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Palaeontology

The changing role of mammal life histories in Late Quaternary extinction vulnerability on continents and islands

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Understanding extinction drivers in a human-dominated world is necessary to preserve biodiversity. We provide an overview of Quaternary extinctions and compare mammalian extinction events on continents and islands after human arrival in system-specific prehistoric and historic contexts. We highlight the role of body size and life-history traits in these extinctions. We find a significant size-bias except for extinctions on small islands in historic times. Using phylogenetic regression and classification trees, we find that while life-history traits are poor predictors of historic extinctions, those associated with difficulty in responding quickly to perturbations, such as small litter size, are good predictors of prehistoric extinctions. Our results are consistent with the idea that prehistoric and historic extinctions form a single continuing event with the same likely primary driver, humans, but the diversity of impacts and affected faunas is much greater in historic extinctions.

1. Background

Mammal faunas around the globe are depauperate today. As recently as the Late Pleistocene, ecosystems contained some of the largest land mammals ever to walk the earth [1]. The timing and intensity of the extinction differed, but by the terminal Pleistocene all continental landmasses had suffered a significantly size-biased extinction [2,3]. The loss of species has continued in recent times, with island faunas being particularly vulnerable [4].

Late Quaternary extinctions were unique in several important respects. First, the size selectivity was extreme when compared with previous extinction pulses [2,5]; over the past 65 Ma, large body size does not make mammals more vulnerable to extinction [6,7] except in the terminal Pleistocene and the present [8]. Second, this size bias was present within mammalian orders as well as across all mammals, suggesting that the extinction could not be explained solely by shared ecological and life-history traits [2]. Finally, on every continent, extinctions happened after the arrival of humans and not always at a time of changing climate [3,9].

Several hypotheses have been proposed to explain the megafaunal extinction, including human hunting [10], climate change and community disassembly [11], removal of keystone species [12], hyperdisease [13], synergy between anthropogenic and climate impacts [14], and a comet [15]. Except for human hunting,

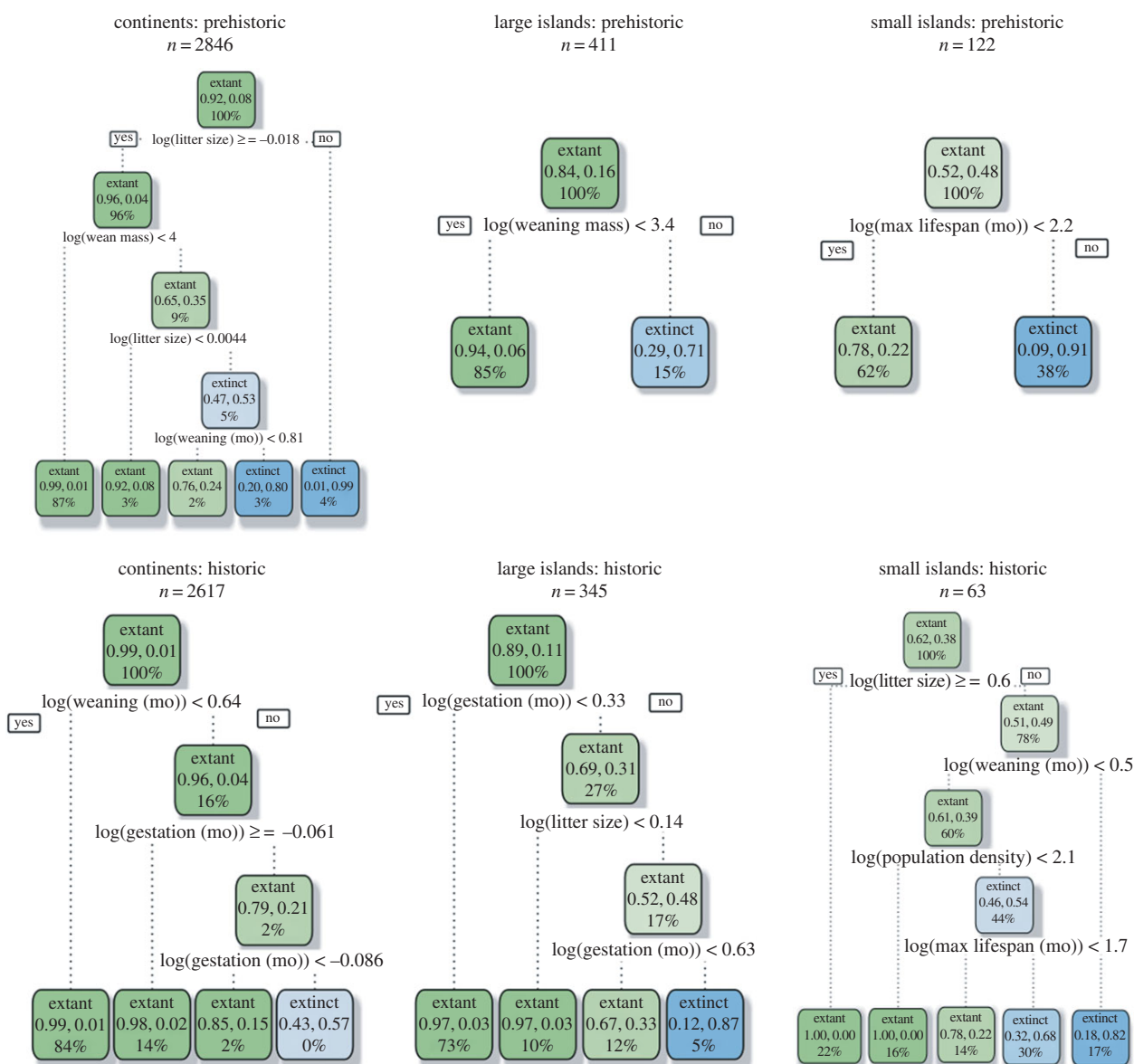


Figure 1. Classification trees for prehistoric and historic extinctions on continents, large and small islands. Historic trees are pruned to the least complex tree (i.e. not following the one-standard error rule) owing to low support (electronic supplementary material, figure S4). Colour of terminal leaves indicates dominance by either extant (green) or extinct (blue) taxa. mo, months.

all of these hypotheses require large mammals to be intrinsically more vulnerable to extinction in order to account for the striking size bias.

Here, we provide an overview of Quaternary extinctions and examine the role of life history on mammalian extinctions on both continents and islands. We compare prehistoric and historic extinctions to determine if they resulted from similar drivers. We define 'prehistoric' as extinctions that occurred in the Late Pleistocene and Holocene (50–2 kBP), but prior to the spread of Europeans and/or major cultural shifts *in situ* (e.g. Japan). 'Historic' is defined as extinctions occurring after the spread of Europeans and their associated commensal species (i.e. 1500–1950 AD). Because the timing of the extinctions and the timing of human arrival and cultural changes varied, prehistoric/historic designations are made individually for each system. We ask whether the size selectivity of the extinctions is similar across continents, large islands and small islands, and whether prehistoric extinctions show similar life-history signatures to more recent extinctions.

2. Material and Methods

(a) Data

Species lists and body size data for five continents and seven large islands (electronic supplementary material, table S1) were taken from an updated version of Smith *et al.* [16]. Data for South American megafauna were revised using updated information from Barnosky & Lindsey [14]. Species lists and body sizes for species on small islands ($n = 31$) were compiled from a variety of literature sources (electronic supplementary material, table S1). The size cut-off for small islands was set at less than 40 000 km², which coincides with a small, but natural break in the distribution of our island areas. Islands were also categorized as continental or oceanic, and analyses were rerun to evaluate the effects of island classification. Taxonomic information was standardized using a global phylogeny of Late Quaternary mammals [17]. Life-history and ecological data for extant species were taken from panTHERIA [18] and Ernest [19]. Life history of extinct mammals and missing data for extant mammals were estimated, using regressions on body size (electronic supplementary material, table S2). Ecological traits for

Table 1. Model statistics for classification trees and random forests. Accuracy represents the proportion of faunas correctly identified as either extant or extinct (and associated statistical significance). Null accuracy is the expectation of overall accuracy, given the structure of the data. Specificity and sensitivity are the proportions of species correctly identified as extant and extinct, respectively. Cohen's Kappa evaluates agreement between model output and true values, with a correction for agreement by random chance. Low values (close to 0) indicate agreement by chance whereas high values (closer to 1) indicate agreement in excess of chance. Significance value for Kappa reflects only the Kappa statistic (not the overall model).

	accuracy	null accuracy	specificity	sensitivity	kappa
classification tree					
prehistoric					
continents	0.988 ($\ll 0.001$)	0.919	0.909	0.995	0.916 ($\ll 0.001$)
large islands	0.922 ($\ll 0.001$)	0.839	0.682	0.968	0.692 ($\ll 0.001$)
small islands	0.861 ($\ll 0.001$)	0.516	0.746	0.968	0.719 ($\ll 0.001$)
historic					
continents	0.989 (0.475)	0.989	0.138	0.999	0.219 ($\ll 0.001$)
large Islands	0.939 (0.002)	0.893	0.676	0.971	0.670 ($\ll 0.001$)
small islands	0.841 (< 0.001)	0.619	0.917	0.795	0.679 (< 0.001)
random forest					
prehistoric					
continents	1.000 ($\ll 0.001$)	0.935	1.000	1.000	1.000 ($\ll 0.001$)
large Islands	0.997 ($\ll 0.001$)	0.857	1.000	0.996	0.988 ($\ll 0.001$)
small Islands	1.000 ($\ll 0.001$)	0.545	1.000	1.000	1.000 ($\ll 0.001$)
historic					
continents	0.999 ($\ll 0.001$)	0.987	0.966	1.000	0.965 ($\ll 0.001$)
large Islands	1.000 ($\ll 0.001$)	0.932	1.000	1.000	1.000 ($\ll 0.001$)
small Islands	1.000 ($\ll 0.001$)	0.610	1.000	1.000	1.000 ($\ll 0.001$)

extinct mammals and missing data for extant mammals were estimated using ancestral character state reconstruction [20]. We explored 12 ecological and life-history traits: trophic level, life habit (terrestrial, arboreal, volant), gestation length (months), newborn mass (g), weaning age (months), weaning mass (g), age at first reproduction (months), maximum lifespan (months), litter size, litters per year, home range (km^2) and population density (n km^{-2}). Continuous variables were log-transformed before analysis. Body size was not included in analyses evaluating life history and extinction risk, because some life-history data were estimated using body size.

(b) Statistical analyses

We employed classification trees and random forests to model the relationship between ecological and life-history traits and extinction risk. This approach is particularly well-suited because it accommodates nonlinear behaviours among variables and allows for complex interactions among intercorrelated variables [8,21,22]. Unless noted elsewhere, classification trees were pruned to the least complex tree with cross-validated error within that of the lowest-error tree (the one-standard error rule) [21]. We used the R packages 'rpart' and 'randomForest' to construct the models. Body size distributions and trait distributions identified as important by the random forests were compared between extinct and extant mammals for each landmass and time category. Species present on multiple landmasses were recorded only once and species that went extinct on one landmass, but were extant on another were excluded from further analyses (see the electronic supplementary material). To evaluate whether phylogenetic autocorrelation was an important driver of our results, we used a multivariate phylogenetic logistic regression to control for phylogeny while evaluating the relationship between

extinction risk and life-history traits [23]. Ecological traits were not included in this analysis, because missing data were estimated using the phylogeny. Analyses were performed separately for historical and prehistoric extinctions on continents, large islands and small islands.

3. Results and discussion

We find that large mammals are more prone to extinction during the Late Quaternary (electronic supplementary material, figure S1). This is true for both historic and prehistoric extinctions, but the effect size decreases considerably in historic extinctions (electronic supplementary material, table S3). The time-transgressive nature of the size bias suggests that these extinctions, both prehistoric and historic, are part of a single prolonged event [24]. This consistency, combined with findings that large body size does not correlate with higher extinction risk outside the Quaternary [6,7], and the timing of the extinctions after human arrival [3], suggests that either large-bodied mammals are selectively targeted by humans when they enter a new area, that large-bodied mammals are more vulnerable to human impacts [25], or both.

We find a consistent and important role of life history across landmasses (figure 1), with similar results for continental and oceanic islands (electronic supplementary material, figure S2). Although the trait with the most explanatory power is not always the same (figure 1 and electronic supplementary material, figure S3), the values of the traits associated with survival indicate increased 'resilience', that is the ability to recover from perturbation. For example, species

Table 2. Multiple phylogenetic logistic regression of extinction risk against life history traits. * indicates predictors that are significant at the 0.05 level.

	independent variable	slope estimate	z-value	p-value
prehistoric				
continents	gestation month	4.18	4.47	<0.001*
	log newborn mass	−0.84	−2.63	0.009*
	weaning month	−2.88	−3.02	0.003*
	log weaning mass	−0.13	−0.33	0.743
	age at first reproduction (months)	1.28	1.72	0.085
	maximum life span (months)	−2.49	−1.96	0.050*
	litter size	4.77	4.86	<0.001*
	litters per year	−2.60	−3.13	0.002*
	log home range size	−0.60	−2.86	0.004*
	log population density	0.78	3.80	<0.001*
large Islands	gestation month	1.09	0.75	0.453
	log newborn mass	−0.84	−1.58	0.114
	weaning month	−1.25	−1.00	0.318
	log weaning mass	−0.84	−1.45	0.148
	age at first reproduction (months)	0.77	0.52	0.602
	maximum life span (months)	1.50	1.08	0.279
	litter size	2.34	2.41	0.016*
	litters per year	−1.70	−1.22	0.223
	log home range size	−0.45	−1.05	0.296
	log population density	−0.19	−0.52	0.607
small Islands	gestation month	−1.05	−0.45	0.656
	log newborn mass	2.54	1.15	0.251
	weaning month	−2.78	−1.08	0.280
	log weaning mass	−2.92	−1.06	0.289
	age at first reproduction (months)	5.50	2.36	0.018*
	maximum life span (months)	0.75	0.21	0.833
	litter size	5.87	1.96	0.050*
	litters per year	3.53	1.18	0.238
	log home range size	0.50	0.57	0.570
	log population density	0.76	1.40	0.161
historic				
continents	gestation month	0.98	1.09	0.278
	log newborn mass	0.22	0.80	0.421
	weaning month	−2.21	−2.12	0.034*
	log weaning mass	−0.35	−0.82	0.413
	age at first reproduction (months)	0.86	1.18	0.239
	maximum life span (months)	0.37	0.49	0.625
	litter size	0.93	1.14	0.254
	litters per year	−0.87	−0.84	0.404
	log home range size	−0.70	−2.18	0.030*
	log population density	−0.30	−1.28	0.201
large Islands	gestation month	−3.00	−2.03	0.042*
	log newborn mass	−0.83	−1.46	0.144
	weaning month	−1.51	−1.24	0.216
	log weaning mass	0.78	1.21	0.227

(Continued.)

Table 2. (Continued.)

	independent variable	slope estimate	z-value	p-value
	age at first reproduction (months)	0.04	0.04	0.968
	maximum life span (months)	2.00	1.50	0.135
	litter size	-2.83	-2.17	0.030*
	litters per year	0.94	0.77	0.443
	log home range size	0.23	0.59	0.552
	log population density	0.55	1.33	0.184
small islands	gestation month	0.22	0.10	0.920
	log newborn mass	-1.27	-0.38	0.710
	weaning month	-0.55	-0.36	0.720
	log weaning mass	0.22	0.06	0.950
	age at first reproduction (months)	0.53	0.16	0.870
	maximum life span (months)	0.62	0.12	0.900
	litter size	0.45	0.09	0.930
	litters per year	0.56	0.14	0.890
	log home range size	0.10	0.07	0.940
	log population density	-0.94	-0.74	0.460

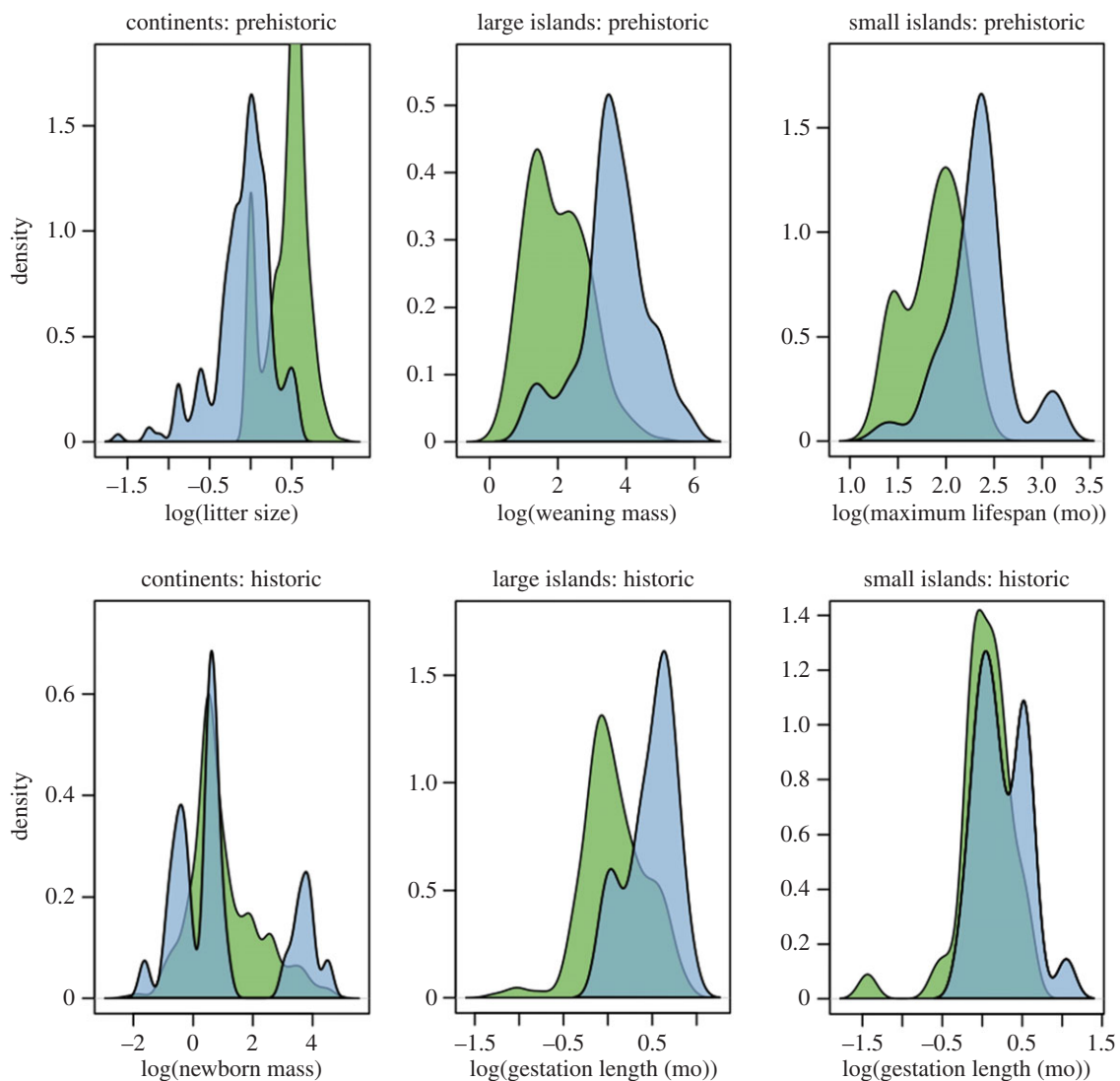


Figure 2. Density plots of most important life-history traits predicting extinction risk identified by random forests (electronic supplementary material, figure S3). Blue, extinct; green, extant. For each panel, kernel density estimates were calculated using the same bandwidth for extant and extinct taxa. mo, months.

more likely to go extinct prehistorically had smaller litter sizes (continents), larger weaning masses (large islands) and longer lifespans (small islands). In historic extinctions, the most important traits identified by random forest models were newborn mass and gestation length (electronic supplementary material, figure S3); again, extinct species had values that indicated longer population recovery times (e.g. larger newborns, longer gestation lengths). It is important to note that the classification trees predicting the historic extinctions have poor support, suggesting that life histories play a reduced role in these extinctions (table 1 and electronic supplementary material, table S4 and figure S4). For continents, this may be because of sample size; only 29 species, or 1% of the fauna have gone globally extinct in historic times, whereas 8% went extinct in prehistoric times (electronic supplementary material, table S1). This is less of an issue for islands as the extinctions have been of similar magnitude (large islands: 10% historic, 15% prehistoric; small islands: 36% historic, 49% prehistoric). The multivariate phylogenetic logistic regression also identified traits associated with increased resilience (e.g. litter size) as being important after controlling for phylogenetic autocorrelation (table 2). Similar to the classification trees, life-history traits play an important role in the prehistoric extinctions, especially on continents, and a lesser role in historic extinctions.

The difference in the important life-history traits between extinct and extant species was more pronounced during prehistoric extinctions on all landmasses (figure 2 and electronic supplementary material, table S3). Trait distributions differed significantly and had much larger effect sizes for all landmasses during the prehistoric extinctions. For the historic extinctions, effect sizes were smaller, and only the trait distributions for large islands were significantly different. The lack of signal in historic extinctions (table 1 and electronic supplementary material, figure S4) may be a result of larger numbers of driving factors compared with prehistoric extinctions [26].

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4. Conclusion

Comparison of prehistoric and historic extinctions on different landmasses provides insights into potential causes. Similar to others, our results suggest that these extinctions are all part of a single, prolonged, global extinction event that is still ongoing [24]. The timing of extinctions [3,9] and similarity in size selectivity suggest that the main driver of these extinctions is human impacts rather than other causes such as climate change. Extinction vulnerability in the prehistoric is closely tied with life-history traits, indicative of reduced capacity to quickly recover from a perturbation. Vulnerability to historic extinctions has far weaker ties to life-history characteristics, suggesting a change in the suite of extinction pressures; this is likely a consequence of increasing intensities and varieties of human perturbations [26]. Identifying these diverse, and potentially synergistic extinction drivers across ecosystems worldwide will be a challenging but necessary component for managing the future of mammalian biodiversity.

Ethics. Ethical approval was not required.

Data accessibility. Body size and ecological trait data can be downloaded from <http://biology.unm.edu/fasmith/Datasets/> [16]. Life-history data [20,21] are from *Ecological Archives*. Data estimated from regression equations are available from S.K.L.

Authors' contributions. S.K.L. designed the study with J.H.M. and F.A.S. J.H.M. conducted most analyses. D.F. conducted phylogenetic analyses. A.B. provided R code. E.L. provided data on extinct South American mammals and A.M.M. provided data on mammal extinctions on small islands. S.K.L. wrote the paper and all authors provided input into revisions. All authors agree to be held accountable for the content therein.

Competing interests. We have no competing interests.

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