

# Human impacts on the rates of recent, present, and future bird extinctions

Stuart Pimm<sup>\*†</sup>, Peter Raven<sup>†‡</sup>, Alan Peterson<sup>§</sup>, Çağan H. Şekercioğlu<sup>¶</sup>, and Paul R. Ehrlich<sup>¶</sup>

<sup>\*</sup>Nicholas School of the Environment and Earth Sciences, Duke University, Box 90328, Durham, NC 27708; <sup>†</sup>Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166; <sup>§</sup>P.O. Box 1999, Walla Walla, WA 99362; and <sup>¶</sup>Center for Conservation Biology, Department of Biological Sciences, Stanford University, 371 Serra Mall, Stanford, CA 94305-5020

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**Unqualified, the statement that  $\approx 1.3\%$  of the  $\approx 10,000$  presently known bird species have become extinct since A.D. 1500 yields an estimate of  $\approx 26$  extinctions per million species per year (or 26 E/MSY). This is higher than the benchmark rate of  $\approx 1$  E/MSY before human impacts, but is a serious underestimate. First, Polynesian expansion across the Pacific also exterminated many species well before European explorations. Second, three factors increase the rate: (i) The number of known extinctions before 1800 is increasing as taxonomists describe new species from skeletal remains. (ii) One should calculate extinction rates over the years since taxonomists described the species. Most bird species were described only after 1850. (iii) Some species are probably extinct; there is reluctance to declare them so prematurely. Thus corrected, recent extinction rates are  $\approx 100$  E/MSY. In the last decades, the rate is  $< 50$  E/MSY, but would be 150 E/MSY were it not for conservation efforts. Increasing numbers of extinctions are on continents, whereas previously most were on islands. We predict a 21st century rate of  $\approx 1,000$  E/MSY. Extinction threatens 12% of bird species; another 12% have small geographical ranges and live where human actions rapidly destroy their habitats. If present forest losses continue, extinction rates will reach 1,500 E/MSY by the century's end. Invasive species, expanding human technologies, and global change will harm additional species. Birds are poor models for predicting extinction rates for other taxa. Human actions threaten higher fractions of other well known taxa than they do birds. Moreover, people take special efforts to protect birds.**

The  $\approx 10,000$  species of birds are better known than any other comparably sized group of species. Estimates of their extinction rates influence estimates for other taxa (1) and provide the foundation for concerns about human impacts on the global rates of biodiversity loss (2). Considerable care is necessary in interpreting statements about how many bird species have already gone extinct and how many will do so in the future. Of course, listing all of the caveats necessary to such broad statements quickly becomes cumbersome. Authors sometimes drop them from statements about extinctions so as not to distract from their main message. Nonetheless, statements such as “ $n$  bird species have become extinct since the year 1500” really mean “are known to have become extinct.” This added qualification hides large differences in estimated extinction rates. Europe's exploration of the rest of the world merely continued to extinguish species at rates similar to those caused by the earlier Polynesian expansion across the Pacific. Statements of the kind “ $y$  percent of bird species are likely to become extinct in the coming century” generally imply “on the basis of current human impacts.” If human impacts expand at their present rate, they will threaten many species not presently at risk.

Exacerbating these problems, publications usually emphasize the names and images of well known extinct species. Such species are ordinarily only a small subset of the total of extinct species. Other more subtle problems similarly lead to underestimates of the extinction count. In assessing extinct species, conservationists follow the principle that a species survives even if it is

“missing in action,” not recently recorded in its native habitat that human actions have largely destroyed. This assumption prevents terminating conservation efforts prematurely, even as it again underestimates the total number of extinctions. Finally, rapidly declining species will lose most of their populations and thus their functional roles within ecosystems long before their actual demise (3, 4).

We explore the often-unstated assumptions about extinction numbers to understand the various estimates. Starting before 1500 and the period of first human contact with bird species, we consider the estimates in chronological sequence. We continue with the effects of first European contact, the period from 1500 to 1800. Finally, we consider extinctions to the present, proceed to those expected from human impacts to date, and conclude with those expected if human actions continue to expand at their present rate. To estimate extinctions, we calculate the extinction rate as the number of extinctions (E) per year per species or, to make the numbers more reasonable, per million species years (MSY) (ref. 5; see *Methods* below).

## Results

**Pre-European Extinctions.** On continents, the first contact with modern humans likely occurred 15,000 years ago in the Americas and earlier elsewhere, too far back to allow quantitative estimates of impacts on birds. The colonization of oceanic islands happened much more recently. Europeans were not the first transoceanic explorers. Many islands in the Pacific and Indian Oceans received their first human contact within the last two millennia (6). There are two methods to estimate how many species succumbed.

First, there are island surveys for bird skeletal remains found in caves and similar locations that protect them. These surveys routinely result in the descriptions of many species that survived until, but not through, the first human contact. They also find the remains of living species or those that survived until recently, species that taxonomists have described from complete specimens. Of course, not all such recent species appear in surveys of skeletal remains. For the Hawaiian Islands, for example, about half the species described from recent specimens also turn up as remains, suggesting that the surveys also find only half of the now-extinct species, other things being equal (7). For every species known from its remains, the remains of another await discovery. This prediction fits well with the continuing finds of new species known only from remains (Helen James, personal communication). Counting the species known to have and estimated to have succumbed to first contact suggests that between 70 and 90 endemic species were lost to human contact in the Hawaiian Islands alone, from an original terrestrial avifauna estimated to be 125–145 species (7). Comparable

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Abbreviation: E/MSY, extinctions per million species years.

<sup>†</sup>To whom correspondence may be addressed. E-mail: stuartpimm@aol.com or peter.raven@mobot.org.

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numbers emerge from similar studies across the larger islands of the Polynesian expansion (7). New Zealand stands as an exception to the modern/remains-only ratio because all modern native species have been found as remains in addition to the many now-extinct species (8).

Second, one can recreate the likely species composition of Pacific islands. Steadman (6), for example, examined the distribution of rail species. Each archaeologically well explored Pacific island has (or had) at least one unique species and larger islands more than one. He informally suggested that the Polynesians eliminated 2,000 species of rails alone. A more formal analysis by Curnutt and Pimm (9) examined the islands above the threshold size of supporting one or more rail species. The authors further restricted the set of sufficiently large islands to those geographically isolated enough to have a unique rail species. They also examined whether islands were high enough to survive defaunation by periodic tsunamis and, finally, whether they were in the region of the Pacific that rails could reach. Their estimated total number of extinctions involved far fewer extinct rails than did Steadman, but they also applied the methods to pigeons, parrots, and other taxa. They estimated that, in addition to the  $\approx 200$  terrestrial bird species taxonomists described from the Pacific islands from complete specimens,  $\approx 1,000$  species fell to first contact with the Polynesians.

Species on other oceanic islands are likely to have suffered similar fates within the last 1,500 years. Madagascar lost 40% of its large mammals after first human contact, for example (10). The Pacific extinctions alone suggest one species became extinct every few years and there were surely other extinctions after first human contact on the islands of other tropical oceans. An extinction every year is 100 times higher than benchmark rate before human impacts. As we will soon show, the rate is broadly comparable to those in the last few centuries.

First contact was locally even more destructive than these numbers suggest. Some islands lost all their terrestrial land birds. Oceanic birds suffered even greater losses. The explorations of Pacific islands for fossil bird uncover many islands with once abundant seabird colonies. Oahu, in the Hawaiian Islands, housed a massive colony of 18 species of seabird, for example (6). The introduction of rats by Polynesians and Europeans greatly reduced seabird colonies worldwide (11). Only a few islands remain that are people- and rat-free. These vulnerabilities persist to the present. Of  $\approx 450$  species of seabird,  $\approx 130$  are at risk of extinction (12).

**Counting Historical Extinctions.** Birdlife International produces the consensus list of extinct birds (12, 13) and a regularly updated web site [www.birdlife.org/datazone/species/index.html](http://www.birdlife.org/datazone/species/index.html). Henceforth, we call these sources simply Birdlife. Until the May 2006 revision, the list of recent extinctions totaled 129 species, or 1.3% (12). To these, we add newly recognized extinctions in the May 2006 revision to the web site. There are an additional five species that became extinct in the wild, but survive in captivity with various attempts to return them to the wild. Finally, there are species that have not been seen recently in places that suffer extensive habitat loss. While this manuscript was in preparation, Butchart *et al.* (14) saved us the task of justifying our decisions by providing details on 15 species that they (and we) consider unlikely to survive. (One survives in captivity.)

The names of these 154 extinct or presumed extinct species and the names of the 9,975 bird species known since 1500 that we deem valid for this study are provided in supporting information, which is published on the PNAS web site. Without qualification, this would seem to be an extinction rate of  $\approx 31$  E/MSY; we divide the 154 extinctions by  $\approx 500$  years times  $\approx 10,000$  species (i.e., 5 MSY). This extinction rate is certainly higher than the estimated geological background rate, but still much lower than our previous estimates for various taxa of 100–1,000 E/MSY (5).

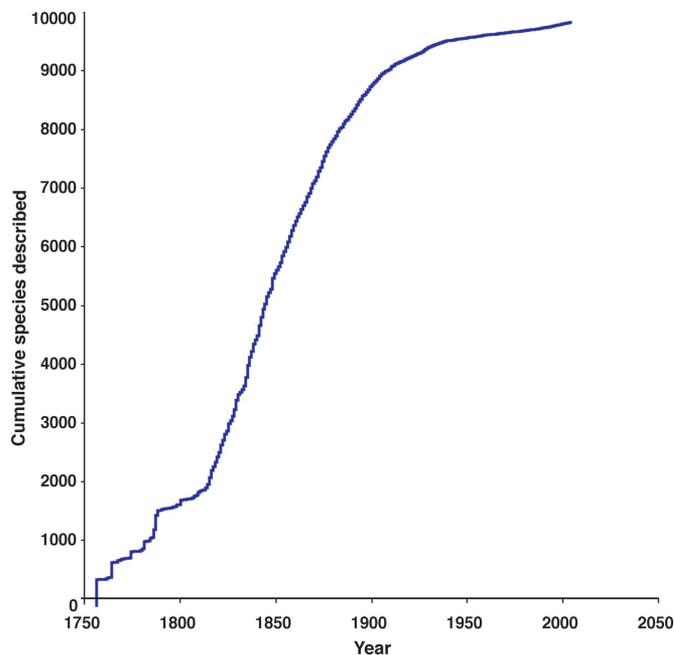


Fig. 1. Dates of description of the world's bird species. Data are available in supporting information, which is published on the PNAS web site.

The count of extinctions over a little more than 500 years has an unstated assumption that science has followed the fates of all the presently known species of bird over all these years. Our supporting information compiles the year in which taxonomists described each species. Taxonomists have given birds  $>20,000$  specific names, of which half are considered valid today. The remainder include synonyms for the same species, names for populations now considered to be only subspecies, and outright mistakes. We count only those species names presently accepted. As Fig. 1 shows, scientific description began in the 1700s, increased through the 1800s, and continues to the present.

Taxonomists described 47 species that were likely extinct, often long extinct, when described (see supporting information). For the remaining species, we sum the years over from when taxonomists described them until their extinction or to the present. For examples, Linnaeus described many species that survive to the present. Of those that did not, the Alagoas curassow (*Mitu mitu*) became extinct in the wild  $\approx 220$  years later, and the whooping crane (*Grus americana*) would have likely become extinct before 1994 were it not for conservation actions (14). By contrast, the po'o uli (*Melamprosops phaeosoma*), described in 1974, survived a mere 31 years after its description.

The sum of years over all of the species is 1.56 MSY. This is a substantially smaller sample than assuming all  $\approx 10,000$  species have been followed since 1500. In fact, taxonomists described half of all bird species after 1850.

Adding conservation dependent species (see below) the corrected extinction rate is  $\approx 85$  E/MSY, that is, slightly less than one bird extinction per year; this still underestimates the true extinction rate, as we now show.

**Historical Extinctions from 1500 to 1800.** In the decade up to 1500, the voyages of Cabot to North America, Colon to the Caribbean, and Cabral to South America marked the start of European exploration of the Americas. Exploration of Africa started earlier, and by the time of Cook's death in Hawai'i in 1779, Europeans had visited most of the world's islands and coastlines. What was the consequence of this European contact? To assess

**Table 1. Dates of descriptions of 9,975 bird species, their dates of extinction, those that are conservation-dependent (CD), and additional species that are critically endangered**

	Description					Sum
	Before				After 1900	
	<1600	<1700	<1800	<1900		
Extinction date						
Before						
1600	0	0	0	0	6	6
1700	0	0	2	4	4	10
1800	0	0	4	10	13	27
1900	0	0	10	37	1	48
After 1900	0	0	12	39	12	63
Sum	0	0	28	90	36	154
CD	0	0	5	16	4	25
Critically endangered	0	0	13	91	53	157
All	0	0	1,689	7,079	1,207	9,975

their impact, we combined the data on the dates of scientific description with the dates of species extinction (Table 1).

Modern scientific description began with Linnaeus in 1758. Of the 446 bird species he described (see supporting information), the dodo (*Raphus cucullatus*) is the famous member of a pair of species expiring in the late 1600s before he described them. (The Mauritian shelduck, *Alopochen mauritianus*, is the other.) Before 1800, the count of described species had grown to 1,689, and six were known to be extinct (Table 1).

In the 19th century, taxonomists added another 7,079 species, four more of which had become extinct before 1700 and 10 more before 1800. Another 1,207 species were added since 1900, of which six had gone extinct before 1600, another four before 1700, and another 13 before 1800 (Table 1). Some 13 of these species were described after 1970. Thus, as knowledge accumulates, we add to the totals of extinctions in earlier centuries.

The total of 43 extinctions before 1800 is still likely to be a considerable underestimate. All are nonpasserines from islands. First, it is unlikely that islands alone suffered human impacts; their predominance reflects the fact that European exploration emphasized strategically important islands, whereas continental interiors remained unknown. St. Helena (Atlantic Ocean) provides seven extinct species, and Réunion, Mauritius, and related Indian Ocean islands provide another 19. This list is likely to increase as more tropical islands are searched for now-extinct species.

Second, there are almost twice as many passerines as nonpasserine bird species, and so one expects more passerine than nonpasserine extinctions simply by proportion. Certainly, nonpasserines might be more vulnerable than passerines, because they are larger and so more likely to be hunted. Moreover, nonpasserines are generally larger-bodied than passerines and so often have lower reproductive rates, making their populations more sensitive to hunting or collecting. In addition, the bones of these larger species are more likely to have been preserved than those of the smaller, more fragile passerines, species that may easily have gone extinct without leaving a record.

Third, even the list of nonpasserines is incomplete. Three extinct species are known merely from writings or drawings compiled well after the species expired (see supporting information). Explorers' logs report distinctive island species, such as parrots, pigeons, and rails, for which there are neither specimens nor drawings (7, 9).

**Extinctions from 1800 to the Present.** Table 1 illustrates two nonintuitive trends. The first is that the extinction rate among a

given group of species declines over time, the second is that more recently described groups have higher rates of extinction.

The largest group of species for which we can make a comparison are the 7,079 species described in the 19th century. Some 37 species became extinct in the 19th century, and 39 species became extinct in the 20th century (Table 1). The numbers are roughly the same, but the total of years-times-species over which we could record extinctions is very different. For the 19th century, the species were followed only from their dates of description in that century to the century's end. For the 20th century, all surviving species were followed from the century's start to its end or to their date of extinction. The rates of extinction drop by almost half: 115 E/MSY in 19th century, to 65 E/MSY in the 20th century.

Increasing human impacts have accelerated the rate of extinction in the 20th century over that in the 19th, as we shall document below. However, there is a counter effect. Species differ greatly in their risk of extinction, so the most vulnerable species will be lost quickly and the rate of extinction will then slow. The great majority of recorded extinctions before 1900 were on islands in the Caribbean, Atlantic, Pacific, and Indian oceans (15). Extinction rates on these islands will slow down, other things being equal, because the vulnerable species have already become extinct. We observe this effect across Pacific Islands, where the islands colonized early have almost no recently extinct or threatened species, whereas those colonized later have many (7). Those species vulnerable to human impacts have already succumbed on long-colonized islands, whereas comparably vulnerable species linger on more recently colonized ones.

Second, we compare the rates of extinctions in terms of the century in which taxonomists described the species. Newly described species have higher rates of extinction than those species science has known for centuries. The largest sample involves the extinctions since 1900 comparing the 7,079 species described in the century before 1900 with the 1,207 species described since. There were 39 extinctions in former, only 12 in the latter. There are far fewer species in the latter, but also fewer years in which to observe them, only from their dates of description to the present. The corresponding extinction rates are 55 E/MSY and 139 E/MSY, respectively. Later, we discuss 182 extremely rare species that are at very high risk of extinction. About 5% of the species described since 1900 are among these 182, but only 1.4% from the species described in the 19th century. The simple explanation of these facts is that the earliest species taxonomists described are generally widespread, abundant species, whereas the newest discoveries are rare and local, and therefore much more prone to extinction.

This finding raises the distinct possibility that rare, local species may have disappeared without a trace after 1500 but before taxonomists described them. We have already commented that the number of historical island extinctions is increasing as more islands are explored for fossil remains, but what about continents?

Bird species have highly skewed geographical range sizes; a few, familiar species have almost continent-sized ranges, but a quarter of the world's birds have ranges <50,000 km<sup>2</sup> (16). Such range-restricted species are overwhelmingly the most threatened species (35% threatened compared to 4% of larger-ranging species) and they are geographically concentrated (16). Major concentrations of continental, range-restricted species are the Andes, Central America, the Atlantic coast of Brazil, and West Africa (17). Europeans explored all these areas before 1600 and used their native peoples or introduced slaves to clear land for crops. One might expect that many species were lost before taxonomic description. The species collected from one location (and not seen since) and species new to science in the last few

decades hint that others were present but missed being collected (see supporting information).

For example, Birdlife considers Brazil to have 89 terrestrial species at risk of extinction (12). Taxonomists described 13 of these species since 1980, all from the Atlantic Coast forests of Brazil (see supporting information). In these forests, only one species is known to have become globally extinct (it survives in captivity), several others have been rediscovered after many decades of being presumed extinct (see supporting information). This area originally had 1.1 million km<sup>2</sup> of forest, but retains <10% of its forest cover, about a quarter of which is in fragments of <10 km<sup>2</sup> (18). The remaining forest is mostly montane, and seven of the 13 new species live >400 m above sea level (18). The seven species' geographical ranges are all <500 km<sup>2</sup>, except one that is <1,500 km<sup>2</sup>. The remaining six species occur in lowlands, with ranges <5,000 km<sup>2</sup>; one has a known range size of ≈1 km<sup>2</sup>.

These examples from coastal Brazil strongly suggest that recently described or rediscovered species are the geographically fortunate survivors of the deforestation that cleared >1 million km<sup>2</sup> of mostly lowland forests. Many more species may have been lost before scientific description in those now-cleared lowland forests. Similar stories come from other regions where species with small ranges survive in massively deforested landscapes.

Following Butchart *et al.* (14), we have designated 15 species as extinct, even though there is some possibility that they still survive. Our supporting information lists another 34 species that have been thought to be extinct at one time, but either they or we considered as probably surviving or, in some cases, have been rediscovered after very long absences. "Not giving up hope" can be an important conservation strategy, necessary to protect the remaining habitats of the species that just might have survived. If more "extinct" species are rediscovered then our estimates of extinction rates would be too high. Not all "rediscoveries" are equal, we must add: many claims lack credible photographic evidence, for example.

**The Impact of Conservation.** Since 1975, there have been 20 extinctions in the wild, six of which involve species that survive in captivity with efforts to return them to the wild (see supporting information). How many more species would have become extinct were it not for conservation actions? Intensive conservation efforts protect many of the surviving species that Birdlife classifies in the two most dire categories of threat: "Critical" and "Endangered." We considered the status of each species to assess how many would likely be extinct were it not for efforts to save them. Again, while this manuscript was in preparation, Butchart *et al.* (19) did the same task, again sparing us the need to provide details. They conclude (and we agree) that were it not for these efforts that another 25 species would have become extinct, 10 within the last decade. We assume the other 15 would have expired within the prior two decades before the last one. Were it not for conservation actions, there would have been these 25 prevented extinctions plus the actual 20 extinctions in the wild over the last 30 years, a rate of 150 E/MSY. Conservation has reduced that extinction rate by two-thirds. The overarching conservation concern is whether this proportional reduction in the extinction rate can be maintained in the face of the predicted rapidly accelerating extinctions rates we now discuss.

**Extinction Estimates for the 21st Century.** Birdlife lists 1,210 bird species in various classes of risk of extinction, plus another 74 species they deem "data deficient" (12). The latter are insufficiently known (usually they are rare) to allow a proper determination of threat level. The most threatened class is "critically endangered." Our supporting information lists 182 such species, including the species thought likely to have gone extinct but for conservation actions. For many of these species, there are doubts

about their continued existence. For all of these species, expert opinion foresees extinction with a few decades without effective efforts to protect them. Were they to expire over the next 30 years, the extinction rate would average five species per year or 500 E/MSY. If the nearly 1,300 threatened or data deficient species were to expire over the next century, the average extinction rate would exceed 1,300 E/MSY. This is an order of magnitude increase over extinctions-to-date.

Such calculations suggest that species extinction rates will now increase rapidly. Does this make sense, especially given our suggestion that the major process up to now, the extinction on islands, might slow because those species already sensitive to human impacts have already perished? Indeed, it does, precisely because of rapid increase in extinction on continents where there have been few recorded extinctions to date.

**Species Threatened by Habitat Destruction.** The predominant cause of species endangerment is habitat destruction (12). Although large tracts of little changed habitat remain worldwide, most of the planet's natural ecosystems have been replaced or fragmented (2). Some species have benefited from those changes, but large numbers have not. The most important changes are to forests, particularly tropical forests for these ecosystems house most of the world's bird species (and likely other taxa as well). We now show that the numbers of extinctions predicted by a simple quantitative model match what we expected from the amount of forest lost. We then extend these ideas to more recently deforested areas to predict the numbers of species likely to become extinct eventually. The observed numbers of threatened species match those predictions, suggesting that we understand the mechanisms generating the predicted increase in extinction rate.

A well established empirical relationship predicts how the number of species (*S*) on islands increases with increasing area (*A*):  $S = cA^z$ , where *c* is a case-specific constant and  $z \approx 1/4$  (20). An extension is to suppose this same species–area relationship will hold as human actions shrink suitable habitat (21). For example, European colonists and their descendants cleared the forests of eastern North America starting in 1620 (21). The low point was about 1870, when half the forests remained. Applying the relationship, we predict that ≈15% of the region's 30 endemic species (=4.5) would go extinct (21). Those not endemic could have survived elsewhere. In eastern North America, three species became extinct. The rediscovery of a fourth, the ivory-billed woodpecker, has yet to be universally accepted. Another endemic, the red-cockaded woodpecker (*Picoides borealis*), is at risk (7). Thus, there is good agreement between the predicted and observed numbers.

Comparably good matches of the numbers of species extinct and predicted to become extinct (plus those presently threatened with extinction) hold for the species-rich insular Southeast Asia (22) and the Atlantic coast forests of Brazil (23).

These matches allow cautious extrapolation to other areas with extensive habitat destruction and containing many vulnerable species. Myers *et al.* (17) defined 25 "hotspots" worldwide based on their high levels of endemism and >70% habitat destruction. There are 2,821 bird species endemic to these 25 hotspots; 1,639 (58%) of which are on continents, the remainder on islands. These 25 areas broadly overlap with 218 "Endemic Bird Areas" that house 2,451 species with ranges <50,000 km<sup>2</sup> (16).

We applied the species–area relationship to each of the 25 hotspots by using the statistics on endemic bird species, original area, and the present area of remaining natural vegetation. This provides a best-case scenario of what habitat might remain (24). Some 1,700 species of birds should be lost eventually. Species can obviously linger in small habitat fragments for decades before they expire, as evidenced by the rediscovery of species thought



