Extensive population decline in the Tasmanian devil predates European settlement and devil facial tumour disease

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The Tasmanian devil (Sarcophilus harrisii) was widespread in Australia during the Late Pleistocene but is now endemic to the island of Tasmania. Low genetic diversity combined with the spread of devil facial tumour disease have raised concerns for the species’ long-term survival. Here, we investigate the origin of low genetic diversity by inferring the species’ demographic history using temporal sampling with summary statistics, full-likelihood and approximate Bayesian computation methods. Our results show extensive population declines across Tasmania correlating with environmental changes around the last glacial maximum and following unstable climate related to increased ‘El Niño–Southern Oscillation’ activity.

1. Introduction

Insular species often have low genetic diversity [1]. The Tasmanian devil (Sarcophilus harrisii) is no exception. The species has low diversity at microsatellite [2], mitochondrial, nuclear [3] and immune-system genes [4]. Combined with the spread of a transmissible cancer, devil facial tumour disease (DFTD), concerns have been raised for the species’ long-term survival. As a specialized scavenger, devils have an influential ecological function in Tasmanian ecosystems, for example suppressing alien mesopredators such as the feral cat [5] and removing carcasses from the landscape. Formerly widespread in Australia during the Late Pleistocene and Early Holocene, the devils are now restricted to the island of Tasmania.

Four major events may have influenced the current distribution and low genetic diversity of Tasmanian devils. First, environmental change around the last glacial maximum (LGM) (approx. 20 k years before present (YBP)) resulted in a colder and drier climate with vegetation dominated by open scrub and grassland [6], limiting prey distribution and thereby devil distribution. Second, increased ‘El Niño–Southern Oscillation’ (ENSO) activity during the mid-Holocene (3–5 k YBP) led to a more arid climate with periods of extensive droughts [7], which would reduce prey abundance and favourable devil habitat. Third, extensive bounty hunting following European settlement of Tasmania (approx. 200 YBP) might have led to population declines [8]. Fourth, the current spread of DFTD has already caused 80% population declines and is expected to reduce Tasmanian devil abundance even further [8].

We inferred the demographic history of the Tasmanian devil based on 10 microsatellite loci using temporal sampling and a combination of summary
statistics, full-likelihood methods and approximate Bayesian computation (ABC). We address the possibility that different regions may have different evolutionary histories, explore the confounding effects of population structure on demographic inference and investigate whether the three different methods provide congruent results. Our study provides the first quantitative assessment of devil population size changes through time.

2. Material and methods

An extensive description of the methods can be found in the electronic supplementary material, SI 1. In brief, modern samples collected from nine sites (figure 1a) during 2004–2005 (n = 306) and historical museum specimens collected in 1964 at the Mt William site (n = 24) were genotyped at 10 microsatellite loci [9]. We quantified genetic diversity as the observed (A0) and effective number of alleles (Ae), observed (H0) and expected heterozygosity (He), and inbreeding coefficient (f) using GENODIVE v. 2.0b25 [10]. We investigated possible population genetic subdivision using pairwise FST values [11] and Bayesian clustering methods implemented in STRUCTURE v. 2.3.4 [12]. Population decline was addressed using summary statistics in BOTTLENECK v. 1.2.02 [13]. Two different but complimentary full-likelihood methods were used to assess and quantify population size changes: MSVAR v. 0.4.1b [14] and MSVAR v. 1.3 [15]. We identified the most likely evolutionary scenario for the devils using ABC as implemented in DIYABC v. 2.0.4 [16].

3. Results

The 10 loci had low polymorphism, with an average 3.9 alleles and mean observed heterozygosity of 0.39. All population pairwise FST comparisons were significant and remained so after sequential Bonferroni correction (electronic supplementary material, SI 2). Our STRUCTURE analysis identified two clusters (k = 2; Ln P(k) = −4561; Δk = 173) as the most likely structure for the devil samples (figure 1b). The northwest (Milkshake Hills, Surrey Hills and Granville Harbour) assigned to one cluster and the west coast (Macquarie Heads) to the other cluster. All of these sites were free of DFTD at the time of sampling. The remaining five sites (Bronte Park, Lake Rowallan, Mt William, Freycinet and Forestier) had ancestry in both clusters, suggesting a cline. To limit possible effects of DFTD on inference of demographic parameters for this group, we partitioned it into a non-DFTD group that were not impacted at the time of sampling—the Central Plateau (Bronte Park and Lake Rowallan)—and a DFTD group—the east coast (Mt William, Freycinet and Forestier) (figure 1a).

Figure 1. (a) Map showing the nine sampling localities in Tasmania. Black dashed line indicates the approximate DFTD front in 2004 with disease-affected sites east of the front. (b) Population structure among the Tasmanian devil populations inferred from Bayesian clustering. Each bar represents the proportion of ancestry in each of the two (k = 2) clusters. Geographical regions are given above and the sampling locations below. Only samples from 2004 to 2005 are shown. (c) Most likely model of demographic history for Tasmanian devil populations tested in DIYABC (electronic supplementary material, SI 8). Abbreviations correspond to: times of divergence (TWN and TNE), admixture (Tc), times of population size change (TN and TE) and effective population sizes (Nw, Ne, Nb, Na, Na, Ne, Nc, Na and Ne). The arrows correspond to admixture rates (rN and rE). The figure is not drawn to scale.
Summary statistics can be found in the electronic supplementary material, SI 3. Bottlenecks were detected for the entire devil population and all regions except the west coast (electronic supplementary material, SI 4). This corresponds to a bottleneck 1.7–5.7 k YBP assuming an estimated effective population size of 432–714 individuals (electronic supplementary material, SI 9).

We found substantial evidence for population decline using the ‘basic’ MSVAR model [14], for both the exponential (Bayes factors (BF) = 3.6–18.4) and the linear model (BF = 3.7–25.0) (figure 2a; electronic supplementary material, SI 5). The parameter describing the timing of population size change (\(t_f\)) was lowest for the ‘pooled’ population (mean log10(\(t_f\)) = 0.13 exponential model; mean log10(\(t_f\)) = 1.23 exponential model).

Figure 2. (a) Posterior density distributions of effective population size change parameter log10(\(r\)) from MSVAR v. 0.4.1b. The magnitude of change in population size (\(r = N_0/N_1\)) is estimated based on the ratio of the effective number of chromosomes in the current (\(N_0\)) and the ancestral (\(N_1\)) populations. Three independent Markov chain Monte Carlo runs were performed under a model of exponential change (solid lines) and linear change (dashed lines), respectively. The dotted horizontal line represents the prior. Log10(\(r\)) < 0 corresponds to a population decline and log10(\(r\)) > 0 a population expansion. Whichever demographic model was used, we did not find support for positive values (increase in population size) or for values close to zero (stable population size). (b) Posterior density distributions of current (log10(\(N_0\))) and ancestral (log10(\(N_1\))) effective population sizes from MSVAR v. 1.3 under the exponential model. Black solid lines represent log10 estimates of current population size (\(N_0\)) and grey solid lines ancestral (\(N_1\)) population size. The dotted lines represent the prior distributions. All posterior distributions show a decline in population size (\(N_0 < N_1\)) over time.
linear model) and varied among the geographical regions (electronic supplementary material, SI 5 and S6). This corresponds to a decline of approximately 2.4–3.9 k YBP (exponential model) and a decline of approximately 29–48 k YBP (linear model) for the ‘pooled’ sample if we assume that the effective population size is 432–714 individuals (electronic supplementary material, SI 9).

Population declines were identified for all regions, except the west coast (figure 2b; electronic supplementary material, SI 7) under the ‘hierarchical’ MSVAR model [15]. Ratios of the current population size to ancestral population size (\(N_0/N_1\)), equivalent to population declines of 78–90% for the regions—

with an overall 83% decline—were identified. Estimates of effective population sizes differed between regions for both current (mean \(N_E\) estimates: northwest \(N_0 = 308\); west coast \(N_0 = 414\); Central Plateau \(N_0 = 225\) and east coast \(N_0 = 195\)) and ancestral population sizes (mean \(N_1\) estimates: northwest \(N_1 = 1412\); west coast \(N_1 = 971\); Central Plateau \(N_1 = 1912\) and east coast \(N_1 = 2023\)), with the ‘pooled’ sample estimate within these ranges (mean \(N_E = 318\) and mean \(N_1 = 1903\); figure 2b; electronic supplementary material, SI 7).

The ABC analyses identified ‘Sc1’ as the most likely scenario for the devils’ recent demographic history (figure 1c; electronic supplementary material, SI 8). This scenario has an ancestral split between the west coast region and northwest/east coast regions, with a constant population size over time for the west coast region. The northwest and the east coast experienced declines after having diverged. The Central Plateau region experienced admixture between the northwest and east coast, with no evidence of decline for this region (electronic supplementary material, SI 9). Compared with information in priors alone, the data-informed model provided improvement for all parameter estimates of current demographic parameters (\(N_N, N_W, N_C, N_E, T_C\) and \(T_0\)) and timing parameters (\(T_N, T_{NE}\) and \(T_{WNE}\)) (electronic supplementary material, SI 10).

4. Discussion

We found evidence for demographic declines in the Tasmanian devil coinciding with increased ENSO activity (approx. 2–4 k YBP) and the LGM (approx. 22–48 k YBP), respectively (figure 2a; electronic supplementary material, SI 6a). We believe these dates of decline are robust because the ABC approach accounts for uncertainty in key parameter estimates (electronic supplementary material, SI 7). During the Mid-Holocene, the thylacine (Thylacinus cynocephalus) and devils went extinct on mainland Australia [17]. Evidence suggests roles for climate change, an increase in human population density, and the introduction of the dingo (Canis lupus dingo) as driving factors [17–19]. In Tasmania, the aboriginal population density remained low during the Holocene [20], and the dingo was never introduced, suggesting that changes in climate were the primary cause of population declines in Tasmania. Increased climate fluctuations can lead to variation in availability of prey and carrion. Devil density is likely primarily driven by food availability and periods of limited prey and carrion would lead to declines in devil population size.

The extensive population declines in the order of 78–90% that we observe (figure 2a,b) are expected to cause reductions in genetic diversity. The devil’s small current effective population size (\(N_0 = 318\); electronic supplementary material, SI 7) raises concern for accelerated loss of genetic diversity should the decline continue. Demographic processes, such as population structure and gene flow, can have confounding effects on detection of genetic bottlenecks and may lead to false assignment of bottlenecks [21]. These may have influenced the equivocal signals of decline that we observed for the west coast and the Central Plateau (figures 1 and 2). The increase in decline at Mt William over time (84–90%; figure 2) is likely reflecting the impacts of DFTD on population size at this site. An excess of heterozygotes—as observed for the devils (electronic supplementary material, SI 4)—may result from mate choice and selection on linked traits. The contributions of these factors are not known for devils, but given the consistency of bottleneck detection across all applied methods, we believe they may be negligible for the species. Among the four regions, the severity of decline varied and differed between methods, and our ‘pooled’ results also showed an extensive range-wide population decline. This congruence suggests that the results are not an artefact of population structure.

The concurrence of declines with ENSO activity and the LGM both had substantial to strong support (electronic supplementary material, SI 5). Therefore, we were not able to determine—solely from the full-likelihood results—which event has been the dominant cause of the extensive population decline or if both contributed. Given that we detect bottlenecks using summary statistics (electronic supplementary material, SI 4), which suggest a bottleneck 2–4Ne generations ago and identify recent declines using ABC (electronic supplementary material, SI 9), we are most likely capturing the recent ENSO-induced population decline.

Climate predictions for Australia suggest a hotter and more arid climate [22], which is likely to contribute to fluctuations in devil density [17,18]. To limit further loss of genetic diversity, it is therefore important that conservation measures, e.g. translocations and reintroductions, be taken to ensure survival of devils in the wild.

Data accessibility. Microsatellite genotypes are included in the electronic supplementary material, table SI1.

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References


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