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Bird Extinctions in the Central Pacific [and Discussion]

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Bird extinctions in the central Pacific

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SUMMARY

The first wave of human colonists spread across the Pacific from 4000 to 1000 years ago. That they caused many extinctions is well known from fossil finds. We estimate how many fossil species were missed – the answer is roughly half – and so estimate the true extinction rate. The first colonists exterminated roughly half the species on each island group. Some of these extinctions are falsely attributed to the first colonists, because intensive collection often began a half century after the damage initiated by European discovery. Even taken at face value, these recent extinctions are too few. Many species are so critically endangered that we know neither whether they still survive or how to save them. Interestingly, there are fewer recent extinctions and currently endangered species in the islands of the western Pacific, which were the islands occupied first by humans. We suggest that the species sensitive to human occupation died out long ago in these areas. If so, these islands would have lost even more than half of their bird species.

1. INTRODUCTION

The Pacific islands faunas and floras are well known for their high extinction rates (Diamond 1984*a*,*b*; Smith *et al.* 1993; Milberg & Tyrberg 1993; Humphries & Fisher, this symposium). Human colonization has driven these changes in the last few millennia. The first wave spread eastwards from the east Indies reaching Melanesia and Micronesia about 4000 years ago, Fiji and Samoa 3500 years ago, the Marquesas 2000 years ago, and the outliers of Hawai'i, Easter Island and New Zealand within the last 1500 years. European exploration started with Magellan and Mendaña in the sixteenth century and was all but complete when Cook died at Kealakekua, Hawai'i in 1779. Colonization started later: the first missionaries arrived in Tahiti in 1795 and Hawai'i in 1820, for example. Both waves brought alien species to the region although the peak period of introductions is much more recent. Most bird introductions to Hawai'i have occurred since 1920.

Before humans arrived, Pacific islands housed a diverse avifauna. The first human colonizations caused extensive extinctions (Olson & James 1982). However, estimating the true extent of the depredation is not trivial. The second wave of colonists also caused extinctions; and they continue to the present with many species surviving at population sizes too low for long-term persistence.

The purpose of this paper is to document the depressing statistics. We restrict our analyses to the land birds of the central Pacific: the area between 30°N and 30°S and 140°E and 100°W. By land birds, we mean those species not tied to the ocean for feeding. We exclude terns, boobies and shearwaters, for example, but include ducks, most herons (but exclude reef heron) and other birds of freshwater habitats. We start with the Hawaiian islands. They have been the most thoroughly explored and documented. We will then consider the islands of south-eastern Polynesia and finally move westwards.

2. THE HAWAIIAN ISLANDS

The Hawaiian Islands are of two types: from north to south, the six main islands (Kaua'i, O'ahu, Moloka'i, Maui, Lana'i and Hawai'i) and their smaller attendants are relatively young, shield volcanoes in various stages of erosion. From every island, one can see at least one other island. To the north and west, the much smaller, older and more isolated islands consist of coral atolls atop the eroded bases of once-huge volcanoes. Only Laysan, Lisianski and Nihoa supported land birds. On the main islands, the remains of birds in caves in lava tubes (and other such places) provide an unusually detailed record of the islands' faunas (Olson & James 1982, 1991; James & Olson 1991).

(*a*) *The not-so-noble savages*

The total set of species consists of those that survived Polynesian contact, to be collected or observed by two centuries of biologists ('skins') and

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those that did not ('no skins'). A second dichotomy is between those species for which we have fossils ('bones') and those for which we do not ('no bones'). The combination of the two sets gives four subsets. Obviously, we are totally ignorant of those species lost during contact and for which we have no fossils ('no bones and no skins'). Other things being equal, we can estimate their number as:

$$\frac{\text{'bones but no skins'} \times \text{'skins but no bones'}}{\text{'bones plus skins'}}.$$

The analogy to familiar mark recapture method of estimating numbers is obvious. As an example, 29 species of non-passerine birds have been found only as fossils in Hawai'i, while two are known only from modern collections or observations, and seven are known from both fossils and collections. The estimated number of missing species is eight (to the nearest integer value).

The formula is obviously sensitive to the errors that come with small samples. Nor do all species fossilize well. A bone from a large-bodied species may survive better than its fragile equivalent from a small-bodied species. Common species are more likely to be found than rare ones. Some species are more vulnerable to extinction: not only the rare ones, but also those that were the perfect accompaniment to poi (a dish made from taro root). We may never know how many rare small-bodied species have disappeared. None the less, there are two ways in which we can refine our estimates. We can distinguish the large, likely to fossilize, good-for-the-calabash species from the small species. Ancient Polynesians may have understood our modern division of non-passerines and passerines, for it mirrors that distinction. In an independent classification, we can assume that we are more likely to find widespread species than those restricted to one island. Even within an island, those restricted to it may have been less numerous than those found more widely (see Lawton, this symposium). This is true of the species that still survive in the Hawaiian islands. Finally, not all islands yield fossils equally. Kaua'i provides Olson and James with one site, O'ahu with three, Moloka'i with two, Maui with 11, and Lana'i and Hawai'i have no 'representative' sites (Olson & James 1991).

Separating the species into non-passerines and passerines leads to estimates of eight and 21 missing species respectively. Dividing the passerines into those found on only one island and those found on several yields estimates of 20 and one respectively. (That these add to 21 – the estimated number for both passerine groups combined – is reassuring, but coincidental.) The number of missing non-passerines found on more than one island we estimate as 12 and there are too few data to estimate the number of non-passerines found on only one island. We conclude that there are 21 species of passerines and between eight and 12 species of non-passerine bird that fell to the Polynesians without trace. We think these estimates are conservative.

Separating all species into those found on only one island and those found on several, leads to estimates of 46 and three respectively. The latter number is smaller than our estimate for the non-passerines alone. The former number would be increased almost in direct proportion by new finds of species known only from fossils and only from Lana'i or Hawai'i. Almost all (25 of 26) species of non-passerine found on only one island are found only as bones. Many were of flightless species that could not have occupied more than one island. Thus the number of missing non-passerines restricted to one island is likely to be large. On the four islands for which we have good fossil records, the estimated numbers of missing non-passerines on those islands equals or exceeds the number of missing passerines. The estimate of 8–12 missing non-passerines is surely too low: there are likely to be more missing species and they are likely to be restricted to just one island.

(*b*) *Missing skins and false accusations*

The extinctions occurring within the last two hundred years would seem to be easier to document. Since 1800, 18 species have gone extinct on the main islands and one more species and two endemic subspecies have gone extinct on Laysan. This is also an underestimate, because distinguishing Polynesian- from European-caused extinctions is not always easy. How many species survived the Polynesians yet disappeared before collectors could shoot them? Sampling distributions are often Poisson. Given that we have the number of species collected once, twice, or n times, we could estimate the number of species that were not collected at all. This calculation eludes us, for we do not know the numbers of specimens collected and there would be enormous uncertainties in both the numbers and the method itself. Yet we can apply its principles. Obviously, if only large numbers of specimens are collected for most species, we would conclude that we had not missed any.

The late nineteenth century saw the most intensive bird collections. By then, trade (including whaling and ranching), the introduced species it brought in general, and rats in particular, had been a feature of the islands for 60 years. The collectors may have missed species that went extinct quickly for they even missed some that did not. One species, the po'ouli, was first described as recently as 1973. Twenty years later, it is so rare that in the last two years only one of several extensive and intensive surveys has found isolated individuals. It is likely to go extinct soon and it could well have disappeared without a trace. There are fossil po'ouli. Had there been no sightings, its loss would have been blamed on the Polynesians.

Given near misses like the po'ouli (and other species) known from very few specimens, it is likely that there are several species missing from the recent record. Whereas it is likely that the Polynesians did exterminate most of the 43 species we know only as fossils, and the roughly 30–50 we estimate are missing, they may not have killed them all. Attributing nineteenth century extinctions to the Polynesians is doubly unfair. First it places false blame. Second, if causes us to underestimate the number of species we count as both fossils and skins and to overestimate the number of species found only as fossils. Both effects inflate our estimates of the number of missing species and we attribute their loss to the Polynesians. Of course, the species may not be found as fossils and their loss from the 'skins only' category would reduce the estimate of missing species.

(*c*) *Taxonomy*

Some of the taxonomic problems in estimating extinction rates are familiar. For example, are the various island forms of 'akialoa, 'akepa and creeper sub-species or species? The once single species of Hawaiian creeper now contains species placed in two separate genera, two species of which once occupied the same island (James & Olson 1991). The 'akepa of Hawai'i (males are bright orange) and the 'akeke'e of Kaua'i (green with black masks on yellow faces) were once considered conspecifics. Our impression of these and other cases, including the once-overlooked Lana'i hookbill, is that Hawaiian taxonomy was unusually poor until recently. We follow Olson & James' (1991) classification.

Whatever its explanation, poor taxonomy will underestimate the true extinction rate. Indeed, it may lead to species extinction. One of the creeper species formed by revision is the 'akikiki, a species that to us seems distinctive in its appearance and behaviour. It is obviously endangered, but not Endangered (and so specially protected) by United States' law.

Some of the taxonomic challenges are the result of new methods. Whether the forms of 'amakihi across the main islands constitute several species or sub-species would seem to be the same call as that for the 'akialoa. Yet, recent work by Tarr & Fleischer (1993) shows that the 'anianiau is most closely related genetically to Kaua'i 'amakihi and O'ahu 'amakihi. Thus we should treat the Kaua'i 'amakihi as a separate species. Their results also split out the O'ahu 'amakihi: another species that would need to become legally endangered.

(*d*) *The ghosts of Christmas future*

The most difficult task is identifying those species whose fates are already sealed, those merely in danger and those that never were in danger or which have 'recovered': a term with legal connotations in the United States. Even if we manage to save some of the rarest species by active intervention, we should still add the former to the extinct class when estimating extinction rates. The task reduces to asking: How long will a species last? The Pacific Avifauna Recovery Coordinating (PARC) Committee of the United States Fish and Wildlife Service (of which Pimm is a member) has adopted guidelines, based on its collective wisdom, and a recipe for predicting likely times to extinction.

The recipe has three parts. First, we know that there are population levels below which extinction will be rapid (Pimm *et al.* 1988; Pimm 1991). Second, some populations are declining continuously. Even those that are not declining will still fluctuate in numbers and some populations fluctuate more than others. Other things being equal, these more variable populations will reach the dangerously low levels more quickly than populations than vary less. The numbers of fragmented populations may vary independently, reducing their combined risk, although the individual sub-populations may be at dangerously low levels. Third, there is the nature of how the population minimum drops over time (Pimm & Redfearn 1988). All three components of this recipe are amenable to estimation from empirical data on species we chose to be similar to the endangered species in question. We typically lack data on the endangered species itself.

For example, the 'alala has probably remained at three breeding pairs for the past fifteen years. In managing the 'alala, Duckworth *et al.* (1992) addressed the question of how fast species become extinct at very low levels using data on congeners from Britain (Pimm *et al.* 1993). They recommended active intervention, but leaving adults in the wild. This strategy was on the expectation that this population would become extinct eventually, but not for a decade or two. The species' survival to date has been due to an unlikely combination of legal and social factors, conservation advocacy, and the population's good luck in avoiding demographic accidents. The goodwill of the ranch owner on whose land the birds survived has been crucial. Several other species have not been as lucky. They are so rare that we do not know if they still survive and we cannot help them if we cannot find them. Even if we do, there are no facilities and no detailed, funded plans to provide them with expert care. We consider 12 species to be so rare that their extinction is assured without immediate and active intervention.

The more difficult group involves species with numbers greater than one hundred but less than a several thousand. Using knowledge of long-term population variability and its distribution in time and space, the PARC Committee concluded that 12 species have not yet recovered. It is likely that many of them cannot recover.

(*e*) *Haole Moas: foreign birds*

How Hawai'i acquired an introduced avifauna larger than any other area is a story we have told before (Moulton & Lockwood 1992; Moulton & Pimm 1985, 1987). Here, we will mention only the consequences to β-diversity, and use percentage endemism as its measure. The original land birds of Hawai'i contain only three species (pueo, moorhen and night heron) that are not endemic to the islands. All the passerines are endemic. Polynesian extinctions and introductions reduced non-passerine endemism from 93% to 67%, and recent extinctions to 62%. Yet modern species introductions reduced non-passerine endemism to a mere 16%. Currently, only about one third of the passerine birds are endemic. Almost all of the birds (species and individuals) seen below 1000 m are now alien.

(*f*) *Summary*

Eleven species are abundant enough to not generate immediate concern about their future. Twelve species are endangered, a further 12 are so rare that they are unlikely to survive in the wild (even if they still exist) and 18 are extinct. Forty-three species are know only from fossils, and we estimate that between 30 and 50 species have been lost without a trace. Of the roughly 125–145 species that once inhabited the main Hawaiian islands, 90–110 are extinct and, based on recent experience, 100–120 will be the figure by the end of the decade. Less than 10% of the species have really survived human impact; and humans brought most of the species now present in the islands.

We have discussed Hawai'i in detail because those details cause important and systematic biases to the extinction rates, raise difficult questions about the timing of extinctions and point to the importance of introductions in further reducing endemism. We turn to the other islands within the tropical Pacific and will not repeat the details, although they apply throughout.

3. SOUTHEASTERN POLYNESIA

Southeastern Polynesia is a loose group of island clusters, consisting of the Cooks, Societies, the Tuamotus, the Marquesas, and the remote islands of Henderson and Pitcairn. We justify their joint consideration because only six of the more than 60 species are found outside the area. Most of the islands are atolls, but some are the relatively large remains of old volcanoes. They also introduce the third island type, Makatea islands, of which Makatea in the Tuamotus is the type specimen. These are high islands of uplifted corals and have limestone substrates. (Islands can be mixtures; the north of Guam in the Marianas is of this type, the south is volcanic.)

Steadman (1989, 1991) and Steadman & Kirch (1990) describe fossil faunas from Henderson, Huahine (in the Societies), three islands in the Cooks and four islands in the Marquesas. For all species combined, we estimate the missing species to be 0, 11, 4 and 6 respectively. Of course, some of these 21 species might survive elsewhere in the group because the islands share many of their species. For the entire region, we estimate that there are 16 missing non-passerines and four missing passerines. We also estimate that for both groups combined, there are 22 missing species that occurred on only one island group, and one species missing across the entire region. We cannot separate the data further.

The range of missing species is thus 20 to 23. A further 20 species are known only as fossils. Forty-seven species survived the Polynesians, suggesting they may have exterminated about 45% of the fauna. Again, although estimates of missing species increase the Polynesian impact, we simply do not know how many of these species fell, for example, to the cats deliberately introduced to Tahiti on the expedition that carried Banks. Of the 47 survivors, only eight are known to have become extinct since European exploration. Four more species are endangered, three occur only on uninhabited islands, and three more have such low numbers that their existence is uncertain (Pratt *et al.* 1987; Holyoak 1980). About one third of the bird species have survived human impact.

These islands have introduced species too. As always, the Polynesians brought moas (jungle fowl, *Gallus gallus*) and more recent efforts brought 41 passerine species to Tahiti of which seven survived (Lockwood *et al.* 1993). There are three other non-passerines introductions.

4. THE MARIANAS

The largest islands in the Marianas are of Makatea type. Their frequent caves were defended vigorously during World War II. Those on Guam, Tinian, and Saipan were badly damaged in the fighting. Rota, in contrast, was not contested, and Steadman has explored its caves (Steadman 1992). Seven species are found only as fossils on Rota, and there is a further species found only on Tinian. Of these eight species, two are known from elsewhere (Micronesian pigeon, purple swamphen), two are of uncertain affiliation and may be of species found elsewhere in the islands. Four species are thought to be new ones, including a flightless duck and a giant ground dove.

We estimate that five non-passerines and two passerines are missing from the fossil record. These numbers would be increased by finds of species restricted to one island, but several of Steadman's finds show that species were once more extensively distributed. Twenty species survived to recent times. Of the 28 known species, 14 are endemic and three more are distinctive endemic sub-species. Of the 20 survivors to modern times, five are extinct, one, the Guam rail, occurs only in captivity (although attempts are being made to re-introduce it to the wild; Witteman *et al.* 1990), and three species are endangered. Only the Guam rail, the Guam kingfisher (possibly only a sub-species, although a distinctive one), the Guam flycatcher, and the taxonomically debatable Marianas mallard have gone from the wild.

In summary, of an estimated 35 species, 15 fell to the islands' first colonists, five more since then, but 12 have survived human occupation, at least until now. Consider the island of Guam. It has only one species that may be considered safe, two are endangered, one more (the Marianas crow) survives but rarely breeds, and the island has lost a dozen species. The cause of these extinctions – the introduced brown tree snake – is well known (Savidge 1987; Pimm 1987). So, too, is the snake's spread to Saipan and the occurrence of dead snakes in Hawai'i. The potential consequences to the remaining Pacific faunas are obvious.

5. THE WESTERN PACIFIC

Finally, we turn to the faunas of New Caledonia, Vanuatu, and the group of islands than contains the Fiji, Samoa and Tonga. There are many atolls in this cluster, but it also contains many large islands, in fact, islands larger than any we have discussed so far. We start with Fiji and our personal, identical yet independent impression of its largest island, Viti Levu.

Our first impressions of the islands examined so far were not favourable. Guam has no forest birds and lowland Hawai'i has only a few rare and local native forest birds. To see native Hawaiian birds, one gets cold, wet and tired. On Viti Levu, in contrast, one can see native birds from one's beach front condominium. Indeed, only four of Viti Levu's 47 land birds occur only in the rainforest, and 17 occur commonly in agricultural and suburban habitats (Watling 1982). Viti Levu has introduced species (nine of them), but they do not comprise the majority of the islands individuals or species. This impression of paradise continues as one studies Watling's book on the birds of Fiji, Tonga and Samoa. There are 67 land bird species in the region and 46 are confined to it. Of these, only four have become extinct in historical times, only four more are considered 'rare'. One species is endangered (the Niuafo'ou megapode), in part because it occurs on only one island and in part because of its peculiar habits (it incubates its eggs in hot, volcanic ash). One further species (the long-legged warbler) was once considered rare, but Watling considers it merely hard to find.

Fossil data are few. Steadman has explored 'Eua of the Tonga group. Our analyses of this single island predict only one missing species. Three more species are know only from bones, there are three extinctions in historical times, but all occur widely throughout the region and 12 species survive until the present.

This scarcity of recent extinctions extends to Vanuatu, where Bregulla (1992) reports no recent extinctions in his discussion of the islands' 55 species. He reports only one species near extinction and it is widespread elsewhere. There are two species that are restricted to montane forest on just one island each and both are common in their very restricted ranges. (There are about 30 islands or island groups in the Vanuatu chain, stretching over 1000 km from north to south.)

New Caledonia has 56 species (31 non-passerines) of birds known historically, of which four, all non-passerines, have become extinct in recent times (Hannecart & Letocard 1980). So far, only fossil non-passerines have been described (Balouet & Olson 1989). These add 12 species known only as fossils and we estimate that there are another 12 missing. This island's species include an endemic family (the kagu, Rhynochetidae) with two species, one fossil and one modern, and one fossil species of uncertain familial affinities, the giant, flightless *Sylviornis neocaledoniae*. As the numbers of non-passerines are roughly the same, an even rougher guess for the number of lost and fossil passerines might be the same as for the non-passerines, i.e. 24. This would bring New Caledonia's total to 104 species.

6. PARADISE OR SLAUGHTERHOUSE?

Something is very wrong in this paradise. First, recall our estimates of pre-colonization species richness: Hawai'i, 125–145 species; southeastern Polynesia, 87–90 species; the Marianas, 35 species; Fiji, Tonga and Samoa, 67 plus extinctions; New Caledonia, 104; and Vanuatu, 55 plus extinctions. Exclude the Marianas, for they are low and dry islands; the rest have both small atolls and large, high, volcanic islands. Should we conclude (approximately) that islands have *more* bird species on them the *smaller* they are and the *further* they are to source areas for potential colonists? No, we do not actually believe that a quarter of a century of island biogeography has got the patterns exactly the wrong way around.

When all the fossils are found, we predict that the actual species richness of the Fiji, Tonga and Somoa group should be at least that of the Hawaiian islands: the 'plus extinctions' should exceed the 67 known species. The Hawaiian islands are more remote and they are closer to each other, so allowing less between island diversity. It would be a considerable biogeographic anomaly if the Fiji, Tonga and Somoa group did not have more species than the smaller, more distant group of islands in southeastern Polynesia! First-wave colonizations seem to remove about 50% of an archipelago's fauna. A reasonable prediction would be that the Fiji, Tonga and Somoa group lost 60 or more species.

Similarly, we predict that the missing fossils of Vanuatu will also roughly double its numbers of species. This would be broadly comparable with the situation in nearby New Caledonia as well as the other islands.

Less confidently and more controversially, we suggest that even these numbers (roughly 50 species for each of New Caledonia and Vanuatu) are underestimates. These numbers lead to an almost flat distribution of species richness with increasing distance from sources of colonists across the Pacific. This may be correct. For remote islands speciation, not colonization, is the principal factor increasing species richness. None the less, the increased colonization rates we expect for the islands in the western Pacific, not only provide more species directly (their faunas have less endemics than those in the east and north), but these colonists may seed the process of speciation. Speciation on New Caledonia was sufficiently vigorous to produce at least one endemic family (the kagus) and the bizarre *Sylviornis*.

Another reason for considering the western Pacific estimates of extinction to be on the low side comes from considering the proportion of modern species that are endangered or known to have gone extinct in the last two centuries. This proportion is high in Hawai'i and drops towards the west, roughly linearly with the age of human settlement.

Perhaps the islands in the western Pacific lost the 'wimps' – the species that were in any way sensitive to human activities – a long time ago. This would explain why so many Fijian species occur around human disturbance and so few in the forest and why the pattern is reversed in Hawai'i. Fiji may have lost its forest specialists a long time ago. We would explain Europe's lack of rare birds the same way: the wimps are long gone. (Jared Diamond, personal communication, suggests that elsewhere, frequent cyclones preclude forest specialists, because the forest is so frequently disturbed.)

The consequence of this explanation is that New Caledonia, Vanuatu, and the Fiji, Tonga and Samoa group should have lost even more than the half of their fauna typical of more recently colonized islands. These recently colonized islands are still losing the wimps.

Will the missing species be found? We are not sure. As one moves westwards across the Pacific, humans arrived and birds were lost at earlier dates. Not only might intact bones become scarcer, but their hiding places may be more likely to be destroyed.

It is possible, of course, that the numbers of species may be determined by local factors, such as island height and isolation, the range of habitats, the presence of land crabs (Atkinson 1985) and many other details. If these factors are really important in determining diversity, their effects would not lead to a predictable decline in species richness eastwards across the Pacific.

7. CONCLUSIONS

The number of species lost when humans colonized Pacific islands is approximately double the number of known fossil species and involved about half the species present. Estimated rates of extinction and current endangerment drop with the period of human occupancy, suggesting that those areas colonized first have lost most of their sensitive species.

While adding further crimes to the first colonists, we point to the considerable uncertainties about which species survived to the modern era. In Hawai'i, for example, intensive collecting followed European contact by half a century. This period is certainly long enough for many species to have been lost except as fossils. Indeed, several species were not collected and there were several 'near misses'.

Extinction rates for the last two hundred years frequently ignore a substantial number of species whose numbers are too small to survive without immediate active human intervention. Even more species are endangered, meaning that their long-term survival is unlikely.

Faunal changes have done more than reduce local diversity. Single-island endemics predominate among the species that are lost. There are several explanations for this. Obviously, they would be more vulnerable than species that occur on several islands, even if the per island extinction probabilities were similar for all species. Their probabilities may be higher, because such species may adopt life histories that lead them to being vulnerable (flightlessness, for example). (Their per island extinction rates may appear higher spuriously, because all species on the way to extinction must eventually be found on only one island.) Whatever the reasons, their extinction reduces β-diversity: the percentage of endemic species drops. Even more dramatic in its effects on endemism is the introduction of alien species. Introductions reduce endemism to levels where, in Hawai'i for example, the great majority of the species are not endemic.

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Discussion

N. J. Collar (*Birdlife International, Cambridge, U.K.*). Reference to extinct island forms as 'wimps' is, I appreciate, a convenient shorthand, not intentionally pejorative, for species that colonized the oceanic islands and found themselves in environments usually free of predators or competitors. This makes such species particularly important to target if we truly wish to conserve a representative (if not the full) complement of the biological diversity of our planet.

D. M. J. S. Bowman (*Conservation Commission of the Northern Territory, Palmerston, Northern Territory, Australia*). There is no doubt that Polynesian and European cultures caused numerous extinctions throughout the Pacific. However, I suggest caution against the conclusion that all human colonists or islands necessarily cause substantial extinctions of vertebrates. The first humans colonized Australia at least 60000 years ago. Their impact on the vertebrate assemblages of the great island continent is unclear, with little direct proof that they caused the demise of the marsupial megafauna. What is clear is that the Australian Aborigines caused fewer extinctions of vertebrates than occurred in the mid-Miocene, or which followed the arrival of Europeans. I suggest that some cultures cause extinctions, rather than the general idea that humans necessarily are destructive of biodiversity.

W. J. Bond (*Botony Department, University of Cape Town, South Africa*). Have the many bird extinctions that Professor Pimm has documented had any cascading effects on other organisms, plants for example?

S. L. Pimm. In Hawai'i, the Hawaiian honeycreepers and the plant genera including *Clermontia* and *Trematolobelia* are famous examples of adaptive radiations. The plant genera including many showy, bird-pollinated species, with long curved corollas, from which birds with appropriate beaks could extract nectar. These plants have had unusually high rates of extinction even among a flora where extinction rates are high (introduced goats and pigs may have been the cause). Interestingly, the birds with long curved beaks have also become extinct (mamo, black mamo) or extinct on some islands (i'iwi). It is tempting to explain the bird extinctions as a consequence of the plant extinctions. Such explanations are always plausible and always untestable.