

Holocene extinctions and the loss of feature diversity

Arne Ø. Mooers, Simon J. Goring, Samuel T. Turvey,
and Tyler S. Kuhn

14.1 Introduction

Species are hard to define, but under all definitions they are unique. Each species can be considered to possess a set of unique characters which comprise its feature diversity, the diversity that would be lost when that species goes extinct. However, because species differentiate via evolution from other species, they also share features as a function of degree of relationship. So, within placental mammals, all mice share all the characteristics that allow us to call something a mouse, whereas the sole living species of aardvark shares very few basic mammal characteristics with anything: it must be true that the Earth loses less diversity when any single mouse species goes extinct than when the last living aardvark shuffles off its mortal coil. This is one well-established way in which species are not created equal (Vane-Wright *et al.* 1991; Faith 1992).

We can start to formalize this simple idea with the help of Fig. 14.1. It depicts the common pattern of a diversifying phylogenetic tree, but also can represent the pattern of shared feature diversity, with branch lengths representing the number of unique features that have evolved along that lineage. Pruning the tree illustrates how species and groups of species may differ in the number of unique features they have: if we prune distinctive species (such as the aardvark in Fig. 14.1) we will lose more of the tree (more unique features) than if we prune less distinctive species (e.g. the cat). Likewise, if we prune species {dog, cat}, we will lose more of the tree than if we prune {beaver,

mouse 2}, because, on the tree, species {mouse 1} preserves much of the feature diversity represented by {beaver, mouse 2}. We can say that each of {beaver, mouse 1, mouse 2} are redundant with respect to the features represented by the rodent lineage that gave rise to them.

The mouse/aardvark comparison and Fig. 14.1 allow us to consider a set of interesting observations about how feature diversity is distributed across biodiversity, and what the impacts of historically and prehistorically recent (i.e. Holocene) extinctions have been on this distribution. First, it is now well known that biodiversity is very unevenly distributed across the tree of life: the fact that at the ordinal level the mammals are approximately 50% rodents (Rodentia) and 0.02% aardvark (Tubulidentata) is typical (reviewed in Purvis and Hector 2000). The few living monotremes are another obvious case within mammals, being only distantly related to the remaining approximately 5500 known Holocene species. In phylogenetic terms, the tree of life is very imbalanced, because clades differ greatly in the net diversification they have experienced. Interestingly, the simplest null models of diversification also lead to imbalance, although they are usually not as extreme as those observed in nature (reviewed in Mooers *et al.* 2007).

The second observation, made most clearly by Nee and May (1997), is that, at least under simple null models of diversification, random loss of species has a mild impact on the total loss of the tree. This is easy to intuit: if loss is random, more

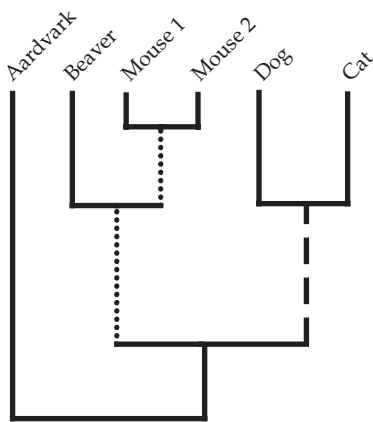


Figure 14.1 Schematic diagram demonstrating clumping of extinction on a phylogenetic tree. Branch lengths represent the number of unique features. The loss of the aardvark would lead to the greatest loss of feature diversity. If both dog and cat go extinct, their shared feature diversity (dashed branch) would also be lost. Extinction of beaver and mouse 2 would lead to less loss, because mouse 1 would represent the shared features of the set (dotted branches).

species will be chosen from the most speciose parts of the tree, which are those parts that contain the most redundancy. From the point of view of conserving the products of evolution in the face of current extinctions, this observation is often cited with some relief (see e.g. Avise 2005). Importantly, Nee and May (1997) highlighted that the actual amount of evolutionary history lost depends strongly on the shape of the tree: the more imbalanced the tree, and the shorter the branches near the root, the more that can be lost (Vazquez and Gittleman 1998; Heard and Mooers 2000). Interestingly, Rauch and Bar-Yam (2004) applied diversification models similar to Nee and May's to make a very different claim: the distribution of genetic redundancy (for them, within species) is highly skewed, such that some lineages (individuals) would be genetically much more distinct than others; that is, *non-random* loss of these lineages would have a large effect on total genetic diversity. This perspective of non-random loss is very important, and the question of the fail-safe of phylogenetic redundancy becomes largely empirical. Heard and Mooers (2000) documented that (1) although non-random loss alone may contribute little to loss overall, (2) non-random loss

concentrated within slowly diversifying groups could lead to very large losses.

The Nee and May (1997) result spurred a series of empirical investigations into how much of the tree of life would be lost if current extinction risk projections were predictive: von Euler (2001) considered birds of the world, Purvis *et al.* (2000a) considered both the world's birds and the world's carnivores and primates, Sechrest *et al.* (2002) looked at these latter two groups in the world's biodiversity hotspots, Johnson *et al.* (2002) studied marsupials in Australia, Russell *et al.* (1998) looked at historical and projected extinctions for all mammals and birds (using taxonomies), and Mooers and Atkins (2003) considered at-risk birds in Indonesia. All these studies agreed that projected losses are significantly greater than if extinctions were random, because projected losses are clumped and/or concentrated in species-poor groups. In addition, von Euler (2001) offered evidence that projected extinctions will make the future bird tree even less balanced than it is today. This means that feature diversity will be even less uniformly distributed among living species than at present, increasing the distinctiveness of some remaining lineages.

It might help to contextualize the main observation (non-random loss of feature diversity) by comparison with past extinctions, and this is the focus of this final chapter. For this we must move from time-based model trees to primarily morphology-based taxonomies, and this presents several interesting issues. Phylogenetic trees are often depicted with all the species an equal distance from their common root, so that we can think of branch lengths as equal to time. Elapsed time must be correlated with feature diversity (Crozier 1997). However, we know of no good quantitative test of the strength of this correlation, partly because the very notion of feature diversity is vague. Williams and Gaston (1994) argue clearly that the correlation may be low, and indeed there is no theoretical reason to expect that morphological evolution should proceed at a constant rate (this is the reason why molecular clocks based on neutral genetic mutations are used instead of cumulative phenotypic character-state changes to estimate phylogenetic divergence dates). So, for example, *Amborella trichopoda* seems to be the sister group to all other living flowering

plants (Mathews and Donoghue 1999). As such it is a monotypic lineage on a very long branch of the tree of life. However, it is presented in textbooks as classically 'primitive', representing a suite of 'basal' characters rather than a suite of novel ones: time seems to have stood still for this particular lineage. The tuatara *Sphenodon punctatus* is another case. Recent genetic studies (Hay *et al.* 2008) suggest that although morphologically unchanged since the Cretaceous, *S. punctatus* may in fact possess one of the fastest rates of molecular evolution for the mitochondrial DNA control region ever observed, making a strong case that although morphologically 'primitive' it might be inappropriate to label *S. punctatus* as primitive in a phylogenetic context. *A. trichopoda* and *S. punctatus* are only two examples of many such small-taxon number lineages, and considerable quantitative work still needs to be done to define and understand the relationships between feature diversity and phylogenetic diversity.

Furthermore, it is important to bear in mind that there are two different hypotheses to explain the existence of small taxonomic groups today. Some small taxa (e.g. obligate river dolphins, most of which represent monotypic families) have persisted for considerable periods but have not diversified further, presumably as a result of the diminished likelihood of diversification under certain ecological settings (see also Vrba 1984). This long persistence at low species diversity provides no intuitive reason to suspect any increased vulnerability to extinction. Conversely, other small taxa were formerly very species-rich (e.g. sloths; see e.g. Kurtén and Anderson 1980), but have experienced disproportionately high levels of extinction. If extinction risk is phylogenetically patterned (see e.g. Purvis *et al.* 2000a), then species from these taxa may be at increased risk of extinction in the future. However, these two different kinds of small taxa are generally not differentiated in analyses of extinction risk, and further research is again required to quantify their relative contributions to present-day feature diversity.

14.2 Holocene extinctions

Here, we use taxonomies as surrogates for phylogenetic trees, and in the case of mammals the

recently published supertree for all mammals (Bininda-Emonds *et al.* 2007), to examine how Holocene extinctions were distributed among taxa. We begin by examining taxonomies, a classification system based primarily on morphological differences. Taxonomies may offer a crude compound measure of feature diversity and time, in so far as they can often be interpreted as reflections of underlying phylogeny (especially following the incorporation of cladistic methodology into taxonomy from the mid twentieth century onwards). New taxa are probably more likely to be recognized when groups of individuals or species are phenotypically distinct (Scotland and Sanderson 2003), and so a taxonomy must contain at least some information about how feature diversity is shared among its members. We recognize, however, that until we have a better concept of feature diversity, this argument is weak (e.g. *A. trichopoda* had already been assigned to its own order before phylogenetic work was conducted, and it is 'different' because it is primitive, not because it is derived).

Our point of departure is the study by Russell *et al.* (1998) on the taxonomic patterns of recent (post-AD 1600) and projected bird and mammal extinctions. We ask the same two questions these authors did: were Holocene extinctions non-random in that they were concentrated in particular subtaxa, and, if so, were these subtaxa small? The first pattern would point to biological correlates of extinction risk, but would not lead to an appreciable loss of feature diversity (see e.g. fig. 3 in Heard and Mooers 2000), whereas the second pattern could lead to substantial losses of higher-order taxa (see e.g. fig. 4 in Heard and Mooers 2000). Using the recently published mammalian supertree (Bininda-Emonds *et al.* 2007) we examine these same two questions by looking at the change in imbalance from a reconstructed Holocene tree to the pruned-by-extinction current tree. Non-random loss that is not clustered within small taxa might have little effect to the overall balance of the tree (but see Heath *et al.* 2008), while non-random losses clustered within small taxa would increase imbalance, at least until a tipping point is surpassed where monotypic taxa are completely removed from the pruned phylogeny, rendering the tree more balanced.

We made use of the taxonomy and lists of mammals and birds known to have gone extinct in the past 11 000 years presented earlier in this volume (see Chapters 3 and 4 in this volume) cross-checked with the 2007 Red List (IUCN 2007), Wilson and Reeder (2005), and the Systema Naturae 2000 online taxonomic database (Brands 2007) (see Appendix 14.1 for decisions made). This database, which lists many extinct taxa, was also important in checking synonymies for extinct and modern species. Because the taxonomic position of extinct species are sometimes not fully resolved, the genera and family data sets are not fully nested. Our mammal data set lists as extinct 249/5577 species, 70/1276 genera (with 16/5577 extinct species not assigned to a genus), 9/159 families, and 1/14 orders (the enigmatic aardvark-like *Bibymalagasia* of Madagascar). Our bird data set lists as extinct 520/10 324 species, 89/2166 genera (with 38/10 324 species not assigned to a genus), 11/204 families, and 2/24 orders (*Aepyornithiformes* and *Dinornithiformes*). This list is obviously not complete: for instance, an estimated but undocumented 2000 flightless rail species may have gone extinct between 3500 and 1000 years BP in the South Pacific (Steadman 1995; see Chapter 10 in this volume for further discussion).

Extinct species were added into the mammal supertree manually using the program PhyloWidget (Jordan 2008). The taxonomic position of each extinct species from primary literature and the Systema Naturae 2000 database were used to work out the sister taxa and depth of each node added. Only extinct species whose taxonomic position was fully resolved were added to the supertree (i.e. the 233 taxa used in the genus-level analysis).

A first reasonable question is whether approximately 5% of 5500 mammal (or of 10 000 bird species) is an anomalous number to lose over 11 000 years. The following are some very rough calculations based on simple null models of the average tempo of diversification that might help (for a guide, see e.g. Baldwin and Sanderson 1998; Ricklefs 2003). We start with a constant-rate birth/death model of diversification:

$$n_t = n_0 e^{rt}$$

where $r = b - d$ (b and d refer to instantaneous speciation and extinction rates per lineage) and n_0 is

the number of species at time (t) zero. If we set t_0 to 1.66×10^8 years ago (the deepest split in the placental mammal tree; Bininda-Emonds *et al.* 2007) when $n_0 = 2$, and if we set $n_t = 5500$ mammal species (the total number in our data set), then, by rearrangement, we get $r = [\ln(5500) - \ln(2)] / 1.66 \times 10^8$ years = 5×10^{-8} years⁻¹. To try to achieve a high enough number of extinctions, we can set $d = 0.9b$ (a high turnover rate sometimes assumed in modeling diversification; see e.g. Magallon and Sanderson 2001); b would be approximately 5×10^{-7} years⁻¹ and $d = 4.5 \times 10^{-7}$ years⁻¹. If we now look at any time slice when many lineages are extant, then the overall rate of addition of new species is deterministically $n_0 b e^{rt}$, and so the total (deterministic) number of 'births' can be calculated as

$$\text{births} = n_0 \int_{t=0}^{t=t^*} b e^{rt} dt$$

For $n_0 = 5500$ and $t^* = 11 000$ years and the b and d estimates above, this is less than 25, and the number of deaths would be less than that; that is, much less than 0.5% of the standing crop. Increasing turnover further to achieve the observed approximately 240 Holocene extinctions, in line with the surely underestimated record number of mammal extinctions, requires that $d = 0.9875b$, but would imply a birth rate of 4×10^{-6} years⁻¹. This in turn demands that the average species is only $b^{-1} = 250 000$ years old. Given that genetic evidence suggests that new species of vertebrate take on the order of 2 million years to form (Avice *et al.* 1998), and an oft-quoted average species age for mammals is 5 million years (see e.g. Purvis and Hector 2000), this does not seem like a biologically reasonable turnover rate (see also Ricklefs 2003). Calculations for birds lead to similar values. Even including preservation biases, estimates for average species ages taken directly from the fossil record are also on the order of 1 million years (Kemp 1999). Taken together, the evidence suggests that the number of recorded mammal and bird extinctions in the Holocene is unusual and was not compensated for by the production of new species. This is not a controversial conclusion, as it is widely recognized that extinctions have occurred rapidly over ecological rather than evolutionary timescales during the

Late Quaternary. In addition, no Holocene species-level bird or mammal extinctions are considered likely to represent 'natural' (i.e. non-anthropogenic) events (see e.g. Chapter 2 in this volume). These prehistoric Late Quaternary extinctions are interpreted as the beginning of a mass extinction event, comparable to those observed in the Phanerozoic fossil record, and which is ongoing today.

To investigate the taxonomic patterning of these extinctions, we followed the clear procedures outlined in Russell *et al.* (1998). We scored the size n_i of each taxon i (genus or family) and the proportion of species extinct and extant in each. Standard binomial theory allows us to produce numbers of species one would expect to go extinct in taxa of a given size and so the expected number of taxa of each size that would be lost entirely. If extinction were random, then the observed proportion of extinct species p

is our maximum likelihood estimate of the global probability of extinction. For the taxonomically assigned mammals, $p=0.042$, and for taxonomically assigned birds, $p=0.047$. If the number of taxa of each size n is S_n , then the expected number of taxa of S_n that are wholly extinct is just $S_n p^n$. This expectation will have a standard deviation of $[S_n p^n (1-p)^n]^{1/2}$. This pattern of random extinction is presented in the grey bars in Fig. 14.2 and compared with the observed number of extinct taxa. Overall, if we take two standard deviations above the expected value as our guide, roughly twice as many higher taxa than expected under a random extinction scenario have been lost throughout the Holocene (e.g. 70 observed mammal genera extinct compared with a maximum of 24 expected, nine observed compared with one or two expected extinct mammal families, 89 compared with 43 expected extinct bird genera,

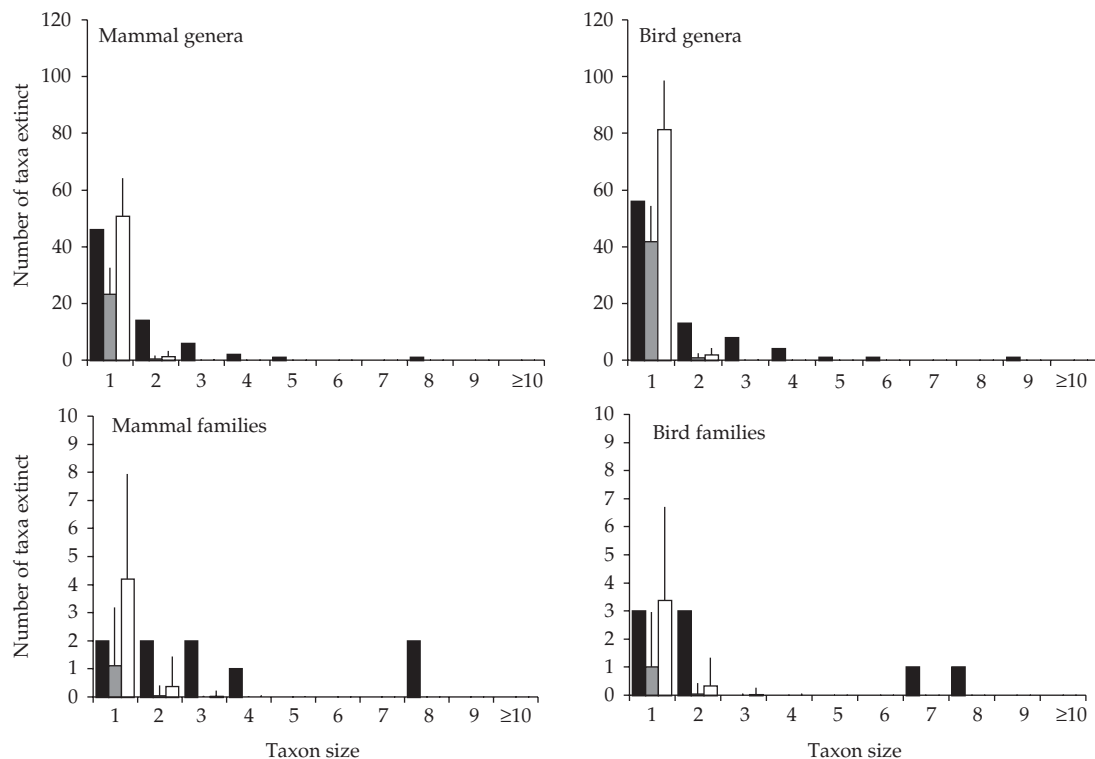


Figure 14.2 The numbers of extinct Holocene taxa of a given size. Dark bars indicate the actual number, grey bars are the expectations if extinction were random, and open bars the expectation under size selectivity (from models presented in Fig. 14.3). Error bars depict two standard deviations under a binomial distribution. Panels are standard for all subsequent figures: top left panel depicts mammal genera; top right panel depicts bird genera; bottom left panel depicts mammal families; and bottom right panel depicts bird families.

and 11 compared with one or two expected extinct bird families).

Russell *et al.* (1998) speak of 'selectivity by size', where probability of extinction is some smooth function of taxon size. Using the standard R-package statistical library (www.r-project.org), and assuming binomial error, we used maximum likelihood to fit our data using the same generalized non-linear model as Russell *et al.* (1998):

$$p_i = \frac{e^{(b_0 + b_1 \ln(n_i))}}{1 - e^{(b_0 + b_1 \ln(n_i))}}$$

where p_i is the proportion of species extinct in taxon i and n_i is its size, and b_0 and b_1 are fitted

parameters. Fig. 14.3 plots the fitted lines of the binomial models of p_i on $\ln(n_i)$ and also the average proportion extinct for taxa of size $\ln(n_i)$. For both mammal and bird genera, and for bird families, there is a significant effect of taxon size on p_i , such that smaller taxa were more likely to lose species to extinction (see Fig. 14.3 legend for values). Outliers in Fig. 14.3 are individual taxon sizes that are ill-fit by the size-selectivity model.

We then used these fitted equations to produce a set of p_n , the probability of extinction for each taxon of size n . This can then be substituted into the simple binomial equations above to produce the expected number of taxa, and associated standard deviations, that would go extinct if there were only

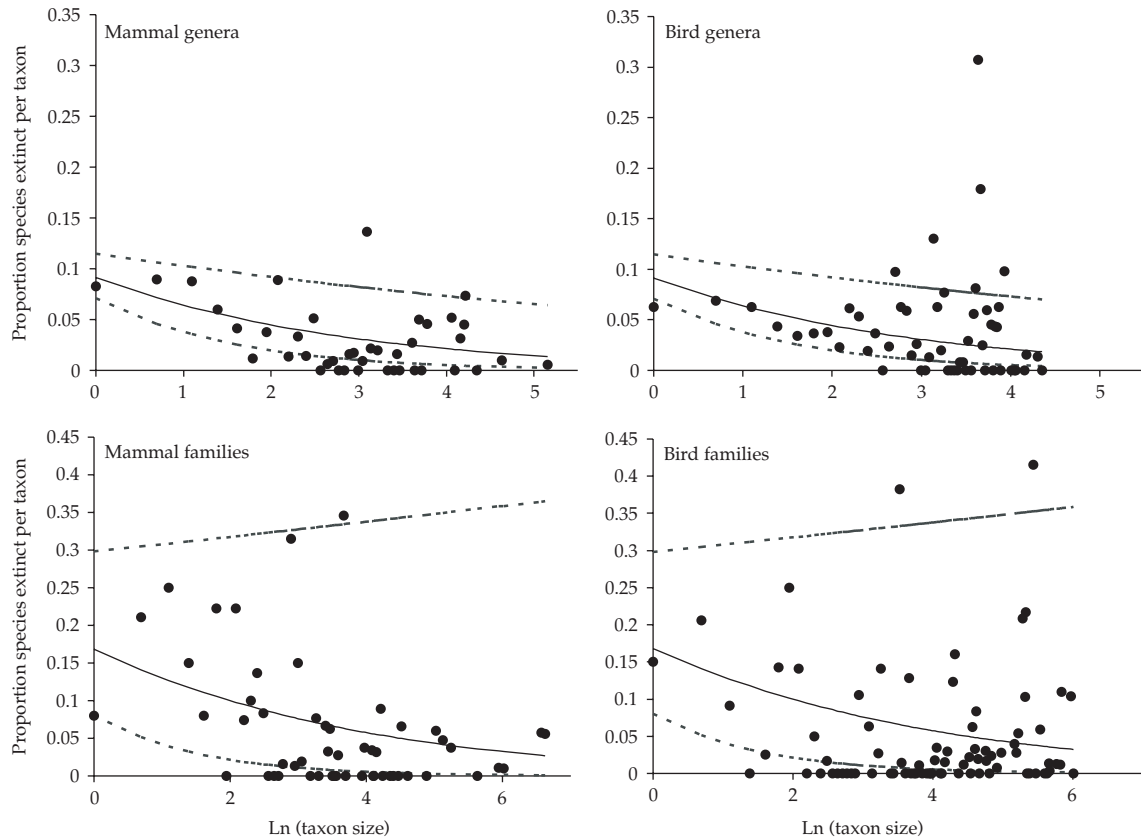


Figure 14.3 Non-linear fits of the proportion of species extinct in a taxon as a function of its size (see equation in the text). The data points are the average proportion of extinct species for taxa of that size. Panels are arranged as in Fig. 14.2. For mammal genera (top left), $b_0 = -2.30$ ($P < 0.0001$) and $b_1 = -0.38$ ($P = 0.005$). Corresponding values for the other data sets are as follows: bird genera (top right), $b_0 = -2.61$ ($P < 0.0001$), $b_1 = -0.20$ ($P = 0.05$); mammal families (bottom left), $b_0 = -1.60$ ($P < 0.0001$), $b_1 = -0.30$ ($P = 0.11$); bird families (bottom right), $b_0 = -1.38$ ($P = 0.0003$), $b_1 = -0.41$ ($P = 0.01$).

selectivity by size. These are depicted in the open bars in Fig. 14.2. Taxa sizes that are not well-fit by this equation are those for which there has been some 'selectivity by taxon'; that is, clumping or dispersion of extinction that is not predicted by taxon size. Risk to monotypic taxa is well described by size selectivity. However, for both mammal and bird genera, taxa with two to five members are at higher risk even than expected based on their size, and a few entire larger-sized genera have also been wiped out, consistent with taxon selectivity not predicted by size. The same general patterns hold at the family level: whereas monotypic families are well-fit by the size-selectivity model, taxa of size two, and the three extinct large-bodied families of Paleognathes (Aepyornithidae (elephant birds), Dinornithidae (giant moas), and Emeidae (smaller moas)) that radiated on islands, show selectivity not predicted by taxon size.

Overall, these patterns we report are similar those reported by Russell *et al.* (1998) for historical extinctions and extinctions projected by IUCN Red List data.

What contributes to this clumping of extinctions within taxa? Holocene extinctions and the subset considered 'historical' (post-AD 1600) by Russell *et al.* exhibit a strong taxon-size bias, where smaller taxa are more likely to be affected. Consistent with Russell *et al.*'s IUCN projections, birds show a weaker taxon-size effect than do mammals for genera. Russell *et al.*'s preferred explanation for this difference was that mammals in larger taxa were understudied, leading to a bias. However, this does not seem to hold here; if anything, we might have better data for mammal than for bird Holocene extinctions. Another possibility may be that this pattern reflects the increased dispersal capabilities of birds, which has led to a difference in the taxonomic distribution of island-dwelling birds compared with mammals: bird taxa tend to contain both (more often extinct) island and (more often extant) mainland taxa. In birds, extent of annual dispersal and diversification rate are positively correlated (Phillimore *et al.* 2006). If high-dispersing and more species-rich avian taxa (e.g. rails, pigeons, parrots) contain species more likely to reach islands, this would weaken (or even reverse) a negative relationship between taxon size and extinction probability.

Superficially, patterns of modern extinctions are not overwhelmed by a contrasting pattern if we extend back over the Holocene. Table 14.1 and Fig. 14.3 highlight that there was also a strong taxon-size-independent component of selectivity: many taxa are ill-fit by the taxon-size selectivity curve. We identified individual taxa with too many extinct species as those that have lost at least $(n_i p_n + (2n_i p_n (1 - p_n))^{1/2})$, rounded up to the nearest integer, and these are listed in Appendix 14.2.

These two types of taxonomic clumping of extinction can be further disentangled by considering a further quantity, the number of taxa of each size affected (i.e. taxa with at least one extinction; Russell *et al.* 1998). The observed numbers can be compared with expected numbers both under a global p [equal to $S_n(1 - (1 - p)^n)$] and the expected numbers under the size-selective model [equal to $S_n(1 - (1 - p^n)^n)$]. These numbers are presented in Table 14.2 and summarized in Fig. 14.4 alongside the total numbers of entire taxa lost and the total expected. The logic, as presented by Russell *et al.* (1998), is straightforward. Selectivity by taxon size (where species in smaller taxa are more likely to be extinct) results in more taxa lost, but can offer a form of compensation in that fewer taxa are affected. However, extreme clumping in the smallest taxa can have the opposite effect (e.g. if every extinction were in a monotypic genus, then the number of taxa affected would equal the total number of extinctions, much higher than any random expectation; Russell *et al.* 1998). If only large taxa were hit with extinctions, or at least if non-size selectivity is concentrated in relatively larger taxa, then fewer taxa might be expected to be lost, with fewer taxa affected. This might be considered the ideal if we are interested in the preservation of evolutionary feature diversity. All four groups show a consistent pattern: size selectivity means more entire taxa are lost than expected, but selectivity in some larger-sized taxa means that there are fewer taxa affected than one would expect from the size-effect model alone. In other words, many of the taxa that are outliers in Fig. 14.3 by virtue of having no recorded extinctions are the result of extinctions being clumped elsewhere. This also brings up a critical issue of scale: whether clumped extinction leads to the overall loss of feature diversity depends on how

Table 14.1 Number of recorded Holocene extinct 'groups' per group size for mammal and bird genera and families.

Group		Group size	Number of groups	p_n	Actual	Predicted	2 SD
Mammals	Genus	1	555	0.091	46	50.628	13.566
		2	234	0.072	14	1.198	2.033
		3	110	0.062	6	0.026	0.294
		4	92	0.056	2	0.001	0.053
		5	53	0.052	1	0.000	0.008
		6	28	0.048	0	0.000	0.001
		7	19	0.046	0	0.000	0.000
		8	31	0.043	1	0.000	0.000
		9	25	0.042	0	0.000	0.000
		10+	129	0.028	0	0.000	0.000
	Family	1	25	0.168	2	4.207	3.741
		2	19	0.141	2	0.379	1.057
		3	8	0.127	2	0.016	0.209
		4	10	0.118	1	0.002	0.068
		5	5	0.111	0	0.000	0.014
		6	3	0.106	0	0.000	0.003
		7	6	0.101	0	0.000	0.001
		8	9	0.098	2	0.000	0.000
		9	3	0.095	0	0.000	0.000
10+		71	0.061	0	0.000	0.000	
Birds	Genus	1	896	0.068	60	61.106	15.092
		2	347	0.060	12	1.247	2.099
		3	211	0.056	7	0.036	0.349
		4	151	0.053	5	0.001	0.061
		5	95	0.050	2	0.000	0.010
		6	63	0.049	1	0.000	0.002
		7	57	0.047	1	0.000	0.000
		8	35	0.046	0	0.000	0.000
		9	46	0.045	1	0.000	0.000
		10+	265	0.036	0	0.000	0.000
	Family	1	21	0.200	4	4.206	3.668
		2	18	0.158	4	0.451	1.130
		3	13	0.137	0	0.034	0.294
		4	7	0.124	0	0.002	0.062
		5	8	0.114	0	0.000	0.018
		6	6	0.107	0	0.000	0.004
		7	4	0.101	1	0.000	0.001
		8	8	0.096	1	0.000	0.000
		9	2	0.092	0	0.000	0.000
		10+	117	0.044	1	0.000	0.000

those features are distributed among taxa through the tree. Our implicit interpretation here is that more diversity is distributed among families than among genera within families. Null models of diversification and feature evolution may offer a guide here, but more empirical work is also needed.

We augment these analyses with a preliminary look of the change in the shape of the mammal supertree (Bininda-Emonds *et al.* 2007) following Holocene extinctions. We made use of a measure of tree shape, I_w , which allows the inclusion of polytomies (Fusco and Cronk 1995, modified by

Table 14.2 Number of groups of mammal and bird genera and families with one or more recorded extinct Holocene species.

Group		Group size	Number of groups	p_n	Actual	Predicted	2 SD
Mammals	Genus	1	0.091	555	46	50.628	13.566
		2	0.138	234	28	32.290	3.639
		3	0.175	110	15	19.201	1.147
		4	0.205	92	10	18.900	0.511
		5	0.233	53	6	12.323	0.196
		6	0.257	28	1	7.189	0.074
		7	0.279	19	1	5.298	0.032
		8	0.299	31	4	9.274	0.022
		9	0.318	25	2	7.950	0.010
	10+	0.560	129	24	1.809	0.000	
	Family	1	0.168	25	2	4.207	3.741
		2	0.262	19	6	4.985	1.687
		3	0.335	8	2	2.678	0.594
		4	0.394	10	2	3.942	0.361
		5	0.445	5	1	2.224	0.136
		6	0.488	3	1	1.465	0.054
		7	0.527	6	0	3.162	0.038
		8	0.561	9	2	5.051	0.022
		9	0.592	3	2	1.775	0.006
10+		0.895	71	30	1.358	0.000	
Birds	Genus	1	0.068	896	60	61.106	15.092
		2	0.116	347	34	40.355	3.829
		3	0.158	211	19	33.252	1.405
		4	0.194	151	11	29.369	0.603
		5	0.228	95	9	21.671	0.254
		6	0.259	63	5	16.325	0.112
		7	0.288	57	7	16.413	0.059
		8	0.315	35	7	11.021	0.026
		9	0.340	46	10	15.650	0.016
		10+	0.670	265	61	2.950	0.000
	Family	1	0.200	21	4	4.206	3.668
		2	0.291	18	5	5.246	1.752
		3	0.358	13	3	4.649	0.794
		4	0.410	7	0	2.872	0.310
		5	0.454	8	1	3.632	0.173
		6	0.492	6	1	2.949	0.076
		7	0.524	4	1	2.097	0.031
		8	0.553	8	2	4.425	0.021
		9	0.579	2	0	1.158	0.005
		10+	0.907	117	51	1.348	0.000

Purvis *et al.* 2002). This measure has an expectation of 0.5 under the simplest null model of random diversification, and approaches 1.0 as trees become more imbalanced. We compared the change in shape from the loss of 233 extinct species that we could place on the mammal supertree with

the expectation if such losses were taxonomically random.

Not surprisingly, the Holocene mammalian phylogeny appears imbalanced ($I_w > 0.5 = 0.633$). When extinct taxa are pruned from the tree imbalance increases ($I_w = 0.645$), and this increase is significant

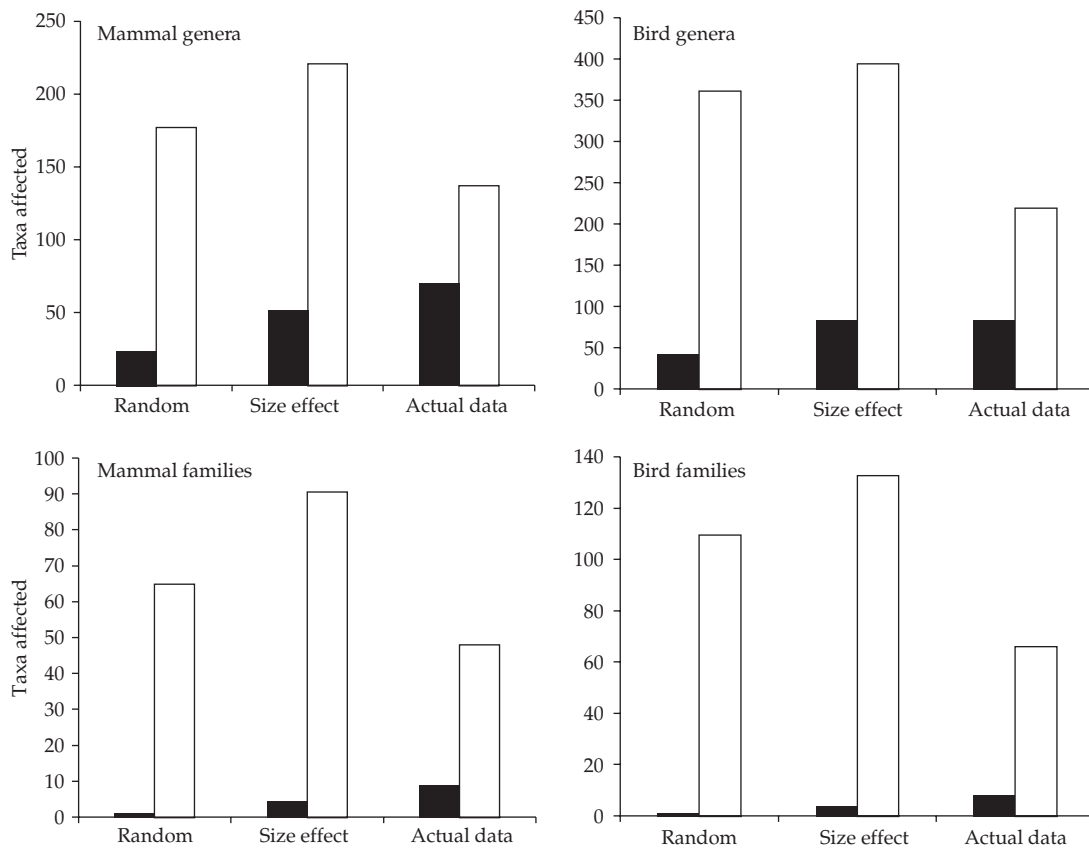


Figure 14.4 In closed bars are the total number of taxa expected to have been lost during the Holocene under taxonomically random extinction [sum across sizes n of $n \times pn$]; the total number under size-selective extinction [sum across sizes n of $n \times pn$], and the observed total number. Open bars depict the total number of taxa with at least one extinction during the Holocene under random extinction [sum across sizes n of $n(1 - (1 - p)n)$], the total under the size selectivity model [sum across sizes n of $n(1 - (1 - pn)n)$], and the observed total. Panels are arranged as in Figs 14.2 and 14.3, with genera above and mammals to the left.

($P < 0.05$) relative to the null expectation of random loss [$E(I_w) = 0.628$, $SD = 0.008$, $n = 1000$ bootstraps]. In agreement with the taxonomic work, the increase in imbalance is most likely due to non-random losses from species-poor clades over the course of the Holocene.

The explanation for the non-random loss of species from small taxa during the Holocene is most certainly the island effect. First, small-range species have experienced the great majority of post-glacial anthropogenic extinctions (for passerine birds, see Manne *et al.* 1999), and island species tend to have small ranges (usually by virtue of geographic isolation of insular populations). Indeed,

207/249 of the extinct mammal species and 495/520 of the extinct bird species were either endemic to islands or geographically restricted to islands or island systems by the start of the Holocene. The three extinct orders were also each endemic to one of two island systems (Madagascar and New Zealand). Island species tend to be placed in their own taxonomic groups, perhaps due to divergent selection imposed by island habitats, or by predetermined biases in taxonomic classification. It is important also to recognize that island systems can act both as refugia for ancient, typically species-poor lineages (e.g. tuatara) and also as centres of evolutionary radiation of more recent colonists

(e.g. drepanidine honeycreepers and *Drosophila* in the Hawai'ian archipelago). However, both sets of species appear to be similarly vulnerable to anthropogenic impacts, as they have typically evolved in the absence of many native predators (notably mammalian predators). It remains unclear whether there is any relationship between relative age and size of island taxa and their vulnerability to extinction. Following on from the work reported here, it would be interesting to compare patterns of taxon size selectivity and extinction in the earlier Late Pleistocene extinctions, which had a continental rather than insular focus but which also clearly impacted many mammals that survive today only as small taxa; however, this is beyond the scope of the present volume.

14.3 Holocene effects on present-day distributions

Humans have had a significant impact on global biodiversity during the Holocene. The extinctions recorded here and projected extinctions based on IUCN Red List data (Russell *et al.* 1998) have had, and likely will lead to, a greater than random loss of feature diversity, at least for birds and mammals (the best-studied taxonomic groups for which we currently possess the most meaningful data). In addition, past taxon selectivity could produce present-day small, at-risk taxa. For example, the two living members of the family Elephantidae (*Elephas maximus* and *Loxodonta africana*) that express the unique feature diversity of the entire classical order Proboscidea are the remnants of a clade with at least 10 members that still survived after the Last Glacial Maximum in the terminal Pleistocene. These two remaining species are also at fairly high risk of extinction: *L. africana* is classified as Vulnerable and *E. maximus* is classified as Endangered by IUCN (2007).

Is it possible that past anthropogenic extinction has created extreme skew in present-day feature diversity? Eleven of the top 100 most evolutionarily distinctive mammals as measured by Isaac *et al.* (2007) have had close (confamilial) relatives lost in the Holocene, increasing their taxonomic and phenotypic isolation. Besides the two elephant species, the list includes the two remaining

hippopotamus species *Hexaprotodon liberiensis* and *Hippopotamus amphibius*, the aye aye *Daubentonia madagascarensis*, the greater bilby *Macrotis lagotis*, the two living solenodons *Solenodon cubanus* and *Solenodon paradoxus*, the dugong *Dugong dugon*, the steppe pika *Ochotona pusilla*, and the New Zealand lesser short-tailed bat *Mystacina tuberculata*. Disconcertingly, all 11 of these species are also listed as globally threatened by the IUCN (2007). A combination of evolutionary distinctiveness and global threat is encapsulated in the EDGE of Existence programme administered by the Zoological Society of London. Nine of these evolutionarily distinct species are on the Society's top 100 EDGE mammal conservation priority list (and the missing two, *H. amphibius* and *M. lagotis*, are ranked 137th and 130th respectively). It may be that many of the species now listed by this innovative programme may be current priorities as a result of human-precipitated extinctions of close relatives within the last 11 000 years. However, connections among past losses, current threat, and current distinctiveness would need to be investigated more formally. So, while many of the top 100 EDGE species are insular, the Spearman rank correlation between threat status and evolutionary distinctiveness, as measured by Isaac *et al.* (2007), while significantly positive, has very low explanatory power ($\rho=0.05$, $P=0.001$, $n=4507$).

In conclusion, not only have Holocene mammal and bird extinctions occurred at a significantly elevated rate, but taxa containing disproportionately few species are both disproportionately threatened with extinction today (Russell *et al.* 1998) and have also experienced elevated rates of species loss over the past 11 000 years (our results) as well as farther back in time (McKinney 1997). We end this short chapter by noting that it is not immediately obvious how to evaluate the importance of the non-random loss of feature diversity through the Holocene that we document here. If the same number of extinctions had taken place but they had been random with respect to the tree of life, would the world be better off? Implicit in the research agenda that looks at the loss of feature diversity through extinction is the idea that species are of different value: to quote George Orwell

from *Animal Farm*, 'all animals are equal, but some animals are more equal than others'. But it need not be true from first principles that more feature diversity as we are measuring it is much better in any ecologically or evolutionarily meaningful way. For example, the species-richness/ecosystem function debate (Cardinale *et al.* 2006; Worm *et al.* 2006) is ongoing. We need more work on the relationship between feature diversity and phylogenetic diversity. We also need more work on the use and non-use values of each.

Acknowledgements

AOM, TSK and SJG thank NSERC Canada, and AOM thanks the Institute for Advanced Study, Berlin, for financial support. We are grateful to IRMACS and to the fab*-lab, both at SFU, for stimulating environments, and to Sally Otto, Walter Jetz, and Gareth Russell for important intellectual input of various kinds. We thank the two anonymous reviewers, one who made us go back to the mammal supertree, and Jonathan Davies, who directed us to PhyloWidget.

Appendix 14.1 Notes on the taxonomic database used

The data sets used here are from Chapter 3 (for mammals) and Chapter 4 (for birds). Revisions and exclusions are listed below for mammals and birds. Revisions to the taxonomies were only made when extant taxa listed in the IUCN 2007 Red List were affected by the taxonomic discrepancies between data sets.

A. Mammals

Taxa excluded from generic analysis

Rodentia

Cricetidae

Oryzomyini gen. et sp. indet., spp. 1–13

Muridae

Melomys/Pogonomeiomys spp. nov. A–B

Taxa excluded from all analysis

Rodentia

Family Indet.

Tainotherium vaei

Rodentia? gen. et sp. nov.

Chiroptera

Family Indet.

Boryptera alba

B. Birds

Taxonomic conflicts

Columbiformes

Columbidae

Pezophaps solitaria, *Raphus cucullatus*: listed as Raphidae by IUCN (2007)

Gruiformes

Rallidae

Atlantisia elpenor: transferred to *Atlantisia* from *Mundia* to be consistent with IUCN (2007)

Passeriformes

Fringillidae

Loxops sagittirostris: listed as *Hemignathus sagittirostris* by IUCN (2007)

Psittirostra kona: listed as *Chloridops kona* by IUCN (2007)

Struthioniformes

Casuariidae

Dromaius ater, *D. baudinianus*: all *Dromaius* species listed as Dromaiidae by IUCN (2007)

Taxa excluded from generic analysis

Anseriformes

Anatidae

aff. *Anas* undescribed species

aff. *Tadorna* undescribed sp.

cf. *Dendrocygna* undescribed sp.

Anatidae undescribed sp.

Anatidae "supernumerary Oahu goose"

Charadriiformes

Scolopacidae

Coenocorypha? undescribed sp.

Columbiformes

Columbidae

cf. *Alectroenas* undescribed sp.

Gallucolumba? norfolciensis

"*Raperia*" *godmanae*

undescribed gen. et sp.

undescribed gen. et sp. A-C

Falconiformes

Falconidae

Falconidae undescribed small sp.

Galliformes

Megapodiidae

Megapodiidae undescribed sp.

Gruiformes

Rallidae

cf. *Dryolimnas* undescribed sp."Fulica" *podagrica*cf. *Gallinula* sp.cf. *Porzana* undescribed sp.

Rallidae undescribed sp.

Rallidae undescribed spp. A–D

Passeriformes

Campephagidae

cf. *Lalage* sp.

Meliphagidae

cf. *Chaetoptila* undescribed sp.

Passeridae

Foudia belloni: formally described after our analysis was conducted; previously referred to in the literature as *Foudia?* undescribed sp.

Sylviidae

cf. *Cettia* sp.

Timaliidae

Timaliinae undescribed gen. et sp.

Turdidae

Turdidae undescribed sp.

Zosteropidae

Zosteropidae undescribed spp. 1–2

Psittaciformes

Psittacidae

"Necropsittacus" *borbonicus*

cf. Psittacidae undescribed spp. 1–2

Psittacidae undescribed sp.

Strigiformes

Tytonidae

Tyto? *letocarti***Taxa excluded from all analysis**

Aves incertae sedis

"Aquila" *simurgh*

Passeriformes incertae sedis

"Turdus" *ulientensis*aff. *Carduelis* undescribed species

Passeriformes undescribed slender-billed species

Passeriformes undescribed very small species

Appendix 14.2 List of taxa that have undergone more extinctions than expected

Families listed in bold have suffered higher than expected numbers of extinct species. Each taxon is listed with the number of extinct species/total number of species in that taxon. §, Extinct order; ‡, extinct family; †, extinct genus.

A. Mammals	Genus	Family	Genus	Family
Artiodactyla			Rodentia	
Bovidae			Capromyidae	27/39
<i>Bubalus</i>	2/6		<i>Capromys</i>	6/8
Hippopotamidae		4/6	<i>Geocapromys</i>	5/7
<i>Hippopotamus</i>	3/4		† <i>Isolobodon</i>	2/2
§Bibymalagasia			<i>Mesocapromys</i>	8/12
†Plesiorcyteropodidae		2/2	<i>Plagiodontia</i>	2/3
† <i>Plesiorcyteropus</i>	2/2		Cricetidae	41/710
Carnivora			† <i>Megalomys</i>	4/4
Canidae			† <i>Megaoryzomys</i>	2/2
† <i>Dusicyon</i>	2/2		<i>Neotoma</i>	3/22
Chiroptera			<i>Nesoryzomys</i>	6/8
Phyllostomidae			Echimyidae	
<i>Desmodus</i>	3/4		† <i>Boromys</i>	2/2
Phyllostomidae			† <i>Brotomys</i>	2/2
<i>Phyllops</i>	2/3		Gliiridae	
			<i>Eliomys</i>	2/5
			†Heptaxodontidae	4/4
			Muridae	42/754

Table continued

A. Mammals	Genus	Family	Genus	Family
Pteropodidae			† <i>Canariomys</i>	2/2
<i>Pteropus</i>	6/67		† <i>Coryphomys</i>	2/2
			†gen. 1	3/3
Dasyuromorphia			†gen. 2	3/3
†Thylacnidae		2/2	†gen. 4	2/2
† <i>Thylacinus</i>	2/2		<i>Notomys</i>	5/10
			<i>Rattus</i>	5/68
Diprotodontia				
Macropodidae			Soricomorpha	
<i>Lagorchestes</i>	2/4		† <i>Nesophontidae</i>	8/8
			† <i>Nesophontes</i>	8/8
Pilosa			Solenodontidae	
Megalonychidae	16/18		<i>Solenodon</i>	2/4
† <i>Acratocnus</i>	4/4		Soricidae	
† <i>Megalocnus</i>	2/2		† <i>Asoriculus</i>	3/3
† <i>Neocnus</i>	5/5			
† <i>Parocnus</i>	2/2			
Primates				
†Archaeolemuridae		3/3		
† <i>Archaeolemur</i>	2/2			
Lemuridae				
† <i>Pachylemur</i>	2/2			
†Megaladapidae		3/3		
† <i>Megaladapis</i>	3/3			
†Palaeopropithecidae		8/8		
† <i>Mesopropithecus</i>	3/3			
† <i>Palaeopropithecus</i>	3/3			
<hr/>				
B. Birds	Genus	Family	Genus	Family
‡Aepyornithiformes			Galliformes	
†Aepyornithidae		7/7	Phasianidae	
† <i>Aepyornis</i>	4/4		<i>Coturnix</i>	3/11
† <i>Mullerornis</i>	3/3			
			Gruiformes	
Anseriformes			†Aptornithidae	2/2
Anatidae		41/197	† <i>Aptornis</i>	2/2
<i>Alopochen</i>	3/4		Rallidae	96/231
<i>Anas</i>	6/48		† <i>Aphanapteryx</i>	2/2
<i>Branta</i>	4/10		<i>Atlantisia</i>	2/3
† <i>Cnemiornis</i>	2/2		<i>Fulica</i>	4/15
<i>Cygnus</i>	3/9		<i>Gallirallus</i>	28/38
† <i>Thambetochen</i>	2/2		† <i>Nesotrochis</i>	3/3
			† <i>Pareudiastes</i>	2/2
Ciconiiformes			<i>Porphyrio</i>	10/15
Accipitridae		15/255	<i>Porzana</i>	26/39
<i>Aquila</i>	3/15		<i>Rallus</i>	3/12

Table continued

B. Birds	Genus	Family	Genus	Family
[†] <i>Titanohierax</i>	2/2		Gruidae	
Ardeidae		12/75	<i>Grus</i>	4/17
<i>Nycticorax</i>	8/10			
Falconidae		9/73	Passeriformes	
<i>Caracara</i>	3/5		Acanthisittidae	4/6
<i>Milvago</i>	2/4		Corvidae	
Procellariidae		17/96	<i>Corvus</i>	8/51
<i>Pterodroma</i>	7/38		Fringillidae	45/207
<i>Puffinus</i>	7/26		[†] <i>Aidemia</i>	3/3
Scolopacidae		14/102	[†] <i>Akialoa</i>	9/9
<i>Coenocorypha</i>	5/7		[†] <i>Chloridops</i>	3/3
[†] <i>Prosobonia</i>	6/6		[†] <i>Ciridops</i>	4/4
Threskiornithidae			[†] <i>Drepanis</i>	2/2
[†] <i>Apteribis</i>	3/3		<i>Loxoides</i>	2/3
Columbiformes			[†] <i>Rhodacanthis</i>	4/4
Columbidae		38/345	<i>Telespiza</i>	4/6
<i>Alectroenas</i>	2/5		[†] <i>Vangulifer</i>	2/2
<i>Ducula</i>	5/42		[†] <i>Xestospiza</i>	2/2
<i>Gallinula</i>	6/24		Meliphagidae	
			[†] <i>Chaetoptila</i>	3/3
			[†] <i>Moho</i>	5/5
Craciformes			Monarchidae	
Megapodiidae		13/34	<i>Pomarea</i>	4/9
<i>Megapodius</i>	11/23		Turdidae	
			<i>Myadestes</i>	3/14
Cuculiformes			†Turnagridae	2/2
Cuculidae			[†] <i>Turnagra</i>	2/2
<i>Coua</i>	3/12		Sturnidae	
			<i>Aplonis</i>	5/26
§Dinornithiformes			Psittacidae	41/394
†Dinornithidae		2/2	<i>Amazona</i>	6/37
[†] <i>Dinornis</i>	2/2		<i>Ara</i>	8/16
†Emeidae		8/8	<i>Eclectus</i>	2/3
[†] <i>Eurapteryx</i>	2/2		<i>Nestor</i>	2/4
[†] <i>Pachyornis</i>	3/3		<i>Psittacula</i>	4/17
			<i>Vini</i>	2/7
Strigiformes				
Caprimulgidae				
<i>Siphonorhis</i>	2/3			
Strigidae		21/204		
<i>Athene</i>	4/7			
[†] <i>Gallistrix</i>	4/4			
[†] <i>Mascarenotus</i>	3/3			
[†] <i>Ornimegalonyx</i>	2/2			
Tytonidae		11/26		
<i>Tyto</i>	10/23			
Struthioniformes				
Casuariidae				
<i>Dromaius</i>	2/3			

