown & Kotler 2004) and limit their intake of plants. In one of the few large scale, experimental exclusions of vertebrate predators, including raptors, Lagos *et al.* (1995) discovered that individuals of the herbivorous rodent *Octodon degus* in northern Chile had smaller home ranges and had more runways between shrubs when predators were absent, indicating the importance of perceived predation risk for altering the behavior and ecological impact of prey populations. Field experiments in Israel with a trained Barn Owl (*Tyto alba*) revealed that two gerbil species, *Gerbillus allenbyi* and *G. pyramidum*, not only reduced their activity and spent more time in bushes in the presence of owls, but their activity increased rapidly following the removal of owls (Abramsky *et al.* 1996).

Abramsky *et al.* (2002) also revealed that the presence of avian predators can significantly reduce seed consumption by small rodents.

These studies of indirect effects emphasize the role avian predators can have on their prey, not only as a result of direct mortality, but also via more subtle, but equally or more important behavioral, ecological, and evolutionary influences induced by these birds' very presence. Reductions in avian predators can cause their prey to perceive less predation risk, potentially leading to significant increases in foraging activity, body condition, and population size. Thus, declines in avian predators are likely to have cascading effects in ecosystems. As avian prey no longer experience mortality from birds, their behavior, population dynamics, and evolution will change accordingly.

Aquatic predation

One of the first studies of the indirect effects of avian predators was conducted in an aquatic system, where Power (1984) quantified the predator-induced resource avoidance of armored catfish in Panama. Similarly, bird predation risk of fish in Tennessee streams was considerably higher for larger fish in shallow waters than in deeper waters or than smaller fish, and this risk affected the fish community composition in these streams (Harvey & Stewart 1991). In a study of chub predation in an experimental stream, Allouche & Gaudin (2001) proved that avian predation pressure significantly reduced chubs' growth variances, reducing the fitness differences between individuals. In fact, the threat of avian predation had a higher impact on fitness, via sub-lethal effects on growth rates, than the direct mortality caused by predation.

This interest in aquatic predation by birds is not limited to the academia. Fish predation by aquatic birds has been blamed for economic losses to hatcheries (Pitt & Conover 1996), fish ponds (Avery *et al.* 1999; Wywiałowski 1999), and fisheries, often resulting in the culling of thousands of cormorants and other "culprits" (Anon. 2004e, 2004f). However, there have been few rigorous studies on the effects of birds on fish stocks, economical damage is mostly limited to captive fish populations and birds are frequently blamed for other sources of mortality. Because waterbirds often prey on species with no economic value, they may actually trigger the competitive release of commercial fish species (Suter 1991). Furthermore, since fish diseases can cause substantial economic losses to fisheries (Wagner *et al.* 2002; Lillehaug *et al.* 2003), birds may provide a service to hatcheries by limiting epidemics via the consumption of diseased fish that are easier to catch.

Even though cormorants are thought to consume disproportionately large quantities of fish to heat their bodies covered in wettable plumage, these birds have extraordinarily efficient energy budgets. In Greenland the food intake of Great Cormorants (*Phalacrocorax carbo*) was shown to be lower than those of better-insulated seabirds (Gremillet *et al.* 1999). In two Swiss rivers, Great Cormorant predation had no impact on the dynamics of trout and grayling populations (Suter 1995). One study of the effects of Great Cormorants on a commercial fishery in a Swedish lake showed that non-commercial fish comprised 88% of cormorant diets, and economically important eels were absent from cormorant diets (Engstrom 2001).

Interviews (Glahn, Rasmussen *et al.* 1999), observations (Glahn, Rasmussen *et al.* 1999), and stomach content analyses (Glahn, Tomsa & Preusser 1999) indicate that at aquaculture facilities in the northeastern United States, Great Blue Herons (*Ardea herodias*) are the most important predators of commercial fish. However, a detailed study of Great Blue Heron predation on stocked rainbow trout in Arkansas tailwaters estimated that these birds consumed only 2.4% of the stocked trout in the area and represented a minor source of mortality (Hodgens *et al.* 2004). Heron activity was 40 times greater at diseased ponds in Mississippi catfish farms and 85% of the fish herons captured were diseased (Glahn, Tomsa & Preusser 1999).

The perceptions of fish losses to birds, usually based on surveys (Wywiałowski 1999), may be much greater than or even the reverse of the reality (Glahn *et al.* 2000; Anon. 2004g). In contrast to the findings of a telephone and mail survey of catfish producers (Wywiałowski 1999), an empirical study of Mississippi catfish farms (Glahn *et al.* 2000) showed that there was no difference in catfish lost over time between heron-exclusion ponds and test ponds where herons fed at a density about 20 times greater than normally reported from commercial farms. Furthermore, this study confirmed that herons prefer to feed on unhealthy catfish or commercially undesirable fish. These findings suggest not only that Great Blue Herons and other aquatic birds may have negligible impacts on certain commercial fish, but that these birds may also provide a service by removing diseased fish and competitors of commercially valuable species (Vaneerden *et al.* 1995).

Economic value of the birds of prey

Fisheries are not the only places where predatory birds provide economical services. In its lifetime, a Barn Owl (*Tyto alba*) is thought to eat over 11,000 mice that would have consumed 13 tons of crops (Anon. 2002b). Given the potential importance of raptors on the behavior, populations, and consumption levels of rodents, birds of prey may greatly influence the populations of rodent and avian agricultural pests, or at least limit their activities and consumption by establishing a landscape of fear (Laundre *et al.* 2001). Even though raptors have been encouraged in some agricultural areas via the construction of nest boxes (Anon. 2002b; Wood & Fee 2003), it is unfortunate that there has been very little research on raptors' roles in controlling the vertebrate pests of agriculture.

Some of the best examples of the financial value of raptors come from an unexpected but appropriate source: The Wall Street Journal. In an article on January 22, 2005 (Warren 2005), the WSJ reported that the city of Fort Worth, Texas, was paying a falconer US\$ 4000 per month to prevent the expanding flocks of Great-tailed Grackles (*Quiscalus mexicanus*) from soiling the city and making noise. Another article published on February 11, 2005 (Stecklow 2005) mentioned that the city of London, in order to control Rock Pigeons (*Columba livia*) of the Trafalgar Square, had paid about \$220,000 in one year to hire trained Harris' Hawks (*Parabuteo unicinctus*) at \$93 per hour. In response to the landscape of fear created by these birds, many pigeons left the area and the Trafalgar Square population dropped from 4000 to "a couple of hundred". Ironically, in Turkey, where being hit by a bird dropping is considered good luck, pigeon droppings themselves constitute a socio-economic service, at least for the vendors of lottery tickets. In Istanbul, the vendors are most concentrated around Yeni Cami (Mosque), where people regularly feed the city's largest flock of Rock Pigeons, a deed considered a religious service.

Although the raptor program of Fort Worth has been discontinued due to its expense, and the effectiveness of the Trafalgar program has been questioned (Stecklow 2005), there is growing interest in using raptors to control or at least drive away pest bird populations, especially with the growing possibility of avian flu in city birds. Raptors can be especially important around airfields, where they can keep away birds that regularly collide with aircraft. As reported in a New York Times article on February 25, 2005 (Kelley 2005), in 2004 alone, the US Air Force logged 4318 aircraft-wildlife collisions, mostly with birds, and this number was estimated to be around 30,000 for civilian aircraft. In this article, the author also reported on the US Air Force paying \$200,000 per year for trained Peregrine Falcons (*Falco peregrinus*) to drive away European Starlings (*Sturnus vulgaris*), Canada Geese (*Branta canadensis*), and other birds that gather around the airfield of McGuire Air Force Base. Although raptors themselves often collide with airplanes (Satheesan 1996), with such collisions even forcing the Israeli Air Force to stay away from certain areas during raptor migration (Pearce 2004), in the case of McGuire Air Force Base, air force officials praised the falcons, stating that "they help keep our aircraft up in the sky and our pilots safe".

As avian pests, especially introduced species, become increasingly problematic, partially due to the growing influence of the animal rights movement in preventing cullings, raptors will grow in importance and value in controlling or driving away avian pest populations. Many raptors, such as Peregrine Falcons, possibly perceive skyscrapers and other large buildings as urban canyons filled with naïve prey, and these birds, along with Red-tailed Hawks (*Buteo jamaicensis*), Ospreys (*Pandion haliaetus*), and other species are increasingly present in large cities and suburban areas (Bird *et al.* 1996). Most city dwellers welcome this comeback, so much so that the recent removal of the nest of a Red-tailed Hawk, "Pale Male", from a Manhattan luxury condominium led to daily protests, ten New York Times articles in two weeks, and the reinstatement of the nest (Edidin 2004). Increasing research on raptors in human-dominated habitats indicates that there is often plenty of prey and that many raptors usually do quite well when they are not limited by nesting sites (Bird *et al.* 1996). Avian pest control funds would be put to much better use in protecting and promoting the populations of native raptor species and providing them with suitable nesting sites.

Summary

Although raptors as a group have a lower percentage of extinction-prone species than most other functional groups (Figure 2), large raptor species are more sensitive to disturbance and are more threatened than average. Furthermore, the expected functional extinctions of 13%-22% of raptor species (Figure 3) may lead to trophic cascades in

some ecosystems, particularly in the tropics where most of these extinctions are expected to take place. Declines in the largest tropical forest raptors, such as Crowned Eagles (*Harpyhaliaetus coronatus*, vulnerable), Harpy Eagles (near threatened), New Guinea Eagles (*Harpyopsis novaeguinae*, vulnerable), and Phillipine Eagles (*Pithecophaga jefferyi*, critically endangered), may have significant impacts on the numbers (Mitani *et al.* 2001) and behavior (Cordeiro 1992) of their prey, with further changes possible at lower trophic levels (Terborgh *et al.* 2001). Birds of prey often feed on many species and are well-connected hubs. Human-caused extinctions usually select against such large top predators (Ebenman *et al.* 2004) and food webs are very vulnerable to the selective losses of hubs (Allesina & Bodini 2004). Consequently, as populations of raptors, particularly large, tropical species decline and disappear, not only are we deprived of the thrill of observing some of the most majestic, inspirational, and symbolic creatures in existence, but we may also have to deal with the ecological and economical consequences of eliminating the drivers of crucial ecosystem processes.

Scavenging

Since most scavenging birds are highly specialized to rapidly dispose of the bodies of large animals, these birds are important in the recycling of nutrients, leading other scavengers, including people (Mundy *et al.* 1992; Eaton 2003), to dead animals (Houston 1979, 1994), consuming the majority of carcasses mammalian scavengers never find (Houston 1974), keeping energy flows higher in food webs (Putnam 1983 in DeVault *et al.* 2003), and limiting the spread of diseases to human communities that would be facilitated by slowly decomposing carcasses. Vultures are the only known obligate vertebrate scavengers since energetics necessitate obligate terrestrial vertebrate scavengers to be large, soaring fliers (Ruxton & Houston 2004). Vultures may well be the most accomplished fliers in existence (Figure 9), patrolling the heights of the Andes and the Himalayas, effortlessly soaring to thousands of meters, and covering hundreds of kilometers in a day's work. A collision at 11,278 m over Ivory Coast between a plane and a White-backed Vulture (*Gyps africanus*) is by far the highest altitude at which any bird has been recorded (Laybourne 1974).

Ecological significance

Even though we tend to think of large mammalian predators as the dominant meat eaters, in many ecosystems, such as African savannas (Houston 1979), Indian woodlands (Houston 1983), and Neotropical forests (Houston 1986), vultures are (or were) the major carnivores due to their efficiency in finding and consuming dead animals. Houston (1983) observed that 86% of experimental carcasses he put out in the Tanzanian savanna were discovered only by vultures. He estimated that in the Serengeti, vultures consume at least 370 kg of meat per km²/year, as much as all mammalian carnivores combined. In fact, vulture community richness can even give us an idea of the importance of predation in some communities, since when predators are the major source of mortality, large avian scavenger species are reduced or absent (Houston 1986). Avian scavengers rely on finding carcasses before predators can get to them, which is often by following vultures. In the Serengeti, lions locate at least 11% of the carcasses they scavenge by watching vultures (Schaller 1968), and this likely applies to many other species of mammals.

Vultures, especially rapidly declining *Gyps* species, are highly effective in quickly discovering and disposing of carcasses (Houston 1983). Since Old World vultures cannot smell, they are mostly absent from tropical forests (Houston 1994). New World vultures of the genus *Cathartes* can smell and members of this genus and the other vultures that follow them to carcasses are the major scavengers in Neotropical forest ecosystems (Houston 1986). For example, Greater Yellow-headed Vultures (*Cathartes melambrotus*) found 63% of experimental carcasses in Colombia, whereas mammals found only 5% (Gómez *et al.* 1994). Houston (1986, 1988) observed that 116 out of 120 domestic chicken carcasses he placed in Panamanian and Venezuelan forests were discovered and consumed by Turkey Vultures (*Cathartes aura*) in three days. Interestingly, he also observed that in forests with reduced mammal abundance, Turkey Vultures missed many of the carcasses which were mainly consumed by invertebrates (Houston 1987). This not only indicates a change in scavenging dynamics as a result of mammalian reductions and reduced specialization of vultures on mammalian carcasses, but also suggests that *Cathartes* vulture numbers can be used to make rapid assessments of Neotropical mammal numbers, serving as an index of mammalian defaunation (Dirzo & Miranda 1990).



Figure 9.
Lappet-faced Vulture (*Torgos tracheliotus*),
scavenging trophic process linker.

Masai Mara Game Reserve, Kenya.
Cagan H. Sekercioglu.

Sanitary services

Besides their ecological significance, vultures are particularly important in many tropical developing countries where sanitary waste and carcass disposal programs may be limited or non-existent (Prakash *et al.* 2003), and where vultures contribute to human and ecosystem health by getting rid of refuse (Pomeroy 1975), faeces (Negro, 2002), and dead animals (Prakash *et al.* 2003). 66% of the Indian population practices open defecation (Jha 2003) and coprophagy by vultures can improve community hygiene and may reduce disease. The alarming population crash of the Indian subcontinent vultures may result in an increase in exposed faeces and augment rat populations. Vultures have an impressive ability to resist and possibly detoxify bacterial toxins in rotting flesh. Extremely acidic secretions of the vulture stomach, with a pH as low as 1, kill all but the most resistant spores and this is thought to significantly reduce the bacterial sources of infection from the carcasses vultures feed on (Houston & Cooper 1975). Understanding the physiological mechanisms of vulture resistance to infectious agents may even lead to medical discoveries.

Marine scavengers

Even though no seabird species is an obligate scavenger, like various bird species (DeVault *et al.* 2003), most seabirds will scavenge opportunistically, especially since many live in harsh climates with unpredictable food resources. The two sheathbill species of the genus *Chionis* comprise a fascinating family (Chionididae) of avian scavengers that are dependent on seabird and pinniped colonies in the temperate and polar zones of the southern hemisphere (Favero 1996). These birds are the “garbage collectors” of these colonies, mostly feeding on pup carcasses, dead chicks, afterbirth blood, and faeces, but also stealing bird eggs and even seal milk (Favero 1996). Giant petrels (genus *Macronectes*) are sometimes considered the marine equivalents of vultures although giant petrels also feed on marine invertebrates and chicks of various marine birds (Hunter 1991). Nevertheless, they are the most important, if not the only large scavengers on many oceanic islands and Antarctica. Interestingly, scavenging is mainly done by male giant petrels whereas females generally feed at sea, resulting in higher female mortality on fishing lines (González-Solís *et al.* 2000).

Although many seabirds scavenge from fishing boats, they do not depend on them completely (Camphuysen & Garthe 1997), and numerous seabird species, including some scavengers, have rapidly declining populations as a result of the accidental mortality caused by being caught on fishing lines (Tasker *et al.* 2000). Currently, Southern Giant Petrels (*Macronectes giganteus*) are listed as vulnerable and Northern Giant Petrels (*Macronectes halli*) are near threatened, with the former declining mainly as a result of being bycaught on longlines and the latter increasing around South Georgia, possibly as a result of an increase in Antarctic fur seal populations (González-Solís *et al.* 2000). Unfortunately, we know little about the potential ecological consequences of the changes in the numbers of these scavenging seabirds.

Worldwide declines

Indeed, avian scavengers worldwide comprise the most threatened avian functional group, with about 40% of the species being threatened or near threatened with extinction (Figure 2). Sadly, this is not surprising. The same factors that make vultures efficient scavengers (Ruxton & Houston 2004), namely large body size, long travel distances, and the consumption of many carcasses, also make them vulnerable to accidental and deliberate poisoning, persecution, collisions with powerlines, habitat loss, disturbance, and even ritualistic killings inspired by their majesty (Mundy *et al.* 1992; Houston 1994; Snyder & Snyder 2000). Therefore, even non-threatened species such as Egyptian Vultures (*Neophron percnopterus*) (Liberatori & Penteriani 2001; Donazar *et al.* 2002) and Bearded Vultures (*Gypaetus barbatus*) (Brown 1991), have been experiencing extensive and steady declines. Avian scavengers are also highly susceptible to poisoning as a result of swallowing lead bullets while consuming carcasses unclaimed by hunters (Clark & Scheuhammer 2003). This is a serious problem for many bird species and is one of the leading causes of death for California Condors (*Gymnogyps californianus*). Disconcertingly, like birds in general, more specialized Neotropical vulture species are more prone to extinction, and some of the largest species in the New World have become extinct in the Pleistocene (Hertel 1994). African vultures are exposed to many anthropogenic threats including habitat destruction, reductions in food availability, inadvertent killing during “problem animal” control

campaigns (poisons, gin traps, etc.), electrocution on electricity pylons, nest disturbance, and harvesting for traditional medicine (Schüz & König 1983; Mundy *et al.* 1992). Since 1970, the numbers of West African vultures, with the exception of Hooded Vultures (*Necrosyrstes monarchus*), declined by an average of 95% and White-headed (*Trigonoceps occipitalis*) and Lappet-faced Vultures (*Torgos tracheliotus*; Figure 9) have virtually disappeared from the region (Thiollay & Rondeau 2004). Ironically, the US Department of Agriculture's Wildlife Services has recently increased its take of vultures, including Black Vultures (*Coragyps atratus*), one of the few vulture species that is doing well (Anon. 2004h). According to the same source, in 2003, 2884 vultures were killed and the Wildlife Services has refused to release data on vultures killed in 2004.

Disappearance of south Asian vultures

Vulture declines have been particularly severe in south Asia (Prakash 1999; Oaks *et al.* 2004). Once some of the most common raptors in the world and with large urban populations (Galushin 1971), White-rumped (*Gyps bengalensis*), Indian (*Gyps indicus*), and Slender-billed Vultures (*Gyps tenuirostris*); the latter two split from Long-billed Vulture (*Gyps indicus*) of the Indian subcontinent have declined faster than any other bird species, from least concern in 1994 (Collar *et al.* 1994) to critically endangered by 2000 (Stattersfield & Capper 2000). Prakash (1999) was the first to report on declines of 96%-97% in the Keoladeo National Park between 1988 and 1999, and in a carcass dump at Uttar Pradesh, Long-billed Vultures declined from 6000 in 1991-92 to five in 1994 (Eaton 2003). Although infectious disease initially seemed most consistent with the observed symptoms (Cunningham *et al.* 2003), further studies have confirmed renal failure caused by the cattle anti-inflammatory drug diclofenac as the underlying cause (Green *et al.* 2004; Oaks *et al.* 2004). The combination of this sudden population crash and a potential increase in carcass numbers, combined with infectious agents and high human population density, may cause increases in incidences of anthrax, bubonic plague, and rabies (Pain *et al.* 2003), but these crucial interactions have not been studied.

Costs and consequences

Even though no one has estimated the potential cost of the loss of decomposition services provided by vultures, increased disease transmission and consequent health spending is likely. Observations in India, where most people do not consume cattle and where most animal carcasses are simply left outside for vultures, indicate substantial increases in the numbers of rotting carcasses, especially around human habitations (Prakash *et al.* 2003). Between 1992 and 2001, V. Prakash observed a 20-fold increase in the numbers of feral dogs at an Indian garbage dump (Prakash *et al.* 2003). In 1998, more than 30,000 of the world's 35,000-50,000 rabies deaths took place in India (Anon. 1998f), where approximately 1,000,000 post-exposure treatments of rabies were reported, mostly caused by dogs (Anon. 1998f). Increased numbers of cattle carcasses also increase the chances of the spreading of livestock diseases such as anthrax (Prakash *et al.* 2003). It may be no coincidence that the 1994 outbreak of bubonic plague in western India occurred soon after the start of the crash of vulture populations. Although the ecological factors behind this outbreak were not systematically studied (Gratz 1999), it is thought to have been initiated by an unusually hot summer killing many cattle, the carcasses of which led to an explosion in rat numbers (Kaplan 1997). The plague infected at least 876 people, killed 54, resulted in quarantines and evacuations, and the resulting media attention led to trade and tourism boycotts (Gratz 1999). The whole episode cost India over US\$2 billion (Kaplan 1997).

Even though feral dogs seem to be replacing vultures in parts of India, their scavenging is less efficient and less sanitary than the vultures'. While vultures can remove all soft tissues extremely rapidly (Houston & Cooper 1975), dogs eat only the choice bits, leaving much rotting flesh behind. This not only provides a breeding ground for pathogenic bacteria, it also allows resistant spores to form (Houston & Cooper 1975). Dogs' stomachs are about four times less acidic (Lui *et al.* 1986) than those of vultures (Houston & Cooper 1975), increasing the likelihood of survival and transmission of pathogenic bacteria such as *Brucella abortus* or *Bacillus anthracis*, found in carcasses fed on by dogs. In addition, increasing numbers of feral dogs and rats mean more vectors of human diseases such as rabies and bubonic plague, as well as wildlife and livestock diseases caused by canine distemper virus, canine parvovirus, *Leptospira* bacteria and other pathogens (Pain *et al.* 2003; Butler *et al.* 2004). Furthermore, subsidized by a carcass surplus, the increased populations of these opportunistic mamma-

lian scavenger-predators are likely to put a higher predation pressure on vulnerable wildlife (Pain *et al.* 2003).

Socioeconomical effects

The disappearance of vultures from India has also had social, economical, and even religious consequences. Their loss has meant the loss of income for the impoverished “bone collectors” who rely on the efficient and relatively hygienic cleaning of vultures (Pain *et al.* 2003). Since the Parsis, which comprise a sect of Zoroastrianism, believe that death pollutes the sacred elements of earth, fire, and water, they cannot use any of these elements to dispose of their dead. For centuries the Parsis have been leaving their dead to the elements, to be cleaned by avian scavengers. This is a practice whose roots go back 8000 years, to the Neolithic site of Çatalhöyük, Turkey (Eaton 2003), where drawings of Cinerous Vultures (*Aegypius monachus*) circling headless bodies have been found. On *dakhmas* or “Towers of Silence” constructed for this purpose, vultures would normally take about half an hour to clean a corpse and three corpses would be left each day. After the crash of vulture populations, however, hardly any vultures visit and smaller avian scavengers are not effective. The corpses can no longer be disposed of according to the Parsi religious doctrine, which has resulted in a spiritual crisis (Parry-Jones 2001).

Summary

Scavengers, especially the obligate scavengers consisting of the Old and New World vultures (Houston 1979), provide one of the most important yet under-appreciated and little-studied ecosystem services of any avian group due to the difficulty of and human aversion towards studying rotting substances (DeVault *et al.* 2003). Although there are some studies quantifying carrion consumption by avian scavengers (Houston 1988; DeVault *et al.* 2003, and references therein), despite an extensive literature search, I was unable to find a published study that compared carcass decomposition rates between two areas with intact and reduced avian scavenger communities. Such a “before and after” study would have been especially valuable in quantifying the effects of the Indian subcontinent vulture population crash (Prakash *et al.* 2003). As such, this and many other unconduted studies on the ecological roles of avian scavengers represent significant and urgent research opportunities for avian ecologists. If the declines in vulture populations continue, it may soon be too late to find an intact “before” community in most parts of the world.

Compared to other avian functional groups, the obligate scavenger guild is tiny, comprised of only a few dozen species whose food consumption is predominantly based on scavenging. As such, even the declines or extinctions of a small number of species can result in significant reductions in avian scavenging, especially when one considers that in any one part of the world there are at most seven species of vultures. Their scavenging nature requires that these birds represent the epitome of animal flight, and, ecologically and evolutionarily, vultures are in a unique and highly threatened class of their own. From prehistoric Africans likely following vultures to obtain carcasses to Andean and Californian natives revering condors to Neolithic Anatolians and present-day Parsis leaving their dead on *dakhmas*, vultures’ unique status in ecosystems has always been paralleled in their special place in the human cultural landscape. It is now upon us to make sure that these majestic birds can continue to play their crucial roles in the biosphere and in the human psyche for the millennia to come.

Nutrient deposition

An underappreciated role of birds is transporting nutrients from one habitat to another. This is particularly important in the case of seabirds transferring marine productivity to terrestrial ecosystems, especially in coastal areas and unproductive island systems (Sánchez-Piñero & Polis 2000). Seabird droppings are enriched in important plant nutrients such as calcium, magnesium, nitrogen, phosphorous, and potassium (Gillham 1956). Murphy (1981) estimated that seabirds around the world transfer 10^4 to 10^5 tons of phosphorous from sea to land every year, and this guano also provides an important source of fertilizer and income to many people living near seabird colonies. Ironically, the very currents such as Benguela, California, and Humboldt that facilitate spectacular marine productivity, also create temperature inversions that result in low productivity deserts on nearby landmasses. Marine birds (Figure 10), by providing allochthonous

inputs in the form of guano and carcasses, help offset this imbalance and are crucial conduits between some marine and terrestrial areas (Sánchez-Piñero & Polis 2000; Croll *et al.* 2005). Avian enrichment of soils with nutrient-rich guano can have indirect but significant and cascading effects on the populations of plants (Stapp *et al.* 1999; Croll *et al.* 2005), invertebrates (Polis & Hurd 1995, 1996), rodents (Stapp & Polis 2003a, 2003b), and even large mammals (Iason *et al.* 1986; Wolfe *et al.* 2004).

Gulf of California Islands

The nutrient-poor desert islands of the Gulf of California, Mexico provide a natural laboratory for studying the role seabird allochthonous inputs play in shaping island ecosystems (Polis & Hurd 1995, 1996; Anderson & Polis 1999; Stapp *et al.* 1999; Sánchez-Piñero & Polis 2000). In a detailed study of this system, Polis & Hurd (1996) found that on islands with seabird colonies, arthropods were 2.2 times more abundant than on islands without colonies. Sánchez-Piñero & Polis (2000) showed that tenebrionid beetles, a dominant consumer group on the Gulf of California islands, were five times more abundant on nesting and roosting islands, and on these islands, six times more abundant inside versus outside the bird colonies. On roosting islands, birds' primary effect was to increase plant productivity through guano input, whereas on nesting islands, bird carcasses provided significant amounts of food for tenebrionids. Using stable isotopes, Stapp *et al.* (1999) revealed that seabird nutrient subsidies to these desert islands are particularly important during the wet El Niño years when the availability of seabird-derived nutrients significantly increased plant productivity. More detailed studies of rodent populations on these islands confirmed the direct and indirect effects of marine subsidies in affecting consumer population dynamics (Stapp & Polis 2003a, 2003b), emphasizing the role seabirds play in shaping community composition on resource-limited islands.

Community and ecosystem-level effects

Besides affecting productivity and abundance of organisms, increased influence of seabird colonies can also change invertebrate community composition. On the Mediterranean island of Bagaud, the presence of Yellow-legged Gull (*Larus cachinnans*) colonies significantly changed beetle assemblages, with a marked shift from polyphagous species to polyphagous tenebrionid species (Orgeas *et al.* 2003), which seem to benefit from bird colonies more than other beetle families (Sánchez-Piñero & Polis 2000). Seabird colonies can also have dramatic impacts on the productivity, diversity, and composition of nearby plant communities (Anderson & Polis 1999), sometimes at the expense of native taxa (Vidal, Jouventin & Frenot 2003; Vidal, Medail *et al.* 2000). Moderate disturbance by seabirds may maximize diversity (Vidal *et al.* 2003), with increased disturbance resulting in an increase of alien species at the expense of native species (Vidal *et al.* 2003). On the other hand, some plant species, such as those found in the genus *Lepidium* (Brassicaceae) endemic to New Zealand, have so adapted to the nutrient enrichment and disturbance regimes associated with seabird (and seal) colonies that some are extinct or threatened with extinction as a result of seabird and seal declines (Norton *et al.* 1997).

Although many studies on the effects of seabird allochthonous input have focused on specific taxa, these inputs often influence entire ecosystems. Simultaneous increases in invertebrates and lizards as a result of the addition of nutrients by seabirds has been documented on islands off New Zealand (Markwell & Daugherty 2002). Seabird-derived nutrients were found in the tissues of plants, invertebrates, and lizards, and the addition of this resource led to a significant increase in organismal abundance across the board. Harding *et al.* (2004) showed that 28-38% of the nitrogen in the biota of streams near Westland Petrel (*Procellaria westlandica*) breeding colonies in New Zealand were marine-derived. The authors also emphasized the potential consequences for nitrogen cycling and ecosystem productivity of the reduction in marine-derived nutrients following extensive population declines in seabird colonies on the New Zealand mainland.

Perhaps the most striking example of the importance of seabird nutrient input comes from the remote Aleutian islands of Alaska (Croll *et al.* 2005; Maron *et al.* 2006). The former lack of native mammals on these islands had made them a haven for seabirds, and more than 10 million individuals that belong to 29 species still breed on the Aleutians. Before the introduction of arctic foxes (*Alopex lagopus*) to over 400 Aleutian islands, however, these numbers were probably far greater, since fox removal from 40 islands has resulted in a two order-of-magnitude increase in Whiskered Auklet (*Aethia*

pygmaea) populations (Williams *et al.* 2003; Croll *et al.* 2005). Similarly, nine fox-free islands have nearly 100 times more seabirds than nine comparable but fox-infested islands (Anon. 2004i; Croll *et al.* 2005). Croll *et al.* (2005) and Maron *et al.* (2006) recently showed that this reduction by foxes reduced the annual input of guano from 362 g to 5.7 g per m². This has resulted in substantial declines in soil phosphorous, marine-derived nitrogen, and plant nitrogen content, triggering an ecosystem switch from grassland to maritime tundra on fox-infested islands. Given that countless formerly predator-free oceanic islands lost their immense seabird populations to introduced predators (Pimm *et al.* 2006), it is most likely that trophic cascades and ecosystem shifts triggered by the loss of seabirds are more the rule than the exception.

Life history consequences

The effects of seabird nutrient input on the life histories of island species can be substantial, even affecting the survival of small mammals (Wolfe *et al.* 2004) and the reproductive success of large ones (Iason *et al.* 1986). Iason *et al.* (1986) found that local nutrient addition by Herring Gulls (*Larus argentatus*) on the Isle of Rhum, Scotland, resulted in an enrichment of soil nitrogen and phosphorus, followed by an increase in the nitrogen content of vegetation, which led to a rise in the lifetime reproductive success of red deer (*Cervus elaphus*) females feeding on this vegetation. The populations of the endangered marsupial dibbler (*Parantechinus apicalis*) on two islands off western Australia provide a particularly fascinating example of nutrient subsidies (Wolfe *et al.* 2004). Males of some dasyurid species such as dibblers experience substantial to complete stress-related post-breeding mortality, which is reduced by improved body condition (Wolfe *et al.* 2004). On the island with greater nesting seabird density, plant-available soil nutrients were 5-18 times more enriched, there were more invertebrates, and the body conditions of insectivorous dibblers were significantly better. This led to higher post-breeding survivorship of males, highlighting the crucial importance of seabird-derived resources for these animals.

Disappearing seabirds



Figure 10.
Black-browed albatross
(*Thalassarche melanophris*),
nutrient depositing resource linker.

Off Cape Town, South Africa.
Cagan H. Sekercioglu.

Unfortunately, guano production by seabirds is one of the most threatened of avian ecosystem services, due to the rapid decline in seabirds worldwide (Anon. 2004d). In general, seabirds are long-lived, ground-nesting species with low reproductive rates, and as such, are very prone to adult mortality and introduced predators. The recent crash of the populations of seabirds, particularly albatrosses (Anon. 2003e) is mainly caused by these birds accidentally getting caught on fishing longlines. Although fishery waste can be rather important as a food source for seabirds, with about six million birds being supported in the North Sea alone (Garthe & Scherp 2003), a large portion of birds supported are generalist gulls that may even exclude more specialized seabird species from limited nesting grounds. The high bycatch mortality seen in more specialized and declining seabird families, such as Procellariidae and Diomedidae, more than offsets the population increases enabled by the food subsidies originating from fishery waste. The magnitude of the bycatch mortality is exemplified by Black-browed Albatrosses (*Thalassarche melanophris*; Figure 10), which declined from least concern status in 1998 to near threatened in 2000, vulnerable in 2002, and endangered in 2003, a rate not seen in other bird species except Indian vultures. There are various cost-effective methods for reducing bycatch-related seabird mortality, with bird-scaring lines being particularly successful (Lokkeborg 2003). However, effectively implementing these measures has been hindered by the political and logistical constraints inherent to monitoring fisheries and fishermen, many of whom fish illegally in remote international waters.

Aquatic communities

Avian nutrient inputs are not limited to terrestrial ecosystems. Many water-associated birds breed in large colonies, which often contribute significant amounts of nutrients to coastal and wetland aquatic communities. In Florida Bay, USA, guano produced by a seabird colony fertilized seagrasses, which are critical habitats for the young of many reef fish (Powell *et al.* 1991). Black Skimmers (*Rhynchops niger*), South American Terns (*Sterna hirundinaceae*), Snowy-crowned Terns (*Sterna trudeaui*), Common Terns (*Sterna hirundo*), and other piscivorous seabirds at an Atlantic coastal lagoon in Argentina produced 0.27 g of guano/m²/day, which increased the density of soft bot-

tom benthic macrofauna and affected the abundance and behavior of several species (Palomo *et al.* 1999). The guano of thousands of White Ibis (*Eudocimus albus*) nesting in the Okefenokee Swamp of Georgia, USA fertilized this macronutrient-limited blackwater marsh, increased phosphorous levels, and augmented the biomass of phytoplankton and planktivorous fish (Oliver & Schoenberg 1989). The nutrient additions were so substantial that even two years after birds abandoned this colony, the effects of nutrient enrichment were still visible.

Excessive nutrient inputs

Although avian nutrient inputs benefit many species, communities, and ecosystems, there can be too much of a good thing. Excessive inputs of avian guano can inhibit plant growth (Gillham 1960). Abundance and species richness of invasive plant species may increase in areas of greatest intensity of bird colonies (Vidal, Jouventin & Frenot 2003; Vidal, Medail *et al.* 1998), since these plants often have high disturbance tolerance and colonizing capacity. Human presence can increase the establishment success of invasive plants near bird colonies, as exemplified by the increased number of alien plants in the King Penguin (*Aptenodytes patagonicus*) colonies closer to the scientific research station on Possession Island, in the Crozet archipelago (Vidal *et al.* 2003). Interactions with people can also result in population explosions of opportunistic species, such as Yellow-legged Gulls, whose breeding colonies can damage to fragile and rare plants and animals (Vidal *et al.* 1998). As also exemplified by invasive plant species dispersed by birds (Cronk & Fuller 1995) and introduced pigs catalyzing the elimination of Channel island foxes by Golden Eagles (Roemer *et al.* 2002), human activity and the species that benefit from it can significantly modify ecological interactions and turn positive synergisms into negative ones (Lundberg & Moberg 2003).

Land use changes in many parts of North America have led to population increases of some goose species, particularly Canada Geese, due to the increased availability of food from agricultural areas, golf courses, and other human-modified habitats. Although this is preferable to the population declines seen in many anatids, large concentrations of ducks and geese can add excessive amounts of nutrients to wetlands, parks, and other open areas, reducing water quality, destroying vegetation, creating pollution, and even causing disease outbreaks (Post *et al.* 1998). Manny *et al.* (1994) calculated that of all outside nutrients that entered Michigan's Wintergreen Lake, waterfowl added 69% of carbon, 27% of nitrogen, and 70% of phosphorous, the last two of which can lead to eutrophication. While more than 40,000 Snow Geese (*Chen caerulescens*) and Ross' Geese (*Chen rossii*) in the Bosque del Apache National Wildlife Refuge of New Mexico constitute one of the most impressive avian spectacles of North America, they also add 40% of all nitrogen and 75% of all phosphorous to the wetland where they roost (Post *et al.* 1998). Increases in the numbers of these birds as a result of agricultural practices have resulted in excessive nutrient additions to this wetland, as well as to the destruction of salt marshes on the shores of Hudson Bay, where Snow Geese graze during summer (Kerbes *et al.* 1990).

Summary

Avian allochthonous inputs, particularly by seabirds, can provide substantial nutrient subsidies that are especially valuable in nutrient-poor ecosystems. Although in some guano-rich ecosystems, such as the Pacific coast of North America, guano-derived nutrients may be of limited consequence (Wootton 1991) and excessive inputs can lead to pollution and eutrophication (Post *et al.* 1998), on many low productivity islands the terrestrial ecosystem is largely subsidized by avian inputs (Sánchez-Piñero & Polis 2000). On oceanic islands, many of which are nutrient poor (Anderson & Polis 1999), nutrient inputs from sea to land can greatly increase nitrogen and phosphorous concentrations in soils, enriching plants and consequently, affecting the entire food web on these islands (Anderson & Polis 1999). Nutrient deposition by seabirds can be so important that seabird losses can trigger trophic cascades and ecosystem shifts (Croll *et al.* 2005). Besides enriching soils, seabirds may even create them. In polar areas with low levels of biological activity, seabirds may be the main agents of soil formation, as exemplified by Adelie Penguin (*Pygoscelis adeliae*) rookeries on Cape Bird, Antarctica (Heine & Speir 1989). Guano production by seabirds also constitutes a significant socio-economic resource (Haynes-Sutton 1987), especially for impoverished communities that cannot afford commercial fertilizers. Therefore, reductions in seabird guano, in addition to affecting natural communities, can also have agro-economical consequences for many people, particularly in the developing world.

Unfortunately, seabirds are among the most threatened of all avian taxa. Half of all species whose primary habitat is the sea are extinction-prone (Sekercioglu *et al.* 2004), a proportion that is by far the largest among all habitat types. The unprecedented population crash of pelagic birds is one of the most important bird conservation crises of our time and will only get worse if the world fishing community and fish consumers are not fully engaged in finding and enforcing solutions.

Ecosystem engineers and other ecological actors

Birds have a plethora of other roles in ecosystems that cannot be pigeon-holed into the main categories above. For example, grazing birds, such as geese and ducks (Figure 6), can have significant impacts on the vegetation of some areas, particularly in wetlands and coastal areas where anatids are often concentrated. Although intensive grazing can lead to the degradation of some areas, such as the salt marshes on the shores of Hudson Bay damaged by Snow Geese (Kerbes *et al.* 1990), ducks and geese can also reduce agricultural residues in an environmentally-compatible manner, as opposed to open-field burning that has been restricted by legislation (Bird *et al.* 2000).

Ecosystem engineers

Perhaps the least appreciated ecological contribution of birds are as ecosystem engineers (Jones *et al.* 1994). This is partly because avian engineering rarely has the very visible effects of more prominent engineers such as beavers or trees, but nevertheless, some birds are ecosystem engineers, and sometimes in more ways than one (Daily *et al.* 1993). Another reason for the relative lack of awareness is that ecosystem engineering itself has received little recognition until recently (Jones *et al.* 1994). By definition:

“Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain, and/or create habitats” (Jones *et al.* 1994)



Figure 11.
Slaty-tailed Trogon (*Trogon massena*), ecosystem engineering non-trophic process linker, digging a nest in a termite mound.

Pipeline Road, Panama.
Cagan H. Sekercioglu.

Given that birds have limited capacity to change their surroundings physically (as opposed to corals, earthworms, or prairie dogs, for example), some of the best examples of avian engineering come from bird nests (Figure 11). Even small bird nests often house beetles, moths, and other invertebrates (Collias & Collias 1984). At the other extreme, colonial Social Weavers (*Phalacrocorax socius*) construct the largest nest of any bird species. In addition to providing a dwelling to many other organisms, such as snakes, Pygmy Falcons (*Polihierax semitorquatus*), and countless invertebrates, these massive structures can even bring down trees (personal observation). Even though not as extreme, there are various other examples of large avian nests, particularly of raptors, weavers, and oropendolas, that have effects that go beyond the original nest builder. Burrow-nesting European Bee-eaters (*Merops apiaster*) are allogenic ecosystem engineers in arid environments, since they remove large amounts of soil, increase the rate of soil loss, create nest burrows often used by other species, and attract burrow-using invertebrates which are consumed as food by various birds (Casas-Crivillé & Valera 2005). Trogons (Figure 11) engineer in tropical forests (Valdivia-Hoeflich *et al.* 2005) and burrow-nesting seabird colonies can change soil fertility and lead to massive erosion (Furness 1991).

The best examples of nest construction resulting in ecosystem engineering come from woodpeckers. Their unique behavior of drilling nest holes is arguably a more important contribution to ecosystems than the insectivorous habits they share with many other species, although woodpeckers' superior ability to extract invertebrates certainly benefits many trees. Because they drill nesting cavities which are later used by other, secondary cavity-nesting species, woodpeckers provide novel resources to other species by changing the physical structure of their environment and therefore, are ecosystem engineers par excellence. Since cavity nesting bird species often have higher nesting success (Knutson *et al.* 2004), woodpeckers are important components of many avian communities. Therefore, it is encouraging that woodpeckers (Picidae) comprise the only avian family that contains significantly fewer threatened species than expected (Bennett & Owens 1997). This resilience may be a consequence of woodpeckers' ability to extensively engineer their habitats. Some woodpeckers assume further ecological importance as “double keystone” species, as in the case of sapsuckers (*Sphyrapicus* spp.), which provide bird and mammals with nest cavities as well as making nutritious sap available to dozens of vertebrate and invertebrate species (Daily *et al.* 1993). Avian provisioning of sap is not limited to woodpeckers and is also seen in Akiapolaau

(*Hemignathus munroi*), an endangered Hawaiian honeycreeper, whose decline may have averse effects on the species that benefit from this sap (Pejchar & Jeffrey 2004).

Possibly an important bird ecosystem engineer and perhaps one of the most significant of avian ecological actors may also be the one that has received the least recognition. The Passenger Pigeon (*Ectopistes migratorius*) is often presented as an example of a bird species, maybe the world's most abundant, whose decline from billions of birds in the mid 19th century to none by 1914 had no measured effects on its ecosystem (Simberloff 2003). However, the key word here is "measured". Unfortunately, no one thought to study the northern red oak (*Quercus rubra*) and white oak (*Quercus alba*) forests before Passenger Pigeons went extinct. It is likely that Passenger Pigeons, which preferred northern red oaks, had a diverse range of ecological effects on this forest via physical disturbance, nutrient deposition, and acorn consumption (Ellsworth & McComb 2003). Tree branch and stem breakage by billions of roosting birds, in addition to changing the forest structure, also built up fuel loads, and likely led to increased fire frequency and intensity in northern red oak forests. This, in combination with the consumption of vast numbers of acorns, may explain the dominance of white oaks in the range of Passenger Pigeons before their extinction, which possibly facilitated the range expansion of northern red oaks (Ellsworth & McComb 2003).

Seed consumers

Although birds may well be the most important seed dispersers, especially in the tropics, some granivorous birds, such as Passenger Pigeons, finches, and parrots, can be significant seed predators. Red Crossbills (*Loxia curvirostra*) in Spain consume more than 80% of the ripening seeds of relict Scots pines, whose regeneration is limited by the high rate of seed predation (Castro *et al.* 1999). Avian seed predation may increase in tropical forest fragments since many tropical granivorous birds are more common in forest fragments and outside forests than in extensive forest. In the forest fragments of southeast Brazil, where rodent seed predators have declined and granivorous birds have increased, birds have become the most important, if not the main, seed predators of *Croton priscus* (Euphorbiaceae) (Pizo 1997). In fact, granivorous birds are the most important avian pests of agriculture, although damage estimates are often exaggerated and often not collected in a scientific manner (Weatherhead *et al.* 1982). Weatherhead *et al.* (1982) derived corn damage estimates by Red-winged Blackbirds (*Agelaius phoeniceus*) by combining energetics and life history information with a study of captive birds. The resulting damage estimate of 0.41% of total production agreed with the range of 0.25-0.80% obtained by extensive damage sampling in nine other regions and was well below a 1975 government estimate.

The most notorious example of an avian seed predator is the Red-billed Quelea (*Quelea quelea*). It is the world's most numerous bird with 1-3 billion individuals (Elliott & Lenton 1989) and the predominant avian pest in Africa. Nevertheless, detailed studies indicate that although local damage may be high, the impact on continental food production is negligible, with losses to cereal crops amounting to less than 1% of the production (Elliott & Lenton 1989). This is in the region of losses caused by bird pests in other parts of the world (Weatherhead *et al.* 1982; Elliott & Lenton 1989). Also, considering the important ecological roles played by Red-billed Queleas as predators of insects, including pest species, as providers of nutrients that also fertilize fields and orchards, and as important food sources for many birds, mammals, and people (Elliott & Lenton 1989), the extensive environmental damage and non-target deaths caused by explosives, fire bombs, and especially aerially-sprayed fenthion (Meinzingen *et al.* 1989) cannot be justified. Fenthion has especially severe effects on aquatic species found in water bodies near quelea roosting sites and on predatory and scavenging birds (McWilliam & Cheke 2004). Birds of prey can reduce quelea populations significantly (Bruggers & Elliott 1989), but many of them die after spraying operations (Meinzingen *et al.* 1989). Furthermore, many Africans collect and consume queleas killed by avicides and, are thus routinely exposed to dangerous chemicals (Jaeger & Elliott 1989).

Mass killing of the other super-abundant granivorous bird, the Passenger Pigeon, may have had public health consequences as well. Oak masts are known to cause population explosions in white-footed mice (*Peromyscus leucopus*) (Blockstein 1998), which reduce songbird populations directly through nest predation and indirectly by increasing avian predator populations (Schmidt & Ostfeld 2003). It is likely that the consumption of a large portion of the oak mast by 2-3 billion Passenger Pigeons had limited white-footed mice numbers in the past. Most disconcertingly, white-footed mouse and the black-tailed deer (*Odocoileus hemionus*) are both vectors for Lyme disease carrying ticks. The increase in the oak crop available to these mammals after the pigeons went extinct may have increased their populations, contributing to the increased frequency of Lyme disease we observe today (Blockstein 1998).

Beyond ecosystems

Thus far I have focused on typical avian ecosystem services. However, birds provide various other “indirect” services, ranging from the aesthetic to the critical to the esoteric, which contribute to human needs in meaningful ways (Filion 1987). These cover the spectrum from Common Cranes (*Grus grus*) inspiring crane dances, the evidence for which goes back more than 8000 years at the Neolithic site of Çatalhöyük, Turkey (Russell & McGowan 2003) to White-throated Dippers (*Cinclus cinclus*) serving as indicators of stream water quality (Ormerod & Tyler 1993) to the economical contributions of millions of people who spend significant amounts of money and time to study, observe, photograph, and enjoy the birds of the world (Sekercioglu 2002c).

Environmental monitors

Perhaps birds’ most important indirect function in relation to human-dominated ecosystems is as environmental monitors. Their history here is long, particularly if one uses a liberal definition of environmental monitoring. Back in ancient Rome, domestic geese had a guarding function since they would make quite a racket in response to intruders, a service these birds still provide in a few remote places, such as the Kars province of Turkey. The classic example of avian environmental monitoring, however, is the use of caged canaries in coal mines to warn against the accumulation of toxic gases. These birds are much more sensitive than people to the build-up of carbon monoxide, and give distress signals or keel over before men can detect its presence. It was 1986 before some 200 canaries were phased out of the mining pits in Britain, where two per pit had been required since 1911, to be replaced by electronic gas detectors. At the time, the BBC commented that miners, who grew fond of the birds, “are said to be saddened by the latest set of redundancies in their industry, but do not intend to dispute the decision.” (Anon. 1986b). Birds have far more and ongoing significance, however, as indirect monitors. Indeed, the beginnings of the modern environmental movement in the USA can be traced to Rachel Carson’s classic book, *Silent Spring* (Carson 1962). The title alludes to the catastrophic impacts of broadcast DDT spraying on bird populations in the United States – presaging springs without birdsong. Carson’s work had a catalytic effect on the environmental movement, rapidly creating public awareness and political action that culminated in the first Earth Day less than a decade later.

Since *Silent Spring*, birds have remained the leading indicators of environmental disruption in the eyes of both scientists and the general public. Scientists employ birds as monitors of various environmental factors, including overuse of pesticides, radionuclide contamination, fisheries stocks, marine pollution, streamwater quality, and wetland acidification (Diamond & Filion 1987; Furness & Greenwood 1993; Bryce *et al.* 2002). In addition, because so many people are devoted birdwatchers or maintain bird feeders, changes in avian population sizes and distributional status are detected early on and often highly publicized, particularly so with the rapid growth of “citizen science” projects involving bird enthusiasts (Anon. 2003f). The immense publicity in the United States surrounding the decline of the Northern Spotted Owl (*Strix occidentalis occidentalis*), the extinction in the wild and captive breeding of the California Condor, and the recent rediscovery of the Ivory-billed Woodpecker (*Campephilus principalis*) (Fitzpatrick *et al.* 2005) are cases in point. In New South Wales, Australia, there are road signs pointing out breeding areas for the endangered Regent Honeyeater (*Xanthomyza phrygia*). The status of rare and endangered bird species are now regularly detailed in journals such as *Bird Conservation International* and *Bulletin of the British Ornithologists’ Club*. This interest in birdwatching is just one example of the intangible but integral services birds provide for people as sources of entertainment, wonder, and connecting with nature.

Birdwatching and conservation

Birds generate substantial income via birdwatchers who make significant economic contributions to many communities around the world (Sekercioglu 2002c), not to mention creating a market that fuels the production of high-quality ornithological literature. Birdwatchers are one of the best sources of ecotourism income since they form the largest single group of ecotourists, are educated and have above-average earnings (Ceballos-Lascuráin 1996; Cordell & Herbert 2002; Sekercioglu 2002c). Because of the zeal of many birdwatchers and the resources these people are willing to invest in this activity, birdwatching is becoming the most rapidly growing and most environmentally conscious segment of ecotourism and provides economic hope for many natural areas around the world. The high expectations of many birdwatchers, com-

bined with their high average incomes, often result in large financial contributions to the localities visited, especially in the case of self-reliant and independent birdwatchers (Kerlinger & Brett 1995). In addition, information gathered by birdwatchers, such as during breeding bird surveys, Christmas bird counts and other “citizen science” projects (Anon. 2003f) can contribute substantially to ornithological knowledge, especially in tropical areas with few researchers (Mason 1990).

Birdwatchers’ knowledge of birds and expectations of seeing a variety of species provide a direct link between avian biodiversity of a region and local income. Although birdwatchers are sometimes criticized for commodifying nature through “twitching” or “listing”, this commodification actually makes it possible for local communities in areas with many and/or rare bird species to generate more income from hosting birdwatchers than other tourists. Because most birdwatchers know what they want to see and have high expectations of seeing certain species, they are likely to spend more money in order to see bird species in their natural environment than the average ecotourist who is not particularly interested in birds. The consequent increase in the local awareness of the value of bird biodiversity may be key to preserving many natural areas near human population centers. Local people who observe the direct monetary benefits of biodiversity as a result of showing various species to birdwatchers are more likely to conserve ecosystems that harbor unusual birds. Better ecological knowledge and higher expectations of birdwatchers also result in the preservation of many patches of native habitat that host rare birds but do not have official protection.

In many places, indigenous people lack the education and essential financial resources required to invest in ecotourism and they usually qualify for the most menial and low-paid jobs (King & Stewart 1996). Guiding for birdwatchers, however, values knowledge of natural history, has minimal language requirements, and is less demanding and better paid than jobs requiring hard labor. Birdwatching is a most promising branch of ecotourism because birdwatchers comprise a large and growing pool of educated and relatively wealthy individuals who desire to observe birds in their native habitats and whose activities have relatively low environmental impact. Among various kinds of ecotourism, birdwatching has the highest potential to contribute to local communities, educate locals about the value of biodiversity, and create local and national incentives for the successful protection and preservation of natural areas.

Birds as inspiration

As millions of birdwatchers would attest, birds have long been a source of wonder and curiosity for *Homo sapiens*, if for no other reason than their seemingly miraculous ability to fly. The legend of Daedalus and Icarus trying to escape the labyrinth of King Minos of Crete by imitating birds is a classic example and many ancient religions had gods embodied as raptors and other birds (Diamond 1987b). Medieval Europeans were puzzled about where the birds went in the winter, and even came up with the idea that they dove into the sea and spent the season underwater. Owls symbolize wisdom in our own culture, but were considered evil omens in others. There may well be more folklore associated with Strigiformes than with any other bird order, and some of the best examples can be found in the owl family accounts in HBW (Bruce 1999; Marks *et al.* 1999).

Ancient Egyptians associated various birds with gods, with the sun god Horus typically represented as a falcon, Lappet-faced Vulture (*Torgos trachliotus*) pendants being placed in pharaonic graves, and Sacred Ibises (*Threskiornis aethiopicus*) being raised for sale to pilgrims to be placed in tombs as offerings. Birds of prey have had prominent roles as symbols of martial might far back into antiquity. In our own time, eagles still play that role as symbols of the United States and other armed forces, as well as of nations such as Albania and Germany. The legendary beauty of some birds has been a major interest of people for virtually as long as records have been kept. Their feathers have long adorned everything from the warrior headdresses of Papua New Guinea to the robes of Hawaiian kings to the hats of Victorian ladies. Birds have been frequently featured both in secular and religious art (Figure 12), avian mating displays have inspired various forms of human dancing (Russell & McGowan 2003), and John James Audubon’s bird paintings are so admired that some of his original prints now sell for over 100,000 Euros.

The right to exist

Most importantly, birds, like other creatures that share this planet with us, also have an “existence value”. Whether or not I eventually see one, I value the fact that Congo Peacocks (*Afropavo congensis*) and Phillippine Eagles (barely) exist and regret that Haast’s Eagles (*Harpagornis moorei*), Passenger Pigeons, Black Mamos (*Drepanis*



Figure 12.
The Red-crowned Crane (*Grus japonensis*) is a major cultural icon, a symbol of peace, and a source of artistic inspiration in eastern Asia. Popularly believed to live 1000 years, it is ironically endangered, with a declining global population of only 2400 birds.

Hokkaido, Japan.
Cagan H. Sekercioglu.

funerea), and dozens of Pacific island flightless rails survive no longer. As David Ehrenfeld once said, species and communities should be conserved “because they exist and because this existence is itself but the present expression of a continuing historical process of immense antiquity and majesty. Long-standing existence in Nature is deemed to carry with it the unimpeachable right to continued existence” (Ehrenfeld 1978).

Ehrenfeld’s view carries us into an active area of ethics, which in the context of HBW can be seen as centering around the question of what responsibilities people should have to maintain not just the ecological functions of birds, but also their roles in the evolutionary process. Most readers of this Foreword would probably share the view that everything possible should be done to maintain opportunities for avian speciation (Soulé & Lease 1995; Soulé 1999). But technological optimists would claim that we need not worry – threatened or extinct species can be cloned (albeit *sans* their original habitat) and even new kinds of “needed” or “desired” birds will be synthesized by genetic engineers in the future. To what degree is human alteration of the evolutionary trajectories of birds and other life forms ethical (Ehrlich 2001; Van Houtan 2006)? This is the sort of question that can only be answered by broad ethical discourse within society – perhaps by a global *Millennium Assessment of Human Behavior* such as has been proposed (Ehrlich & Ehrlich 2004). Looking at birds in ethical contexts should prove especially useful, considering their manifold interactions with *Homo sapiens*, and the long-standing and intense interest that our species has shown in them. In that process birds may help humanity achieve a sustainable society.

If we fail in our endeavor to reach a sustainable compromise with global biodiversity, including thousands of bird species, not only we will fail morally in our roles as stewards of other species and will be confined to an aesthetically impoverished planet, but we will also be faced with more concrete consequences. Important avian guilds are in rapid decline and consequent reductions in ecosystem processes are to be expected. The societal importance of ecological services is usually appreciated only after their loss. Historically extinct birds are the seemingly-distant rumble before an imminent flash flood of bird declines (Gaston *et al.* 2003) and population losses (Hughes *et al.* 1997), likely to be followed by concomitant decreases in ecological interactions (Sekercioglu *et al.* 2004) and evolutionary processes (Thompson 1996). The ecological and evolutionary consequences of the reductions in bird species and populations are hard enough to estimate, let alone put a price on. However, it is almost certain that there will be financial losses as a result of the reductions in ecological services provided by birds. In areas that suffer heavy avian losses, birdwatching tourism income will decline considerably. Investments in understanding and preventing declines in the populations of birds and other organisms will pay off only while there is still time to act. Even putting ecological and economical consequences aside, one does not have to be a birdwatcher or an ornithologist to feel a profound sense of loss from the disappearance of hundreds, if not thousands, of bird species.

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Bibliography

The full references to the citations included herein can be found towards the back of the volume, in the General List of References.

Acknowledgements

I am grateful to the Christensen, Koret, Moore Family, and Winslow Foundations, National Geographic and Wildlife Conservation Societies, and W. Loewenstern for funding my research. My special thanks go to P.R.

Ehrlich for his thorough revision of this essay, and to G.C. Daily, W.F. Laurance, C. Peterson, S. Renner, and N.S. Sodhi for their valuable comments. I am thankful to D. Wheye for producing such an excellent illustration despite the short notice. I greatly appreciated the assistance and understanding of F.O. Brenes, M.P. Castro, C. Logan, J.F. Sandí, and the rest of my Costa Rican crew, whose help enabled me to keep on writing during my field season. I thank the dedicated staff of HBW for their invitation, patience and for accommodating a review that ended up more detailed than any of us could imagine. Last but not the least, I salute all the ornithologists whose in depth studies enabled me to do an overview that would be difficult to accomplish for any other group.