Historical bird and terrestrial mammal extinction rates and causes

Craig Loehle* and Willis Eschenbach

INTRODUCTION

There are three dominant forces commonly posited to be causing elevated extinction rates: habitat loss; human exploitation; and effects of invasive species, including diseases, as well as their combined effects (De Castro & Bolker, 2005; Smith et al., 2006; Brook et al., 2008; Frick et al., 2010), with climate change assumed to be a future risk factor (Brook et al., 2008; Stork, 2010). Deforestation is presumed to be a future risk factor (Brook et al., 2008; Stork, 2010). Deforestation is presumed to be a future risk factor (Brook et al., 2008; Stork, 2010). Deforestation is presumed to be a future risk factor (Brook et al., 2008; Stork, 2010). Deforestation is presumed to be a future risk factor (Brook et al., 2008; Stork, 2010).

Main conclusions Our analysis suggests that conservation strategies for birds and mammals on continents should not be based on island extinction rates and that on islands the key factor to enhance conservation is to alleviate pressures from uncontrolled hunting and predation.

Keywords Biodiversity, conservation, deforestation, endangered species, extinction risk, reserve design.
did not examine estimated extinctions, predicted extinctions or calculated extinctions (see Stork, 2010). Rather, we conducted an analysis of actual historical record of extinctions with the purpose of understanding the nature and scope of extinctions from habitat reduction or other causes. We have analysed global extinctions of species (not subspecies) rather than local extinction (extirpation), which is a separate and valuable study.

**METHODS**

There are two main lists used by scientists to track extinctions. The ‘Red List’, maintained by the International Union for the Conservation of Nature and Natural Resources (IUCN), lists species that are either extinct or at risk of extinction (http://www.iucnredlist.org). The CREO list, from the Committee on Recently Extinct Organisms at the American Museum of Natural History (http://creo.amnh.org), addresses mammals but not birds. It has established very clear criteria for declaring a species extinct, not extinct or unresolved that have been uniformly applied to the historical record of extinctions of mammals and fish in the last 500 years. These criteria include adequate taxonomy (including DNA comparisons if available), sufficient hypodigm (actual specimens of the species) and adequate surveying of the species’ habitat to verify extinction. The class Mammalia, which includes marsupials and monotremes, was used in our analysis. The conclusions of the CREO list are noted in the Red List and vice versa. Although the two lists are not very different, the CREO list provides a greater level of detail than the Red List. Thus, we have used it for mammal extinctions and the Red List for birds. Both lists are limited in their treatment of older extinctions (> 100 year) because of limited research on the topic, particularly on remote islands.

In evaluating extinction data, it is useful to consider islands as a special case. It is well known that island biota are generally at a higher risk of extinction (Diamond, 1989; Alcover et al., 1998; Baillie et al., 2004; Blackburn et al., 2004; Duncan & Blackburn, 2004; Pimm et al., 2006; Sax & Gaines, 2008; Fordham & Brook, 2010; Lane, 2010). Corlett (2010) showed that the impact of invasive species has been greater on more remote islands. The reasons for greater extinction risk on islands are asserted to be the result of species naive about predators (Cronk, 1997), ground nesting by birds on predator-free islands (e.g. Duncan & Blackburn, 2004), less competition because of reduced species richness (Corlett, 2010), perhaps reflected in slower rates of evolution (Wright et al., 2009), and smaller geographic ranges. If these particular causes are mainly operative on islands, then implications drawn for conservation priorities on much more spacious continents may not be valid (see Walter, 1998, 2004). Thus, we divided extinctions into two groups: (1) extinctions of species living on isolated islands or on Australia, and (2) extinctions of continental species. We excluded Greenland and Antarctica from consideration because they are almost totally covered by ice and have very few species of birds or mammals. We excluded marine mammals from our counts.

To compare extinctions on a per unit area basis, we summed the area in islands and continents. We define islands following Alcover et al. (1998) as those substantially not connected to the continents during the last glaciation. We also included Australia, in spite of its size, because of its lack of exposure to the modern fauna of the major continents before the modern era. The prehistoric human population of Australia also lacked agriculture, which kept population low and did not possess the bow and arrow, which reduced its hunting impact (Trueman et al., 2005; Prideaux et al., 2010). Island area was computed by summing the areas of Australia, New Zealand, Tasmania, Madagascar, Malaysia, Indonesia, Philippines, Japan, Taiwan and other major islands. The high arctic islands were not included because they are connected by ice every winter and are thus not isolated. The British Isles and Mediterranean islands were not included because of Pleistocene land connections and/or early and heavy human occupation (Alcover et al., 1998). To capture smaller islands missed, this number was multiplied by an arbitrary 1.1 to be conservative. This yielded $1.31 \times 10^8$ km$^2$ area for islands. The total world land area is $1.489 \times 10^8$ km$^2$. To obtain the continental land area, we subtracted island area as well as Greenland and Antarctica areas, as these areas are almost entirely covered by ice. This yielded $1.196 \times 10^8$ km$^2$ continental area.

**RESULTS**

Island extinctions have dominated the total record of extinctions. On all continents, only three mammals are recorded as having gone extinct in the last 500 years. These were as follows: Blueebuck antelope, hunted to extinction, South Africa; Algerian gazelle, unknown cause, Algeria; and Omilteme cottontail rabbit, unknown cause, Mexico (Table 1). The remaining global mammal extinctions (58 or 95%) occurred on islands. Alcover et al. (1998) document 188 mammal island species that have gone extinct since the end of the Pleistocene, mostly because of human occupation (according to the authors). Not having access to the exact species they identified, we can only approximately identify 130 island (insular) mammal species as extinct because of prehistoric island invasions by humans and their commensals. Of the 128 extinct bird species, 122 (95.3%) were island extinctions and six were on continents. Of the continental bird species extinctions, three were prolific terrestrial bird species hunted to extinction and three were single-habitat freshwater bird species. These freshwater bird species suffered from hunting pressure, predation from introduced fish and habitat alteration.

Other studies have documented far more island bird (mainly) species that were driven to extinction during prehistoric (outside our 500-year window) or historical times (e.g. Steadman, 1995, 2006; Pimm et al., 2006), perhaps, in the thousands. However, to avoid problems of subjectivity, we have used standard databases. The implications of the higher estimates are mentioned in the discussion.

Per million square kilometres, historical (past 500 years) extinction rates (not per year) for birds were 9.38 species on
This equal area rate was 187 times (not per cent) higher on islands. For mammals, the extinction rates per million square kilometres were 4.43 species on islands and 0.0251 species on continents, and the relative risk was 176.5 times higher on islands. If we consider Australia to be a continent, then there are 23 continental and 38 island extinctions, but the island rate per million square kilometres is still 45 times as high. In this case, we would have to explain why 82% of the mammal extinctions are marsupials, returning us to the conclusion that species of Australia were/are uniquely sensitive. If prehistoric impacts of humans had been included, the difference would be even greater because many species were exterminated prior to our 500 year cut-off. Alcover et al. (1998), for example, estimated that 130 island mammal species went extinct during the prehistoric Holocene, most of which they attributed to human invasion of islands. A similar number of continental species are not available, although Alcover et al. (1998) assert that it is much lower because of long coexistence with humans on the continents. Similarly, they estimate that 60% of 3500 island endemic birds went extinct during the Holocene following human occupation, although this number is very rough. Steadman (1995, 2006) and Pimm et al. (2006) give similar high numbers. Some of these extinctions may have resulted from post-Pleistocene climate changes and sea-level rise.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Extinct continental species.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Year</td>
</tr>
<tr>
<td>Bluebuck (<em>Hippotragus leucophaeus</em>)</td>
<td>1800</td>
</tr>
<tr>
<td>Labrador duck (<em>Camptorhynchus labradorius</em>)</td>
<td>1878</td>
</tr>
<tr>
<td>Algerian gazelle (<em>Gazella rufina</em>)</td>
<td>1894</td>
</tr>
<tr>
<td>Carolina parakeet (<em>Conuropsis carolinensis</em>)</td>
<td>1904</td>
</tr>
<tr>
<td>Slender-billed grackle (<em>Quiscalus palustris</em>)</td>
<td>1910</td>
</tr>
<tr>
<td>Passenger pigeon (<em>C. carolinensis</em>)</td>
<td>1914</td>
</tr>
<tr>
<td>Colombian grebe (<em>Podiceps andinus</em>)</td>
<td>1950s</td>
</tr>
<tr>
<td>Atitlán grebe (<em>Podilymbus gigas</em>) (found only on Lake Atitlan, Guatemala)</td>
<td>1986</td>
</tr>
<tr>
<td>Omilteme cottontail rabbit (<em>Sylvilagus insonus</em>)</td>
<td>1991</td>
</tr>
</tbody>
</table>

CREO, Committee on Recently Extinct Organisms.
*Interestingly, this bird has since been replaced on Lake Atitlan by a similar grebe of the same genus, *Podilymbus podiceps*. In fact, there is significant disagreement among biologists about whether *P. gigas* is just a subspecies of *P. podiceps*, but we have included it to be on the safe side.

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Extinctions since 1500 according to IUCN and CREO, with per species and per unit area rates.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Year</td>
</tr>
<tr>
<td>Bluebuck (<em>Hippotragus leucophaeus</em>)</td>
<td>1800</td>
</tr>
<tr>
<td>Labrador duck (<em>Camptorhynchus labradorius</em>)</td>
<td>1878</td>
</tr>
<tr>
<td>Algerian gazelle (<em>Gazella rufina</em>)</td>
<td>1894</td>
</tr>
<tr>
<td>Carolina parakeet (<em>Conuropsis carolinensis</em>)</td>
<td>1904</td>
</tr>
<tr>
<td>Slender-billed grackle (<em>Quiscalus palustris</em>)</td>
<td>1910</td>
</tr>
<tr>
<td>Passenger pigeon (<em>C. carolinensis</em>)</td>
<td>1914</td>
</tr>
<tr>
<td>Colombian grebe (<em>Podiceps andinus</em>)</td>
<td>1950s</td>
</tr>
<tr>
<td>Atitlán grebe (<em>Podilymbus gigas</em>) (found only on Lake Atitlan, Guatemala)</td>
<td>1986</td>
</tr>
<tr>
<td>Omilteme cottontail rabbit (<em>Sylvilagus insonus</em>)</td>
<td>1991</td>
</tr>
</tbody>
</table>

CREO, Committee on Recently Extinct Organisms.
*Interestingly, this bird has since been replaced on Lake Atitlan by a similar grebe of the same genus, *Podilymbus podiceps*. In fact, there is significant disagreement among biologists about whether *P. gigas* is just a subspecies of *P. podiceps*, but we have included it to be on the safe side.

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Extinctions since 1500 according to IUCN and CREO, with per species and per unit area rates.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Year</td>
</tr>
<tr>
<td>Bluebuck (<em>Hippotragus leucophaeus</em>)</td>
<td>1800</td>
</tr>
<tr>
<td>Labrador duck (<em>Camptorhynchus labradorius</em>)</td>
<td>1878</td>
</tr>
<tr>
<td>Algerian gazelle (<em>Gazella rufina</em>)</td>
<td>1894</td>
</tr>
<tr>
<td>Carolina parakeet (<em>Conuropsis carolinensis</em>)</td>
<td>1904</td>
</tr>
<tr>
<td>Slender-billed grackle (<em>Quiscalus palustris</em>)</td>
<td>1910</td>
</tr>
<tr>
<td>Passenger pigeon (<em>C. carolinensis</em>)</td>
<td>1914</td>
</tr>
<tr>
<td>Colombian grebe (<em>Podiceps andinus</em>)</td>
<td>1950s</td>
</tr>
<tr>
<td>Atitlán grebe (<em>Podilymbus gigas</em>) (found only on Lake Atitlan, Guatemala)</td>
<td>1986</td>
</tr>
<tr>
<td>Omilteme cottontail rabbit (<em>Sylvilagus insonus</em>)</td>
<td>1991</td>
</tr>
</tbody>
</table>

CREO, Committee on Recently Extinct Organisms.
*Interestingly, this bird has since been replaced on Lake Atitlan by a similar grebe of the same genus, *Podilymbus podiceps*. In fact, there is significant disagreement among biologists about whether *P. gigas* is just a subspecies of *P. podiceps*, but we have included it to be on the safe side.
The approximate total number of recent mammal species (including recently extinct) from IUCN (and Alcover et al., 1998) is 4629, of which 117 are marine and 787 are island species. This gives 3725 living continental land species. The continental per species extinction rate is then 3/3725, or 0.081% per 500 years, or 1.61 per million species years (MSY). Similarly, the per capita island extinction rate is 58 of 787 total island species (IUCN) or 7.4% per 500 years or 147.4 per MSY. The island rate per MSY is 91.6 times the continental rate.

We can compare these numbers to estimated fossil mammal turnover rates (species/species per million years) of 0.21 (Alroy, 1998), 0.4 (Regan et al., 2001), 0.46 (Foote, 1997) and 1.8 (Barnosky et al., 2011). This means that continental rates of extinction are 0.89 as high to 7.4 times higher than for fossil faunas. In contrast, assuming comparable island preservation, island extinction rates are 82–702 times higher on a species pool basis. These numbers are subject to great uncertainty because of difficulty in estimating past extinction rates. We used established authorities as our standard, rather than guessing about individual species. Even if the true extinction of < 4% of species extinct since 1500 (Smith et al., 2005; Prideaux et al., 2005; Prideaux et al., 2010). The loss of small bird species and rodent-like species (rodents and small marsupials) can probably be attributed to introduced rats, dogs and (more recently) cats. The correlation of deforestation with species loss on oceanic islands (Didham et al., 2008) may be partially explained by the fact that forest loss is an indicator of population size, which is itself an indicator of exploitation pressure. This would explain why extensive deforestation on continents has not led to many extinctions.

The role of disease is difficult to assess. While theoretically important, it leaves few traces for extinctions not directly observed in recent years. For example, in order to demonstrate even the presence of an introduced disease in an extinct species, Wyatt et al. (2008) had to conduct DNA analyses on museum specimens, and even then, the extent to which the disease contributed to the extinction was only suggestive. Likewise, estimates of the contribution of infectious disease to extinction of < 4% of species extinct since 1500 (Smith et al., 2006) is based on expert opinions expressed in the IUCN database. On the other hand, the argument that introduced disease per se can only predispose a population to extinction (De Castro & Bolker, 2005) ignores the reservoir effect of disease carried by an introduced species and the sensitivity of a naive species (particularly on islands). The fact that flightless birds such as rails were far more likely to have gone extinct (Steadman, 1995, 2006; Pimm et al., 2006) also suggests hunting and introduced predators (e.g. rats) as a major cause of extinctions, rather than disease. Similarly, more rapid loss of
species when human populations were larger also suggests hunting and/or habitat alteration rather than disease. Disease can, of course, have been important in some cases and is clearly important today in cases such as bat decline in eastern North America and amphibian decline in South America.

Invasive species seem to be a major secondary cause of extinctions on islands. Australian and island species were extremely vulnerable to pressure from invasive predators (e.g. Recio et al., 2010), competitors and disease species. This was because of the ground-nesting habit of many island species such as rails (e.g. Pimm et al., 2006) and the tendency of many species to not flee from predators or humans. Many extinct island mammals on the CREO list are rodents, which probably perished because of competition with introduced rats. Although it occurred over a number of years, this initial introduction of continental species into island habitats is now better understood and attempts are being made to avoid new introductions and to actively control old ones. Habitat loss has, of course, played a role in the extinction of some continental species. However, it is worth noting that to date, no continental mammal or bird in our databases has been documented to have gone extinct solely because of habitat reduction. Early prehistoric waves of extinction (America around 12,000BP and Australia over 50,000 year ago) also were not because of habitat alteration (except fire) but largely because of hunting and other exploitation (e.g. egg gathering) (Trueman et al., 2005; Sodhi et al., 2009; Prideaux et al., 2010; Ripple & Van Valkenburgh, 2010). All extinctions of marine mammals are strictly because of hunting and are obviously not because of habitat alteration or introduced predators.

An important point about these documented extinctions is that because of the unique sensitivity of island species, the recent historical rate of island extinctions cannot continue at the same pace into the future. On many islands, most or all of the flightless rails, for example, are already extinct (Steadman, 1995, 2006). Thus, it is not valid to conceive of a rate of X species per year as continuing, although, of course, many species are currently at risk.

Our results do not support statements or projections by others of grossly elevated extinction rates for continental bird and mammal fauna over the last 500 years compared with background rates. This is particularly noteworthy because mammals (Ceballos et al., 2005), large-bodied animals (Sodhi et al., 2009) and carnivores (Saif & Pettorelli, 2010) are widely assumed to be at greater risk than other species. For example, Sodhi et al. (2009) projected that current extinction rates are 100–10,000 times background vs. the very modest rise we estimated of 0.89–7.7 times the background rate for continental mammals and 0.69–5.9 times background for continental birds. We do find very high rates for islands, several hundred times background. Wilson (1992) estimated from theory that 540–1088 continental bird and mammal species had been lost the past few hundred years, depending on which of his assumptions are used. Twenty other studies (Table I in Stork, 2010) make similar high estimates. Sax & Gaines (2008) estimate 13,500–27,000 total species (all taxa) lost or doomed per year just because of tropical deforestation. Most of these estimates are based on the species-area curve, which is an empirical relationship between the number of species found and the area surveyed. The idea is that when area is lost to development, the change in species that can be supported can be estimated from this model. In contrast, our compiled IUCN and CREO continental bird and mammal extinctions and references cited earlier do not support these projections. In fact, habitat loss only contributed to a handful of extinctions, even on islands.

Our relatively low estimates for extinction rates could theoretically be because of some species requiring a relatively long time period to reach extinction (an extinction debt, Labrum, 2011). For example, Wilson (2001) notes that ‘...species in a reduced habitat may take from 25 to 100 years to go extinct’ and that research has shown that the rate of these delayed extinctions drops off exponentially with time. Even with this assumption, the long history of deforestation should have led to hundreds of extinctions. We have, however, seen only a handful. If true extinction debt relaxation times are more like thousands of years (as in prehistoric Australia following human arrival), then the recent continental rates are explainable, but none of the references to current extinction rates we found (e.g. Sax & Gaines, 2008; Stork, 2010) make this assumption. Under this assumption, conservation efforts would be much more hopeful.

Several other factors may at least partially be responsible for lower observed extinction rates than expected based on estimates of background extinctions. Stork (2010) suggests that conservation efforts have been a successful mitigation effort. It is true that species such as the California condor have been saved and reintroduced into the wild. Many other species have been protected or are currently found only in zoos. However, this number is far below what is needed to reconcile our results with extinction rates predicted by others. Stork also suggests that secondary forest could be providing adequate habitat for at least some species assumed to require old growth (undisturbed) forest. Finally, some species predicted as extinct may not have ever been described in the scientific literature. However, it is unlikely that hundreds of extinct continental bird and mammal species have not been documented and only the unknown species should have gone extinct.

We suggest that the ‘habitat loss’ theory of extinction risk is deficient. What might explain this deficiency? On continents, species are often able to roam widely and this mobility prevents speciation except under exceptional circumstances. For example, in the eastern United States, most mammals and birds can move freely and for this reason occupy the entire zone from Florida and into Canada but will be locally found in their preferred habitats such as wetlands or meadows. It does not follow logically that these species require this entire region to persist. Evidence from islands suggests that they do not. On the Galapagos, each of the tiny islands has a unique tortoise species and finch species. These islands are each home to a unique species only because they are isolated but testify to the fact that species can persist in a small area, as documented by Walter
Diversity and Distributions, C. Loehle and W. Eschenbach

Our analysis is not meant to imply that habitat loss, forest fragmentation or loss of species diversity are incidental or unimportant issues or that extinctions will rise or fall in the future. This is an analysis of historical record to date. Because mammals and birds are more mobile than other taxa, we also do not consider our results to necessarily extend to other taxa, which make up a significantly higher proportion of total extinctions.

There are implications from our study for conservation practice. We suggest that conservation should be spatially focused on islands for birds and mammals because species on islands are uniquely sensitive. Furthermore, efforts to restore or protect a given area on islands will, in general, have a much higher pay-off than on continents, if our goal is to prevent extinctions. On islands, it is most important to control invasive species (particularly predators) and exploitation (unregulated hunting). Thus, preserves may not be effective on islands unless introduced predators are controlled. Predator removal can, in fact, lead to dramatic recovery (Jones, 2010). On continents, the role of habitat loss is overemphasized by models that do not predict correct extinction rates (He & Hubbell, 2011). Introduced or altered levels of predators on continents have rarely been documented to be the type of problem they are on islands because continents already have modern efficient predator species. Thus, on continents, it is control of hunting and other exploitation that would yield the largest benefit.

We do not extend our results to plants (e.g. Sax & Gaines, 2008) because they are so different from birds and mammals. Relative to forecasts of climate change effects (e.g. Brook et al., 2008; Stork, 2010), we would note first that many such forecasts have been based on the species–area curve (critiqued by Botkin et al., 2007) and second that before extrapolating to unknown future conditions it would be helpful to properly understand existing extinction records.

ACKNOWLEDGEMENTS

Thanks to Darren Sleep and Jake Verschuyl for helpful comments. This manuscript originated as a blog post by Willis Eschenbach.

REFERENCES


**BIOSKETCHES**

Craig Loehle is a research scientist for NCASI. He conducts research on biodiversity, forest ecosystems, modelling methods, statistics of sampling and distributions and climate change. He developed and refined the analysis in the paper.

Willis Eschenbach is a retired polymath with interests in engineering, ecosystem processes and climate change. He developed the initial insights into relative extinction rates on islands and continents.

Editor: George Stevens