Chapter 4: Demographic history of the Arunachal and bonnet macaques, with implications for their conservation in the future
4.1 Introduction

Significant changes in the environment can influence the biology of species and, in turn, shape their responses. Tracking such changes can not only inform us about the past but also offer insight into the future of these species. One of the large-scale changes that have influenced the biology of many species is constituted by long-term climatic fluctuations (Davis et al. 2005). Studying the response of species to climatic change can also help us understand the mechanisms that may shape the evolution of species. The Pleistocene epoch, with its frequent climatic fluctuations, offers us an ideal model for investigating this and related issues. The Pleistocene epoch is generally divided into episodes with relatively high and low global ice volumes, with the lowest ice volume characterising the interglacial periods. The last such episode with a low ice volume, comparable to that of today, is the Marine Isotope Stage (MIS) 5e, which is also known as the Last Interglacial (LIG). It started approximately 130,000 years ago, peaked 125,000 years ago, and terminated 116,000 years ago (Kukla 2000). The Last Glacial Maximum (LGM), which occurred near the end of the Pleistocene, about 20,000 years ago (Clark et al. 2009), was a dramatic period of glacial advance and global cooling and was followed by a period of warm and humid climate that lasted through the Early Holocene. Later, fluctuations in aridity in the mid- and late Holocene shaped many of the Earth’s modern ecosystems (Williams et al. 2004). Holocene warming also created opportunities for colonisation of new regions by anatomically modern humans, which further triggered profound alterations in world ecosystems (Barnosky 2008). One of the ways we can corroborate these changes is by tracking changes in population size of species over time.

Recent advances in model-based hypothesis-testing of molecular data has allowed us to make statistically robust inference of the timing and magnitude of past changes in the effective population size ($N_e$) of species through this time period (Fontaine et al. 2012; Koblmüller et al. 2012). It is also being increasingly recognised that the separation of ancient and recent demographic events is crucial to know the long-term population dynamics of species in order that we may be able to eventually apply this knowledge for the efficient management of endangered species (Chikhi and Bruford 2005). For instance, a low genetic diversity could be the result of either a long-term, small effective population size or a recent population collapse. In the latter case, it would be urgent to take management measures, whereas in the former case, management measures, for the time being, should focus on alternative conservation efforts other than restoring genetic diversity. It is, however, difficult to quantify the relative importance of
ancient versus recent events as similar genetic patterns can result of very different demographic histories (Chikhi et al. 2010). Nevertheless, in the last two decades, the use of different types of markers, such as mitochondrial DNA and microsatellites, combined with new kinds of statistical analytical methods have shown that it is possible to detect genetic signatures of major demographic events, such as population collapses, admixtures and expansions that may have occurred in different time periods (Fontaine et al. 2012).

Although a vast majority of studies have performed these tests and estimated demographic parameters across taxa, very few studies have been conducted on tropical or sub-tropical ecosystems (but see Goossens et al. 2006; Salmona et al. 2012; Ting et al. 2012). This lack of knowledge is clearly problematic as the threat of negative impacts of climatic and environmental changes on tropical biodiversity is only likely to increase in the near future (Beaumont et al. 2011). If we plan to predict how climate change will affect species in tropical regions, we should, therefore, gather more information and a better understanding of how species have reacted to similar environmental changes during and since the Pleistocene climate change.

It is to address this knowledge gap that we decided to investigate the past demography of two primate species, the sub-tropical habitat generalist Arunachal macaque and the tropical habitat generalist bonnet macaque. The reasons for comparing these two species are many. For instance, it is not clear how the complex climatic history of the Indian subcontinent might have shaped the population history of species depending on their geographic location within its tropical environments. Pleistocene climate change and/or physical barriers have often been described as important forces driving the demographic history of many species from other parts of the tropics (Shapiro et al. 2004; Qu et al. 2010; Lu et al. 2012). Very few studies, however, have specifically examined primate species and most of these tend to suggest that demographic changes in primate populations are relatively recent and driven primarily by anthropogenic factors (Goossens et al. 2006; Bergl et al. 2008; Chang et al. 2012; but see Storz et al. 2002). The only exceptions are two macaque species from the northern hemisphere, the Barbary macaque \textit{M. sylvanus} and the Japanese macaque \textit{M. fuscata}, wherein the effect of glaciation was expected to be much more severe during the Pleistocene. Consequently, the macaque populations did reveal signatures of genetic bottlenecks after the LGM, around 20,000 years ago (Modolo et al. 2005; Kawamoto et al. 2008). We, therefore, thought it important to explore the Eastern Himalaya, a sub-tropical zone, which also marks the southernmost limit of the Pleistocene glaciers.
In addition, the decimation of wildlife by the local tribes in this biodiversity-rich region is a well-documented historical phenomenon. Arunachal Pradesh, home of the Arunachal macaque, is inhabited by a number of animistic tribes who continue to depend heavily on wildlife for subsistence as well as for sport (Aiyadurai et al. 2011). Our knowledge of the histories of these people are, however, fragmentary and incomplete. The peopling of this region seems to have occurred rather late in the subcontinent’s history. According to recorded history, based on folklore and traditional knowledge, the ancestral Tani people migrated to central Arunachal Pradesh approximately 1,500 years ago from the north through the Siang region. These people then settled in the valleys and, due to the topography and warfare among them, were later isolated from one another; subsequently, they are believed to have given rise to the many sub-tribes of today, such as the Adis and Apatanis (Krithika et al. 2008). Most of these tribes continue to follow their ancestral animistic culture. Given the prevalent hunting of the Arunachal macaque in many of these areas (Kumar et al. 2008), it is possible to potentially compare the impact of these two factors, Pleistocene glaciations and anthropogenic activities, on the past and recent history of the Arunachal macaque. More specifically, we can ask whether the species was able to maintain its population size throughout its history on the Tibetan Plateau or whether it changed over time. What are the factors that drove such changes, if any could be detected? Did the Pleistocene climate change affect this primate as it did several other species in the region? Or, was the effect of climatic change limited on such a large mammalian species and were humans the principal driving force that actually shaped its history? We have sought answers to these questions in this chapter.

At the other end of the spectrum lies the bonnet macaque, a unique and endemic primate species, distributed widely across the plains of peninsular India. Although this macaque is today found almost everywhere in the peninsula, the peninsula itself has not always been the same. We now know that it experienced several dramatic changes in its vegetation patterns due to fluctuations in climate over the last hundred thousands of years, cycling between dry and wet spells (Petraglia et al. 2012). Thus, in comparison to the sub-tropical Arunachal macaque, the bonnet macaque offers us a rare opportunity to investigate the extent climate change in the tropics may have affected the demography of a species that is highly successful today.
4.2 Methods

4.2.1 Study area and population sampling

The study area and the biological samples collected for both the study species have been described in Chapter 3.

4.2.2 DNA extraction and PCR amplification

The extraction and amplification of mitochondrial and nuclear DNA (autosomal microsatellites) for both the species have been described in Chapter 3.

4.2.3 Population demographic history

4.2.3.1 Mismatch distribution and Bayesian skyline plots

We used mismatch distribution analysis and Bayesian skyline plots of mitochondrial DNA (mtDNA) to examine the past population dynamics of the study populations for both the species.

A mismatch distribution (Slatkin and Hudson 1991) is the tabulation of the number of the pairwise differences among all DNA sequences in a sample. In a population that has been stationary for a long time, these distributions from non-recombinant DNA sequences become ragged and erratic. On the other hand, rapid population expansion results in a smooth mismatch distribution with one peak and a small raggedness value. The theoretically expected distributions were generated by bootstrap resampling (10,000 replicates) using a model of sudden demographic expansion in Arlequin, version 3.11 (Excoffier et al. 2005). The sum of square deviations between the observed and the expected mismatch and the raggedness indices generated were used as test statistics. P-values were calculated as the probability of the simulated values being greater than the observed value.

We, in addition, estimated Tajima’s $D$ (Tajima 1989) and Fu’s $F_s$ (Fu 1997) for bonnet macaques because of its larger sample size. Large negative values of Tajima’s $D$ and Fu’s $F_s$ are associated with demographic expansion while positive values of Tajima’s $D$ provide evidence of population
Bayesian skyline plots allow for the estimation of effective population size, $N_e$, through time without specifying population change models such as constant size or exponential growth. The age of ‘the most recent common ancestor’ or TMRCA of each clade, estimated in Chapter 3 – Tawang: 0.12 mya (95% HPD, Lower 0.05 and Upper 0.21), Upper Subansiri: 0.46 mya (95% HPD, Lower 0.27 and Upper 0.68) and West Siang: 0.89 mya (95% HPD, Lower 0.53 and Upper 1.3) – were employed as priors for the three populations. Two independent runs were conducted for $10^7$ generations, with a sampling of the parameters once every $10^3$ generations. Ten per cent of the samples were discarded as burn-in. The estimated sample size (ESS) for all parameters was found to be above 200 at the end of each run, indicating good convergence of the Markov chain Monte Carlo (MCMC) simulations. The independent runs were combined using LogCombiner, version 1.5.4, with resampling every $10^5$ generations. After combining all the MCMC runs, the ESS for all parameters was observed to be more than 200.

For bonnet macaques, genealogies were reconstructed under four different models of nucleotide substitution, based on jModelTest 0.1.1 (Posada 2008) results. The models were K3P (partial cytochrome b), K3Puf +I (tRNA-THR), K3Puf (tRNA-PRO) and K3Puf+Γ (hyper-variable segment 1). We used the same methods for assigning the molecular clock model, priors for the parameters and conditions for the MCMC runs as was done above. The root for the phylogenetic tree was calibrated using the estimated split between Arunachal and bonnet macaques during the early Pleistocene, approximately 1.61 (95% HPD 1.14 – 2.12) mya (Chapter 3).

4.2.3.2 The EWCL (Ewens, Watterson, Cornuet and Luikart) method

Demographic events such as recent population bottlenecks are known to leave distinct genetic signatures in the distributions of allele size, expected heterozygosity and in the genealogy of microsatellite loci (Garza and Williamson 2001; Goossens et al. 2006). Here, we used the allelic frequency spectrum, namely the number of alleles ($n_A$) and the expected heterozygosity ($H_e$), to determine the patterns of genetic diversity expected for a demographically stable population (Cornuet and Luikart 1996). We performed simulations in Bottleneck, version 1.2.02 (Piry et al. 1999), for both the species separately, to obtain the distribution of $H_e$ conditional on $n_A$ and on
the sample size for each population and locus. These $H_i$ values were then compared to those obtained from the real dataset. Three mutation models were used: the infinite-allele model (IAM), the stepwise-mutation model (SMM) and the two-phase model (TPM) with various amounts (70% to 95%) of single-step mutations (Di Rienzo et al. 1994). Any departures from the null hypothesis were explained as departures from the model, including selection, population expansion or decline. Consistency across independent loci, however, was unlikely to be caused by selection but rather by demographic events. This approach allowed us to detect population size changes and confirm that the signal was consistent across mutation models. The demographic event, however, could not be dated.

4.2.3.3 The Approximate Bayesian Computation approach

4.2.3.3.1 The Arunachal macaque

We further inferred the demographic history of the Arunachal macaque, based on microsatellite data, using the approximate Bayesian computation (ABC) approach (Beaumont et al. 2002), implemented in the programme DIY-ABC, version 1.0.4.46b (Cornuet et al. 2010). This approach allowed us to choose a demographic scenario among many that best fits the data and infer the posterior probability distributions for the parameters of interest under this preferred scenario. The different steps of the ABC parameter estimation procedure (Beaumont 2010) are briefly described here.

Tested evolutionary scenario: We compared three demographic scenarios, graphically depicted in Fig. 4.1. Scenario 1 consisted of a null hypothesis that assumed a population whose effective size ($N_1$) remained stable over time. Scenario 2 assumed a population of size $N_A$ that declined instantaneously to its current effective size ($N_1$), $T_1$ generations ago. Conversely, Scenario 3 assumed a population of effective size $N_B$ that increased instantaneously $T_1$ generations ago to reach its current effective size ($N_1$). For Scenarios 2 and 3, we considered $T_1$ to be between 20 and 4000 generations, during which time these events could have occurred.
Figure 4.1 Possible alternative scenarios of the demographic history of the Upper Subansiri population of the Arunachal macaque, tested using the ABC approach. Scenario 2 was best fit with the data (Table 4.2). The details of each scenario parameterisation have been given in the Methods. The time-scale is indicated by the arrow on the left. Time has been measured backward in generations before the present. Gen: Generation.

**Approximate Bayesian computation:** For each of the three models, we simulated one million datasets based on a demographic history that described the model, using the programme DIY-ABC. Some or all parameters that defined each model (such as population sizes, timing of the demographic events or mutation rates) were considered as random variables for which some prior distributions were defined, as shown in Table 4.1. For each simulation, the parameter values were drawn from their prior distributions, defining a demographic history that was used to build a specific input file for the DIY-ABC programme. Coalescent-based simulations were run to generate a genetic diversity for each sample, with the same number of gene copies and loci as those originally observed. Summary statistics (S) were then computed for the simulated datasets for each of the observed dataset (S*). Following the method of Storz and Beaumont (2002), a Euclidean distance, δ, was calculated between the normalised S and S* for each simulated dataset.
Table 4.1 Model specifications and prior distributions for demographic parameters and locus-specific mutation model parameters. UN: Uniform distribution, with two parameters – minimum and maximum values; GA: Gamma distribution with three parameters – minimum and maximum values and shape parameter value; LU: Log-Uniform distribution with two parameters – minimum and maximum values. See Figure 4.1 for the demographic parameters of each model tested. The mutation model parameters for the microsatellite loci were the mutation rate ($\mu_{\text{mic}}$), the parameter determining the shape of the gamma distribution of individual loci mutation rate ($P$), and the Single Insertion Nucleotide rate ($\text{SNI}$).

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<th>Priors for the Demographic Parameters</th>
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<td>$T1$</td>
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<td>$NA$</td>
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**Mutation model**: The 10 microsatellite loci were assumed to follow a generalised stepwise mutation model (Estoup et al. 2002) with two parameters: the mean mutation rate ($\mu$) and the mean parameter of the geometrical distribution assumed for the length in repeat numbers of mutation events ($P$) drawn from uniform prior distributions of $10^{-5}$ to $10^{-3}$ and 0.1 to 0.3, respectively. Each locus has a possible range of 40 contiguous allelic states, except Loci 12 (43 states) and was characterised by individual $\mu_{\text{loc}}$ and $P_{\text{loc}}$ values, drawn from gamma distributions with respective means of $\mu$ and $P$, and shape parameter 2 in both cases (Verdu et al. 2009). Using this setting, we allowed for large mutation rate variance across loci (range of $10^{-3}$ to $10^{-7}$). We also considered mutations that insert a single nucleotide into or delete one from the microsatellite sequence. We used default values for all other mutation model settings. The details on model parameterisation and prior settings have been provided in Table 4.1.
Summary statistics: The summary statistics of genetic diversity for the microsatellite loci, calculated with the programme DIY-ABC, included: the mean number of alleles per locus ($A$), mean expected heterozygosity ($H_0$), mean allele size variance ($V$), and mean GW Index across the loci (Garza and Williamson 2001).

Model choice procedure and performance analyses: The posterior probability of each competing scenario was estimated using a polytomous logistic regression (Cornuet et al. 2008, 2010) on 1% of the simulated datasets closest to the observed dataset. We evaluated the ability of our ABC methodology to discriminate between scenarios by analysing simulated datasets with the same number of loci and individuals as in our real dataset. Following the method of Cornuet et al. (2010), we estimated the Type I error probability as the proportion of instances where the selected scenario did not exhibit the highest posterior probability, as compared to the competing scenarios for 500 simulated datasets generated under the best-supported model. We similarly estimated the Type II error probability by simulating 100 datasets for each of two alternative scenarios and calculating the mean proportion of instances in which the best-supported model was incorrectly selected as the most probable model.

Parameter estimation and goodness of fit: We estimated the posterior distributions of the demographic parameters under the best demographic model, using a local linear regression on the closest 1% of $10^6$ simulated datasets, after the application of a logit transformation, the inverse of the logistic function, to the parameter values (Beaumont et al. 2002; Cornuet et al. 2008). Finally, following the method of Gelman et al. (1995), we evaluated whether, under the best model-posterior combination, we were able to reproduce the observed data using the model-checking procedure available in DIY-ABC (Cornuet et al. 2010). Model-checking computations were processed by simulating 1000 pseudo-observed datasets under each studied model-posterior combination, with sets of parameter values drawn with replacement among the 1000 sets of the posterior sample. This generated a posterior cumulative distribution function for each summary statistic, allowing us to estimate the $P$ values for the observed values of these summary statistics. In addition, a principal components analysis (PCA) was performed on the summary statistics. Principal components were computed from the 15000 datasets simulated with parameter values drawn from the prior. The target (observed) dataset, as well as the 1000 datasets simulated from the posterior distributions of parameters, was then added to each plane of the PCA.
4.2.3.3.1 The bonnet macaque

We also inferred the demographic history of the bonnet macaque, on the basis of microsatellite data, using the approximate Bayesian computation (ABC) approach (Beaumont et al. 2002), implemented in the programme DIY-ABC, version 1.0.4.46b (Cornuet et al. 2010). This approach allowed us to choose a demographic scenario among many that best fits the data and infer the posterior probability distributions for the parameters of interest under this preferred scenario. The different steps of the ABC parameter estimation procedure (Beaumont 2010) are briefly described here.

*Tested evolutionary scenarios:* We compared three demographic scenarios, depicted in Fig. 4.2.

![Diagram showing demographic scenarios](image)

**Scenario 1** consisted of a null hypothesis that assumed a population whose effective size ($N_1$) remained stable over time. **Scenario 2** assumed a population of size $N_A$ that declined instantaneously to its current effective size ($N_1$), $T_I$ generations ago. Conversely, **Scenario 3**
assumed a population of effective size \( NB \) that increased instantaneously \( T1 \) generations ago to reach its current effective size \( (N1) \). For Scenarios 2 and 3, we considered \( T1 \) to be between 20 and 30000 generations, during which time these events could have occurred.

**Approximate Bayesian computation:** The approximate Bayesian computation approach was used to infer the demographic history of the bonnet macaque populations in accordance with that adopted for the Arunachal macaque in Chapter 4. Some or all parameters that defined each model (such as population sizes, timing of the demographic events, mutation model and mutation rates) were considered as random variables for which some prior distributions were defined, and these are depicted in Table 4.2.

**Table 4.2** Model specifications and prior distributions for demographic parameters and locus-specific mutation model parameters. UN: Uniform distribution, with two parameters – minimum and maximum values; GA: Gamma distribution with three parameters – minimum and maximum values and shape parameter value; LU: Log-Uniform distribution with two parameters – minimum and maximum values. See Figure 4.2 for the demographic parameters of each model tested. The mutation model parameters for the microsatellite loci were the mutation rate \( (\mu_{\text{mic}}) \), the parameter determining the shape of the gamma distribution of individual loci mutation rate \( (P) \), and the Single Insertion Nucleotide rate \( (SNI) \).

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<td>( \text{MEAN} – P )</td>
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<td>( \text{MEAN} – SNI )</td>
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Summary statistics: We calculated the summary statistics of genetic diversity for the bonnet macaque populations exactly as had been done for the Arunachal macaque above.

Parameter estimation and goodness of fit: We estimated the posterior distributions of demographic parameters for the study species and tested for the goodness of fit of the selected model as was carried out for the Arunachal macaque above.

4.3 Results

4.3.1 The Arunachal macaque

4.3.1.1Mismatch distribution analysis and Bayesian skyline plots

All the three populations showed low raggedness values and a non-significant probability of observing a raggedness value, which is larger than that under the null hypothesis of expansion ($P > 0.05$), suggesting that the observed curves did not significantly differ from the simulated distributions expected under a model of sudden demographic expansion (Fig. 4.3).

Our previous mitochondrial DNA analysis (Chapter 3) demonstrated that the three Arunachal macaque populations are geographically distinct. A Bayesian skyline plot was, therefore, not traced for all the three populations taken together (Chikhi et al. 2010). Of these three populations, the Upper Subansiri has the largest number of sampled individuals and was, therefore, taken up for further analysis.

The Bayesian skyline plot for the Upper Subansiri population indicated a population expansion right after the Last Glacial Maximum (LGM) at around 15000 years before present (Fig. 4.4). The population, however, appeared to have maintained a constant population size before this expansion. Interestingly, the plot also showed a small reduction in effective population size in more recent times, right after the Middle Holocene (between 5000 and 7000 years before present; Fig. 4.4).
Figure 4.3 Histogram showing the observed distribution of pairwise differences between individual sequences in the three Arunachal macaque populations. (A) Tawang, (B) Upper Subansiri and (C) West Siang populations. The maroon line represents the expected distribution under a model of sudden population expansion. $r$, raggedness index; $ssd$, sum of squared deviations (goodness of fit to a simulated population expansion); $P$, probabilities.
**Figure 4.4** Bayesian skyline plot reconstruction of past population size trajectory for the Upper Subansiri population of Arunachal macaques. The plot is the product of female effective population size ($fN_e$) and mutation rate ($\mu$) through time, assuming a substitution rate of 0.1643 substitutions per nucleotide per million years (see Chapter 3). The lower and upper 95% confidence interval for the Upper Subansiri TMRCA is also shown. LGM, Last Glacial Maximum, approximately 18 to 20 thousand years before present.

### 4.3.1.2 The EWCL (Ewens, Watterson, Cornuet and Luikart) method

This test, which attempts to detect the presence of a population bottleneck, indicated that, regardless of the mutation model assumed, the three Arunachal macaque populations, taken together, exhibited a significant signal of bottleneck for a majority of the microsatellite loci tested. It should, however, be remembered that this can be an artefact of the presence of structure in the tested population. We, therefore, decided to treat the populations separately and found that only the Upper Subansiri site had an acceptable sample size for the test. For this population, the infinite-allele model (IAM) and two-phase model (TPM) showed statistical significance, in both one-tailed and two-tailed tests (both $P << 0.05$), for heterozygosity excess,
thus providing clear evidence for a genetic bottleneck in this population in the past. The application of a stepwise-mutation model (SMM), however, yielded non-significant results for both one-tailed \( (P = 0.13) \) and two-tailed \( (P = 0.064) \) tests.

### 4.3.1.3 The Approximate Bayesian Computation approach

We first evaluated the relative posterior probability of each competing scenario using a polytomous logistic regression on 1% of the simulated datasets closest to the observed dataset. The resulting PCA unambiguously pointed to the scenario of population decline (Scenario 2), which assumed an ancient, large population size that declined at some point in the past to reach the present, much smaller population size (Fig. 4.5).

We next evaluated the power of the model choice procedure using the method implemented in DIY-ABC, following the recommendations of Robert et al. (2011). For that purpose, we first simulated 500 random datasets under the selected scenario (Scenario 2) and computed the proportion of cases in which this scenario did not display the highest posterior probability among all scenarios. This empirical estimate of the Type I error was only 16.6%. We then empirically estimated the Type II error rate by simulating 100 random datasets under each alternative scenario (Scenarios 1 and 3) and computing the proportion of cases in which Scenario 2 was incorrectly selected as the most likely scenario in these simulated datasets. The average Type II error rate was only 8%, indicating a statistical strength of 92%. Hence, this simulation-based evaluation of the performance of the ABC model-choice procedure (Robert et al. 2011) clearly showed that, given the size and polymorphism of our dataset, the method had high power to distinguish between the alternative demographic scenarios that we investigated.

We estimated the marginal posterior probability density for each parameter of the decline scenario (Scenario 2) using 1% of the closest simulated datasets from the observed dataset (Table 4.3). Under this model, we estimated that a large population with an effective size of approximately 50,600 macaque individuals [95% highest probability density interval (HPDI): \( (19,600 – 68,300) \)] declined to a present effective population size of approximately 1,700 individuals [95% HPDI: \( (476 – 4,090) \)], that is, approximately 30-fold. Assuming an average generation time of 5 years for macaques (Harvey et al. 1987), we estimated that this expansion occurred approximately 3,500 [95% HPDI: \( (520 – 13,800) \)] years before present.
Figure 4.5 Comparison of the three possible alternative demographic scenarios for the Upper Subansiri population of Arunachal macaques. (A) Estimates of the posterior probability of each scenario and their comparison. Direct estimate: The number of times that a given scenario is found closest to the simulated datasets once the latter, produced under several scenarios, have been sorted by ascending distances to the observed dataset. Logistic regression: Following Beaumont’s suggestion (Fagundes et al. 2007; Beaumont 2008), a polytomic weighted logistic regression was performed on the first closest datasets with the proportion contributed by each scenario as the dependent variable and the differences between the summary statistics of the observed and simulated datasets as the independent variables. The intercept of the regression (corresponding to an identity between simulated and observed summary statistics) was taken as the point estimate. In addition, 95% confidence intervals were computed (Cornuet et al. 2008). In all these cases, Scenario 2 explained the observed data best.
Finally, to assess the goodness-of-fit of the model (Scenario 2) to the data, we simulated 1,000 datasets under each of the three scenarios tested, drawing the values of their parameters into the marginal posterior distributions of these parameters. We thus identified which model was the most capable of reproducing the observed summary statistics computed from the real data, following the model-checking procedure described by Cornuet et al. (2010). Of the three demographic scenarios tested, the datasets simulated under Scenario 2 were most compatible with the observed summary statistics. This can be observed by comparing the values of summary statistics computed from the simulated datasets for each tested scenario against the real values. With the exception of Scenario 2, all competing scenarios generated large numbers of summary statistics that displayed highly significant outlying values (Fig. 4.6). This finding thus strongly supported the very high posterior probability values obtained for Scenario 2 using the model-choice procedure.

Table 4.3 Demographic parameters estimated under the best-supported demographic scenario (Scenario 2) of a recent population decline in the Upper Subansiri population of Arunachal macaques. Population sizes are given in effective number of diploid individuals. Time estimates were calibrated by assuming a generation time of 5 years (Harvey et al. 1987).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Median</th>
<th>25% HPDI</th>
<th>95% HPDI</th>
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<tr>
<td>Current effective population size ($N_1$)</td>
<td>1720</td>
<td>476</td>
<td>4090</td>
</tr>
<tr>
<td>Population size before the decline ($N_A$)</td>
<td>50600</td>
<td>19600</td>
<td>68300</td>
</tr>
<tr>
<td>Magnitude of the population decline ($N_1/N_A$)</td>
<td>0.03</td>
<td>0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Time since the decline ($T_1$), years before present</td>
<td>3575</td>
<td>520</td>
<td>13800</td>
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4.3.2 The bonnet macaque

4.3.2.1 Tests for expansion and Bayesian skyline plots

The bonnet macaque populations showed low raggedness values and a non-significant probability of observing a raggedness value larger than that under the null hypothesis of expansion ($P > 0.05$), suggesting that the observed curves did not significantly differ from the simulated distributions expected under a model of sudden demographic expansion (Fig. 4.7).
These results are in agreement with the neutrality test statistics (\(D = -0.91, P = 0.19; Fs = -23.97, P = 0.001\)), which reject a constant population size through time.

The Bayesian skyline plot indicates two events of historical size expansion in the study bonnet macaque populations (Fig. 4.8). The first population expansion was recorded around 80000 years ago during the last interglacial. The effective female population size was then more or less constant for the next 50000 years till the Last Glacial Maximum (LGM), approximately 20000 years ago. It then increased mildly immediately after the LGM, about 15000 years before present. It should be noted, however, that population declines might be relatively more difficult to infer than expansions on the basis of contemporary samples alone.

**Figure 4.7** Histogram showing the observed distribution of pairwise differences between individual sequences in the bonnet macaque population. The maroon line represents the expected distribution under a model of sudden population expansion. \(r\), raggedness index; \(ssd\), sum of squared deviations (goodness of fit to a simulated population expansion); \(P\), probabilities.
4.3.2.2 The EWCL (Ewens, Watterson, Cornuet and Luikart) method

This test, which is conducted to examine a population for the past occurrence of a genetic bottleneck, showed a mixed inference. While both the IAM ($P = 0.08$) and TPM ($P = 0.85$) could not reject the null hypothesis of a continuous population size, the SMM ($P = 0.001$) suggested a significant change in population size. Thus, the bonnet macaque population does exhibit a signature of a past population bottleneck; the failure of the TPM to detect any such change, however, indicates that the signal might be too weak or too recent to be picked up by this test.

![Bayesian skyline plot reconstruction of past population size trajectory for the bonnet macaque population.](image)

**Figure 4.8** Bayesian skyline plot reconstruction of past population size trajectory for the bonnet macaque population. The plot is the product of female effective population size ($fN_e$) and mutation rate ($\mu$) through time, assuming a substitution rate of 0.1643 substitutions per nucleotide per million years (see Chapter 5). The lower and upper 95% confidence interval for the bonnet macaque TMRCA is also shown. LGM, Last Glacial Maximum, approximately 18 to 20 thousand years before present.
4.3.2.3 The Approximate Bayesian Computation approach

The relative posterior probability of each competing scenario was estimated using a polytomous logistic regression on 1% of the simulated datasets that were closest to the observed dataset. The Principal Components Analysis clearly revealed the scenario of population decline (Scenario 2) to be the model that best fit the data (Fig. 4.9).

The marginal posterior probability density for each parameter of the decline scenario (Scenario 2) was also evaluated using 1% of the simulated datasets that were again closest to the observed dataset (Table 4.4). Under this model, we estimated that a large population with an effective size of > 600 thousand macaque individuals [95% highest probability density interval (HPDI): (120,000 – 967,000)] declined to a present effective population size of approximately 16000 individuals [95% HPDI: (5,200 – 33,000)]; that is, by an approximately 30-fold factor. We estimated that this expansion occurred approximately 70,000 [95% HPDI: (12,150 – 137,500)] years before present. This estimated time was based on a generation time for the bonnet macaque of approximately 5 years (Sinha 2001).

**Table 4.4** Demographic parameters estimated under the best-supported demographic scenario (Scenario 2) of a recent population decline in the bonnet macaque population. Population sizes are given in effective number of diploid individuals. Time estimates were calibrated by assuming a generation time of 5 years (Sinha 2001).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Median</th>
<th>25% HPDI</th>
<th>95% HPDI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current effective population size ($N_t$)</td>
<td>16,400</td>
<td>5,200</td>
<td>33,000</td>
</tr>
<tr>
<td>Population size before the decline ($N_A$)</td>
<td>612,000</td>
<td>120,000</td>
<td>967,000</td>
</tr>
<tr>
<td>Magnitude of the population decline ($N_t/N_A$)</td>
<td>0.027</td>
<td>0.043</td>
<td>0.034</td>
</tr>
<tr>
<td>Time since the decline ($T_t$), years before present</td>
<td>70,000</td>
<td>12,150</td>
<td>137,500</td>
</tr>
</tbody>
</table>

Finally, we assessed the goodness of fit of the estimated model to the data by simulating 1,000 datasets under each scenario tested, drawing the values of their parameters into the marginal posterior distributions of these parameters. We were thus able to identify the model most
Figure 4.9 Comparison of the three possible alternative demographic scenarios for the bonnet macaque population. Estimates of the posterior probability of each scenario and their comparison: (A) direct estimate – the number of times that a given scenario is found closest to the simulated datasets once the latter, produced under several scenarios, have been sorted by ascending distances to the observed dataset and (B) logistic regression – following Beaumont’s suggestion (Fagundes et al. 2007; Beaumont 2008), a polytomic weighted logistic regression was performed on the first closest datasets with the proportion contributed by each scenario as the dependent variable and the differences between the summary statistics of the observed and simulated datasets as the independent variables. The intercept of the regression (corresponding to an identity between simulated and observed summary statistics) was taken as the point estimate. In addition, 95% confidence intervals were computed (Cornuet et al. 2008). In all these cases, Scenario 2 explained the observed data best.
capable of reproducing the observed summary statistics that were computed from the real data (Cornuet et al. 2010). Of the three scenarios tested, the datasets simulated under the decline scenario (Scenario 2) were most compatible with the observed summary statistics computed from the real data. With the exception of Scenario 2, the competing scenarios generated large numbers of summary statistics that displayed highly significant outlying values. Consequently, Scenario 2 was clearly closest to the observed dataset (Fig. 4.10).

Figure 4.10 Model-checking to measure the discrepancy between the model parameter posterior combination and the real dataset for the three alternative demographic scenarios for the bonnet macaque population. The summary statistics using datasets simulated with the prior distributions of the parameters, the observed data and the datasets from the posterior predictive distribution are represented on the plane of the first two principal components. The model (Scenario 2) fits the data well, as the cloud of datasets simulated from the prior (small green dots), datasets from the posterior predictive distribution (larger green dots) and the observed dataset (yellow circle) overlap completely.
4.4 Discussion

Classical bottleneck tests are often used by both evolutionary and conservation biologists to evaluate whether species have experienced historical demographic bottlenecks. In contrast, more recently developed Bayesian approaches offer the potential to draw more detailed inferences with respect to both bottleneck timing and severity (Beaumont et al. 2002; Cornuet et al. 2010) but have not yet been thoroughly evaluated. Consequently, we analysed a multi-marker dataset using both sets of approaches to elucidate the possible impacts of historical climate change and more recent anthropogenic effects on two primate species from Indian subcontinent, an “edge” primate species, the Arunachal macaque, in the northeastern Indian state of Arunachal Pradesh, situated in the southern part of the Tibetan Plateau and, a generalist species, the bonnet macaque, from the peninsular India.

4.4.1 The Arunachal macaque

4.4.1.1 Limited effect of Pleistocene glaciations before the Last Glacial Maximum (LGM)

Pleistocene climate change is known to have influenced the demographic history of many species. The landmass of Europe and a large part of northern America were under continental ice sheets repeatedly over the last three million years. Such inhospitable conditions forced most species to either go extinct or shift their distribution range. Those, which shifted their range, also suffered a concomitant reduction in their population size. The effects of glaciation on species abundance and distribution, however, become more complex in eastern Eurasia where ice cover was never continuous.

The southern part of the Tibetan Plateau is an interesting example in this regard. The southern edge of the plateau was characterised by complex orogenesis, as compared to that experienced by the flatter central regions. This area also marks the southern limit of the glaciers that occur on the plateau. During the Quaternary period, the Tibetan Plateau had undergone four to five glaciations but was less affected by the ice sheets than were other regions in Asia at that time (Zheng et al. 2002). The largest glacier on the plateau occurred in the middle of the Pleistocene (about 0.5 mya) and continued until 0.17 mya (Zheng et al. 2002). During that time, the ice cover may have been permanent in the higher altitudes and central regions of the plateau (Shi et al. 1990; Shi 2002) while the southern and eastern regions experienced relatively less glaciation.
(Zhang et al. 2000). Both these sets of conditions created a fragmented ice cover where most the high-elevation areas on the mountain ranges were ice-clad. Consequently, the prolonged glaciation periods during the late Pleistocene appear to have had a less severe effect on the species inhabiting these areas, as compared to those inhabiting Europe or northern America.

It is now being suggested that the ice sheets possibly retreated more rapidly on the Tibetan Plateau than they did in Europe, as seems to be evident from the demographic history of species like the great tit *Parus major* from the plateau (Zhao et al. 2012). It was observed that contrary to the post-LGM expansion of European animal populations, the demographic histories of species on the Tibetan Plateau indicate expansions only before the LGM; they remained relatively stable or grew slowly subsequently through the LGM (Zhao et al. 2012). The edges of the plateau would have been less under the influence of the glaciations, if at all, at least on the lower elevations. We find support of such a hypothesis in the Bayesian skyline plots, which suggest that the size of Arunachal macaque populations appeared to remain constant during the prolonged pre-LGM climatic fluctuations. A recent comparative study on five avian species from the Tibetan Plateau (Qu et al. 2010) demonstrated that three species distributed on the central platform of the plateau experienced rapid population expansion after the retreat of the extensive glaciers during the pre-LGM (0.5–0.175 mya), results similar to that of Zhao et al. (2012). On the contrary, the population sizes of the other two species, distributed on the edges of the plateau, remained at stable levels throughout the same pre-LGM period. It was concluded that the comparatively ice-free habitats on the edges of the plateau might have experienced milder climates during the glaciation period and this allowed the local species populations to persist in this stable niche (Qu et al. 2010). It is illuminating that we have now reached similar conclusions in our study of the Arunachal macaque populations in the Eastern Himalayas on the southern fringes of the Tibetan Plateau.

4.4.1.2 Effect of elevation and animal physiology

Altitude appears to have played an extremely important role in the demographic history of animal species during the past glacial periods with species at various elevations being affected differently. A very good example of this is in the Alps (Hewitt 1996, 2004). The present climate of this mountain range in central Europe ranges from Mediterranean to glacial at different altitudes. Many present-day species in the high elevations colonised their present range by expanding their range from the lower altitudes and latitudes during specific interglacial periods.
In contrast, species with Arctic–Alpine distributions, which were not annihilated during peaks of glaciation, descended during these periods and may have spread more widely across the cold tundra and steppe plains of continental Europe (Hewitt 1996, 2004). The impact of Pleistocene glacial cycles are thus expected to have varied among species across geographical regions, in part, perhaps due to their biology of differential cold tolerance (Lu et al. 2012).

The first indication of such a historical change in the size of the study Arunachal macaque populations was detected through the mismatch distributions of the sampled individuals. According to Rogers and Harpending (1992), populations that have undergone recent declines tend to exhibit ragged, multimodal mismatch distributions, a proposition that has now received considerable empirical support (Excoffier and Schneider 1999; Johnson et al. 2007). But mismatch distribution analysis also has its limitations, as exemplified by many studies where contemporary samples of a bottlenecked population failed to recover a unimodal mismatch distribution (Hoffman et al. 2011). This is because methods that estimate population parameters based on the distribution of pairwise differences do not make full use of DNA sequence data while methods based on coalescent theory, by incorporating information from genealogy, may better evaluate the demographic histories of populations (Felsenstein 1992; Pybus et al. 2000).

We are, thus, more confident of our results that suggest expansion of the macaque populations after they were independently supported by the Bayesian skyline plots. These plots also propound changes in population size only after the LGM, as has been established for many avian edge species on the Tibetan Plateau (Qu et al. 2010). Moreover, the effective female population size of the Arunachal macaque seems to have increased approximately 15 thousand years ago.

Although the climate on the Tibetan Plateau has been documented to have been colder during the pre-LGM extensive glacial period than during the LGM (Shi et al. 1995), mountain heights below the snowline were not apparently glaciated. The current snowlines on the eastern edge of the plateau extend from 4200 to 5200 m (Shi et al. 1997; Liu et al. 1999). In Arunachal Pradesh, more specifically, the vegetation ends approximately at a 5000-m elevation from where the present snowline starts (Mishra et al. 2004). During the LGM, however, the snowline descended to approximately 3300 m on many mountain ranges on the Tibetan Plateau (Shi et al. 1997; Liu et al. 1999), thus contributing to cooler climates locally (Zheng et al. 2002). Arunachal macaques are known to presently occur at altitudes between 1800 – 3500 m (Sinha et al 2005) although they could also inhabit higher, unexplored, elevations in the region. It now seems clear that at least a part of the current habitat of the macaque was covered by ice during the LGM. It is then
likely that the primate may have colonised even higher elevations by population expansion after the LGM.

It is noteworthy that such a pattern that we propound has now been conclusively established for another lower-elevation avian edge species from the Tibetan plateau, the black redstart *Phoenicurus ochruros* (Qu et al. 2010). The relationship between glaciation, altitude and species demographic history is, however, far from straightforward. Interestingly, Lu et al. (2012) found that the population size of the three low-elevation (1800 – 3200 m) stream salamander species from the Tibetan Plateau were significantly affected from the beginning of the extensive glacial period long before the LGM, in striking contrast to what has been established for the Arunachal macaque and the black redstart. According to Lu et al. (2012), the suitable habitats for the salamanders may have not been covered by ice during both the LGM and the extensive pre-LGM glacial period but the species may have suffered from climatic cooling because they are less cold-tolerant than their high-elevation counterparts. These ideas are consistent with the hypothesis that variation in ecological adaptations may affect geographical patterns of genetic variation in species (Gavrilets 2003; Hewitt 2004). The poikilothermic salamanders may be expected to have a much lower range of tolerance to changes in ambient temperatures than would homoeothermic animals such as birds and mammals. Thus, animal physiology is another important factor that may have differently affected the evolutionary history of species that otherwise occurred at similar elevations and latitudes in a particular geographical region.

### 4.4.1.3 Holocene population decline

The increase in effective female population size of the Arunachal macaque, as revealed by the Bayesian skyline plots, continues till approximately five thousand years ago, after which it appears to have suffered a mild decline. Mitochondrial and nuclear autosomal microsatellite loci are known to be informative at different time scales, highlighting different episodes in the demographic history of a species (Fontaine et al. 2012). The mtDNA diversity tends to reflect comparatively older demographic events in a species’ history. Conversely, microsatellite data are more informative about the contemporary demography of a species. Such a difference in demographic signals, captured by each type of genetic marker, may arise from the differences in their respective mutation rates (Cornuet et al. 2010). The relatively fast mutation rate of microsatellite loci enables them to capture recent and almost contemporaneous events but also increases homoplasy at these loci, which thereby reduces the signal of older demographic events.
(Estoup et al. 2002). These, more ancient, events can, however, still be detected using the slower evolving mtDNA sequences. That is why we employed our microsatellite data to validate the occurrence of a very recent population decline in the Arunachal macaque.

The classical heterozygosity excess test (the EWCL method) suggested a past population bottleneck in at least the Upper Subansiri population, as reflected in its microsatellite data although the statistical significance of this result was highly dependent on the underlying mutational model. A bottleneck was inferred for this population for two particular models – IAM and TPM – but not for a third one, the SMM, despite the IAM being unrealistic for most microsatellites (Di Rienzo et al. 1994). Several other microsatellite-based studies of species thought to have experienced severe, but temporary, reductions in population size had either failed altogether to detect a bottleneck or, as with our study, yielded results that depend on the mutational model (Spong and Hellborg 2002; Hoffman et al. 2011). In at least some of these cases, a few specific markers may have disproportionately influenced the more conservative SMM model. However, in our study, we used 22 microsatellite loci, over twice the minimum number recommended by Luikart and Cornuet (1998). To circumvent this problem, we applied the ABC method that clearly supported the population decline model (Scenario 2) over the constant size and population expansion models.

We could also estimate the extent and time of the decline from the posterior probabilities. It seems that the decline started approximately 3500 years ago, which was climatically a warm period and this is surprising as such climatic conditions are normally conducive for population growth. Several authors have postulated that such idiosyncratic mid-Holocene population declines may have been accelerated and enhanced by major expansions in ancient human civilizations (1500 BC; Stavrianos 1998), the rapid development of agriculture, and the resulting changes in landscapes in recent times. For example, it has been speculated that the expansion and migration of human populations into the erstwhile virgin mountains of the Sichuan region may have caused the decline of the giant panda population during the later part of the mid-Holocene (Zhang et al. 2007). In Arunachal Pradesh too, anthropogenic factors may have significantly influenced the demographic history of the Arunachal macaque over the last few decades or centuries. One of the largest indigenous groups of people that inhabit the districts of Upper Subansiri and West Siang, two areas from which our study samples were derived, and which hunt wildlife extensively for food and sport, is represented by the collective animist Adi people (Lego 2005; Tabi 2006). Recent ethnographic and population genetic studies reveal that
the Adi, alternatively referred to as Luoba Tibetan in Tibet, trace their ancestral migration and settlement history from southern Tibet into Arunachal Pradesh to different time periods during the 5th to 7th century AD, or to the last 1300 to 1500 years before present (Lego 2005; Tabi 2006; Krithika et al. 2009; Kang et al. 2010). Although these estimates do not reject the possibility of a peopling of this region in even earlier times, it is entirely possible that the Arunachal macaque population declines may have actually begun at the time that central Arunachal Pradesh was being peopled by the Adi and other animistic tribes that continue to hunt rampantly even today. It must be reiterated, however, that there is currently no evidence to conclusively establish the definitive contribution of either climatic or anthropogenic factors to this decline in Arunachal macaque populations.

In conclusion, the *M. munzala* populations that we sampled lack strong genetic differentiation possibly due to long-term, low levels of gene flow between them; such gene flow may have increased in contemporary times, perhaps brought about by the prevalent pet trade in the species.

### 4.4.2 The bonnet macaque

#### 4.4.2.1 Effect of historical monsoon fluctuations

Peninsular India apparently did not experience any glaciation during the Pleistocene but came under climatic influences that were different from that experienced by the northern parts of the Eurasian landmass. One of the most important climatic factors that stand out in this part of Asia is the fluctuation in historical monsoon patterns. Due to extensive paleontological investigations in many parts of India, we now have a fairly good idea about the shift in the monsoons over the last 140,000 years, including rather frequent fluctuations in monsoon strength across the peninsula (Fig. 4.11; Petraglia et al. 2012). The MIS 6, approximately 130,000 years ago, saw a drastic reduction in the monsoons though it regained its strength over the next 20,000-30,000 years during the MIS 5. This increase in rainfall corresponded to a significantly wetter environment across the Indian subcontinent. This, in turn, gave rise to an expansion of both tropical and subtropical environments (Achyuthan et al. 2007). It is perhaps illuminating that the expansion of the bonnet macaque populations in peninsular India at around 80 thousand years ago coincides with this shift of habitat condition from a dry to a more wet environment; we can,
Figure 4.11 Historical change in monsoon strength in peninsular India, the occurrence of Toba super-explosion and change in bonnet macaque population size. Toba explosion also coincides with the arrival of modern human in India 70 thousand years ago according to some sources (Oppenheimer 2012). Blue thin lines approximately mark the significant demographic events in the history of bonnet macaque estimated by Bayesian methods. Left facing arrow indicates population decline while right facing arrows indicate expansion. Width of the arrows indicates strength of the events. MIS, Marine Isotope Stage (Modified from Petraglia et al. 2012).

thus, speculate that the availability of a more conducive environment may have actually induced the growth of the species during the late MIS 5.
It should however be noted that significant gene flow between populations may sometimes reflect as population growth in Bayesian skyline plots. For example, Fagundes et al. (2008) showed that the incorporation of admixed non-native American genomes in genomic samples of Native Americans caused these plots to artificially detect a very old expansion in Beringia. This expansion, however, was actually a signature of a much older coastal expansion of humans in Asia, far from Beringia. Fagundes et al. (2008) found that this erroneous conclusion was drawn “because the mtDNA haplogroups and sub-haplogroups in those populations have a strong and extensively studied geographic association”. In the case of the bonnet macaques, we have earlier shown the existence of significant female-mediated gene flow, resulting in a high number of shared haplotypes across geographical locations (see Chapter 3). It is thus possible that the increased gene flow during MIS 5 may have resulted in a signature of population expansion in the Bayesian skyline plots that we obtained. The very weak phylogenetic clade differentiation in the species, therefore, may actually reflect a very old vicariance, which may have later been removed by increased dispersal between populations.

4.4.2.1 Effect of Toba super-explosion

Lake Toba in Sumatra, Indonesia, is the site of the largest volcanic explosion in the late Pleistocene (Oppenheimer 2002). Dating of the various deposits associated with the Toba super-explosion has consistently returned ages of approximately 74,000 ± 2,000 years before present (Oppenheimer 2002). It has been asserted to be one of the most significant events in the course of human evolution, leading to cataclysmic changes in terrestrial ecosystems and the near-extinction of our species (for example, Ambrose 1998; Rampino and Ambrose 2000; Williams et al. 2009). The super-eruption and the subsequent climatic cooling in MIS 4 have, in fact, been implicated in the disappearance of our species from Eurasia 70,000 years ago (Shea 2008) or to changes in the social and ritual behaviours of humans in Asia at that time (Rossano 2009, 2010). Haslam and Petraglia (2010), however, call into question the links invoked between the Toba super-explosion, climate change and ecosystem alterations, and instead argue that proximate and local conditions, such as disruptions caused by deposition of significant quantities of ash, are more parsimonious explanations for the observed historical vegetation changes. In either scenario, evidence for ecological alterations is unequivocal suggesting that there were disruptions to local and regional environments, though the timing and duration of these events continue to remain uncertain (Petraglia et al. 2010). This period also coincides with a considerable weakening of the monsoons although the cause for this change is not very clear. In any case, the occurrence
of a considerable bottleneck in bonnet macaque populations around 70,000 years ago, suggested from the microsatellite data analysis, clearly indicates the negative effect of the contemporary changes in vegetation on a now-generalist species from peninsular India. Although it is not clear if the Toba volcanic eruption indeed was the cause of such a degree of population change, the wide range of the confidence interval in the timing of this change possibly hints at the more wide-ranging fluctuations in the monsoons to be a more likely cause.

Finally, the low, but gradual, increase in the population size of bonnet macaques in the more recent mid-Holocene, as evidenced from the mtDNA analysis, yet again coincides with a more recent change in monsoonal patterns. There can, however, be an alternative or an additional factor that may also explain the growth of bonnet macaque populations during this period. For example, Richard et al. (1989) suggested that the reason behind the bonnet macaque population recovery in the mid-Holocene may have been human-driven. According to them, the ubiquity of the weed macaques such as the bonnet macaque today is probably the result of the spread of disturbed vegetation that accompanied the origin and spread of agriculture over the last 10,000 years than to the effects of Pleistocene glacial episodes. The appearance of new human-modified ecological zones, Richard et al. (1989) speculated, would have brought about replacement of climax forest dwellers by weed species such as bonnet macaques that not only tend to prefer early succession vegetation but also manage to live in close proximity to humans.

4.5 Conclusions

The Tibetan Plateau is an interesting region to study the population history of its native species for more than one reason. First of all, it is a highly variable region with its different parts – the flat central platform and the more altitudinally variable mountainous edges – differing significantly from one another in topography and climatic history. The edge regions of the plateau have had a tumultuous orogenic history and the species of these areas are, thus, also expected to show a more eventful evolutionary history. Our study on an edge primate species has yielded a very complex image of how geographical features such as latitude and altitude, animal physiology, and climate change in the past may have together influenced its demographic history. Unlike in the tropics, where Pleistocene glacial fluctuations were less likely to have been extreme, this region seems to represent a balance between the tropics and the more severe, temperate arctic environments. This study also underscores the possibility that a cold-tolerant species like the Arunachal macaque, which could withstand historical climate change and grow
once the climate became conducive, may actually be extremely vulnerable to anthropogenic exploitation, as is perhaps indicated by its more recent population decline. It is imperative that we need to understand the population dynamics of such a species at a much finer scale, which could be possible with more extensive sampling regimes. What is of greater concern is the clear genetic signature of a serious decline in the populations of the species, possibly mediated by the extensive hunting that it faces across its distribution range. While these threats need to be better documented by on-ground field studies on the affected populations, it is entirely possible that unless immediate action is taken, genetic drift caused by hunting, epidemics or certain natural calamities can rapidly eliminate the remaining genetic diversity of this less-known endemic primate from the remote mountains of northeastern India.

We next turned to the bonnet macaque of the plains of southern India in an effort to forge a comparative understanding of the effects of geography and historical climate change on the population genetic structure and demographic history of a similar primate species, a close genetic relative of the montane Arunachal macaque, but one that lives in a very different environment. In this species, clearly, Pleistocene glaciations did not have any effect; instead, the historical fluctuations in the monsoon patterns appear to have been the most important factor that shaped its populations. Interestingly, however, we would have expected that a generalist species like the bonnet macaque would be extremely adaptable to change in its environment but a large-scale climate change could still play havoc with the species. This is a particularly important point to note as the current rapid rate of habitat modification has driven us to provide conservation priority to only specialist species like the Arunachal macaque while the more generalist “weed” species are overlooked under the belief that they are hardy and that their intrinsic flexibility would protect them from survival threats. Our results clearly indicate, however, that a juggernaut like regional climate change could easily decimate populations of the so-called ecological generalist species like the bonnet macaque.

4.6 References


