Chapter 13
Anthropogenic Influences on Macaque Populations and Their Genetic Consequences

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13.1 Introduction

The impact of human population growth on biodiversity accelerated with the invention and spread of agriculture over the past 10,000 years (Redman 1999; McKee 2003). This lifestyle shift, from nomadic foraging by small bands of people to a sedentary lifestyle, was made possible by the development of primary food production processes, largely mono-cropping and herding techniques (Barrett et al. 1998). Predictable food supplies altered the birth-death rate equilibrium of these early human populations, resulting in increased population densities (Roberts and Manchester 1997). Although the existence of populations of other species continued to be impacted by our growing ecological influences, it was now mediated in a different way. Rather than directly killing off individuals or populations of other species, mainly through hunting or outcompeting them for natural food resources, the new agriculturists promoted wholesale displacement of both plants and animals by utilising swaths of land for crops and herding. Agricultural lands necessarily became less diverse and less productive in biomass as concentrations of domesticates were grown specifically for human consumption, at the expense of more diverse systems that had evolved to sustain different wildlife species. Although reliance on fewer food types decreased nutritional value intake, human populations managed to

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flourish at unprecedented scales (McKee 2003). Meanwhile, large mammal extinctions reached an all-time high during this time. For example, in South Africa alone, 16 species of large mammals went extinct in the past 10,000 years, including nine in historic times (McKee 1995). This is in contrast to the general pattern, prior to the emergence of the genus *Homo*, of an extinction rate of about four large mammal species every 100,000 years (McKee 1995).

Primates, the group that incorporates humans, have traditionally been considered to be the most evolutionarily successful taxon, based on several parameters including maximum lifespan potential (MLP), MLP calorie consumption (MCC), encephalisation quotient (EQ), and extra number of cortical neurons (N_c), as compared to other mammalian orders (Cutler 1976). Interestingly, however, few primate taxa occur outside the tropics, and most taxa are rare due to their small geographical range size or latitudinal extent, low population density, or both. Harcourt (2006) found that rare primate taxa are specialised, but neither use more resources nor breed more slowly than do the common ones. Instead, the correlation of rarity and specialisation was found to be mediated through geographical range: Taxa with small ranges, or small ranges for their density, are specialised, but not so taxa at low density. Furthermore, common taxa are generalised but only so because they consist of more differently specialised sub-taxa, not because each sub-taxon is generalised. One such 'generalist' and, in turn, successful non-human primate group is the genus *Macaca*. Among extant primates, the macaques, with 22 well-accepted species (Thierry 2007), occupy a geographical range that is only smaller than that of humans. In terms of their wide distribution, numerous populations and the range of habitat types exploited, macaques have achieved outstanding evolutionary success among primate groups. Although their distribution and numbers have reduced drastically since the Pleistocene, when macaques reached the peak of their evolution, the ecological adaptability and behavioural flexibility of the genus has undoubtedly contributed to their colonising success and the ability of some species to thrive in habitats undergoing drastic modification by humans (Sinha et al. 2005; Lane 2011).

Although evolutionarily successful, macaques have also been affected by anthropological influences and mostly adversely so. Undocumented historical influences of humans on the range of macaque species in the past might be reflected in the disjunction of some species distributions, origin of hybrid species or the expansion of the range of some species through introductions. Most of the well-documented cases are, however, more recent phenomena. A major part of Asia has undergone an unprecedented industrial growth and a spurt in human population size over the last 50 years. Large parts of erstwhile macaque habitats have been, as a result, converted into human habitations making some of the specialised species such as the lion-tailed macaque (*M. silenus*) of India severely endangered. Even the demand of the biomedical research community for non-human primate models, especially rhesus macaques *M. mulatta* and long-tailed macaques *M. fascicularis*, has fostered the depletion of macaques in many areas of their erstwhile distribution and their wide-scale illegal translocation from areas where captive breeding for sale is not permitted. In the present chapter, we will discuss the effect of such adverse anthropological influences on the distribution, demography, and hybridisation of macaque species from a genetic perspective.

13.2 Anthropogenic Effects on Macaque Demographic Histories

Studies in population genetics usually involve the analyses of genetic variability within and among populations and the various forces that shape it. Recent demographic events such as population bottlenecks or expansions create typical signatures of genetic diversity at selectively neutral loci, such as microsatellites or single nucleotide polymorphisms (SNPs); these are usually characterised by parameters such as the population mutation parameter, estimated, in turn, through other variables such as effective population size and rate of mutation. The comparison of different estimates of these parameters across populations, based on neutral genetic markers such as those mentioned above, can then be used to infer demographic historical events experienced by those populations.

Some studies have used this approach to infer the effect of significant environmental events, which may have occurred thousands of years ago, such as glaciations (Modolo et al. 2005), drop or rise in sea levels (Evans et al. 2003; Ziegler et al. 2007; Li et al. 2011) or volcanic activity (Hayaishi and Kawamoto 2006) on the genetic diversity and structure of macaque populations. Glaciations and subsequent warming periods, for example, have been shown to have strong effects on the phylogeography and demography of populations. During glacial advances, widely distributed populations typically shrink in size and either become extinct or retreat to fragmented pockets of where some environmental conditions favourable for life continue to prevail. There is often a severe restriction in gene flow among such pockets, leading to genetic differentiation among individuals in these different refugia (Fa and Lindburg 1996; Abegg and Thierry 2002). The resulting populations usually decline while genetic bottlenecks leave characteristic signatures in the patterns of genetic diversity among these multiple isolated populations. Relatively rare alleles are eliminated from gene pools, yielding survivor populations with an excess of intermediate frequency alleles and increased levels of genetic subdivisions, often leading to a deficiency of genetic heterozygosity within each refugium. Modolo et al. (2005), for example, reported evidence from mitochondrial DNA that suggested that the ancient ancestral population of Barbary macaques was first isolated during the onset of Pleistocene (Riss) glaciation some 213,000 years ago. The isolation deepened during the actual glaciation period and created several isolated refugia such as those currently extant in Morocco and Kherrata (Algeria), as illustrated in Fig. 13.1. A similar historical demographic pattern has been established for rhesus and long-tailed macaques (Melnick et al. 1993; Smith and McDonough 2005; Smith et al. 2007), for Japanese macaques (Hayaishi and Kawamoto 2006; Kawamoto et al. 2008a) and for Sulawesi macaques (Riley 2010).

The impact of the rise of human populations on macaques is, of course, of much more recent origin as compared to climatic events such as glaciation. Modern humans may have been present in Arabia and southern Asia earlier than previously believed and probably coincident with the documented presence of humans in the Levant sometime between 130,000 and 70,000 years ago (Petraglia et al. 2010). The kind and intensity of their interaction with macaques at that time, however, remains

Fig. 13.1 Map showing seven isolated relict populations of Barbary macaques in Algeria (*shaded*). There are other regions where macaque populations were reported a few decades ago but have since disappeared, most likely due to anthropological interference (*stippled*) (Modified from von Segesser et al. 1999)

undocumented. Reports of human–macaque interactions are known from at least the last 5,000 years (as, e.g. the classical records from the Neolithic Jomon Era of Japan, Mito and Watanabe 1999) but provide little insight into the response of the affected macaque populations to increasing human dominance across their distribution range. Furthermore, evidence of an association between the signature of a demographic event and its cause is mostly circumstantial. To confidently conclude, therefore, that a certain human activity may have caused a historical event such as a genetic bottleneck or a population expansion requires corroboration from the dating of the event using a molecular clock that could potentially display a linear correlation between levels of genetic diversity and time. In addition, such a conclusion would be justified if evidence of human intervention at the same time and place could be identified independently. The absence of early written records and the technical difficulty of differentiating the results of human intervention from environmental causes can, however, complicate such attempts. It is remarkable, nevertheless, that a few studies have indeed been able to draw confident inferences regarding the effect of human interference on macaque demographic histories (Modolo et al. 2005, 2008; Kawamoto et al. 2008a, b).

13.2.1 *Effect of Habitat Destruction: Barbary Macaque Populations in Northern Africa*

The Barbary macaque (*M. sylvanus*), traditionally considered the most primitive of all macaques, is the only primate left in Africa north of the Sahara desert. Once widely distributed across Europe and northern Africa, this species is now restricted to a few relict cedar forests of Algeria and Morocco (Delson 1980) where most populations occur at very low densities in heavily disturbed and fragmented habitats (Camperio Ciani et al. 1999). The important question here is whether such large-scale temporal changes in the demography of the species have left genetic signatures in its genome.

While Barbary macaque populations may have been interconnected through extended forest patches at the beginning of the Holocene, various civilisations appear to have contributed to the almost complete depletion of the once-vast lowland forests of northern Africa within a span of a 1,000 years. Fa (1984) has noted in detail how these forests have provided fuel, timber, pasture and arable land for people, resulting in almost 86% loss of forested lands in Morocco and Algeria since the time of the Romans. Such reduction in forest cover continued with the subsequent influx of the Bedouin people from the east (643–698 AD). In all lands under Arab domination, pastoralists were substituted by sedentary agriculturists, who, in effect, exerted severe pressure on the natural vegetation of the region, especially the lowland forests, but had little influence on the mountains. In these highland areas, therefore, the forests remained largely untouched since historical times. Macaque populations living in high-altitude habitats thus appear to have been less disturbed than were the more threatened lowland ones (Fa 1983).

Such a significant reduction in the extent and quality of the habitat expectedly revealed a strong signature of geographic isolation in mtDNA haplotypes among the seven present-day Barbary macaque populations illustrated (shaded) in Fig. 13.1 (von Segesser et al. 1999). Moreover, additional populations, previously reported from Algeria (stippled in Fig. 13.1), appear to have disappeared over this period of time. While all the four isolated populations under study were found to be genetically distinct, genetic polymorphisms at the microsatellite loci screened were observed to be particularly high among the surviving Algerian populations of the macaque, as compared to other genetic markers used in earlier studies (von Segesser et al. 1999). It is perhaps noteworthy that the Barbary macaque differs from all macaque species in having a highly promiscuous mating system where multiple males in a group achieve paternity successfully at any given time. This system would tend to increase the effective population size and this, in turn, may have mitigated the effect of genetic isolation (von Segesser et al. 1995) as was evident from the observed hyper-variability of the microsatellite loci.

In summary, Barbary macaque populations have clearly undergone a severe population bottleneck that mirrors the historical fragmentation of their habitat. Unexpectedly, however, the extant populations of the species reveal a genetic variability that does not match the intensity of the well-recorded anthropogenic impacts that their ancestors must have faced. Such a mismatch is often a result of the complex interplay of multiple factors including anthropogenic effects, climatic events and the more inherent biological traits of the species, the untangling of which requires long-term genetic monitoring of the populations along with a clear understanding of their reproductive behaviour and its potential genetic impacts. There is, however, hardly any study that has examined these problems adequately in any nonhuman primate system. Nevertheless, von Segesser et al. (1999) have strongly advised conserving the isolated populations of the species in order to maintain the present level of its genetic variability over the long term.

13.2.2 The Case of the Japanese Macaque: Impacts of Glaciation, Volcanic Eruptions and Hunting

The major subspecies of the Japanese macaque, *Macaca fuscata fuscata*, occupies three of the four main islands of Japan (Honshu, Shikoku and Kyushu, being absent only from Hokkaido and the Ryukyu Islands) and a number of smaller islands around these three. A second subspecies, *M. f. yakui*, inhabits the island of Yakushima, the southernmost extent of the species' distribution. The endangered status and very low levels of genetic heterogeneity displayed by this subspecies (Hayaishi and Kawamoto 2006) bespeaks its isolation and extremely limited distribution. The subspecies was hunted almost to extinction by the early twentieth century but rebounded in the post-World War II era with its populations increasing steadily since 1978.

Kawamoto et al. (2008a) found a very weak signature of population bottleneck in the northernmost Shimokita island population of *M. f. fuscata* using autosomal and Y-chromosome microsatellite loci; paleontological evidence suggests that this population has existed here over the last 120,000 years (Iwamoto and Hasegawa 1972; Aimi 2002). The last glacial maxima and the following warm period, as well as more recent hunting and forest destruction, well documented from as early as 120 years ago and which continued until the 1970s, seem to have affected this macaque population to a significant extent (Nozawa et al. 1991; Kawamoto et al. 2008a). Although the low genetic variability of the study population, reported by Kawamoto et al. (2008a), could be expected from a demographically stable population (Cornuet and Luikart 1996), the failure to detect any excess of heterozygosity could be due to the disproportionate loss of low-frequency alleles following a population bottleneck. The authors argue that any signature of population decline brought about by humans would have occurred much more recently and, therefore, be stronger in intensity. The bottleneck was thus assumed to have been an ancient one, with its signature decaying over time to an almost imperceptible level today. The demographic change responsible for the current low genetic variability in the Shimokita macaques, therefore, possibly occurred during the last warming period associated with a concomitant rise in sea levels. It is perhaps significant that this study, akin to that on the Barbary macaques, was also unable to find any genetic signature of the massive hunting, which occurred within a relatively short span of 120 years, on the genetic structure of the study populations.

13.3 Anthropogenic Introduction of Alien Macaque Species

Mammalian invasions have a fairly long history, the anthropogenic introduction of mammals into new areas being recorded at least since the beginning of the Neolithic period. Many ancient introductions involved wild species commensal with humans such as the black rat *Rattus rattus*, anthropophilous species like the wood mouse

Apodemus sylvaticus and domestic species such as the Corsican mouflon *Ovis aries* (Genovesi et al. 2009). Macaques constitute, arguably, one of the worst alien invasive species of the world (Lowe et al. 2000), with documented cases of introduced alien macaque species in novel environments over at least the last 200 years. Some species have been intentionally introduced into new territories such as rhesus macaques in the keys of the Archipelagos of the Canarreos and Camagüey in Cuba in order to create artificial colonies of semi-free-ranging macaques that would generate a supply of monkeys for institutions conducting biomedical research (Borroto-Páez 2009). There are, however, other instances where the introductions were accidental, including escaped animals or the abandonment of pet or zoo or circus monkeys. A notable example of the latter consists of between 10 and 30 Taiwanese macaques (*M. cyclopis*) that escaped from a zoo in Wakayama Prefecture, Japan, in 1955; this population had grown to 270 animals by 2003 (Kawamoto et al. 2007). Such incidents often threaten the local flora and fauna (mostly invertebrates and small mammals) due to sudden predation pressure on them brought about by the introduced macaques. In many cases, alien macaque introductions have resulted in subsequent admixture with populations of the native species effectively reducing the global population of the latter and causing a dilution of its local gene pool. These introductions also mark a bottleneck event, more specifically, a founder effect, in the history of the introduced species and this may be followed by a demographic expansion of the surviving founders of this population. An important case in point is again presented by the newly established population of Taiwanese macaques in western Japan, an alien introduction event that appears to be a major conservation threat to the local Japanese macaque population (Kawamoto et al. 2007).

13.3.1 Founder Effect: Long-Tailed Macaques on the Island of Mauritius

Long-tailed macaques were introduced to the island of Mauritius in the Indian Ocean by Portuguese or Dutch sailors about 400–500 years ago. The number of founders was probably quite small (Bonhomme et al. 2008) and considered to represent a single introduction of pets released by the sailors from an Indonesian source (Sussman and Tattersall 1986). Genetic analyses have, however, implicated multiple geographic origins for the founder population including Java (Bonhomme et al. 2008), supporting an earlier study by Tosi and Coke (2007). The local people have regarded the monkeys, numbering between 15,000 and 60,000 individuals (Bonhomme et al. 2008), as a major agricultural pest for a very long time and the Dutch decision to abandon the island in 1712 was apparently partially due to this problem (Sussman and Tattersall 1986). The demographic history of this introduced macaque population thus suggested a founder effect followed by rapid population expansion. The relatively reduced genetic diversity presented by the Mauritian long-tailed macaques, relative to other regional populations of this species, as demonstrated by their mtDNA (Smith et al. 2007), microsatellite loci (Kanthaswamy et al. 2008) and MHC alleles (Wiseman et al. 2007), was also consistent with a hypothesis of an effective genetic bottleneck. The ultimate confirmatory evidence was provided by Bonhomme et al. (2008), who showed that this population had indeed experienced a genetic bottleneck followed by at least one population expansion and possibly several cycles of later expansion and decline.

13.3.2 Effect of Genetic Variability on Population Survivorship

Classically, a population bottleneck, followed by a founder effect, is thought to give rise to low genetic diversity through a small founder size and eventual inbreeding (Wright 1931; Slatkin 1993; Frankham 1996; Frankham and Ralls 1998; Frankham et al. 2002). Such loss of genetic diversity is intimately associated with an increased risk of inbreeding depression and has been shown, in some cases, to result in decreased growth rates, fertility, fecundity and offspring viability (Keller 1998; Westemeier et al. 1998; Madsen et al. 1999). Populations that have lost genetic diversity may also suffer from an increased probability of extinction as a consequence of increased vulnerability to novel pathogens. The maintenance of genetic diversity has thus been traditionally considered to be of fundamental importance in conservation biology (Frankham 1996; Frankham and Ralls 1998; Madsen et al. 1999). There are, nevertheless, reports of an increasing number of species for which the extent of genetic variability and the ability to respond to diseases or environmental change differ markedly from expectations (Amos and Harwood 1998).

An extremely important factor that influences immunocompetence or the ability of an organism to defend itself from disease consists of the major histocompatibility complex (MHC) genes possessed by that organism. MHC genes are responsible for adaptive immune responses in vertebrates and are, thereby, involved in modulating host resistance to emerging pathogens (Klein 1986). Most natural animal populations exhibit high MHC diversity in terms of the number of alleles present, the extent of sequence variation among these alleles and the levels of heterozygosity (Klein 1986; Hedrick 2003). Very high diversity at MHC loci among and within vertebrate species has been interpreted as adaptations to detect and present a wide array of peptides from rapidly evolving pathogens (Garrigan and Hedrick 2003) whose distributions are often geography-specific. Consequently, high levels of MHC diversity could be the ultimate response of natural selection to unpredictable or temporally varying disease outbreaks (Altizer et al. 2003). Some genetically bottlenecked animal populations including, for example, Scandinavian beavers (*Castor fiber*; Ellegren et al. 1993), fallow deer (*Cervus dama*; Mikko et al. 1999), northern elephant seals (*Mirounga angustirostris*; Weber et al. 2004) and African cheetahs (*Acinonyx jubatus*; Castro-Prieto et al. 2011), however, exhibit low or no detectable polymorphisms in MHC genes but yet have survived, or even increased in numbers, with no apparent increase in susceptibility to infectious diseases (but see

Radwan et al. 2010). In sheer contrast, bottlenecked populations of desert bighorn sheep (*Ovis aries*) are highly susceptible to many infectious diseases despite high levels of MHC diversity (Gutierrez-Espeleta et al. 2001). The precise implications of the extent of genetic diversity at MHC loci for the survivorship of non-primate mammalian species thus remain unclear. Let us now turn to the results of a similar study on the aforementioned introduced population of long-tailed macaques on the island of Mauritius.

The Mauritian long-tailed macaques are particularly valuable for detailed immunological studies due to their remarkably restricted MHC diversity (Wiseman et al. 2007; Mee et al. 2009). Bonhomme et al. (2008) compared the variation of microsatellite loci within and outside the MHC region in these macaques with that of natural populations from the Philippines, Java and some areas of southeast Asia. More polymorphism was expected at the MHC microsatellites as they are closely linked to the functional MHC genes than are the non-MHC microsatellites as a result of balancing selection working on the MHC genes. All the study populations, however, displayed similar levels of genetic diversity at both MHC and non-MHC microsatellites while none of the MHC microsatellites from the Mauritian individuals were found to be under positive or balancing selection. It has thus been suggested that a rapid demographic expansion possibly followed the bottleneck event created by the introduction of the founder individuals (Lawler et al. 1995; Sussman and Tattersall 1986) and this maintained the current substantial and comparable levels of genetic diversity at both the MHC and non-MHC loci without the help of any kind of selection. Bonhomme et al. (2008), however, found high frequencies of some microsatellite alleles in the long-tailed macaque population from the Philippines in agreement with a pattern of directional selection on MHC class II genes. Interestingly, unlike the Mauritian individuals, those from the Philippines are able to survive infection by the malaria parasite *Plasmodium coatneyi* (Migot-Nabias et al. 1999). *Plasmodium* species represent one source of pathogens that may play a role in such directional selection and have even been hypothesised to have influenced speciation between rhesus and long-tailed macaques (Wheatley 1980). It was speculated that some MHC alleles or haplotypes (class II DRB and probably class I), prevailing in the Philippines population, play a role in the greater resistance of the macaques of this population to various *Plasmodium* parasites (Bonhomme et al. 2007). Our current understanding thus suggests that the Mauritian population continues to be susceptible to malaria in spite of their high variability at the MHC loci possibly because these individuals have not been exposed to malaria parasites on Mauritius.

13.3.3 Interspecific Hybridisations in the Wild

Ancient hybridisation events across sympatric macaque species are well known (Zinner et al. 2010). In recent times, human intervention has brought together many macaque species that were historically separated by relatively great distances thus resulting in polyspecific associations in the form of mixed-species troops and hybrids. This has been reported for rhesus macaque × long-tailed macaque and long-tailed macaque × pig-tailed macaque *M. nemestrina* crosses in Malaysia, Tonkean macaque *M. tonkeana* × Heck's macaque *M. hecki*, moor macaque *M. maura* × Tonkean macaque, Tonkean macaque × booted macaque *M. ochreata*, Celebes crested macaque *M. nigra* × Heck's macaque and Gorontalo macaque *M. nigrescens* × Heck's macaque crosses in Sulawesi (Bernstein 1966, 1968; Bynum 2002; Fooden 2006; Supriatna et al. 1992; Watanabe et al. 1991a, b; Watanabe and Matsumura 1991). Malaivijitnond and Hamada (2008) reported an interspecific mating between a released male pig-tailed macaque and female rhesus macaques in a small isolated semi-wild troop of rhesus macaques in northeastern Thailand. Rhesus macaque populations in Thailand are presently rare and isolated from one another due to increasing habitat fragmentation; such isolation could make these populations particularly vulnerable to unwanted hybridisation with released alien macaque species. Finally, mixed troops of rhesus and bonnet macaques *M. radiata* have also been reported along their common distribution boundary in central and southern India although it is uncertain whether any hybridisation has ever occurred between members of the two species in such groups (Kumar et al. 2011).

Theoretical studies have shown that a disturbance that weakens pre-mating isolation between incipient ecological species can sometimes lead to species collapse through hybridisation (Gilman and Behm 2011). Whether a particular species pair collapses is likely to depend on the strength, speed and duration of the disturbance, as well as on the genetic architecture underlying resource use and mate choice in the species pair. In the light of such insights but in the absence of any significant ecological and genetic information on the macaque populations mentioned here, it is difficult to assess the frequency and genetic impacts of human-driven natural hybridisation and its conservation implications for these species.

13.4 Human-Driven Range Expansion of Macaques

The geographic areas occupied by species are often highly dynamic, changing through time, with periods of directional or isotropic growth, of range expansions and of contractions followed by re-expansions (Taberlet and Cheddadi 2002). Range expansions have occurred repeatedly in the history of most, if not all, species and appear to be continuing even today, possibly at an increasing rate owing to rapid climatic changes. Species ranges can also occasionally expand and distribution patterns change due to human interventions. The consequences of range expansion of one species for other closely related species in the communities that are invaded can be considerable. Range expansions are also of interest because they often signal important changes in habitats, may bring together populations that have partially or just completed the process of speciation and may have interesting consequences for the communities that are invaded.

In a recent detailed study, Kumar et al. (2011) documented changes in the distribution of rhesus macaques *M. mulatta* in southeastern India; the species appears to have expanded its geographical range by ca. 3,500 km^2 since the last macaque distribution surveys in that part of the subcontinent (Fooden et al. 1981). Thirty years ago, rhesus macaques invaded the Vijayawada Hills in the southern Indian state of Andhra Pradesh, formerly occupied by bonnet macaques *M. radiata* (Fooden et al. 1981), extending its southern distributional limits. Today, the species appears to have advanced further southwards, having crossed the rivers Godavari and Krishna to intrude into the bonnet macaque distributional range. This distributional overlap region, extending to a maximum width of ca. 45 km, is now virtually devoid of bonnet macaque troops. The pace of irrigation development in the basin of the Krishna River accelerated significantly during the last 30 years, and several dams and bridges have been constructed across the river (Venot et al. 2008). This resulted in the development of large swathes of agricultural lands in the Krishna Basin (Guntur district of Andhra Pradesh) facilitating the expansion of rhesus macaques south of the river into the Guntur and Prakasam districts of the state (Kumar et al. 2011). In addition, the introduction of large numbers of rhesus macaque groups into the eastern and the western flanks of the bonnet macaque range during the last three decades has augmented range expansion by the former and local extinctions of the bonnet macaque populations from this region (Kumar et al. 2011). The larger rhesus macaques are more dominant to the comparatively smaller bonnet macaques and displace them by aggressively driving them away from food sources or preferred habitats (Kumar and Sinha 2011, personal communication). Such dominance by large-bodied primate species of smaller-bodied species and eventual displacement or exclusion of the latter from food resources is well known (Strier 2007) and has been clearly documented elsewhere too as, for example, during interspecific interactions of Neotropical primates including howlers, capuchins and muriquis (Dias and Strier 2000).

Although range expansions have occurred recurrently in the history of most species, their genetic consequences have been little investigated. Theoretical studies show that range expansions are quite different from pure demographic expansions and generally lead to a loss of genetic diversity along the expansion axis owing to recurrent bottleneck effects (Excoffier et al. 2009). Extensive migration between neighbouring populations, however, preserves genetic diversity and leads to consequences of range expansions that are more akin to those of large demographic expansions. Such range expansions appear to be conditioned by the properties and the dynamics of the wave front; the frequency of rare variants in the advancing surf front will determine the genetic structuring of the colonising population and certain distinct sectors of low genetic diversity could appear. There could also be a subsequent introgression of local genes into the genome of the invading species. Interestingly, theoretical analyses indicate that the patterns of genetic diversity generated by such an invading population could be similar to those generated by selective sweeps in an established population and could, thus, be mistakenly interpreted as adaptive events (Currat et al. 2006).

13.5 Conclusions

Human–macaque interactions constitute a complex phenomenon influencing perhaps the biology of the macaque more profoundly than ours. At the population level, humans tend to influence the distribution, demography, immunology and even behaviour of the macaque species they interact with though none of these interactions are ever simple. These work at different levels, interacting, in turn, with other environmental factors. For example, when a macaque population is exposed to a novel disease from an anthropogenic source, its distribution range might contract due to outbreak deaths, which will also have severe demographic consequences. At another level, however, this population could also consequently acquire new genetic variation through its survivors, thus influencing the immune system of its individuals. It is thus clear that the distribution, ecology and behaviour of human populations will have multiple effects on commensal and even wild macaque populations at different organisational levels (see Chap. 12 by Sinha and Mukhopadhyay, this volume for the consequences of anthropogenic impacts on macaque social structures), and most of these impacts are likely to have genetic consequences over the long term. Our current state of knowledge, unfortunately, suffers from a serious lack of insight into such genetic impacts. There is, therefore, a dire need for long-term genetic monitoring programmes to understand the effect of anthropogenic factors on the dispersal and demography of different macaque species. New laboratory and statistical techniques are enabling the use of molecular markers for genetic monitoring of wild populations; effective studies, however, are still very few, even on well-studied taxa (Kruckenhauser et al. 2009). One of the reasons attributed to the tenuous survival displayed by macaques against the onslaught of development is their remarkable capacity to adapt to human-modified landscapes. It seems, however, that time is running out for even many of the most adaptable members of this unique group of primates.

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