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Potential effects of human provisioning on populations and habitats of rhesus macaque in China

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ABSTRACT

Rhesus macaques (*Macaca mulatta*) have demonstrated a potent capability of adapting to human-disturbed environment. In China, they have become popular attractions in ecotourism areas and receive substantial food from tourists, resulting in local booming populations. Previous studies have highlighted human-macaque conflicts and yet ignored their impact on local natural ecosystems. Through reviewing previous researches, we summarized the contributing factors to the thriving populations of rhesus macaque and expounded upon the potential impacts of them on other local organisms. Booming populations of rhesus macaque caused by provisioning could present potential risks to local plant and animal community through lesser seed dispersal and greater predation and competition pressures on other sympatric species, ultimately impacting the diversity and stability of local ecosystems. Thus, it is imperative to draft the relevant laws to strictly control human provisioning for wild rhesus macaques and conduct further studies to elucidate their interspecies relationships. And a higher priority should be devoted to monitoring these potentially overabundant populations and formulating optimal management strategies to achieve harmonious coexistence between humans and rhesus macaques.

Keywords: Rhesus macaque; Monkey-human relationships; Provisioning; Inter-species relationships; Overabundance

INTRODUCTION

Human activities have disrupted approximately 70% of terrestrial ecosystems, forcing many species to struggle in these anthropic land covers (Galán-Acedo et al., 2019). However, some species well-capable of adapting to human disturbance have witnessed dramatic population growth in certain areas (Moore et al., 2023). Whether invasive or native, these overabundant species might endanger natural diversity and even cause local extinctions (Garrott et al., 2003). Globally, rhesus macaque (*Macaca mulatta*) is the most widely distributed non-human primate species residing in multi-male, multi-female mixed groups. Males tend to migrate before adulthood and females stay in their natal group, establishing a dominance hierarchy system based upon matrilineal kinship (Fooden, 2000; Southwick et al., 1996). They have demonstrated a potent capability of adapting to human-disturbed environment (Cooper et al., 2022).

In China, rhesus macaques are potentially distributed in south region of Yellow River Basin (Wu et al., 2023). Their habitats ranged from 250 to 4 000 meters above sea level in 17 Chinese provinces. The southernmost distribution was situated in Hainan Island (N18°23'), northernMountain (N34°54'—N35°42') and westernmost to Southern Qinghai–Xizang Plateau (Lu et al., 2018). They are important attractions in many ecotourism areas for wildlife observation, and they receive a substantial amount of food from tourists, which resulted in locally booming rhesus macaque populations (Wang et al., 2022; Zhu et al., 2019). Under natural environment, the density of rhesus macaque populations can reach 170–200 individuals/km^2 (Chang et al., 2002; Jiang et al., 1998). In human-disturbed environment, the overall density can surpass 2 000 individuals/km^2 at main provisioning sites (Zhu et al., 2019). Previous studies of these high-density populations have focused largely upon their conflicts with humans (Zhang et al., 2018; Zhu et al., 2019). However, scant attention has been paid to their potentially negative effects on other native species.

We summarized existing studies on interspecific relationships between non-human primates and other species. A special focus has been placed upon human-disturbed or provisioned populations. This includes not only rhesus macaques, but also other non-human primates worldwide with similar behavior patterns. The overall objective was to explore the potential effects of provisioned rhesus macaque populations on their habitats in China. Firstly, we discussed

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the reasons why rhesus macaques could thrive in anthropogenic environments of China. The probable causes included high dietary diversity, high reproductive potential, low predation pressure, human provisioning and human-introduced population. Secondly, we examined the potential impacts of provisioning on population growth and behavior patterns of rhesus macaques. Also, how this could further affect their role as seed dispersers, food plants, prey animals, competitors and disease transmission. Finally, some potential remedies were proposed for managing the populations of rhesus macaque in China, including direct culling, sterilization, feeding ban and protecting non-provisioned populations.

WHY RHESUS MACAQUES CAN THRIVE IN ANTHROPOGENIC ENVIRONMENT OF CHINA

High dietary diversity

Rhesus macaques are generalist omnivores with highly diverse and flexible diets (Cooper et al., 2022; Cui et al., 2022). Depending upon the abundance of different food resources in their habitats, they could modify their diets to adapt to diverse environments (Ding et al., 2020; Tang et al., 2016; Zhou et al., 2014). For example, they primarily consume fruits in tropical and subtropical regions and become generalist folivores in temperate and limestone forest areas (Richard et al., 1989; Sengupta & Radhakrishna, 2016; Tang et al., 2016). Besides plants, their diets could be supplemented with termites, grasshoppers, ants, beetles, mushrooms, bird eggs, mollusks and fishes (Fooden, 2000). In Supplementary Table S1, we have summarized the published feeding ecology studies of rhesus macaque. The number of their food species ranged from 25 to 117. Their diets varied greatly according to place, season and even between groups. Such a great flexibility and diversity of diets enabled rhesus macaques to thrive over a wide range of environments, especially those highly disturbed by human activities, such as urbanized surroundings (Saraswat et al., 2015).

High reproductive potential

High reproductive potential is known to help rhesus macaques to thrive in anthropogenic environments. Under favorable nutritional conditions (especially with human provisioning), females might give birth for the first time around 3 to 5 years of age and then maintain an annual birthing cycle until around 17 years of age (Lee et al., 2021; Pittet et al., 2017; Wilson et al., 1983). In Supplementary Table S2, we have summarized the data of birth and growth rates from published studies and our own records for both provisioned and non-provisioned wild groups of rhesus macaques. The greatest growth rate for non-provisioned wild groups was 17.6% in Taihangshan, China (Tian et al., 2013) and 21.4% for provisioned groups in Tughlaqabad, India (Malik et al., 1984). Human provisioning could exacerbate the population growth process. In a natural environment without any provisioning, it generally took around 30 years for rhesus macaque population to recover from 200 individuals to over 1 000 individuals (Chu et al., 2019; Fan et al., 2024). In contrast, provisioned populations at Qianlingshan Park of Guizhou, China have spiked exponentially from about 100 individuals to over 1 000 within merely 25 years (Zhu et al., 2019).

Low predation pressure

Generally, predation significant impacts upon the grouping and behaviors of animals (Orihuela et al., 2014; Schaik & Hörstermann, 1994; Van Schaik & Van Noordwijk, 1985; Van Schaik et al., 1983), efficiently controls the prey species' population (Lwanga et al., 2011; Ritchie & Johnson, 2009). However, predation may not be a major limiting factor for populations of some primate species, including macaques (*Macaca*) (Dittus, 1980; Hall & Gartlan, 1965; Rowell, 1969). Most natural predators of rhesus macaques may prefer not to hunt them while human activities have sharply dwindled the numbers and distribution range of all these predators (Barker & Barker, 2010; Lau et al., 2010), leading to low predation pressure for rhesus macaques in China.

Major predators of genus *Macaca* include members of Canidae and Felidae. Fossil evidence from Europe hinted that member of Felidae and Canidae families, as well as hyenas, could prey on Barbary macaques (*M. sylvanus*) (Meloro & Elton, 2013). And Rhesus macaque was known as an important prey of dholes (*Cuon alpinus*) (Bhatt & Lyngdoh, 2023), tigers (*Panthera tigris*) (Sarkar et al., 2018) and leopards (*Panthera pardu*) (Kshettry et al., 2018). Even though Canidae and Felidae are capable of preying on rhesus macaques, they may not prefer them. In fact, rhesus macaques constituted merely 0.7% in the diet of leopards in Jaipur, northern India (Kumbhojkar et al., 2020). Despite being the most abundant prey species, they were not detected in feces of tigers and leopards in Chhattisgarh, central India (Basak et al., 2020). Rhesus macaque accounted for 15.58% within the diet of Nepalese striped hyenas (*Hyaena hyaena*). However, such primary scavengers as hyenas might simply ingest the carcasses of rhesus macaques and have no praying preference (Bhandari et al., 2020). This phenomenon may be due to arboreal capability of rhesus macaques making them less an ideal prey species as compared to other animals limited to terrestrial locomotion, especially human livestock (Kumbhojkar et al., 2020).

Large raptors are capable of preying on rhesus macaques, but at a relative low frequency. Postulated as a specialized primate targeting raptor, Philippine eagle (*Pithecophaga jefferyi*) preys on long-tailed macaques (*M. fascicularis*). However, detailed observations have revealed that less than 5% of their prey targets were macaques (Fam & Nijman, 2011; Ibañez et al., 2003). A similar low percentage was also found for mountain hawk eagle (*Nisaetus nipalensis*) preying upon Formosan macaques (*M. cyclopis*) to feed their nestlings, accounting for only 3.1% of the prey (Sun et al., 2009). Mountain hawk eagle in Japan (Iida, 1999) and Golden eagles (*Aquila chrysaetos*) (Qu et al., 1993) might hunt macaques. No large raptors preyed upon arboreal primates in Southeast Asia with the exception of the Philippines (Van Schaik & Van Noordwijk, 1985). In short, large raptors may not serve as efficient predators for rhesus macaques within their geographical range.

Some constrictor snakes (e.g., pythons) have been recorded to regularly prey on non-human primates (Headland & Greene, 2011). Snakes, especially pythons, might pose a lethal threat to the survival of primates throughout their evolutionary history. As proposed by Snake Detection Theory, both humans and non-human primates tend to associate fear with snakes so that their brains process visual images of snakes in a specific manner (Kawai, 2019). Pythons might pose a greater threat to macaques than other snakes. For example, wild bonnet macaques (*M. radiata*) only emitted alarm calls as opposed to models of other venomous and non-venomous snakes (Ramakrishnan et al., 2005). However, there were no published data about the hunting efficiency of pythons to rhesus macaques.

Up until now, no convincing evidence from published studies might prove that any predator could efficiently control the population of macaques. Studies of toque monkeys (*M. sinica*) in Sri Lanka have demonstrated that food-related behavior-ecological relationships, rather than predation, contributed to macaque mortality under relatively stable ecological conditions (Dittus, 1977). Furthermore, due to such factors as habitat loss and hunting, the numbers and distribution range of all these predators have sharply declined in China (Barker & Barker, 2010; Lau et al., 2010). And many endangered predators have completely disappeared from their native habitats (Lau et al., 2010; Li et al., 2020b). This has rendered it even more difficult for predation pressure to limit the populations of rhesus macaques (Qu et al., 1993), thus partially fostering a rapid proliferation. Additionally, most potential predators of rhesus macaques posed threats to humans, such as tigers, leopards and pythons (Kelly et al., 2019; Natusch et al., 2021), making it impractical to reintroduce them into areas heavily impacted by human activities (e.g., tourist attractions and agricultural areas), where is more likely to have overabundant rhesus macaque populations.

Human provisioning

Due to unique anthropomorphic characteristics, macaques have been humanized widely with religious and cultural symbolic significance in China and other Asian countries (Kabir, 2019; Knight, 1999; Zhang, 2015; Zhang & Chen, 2013), thereby greatly facilitating human provisioning and mutual coexistence. In Hindu mythology, monkeys are traditionally revered as spiritual reincarnations of monkey god Hanuman so that feeding monkeys has become a sacred duty for Hindus (Kabir & Hawkeswood, 2020, 2021; Pragatheesh, 2011). Also, the popular tale of Monkey King in classic saga Journey to the West is widely circulated in China and beyond. A rebellious and anti-authoritarian cultural image for rhesus macaques has fostered human tolerance and unwavering interests (Fuentes, 2013). As a result, macaques roam freely around Hindu and Buddhist temples and enjoy an ample supply of foodstuffs from both devotees and tourists (Aggimarangsee, 1991; Jones-Engel et al., 2006; Medhi et al., 2007; Zhao & Deng, 1992), basking in the protective sanctity of their own or adjoining temples (Priston & McLennan, 2013).

Due to their cultural and religious significance, rhesus macaques have become significant attractions at many ecotourism parks. To attract more tourists, these parks provide food to confine rhesus macaques to specific areas for observation. Also, rhesus macaques habituated to humans actively often steal or snatch food from tourists. Such a resource-abundant environment without predators resulted in a rapid growth in rhesus macaque populations within these localities (Wang et al., 2022; Wu et al., 2025; Zhang et al., 2018; Zhu et al., 2019). At Qianlingshan Park of Guizhou, China, the population of provisioned rhesus macaques has experienced an average annual growth rate of 8.08% since 1992, reaching around 1 000 individuals by 2018. A whooping density of over 2 000 individuals/km^2 was recorded at major provisioning sites (Zhu et al., 2019). Such a high density was ten folds that of the rhesus macaque population at 200 individuals/km^2 on Neilingding Island, a saturated natural habitat in China (Chu et al., 2019; Fan et al., 2024). The population of macaque dependent on human provisioning is often much higher than natural capacity of local natural environment. Therefore, upon a depletion of human-derived food, macaque population becomes rather difficult to sustain (Kurita et al., 2008).

Human-introduced population

In many instances, human intervention has facilitated the expansion of rhesus macaque population into new habitats. Due to their significant attractive value as mentioned above, rhesus macaques have been introduced to many tourism destinations (Wang et al., 2022). The rhesus macaque populations of Silver River, USA descended from a handful of rhesus macaques released by a tour boat operator to enhance the excitement value of his ‘‘jungle cruises’’ in 1930s. The total count surpassed 300 individuals in 1984 (Riley & Wade, 2016). Similarly in China, there are at least 164 macaque ecotourism attractions, with 53 of them explicitly hosting macaque populations introduced from other regions (Wang et al., 2022). Another reason for cultivating rhesus macaque groups is for scientific research purposes. The famous rhesus macaque population at Cayo Santiago was introduced from India 85 years ago, and has become a valuable source of information for scientific researches on adaptive and evolutionary mechanisms (Wang & Francis, 2024). Also, China has bred experimental breeding populations of rhesus macaque at Dajinshan Island, Shanghai to fulfill the needs of laboratory animals from adjoining research institutions (Shen et al., 1991). In addition, humans have also translocated rhesus macaques for population control and other management or protective reasons. Rhesus macaques have been translocated from urban sites to rural places in India to mitigate human-monkey conflicts (Imam et al., 2002). The feasibility of introducing rhesus macaques as a way of ex-situ conservation and rational utilization has been explored at Yinpingshan Forest Park in Dongguan, Guangdong, China (Yang, 2023). The introduction of rhesus macaques may have unintended adverse impacts on local ecosystems. In Puerto Rico, USA, the populations of rhesus macaques were introduced for examining the process of adaptation and have resulted in significant agricultural losses with a complete depletion of seabird breeding colonies on Desecheo Island (Evans, 1989; USDA, 2021). However, little is known about the number and origin of these introduced macaque populations in ecotourism areas and whether they have a negative impact on local ecosystem in China (Wang et al., 2022).

POTENTIAL IMPACTS OF HUMAN ACTIVITY ON RHESUS MACAQUES AND THEIR HABITATS

Population growth and behavior patterns

Provisioning could have significant effects on non-human primates in terms of population growth, competitive behavior, space use and activity budget (Sugiyama, 2015). Large quantities of high-nutritional food from provisioning could significantly boost the physical wellbeing of macaques, accelerate population growth through enhanced fertility, shortening birth intervals and lowering infant mortality (Kurita et al., 2008; Sugiyama & Ohsawa, 1982). As compared to food resources in natural forest, provisioning food is prevalent in a restricted area that could be monopolized by dominant individuals through contest competition, leading to larger gaps in dominance and more aggressive conflicts between individuals (Furuichi, 1984; Mori, 1977; Southwick et al., 1976). The concentrated distribution of provisioning food also altered the space use pattern of non-human primates. Provisioned Northern pig-tailed macaques (*M. leonina*) had significantly smaller home rage and daily path lengths than wild-feeding groups (José-Domínguez et al., 2015). Similar alterations in space use were also noted for provisioned rhesus macaques in India (Sengupta et al., 2015). The concentrated distribution, together with the predictability of provisioning food, could potentially shorten the time allocated to foraging behavior (Ding, 2017; Jaman & Huffman, 2013; Unwin & Smith, 2015). Time saved from foraging created extra time in activity budget. It allowed for the emergence of new behavioral patterns and more rare behaviors within the provisioned population (Sugiyama, 2015). All these changes in population growth, space use and behavior patterns of rhesus macaques could impact their inter-species relationships with other creatures in local habitats.

Curtained seed dispersal

In natural conditions, rhesus macaques play some role as seed dispersers for their food plants in ecosystems. Due to a flexible diet (Fooden, 2000), broad habitat adaptability, large group size and long-haul movement capabilities (Albert et al., 2013), macaques are deemed as efficient seed dispersers (Lucas & Corlett, 1998; Tsuji & Su, 2018). In fragmented forests of tropical and subtropical Asia, where mammal species have been largely extirpated due to anthropogenic disturbances, rhesus macaques with high tolerance to human activities are viewed as essential and sometimes the only dispersers of large-seeded plant species (Lucas & Corlett, 1998; Tsuji & Su, 2018). Studies of rhesus macaque populations in Buxa Tiger Reserve in India revealed that they could disperse seeds of 84% of ingested plant species, confirming their significant role as seed dispersers in forest ecosystems (Sengupta et al., 2014).

It is also worth noting that human provisioning might hinder the dispersal of seeds by macaques. Firstly, a heavy reliance on human food inevitably leads to a reduction in consumption of natural fruits and seeds (Southwick & Siddiqi, 1994). The proportion of dietary fruits dropped from 70.8% in non-provisioning period to 28.8% in provisioning period (Sengupta et al., 2015). Secondly, provisioning causes aggregation effects, shrinking their home ranges, shortening daily travel distances (Zhang, 2008) and thus diminishing their capability of dispersing seeds. The home range size of long-tailed macaques was 23 folds smaller for provisioned group than for non-provisioned group (Hansen et al., 2020). Furthermore, provisioning sites are typically located in human-modified areas with solid paved roads unsuitable for seed germination (Pragatheesh, 2011; Senguptaet al., 2015). During provisioning periods, 41% of fecal seeds were deposited on roads compared to only 9% during non-provisioning periods, resulting in significant wastes of seeds (Sengupta et al., 2015).

Greater pressure on food plants

Moderate foraging of leaves and buds by monkeys might minimize top dominance, trigger compensatory effects and thereby promote plant growth. Studies of white-faced monkeys (*Cebus capucinus*) have demonstrated that areas inhabited by monkey troops tended to have more tree branches compared to areas without them (Oppenheimer & Lang, 1969). Moderate foraging by Japanese macaques stimulated compensatory effects in plants, leading to the growth of more shoots and consequently a greater branch density (Enari & Enari, 2021; Enari & Sakamaki, 2010). However, in cases where rhesus macaque populations underwent a rapid expansion due to human provisioning, foraging might disrupt this equilibrium and result in the destruction and deterioration of vegetation. Given the limited research on rhesus macaques, we primarily drew upon findings from other primate species in this section.

Excessive foraging by monkeys may first affect the plants they prefer to feed on. For example, a study in Sri Lanka revealed that a shortage of food caused by a cyclone led to relative overfeeding by langur monkeys (*Semnopithecus entellus* and *S. vetulus*) and a higher mortality rate of their preferred plants (Dittus, 1985). Another study has found that the preference of red howler monkeys (*Alouatta seniculus*) for certain plants may promote the expansion of non-preferred plants within local communities, ultimately resulting in a reduction in forest nutrient cycling and productivity (Feeley & Terborgh, 2005).

In addition to leaves, intensive consumption of other plant parts could also affect plant reproduction and growth. For example, spider monkeys (*Ateles geoffroyi*) in Costa Rica have been observed completely removing all flowers after their feeding on *Symphonia globulifera*, resulting in no fruit production (Riba- Hernández & Stoner, 2005). A similar situation also found for baboons (*Papio hamadryas*), who damaged 30% to 80% of inflorescences while feeding on *Aloe marlothii* (Symes & Nicolson, 2008). Rhesus macaques in Asola-Bhatti Wildlife Sanctuary of India spent 22.9% of their feeding time on flowers (Ganguly & Chauhan, 2018), highlighting their potential for excessive consumption of flowers.

Barks and roots are also part of the diets of rhesus macaques (Aslam et al., 2024; Shao et al., 2023; Zhang et al., 2022). Bark damage could increase the likelihood of plants being attacked by pathogens and insects, and even directly lead to the death of trees (Mikich & Liebsch, 2014), while root herbivory can damage plants and alter their physiology by decreasing nutrient and water uptake, as well as aggravating pathogen infection (Moore & Johnson, 2017). Many primates have been known to damage the tree bark (Di Bitetti, 2019). A decade-long tracking study revealed that capuchin monkeys (*Sapajus nigritus*) caused extensive damage to the bark of loblolly pine trees (*Pinustaeda*), significantly impeding tree growth (Liebsch et al., 2015). In Western Sichuan Plateau of China, rhesus macaques ingested plant roots (30.9%, main food type), barks (2.4%) and fallen leaves as alterative food when the availability of preferred foods became too low (Zhang et al., 2022). Therefore, high-density populations of macaque might cause damage to the root systems of plants in their surrounding environment when facing food scarcity.

The movement and resting behavior of primates could also lead to vegetation loss as they require plant branches to bear weight (Figure 1). The increased population of baboons using plant branches causes significant damage to the tree crowns and upper branches of their preferred plant species (Lent et al., 2010). A study of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) found that long-term provisioning at a small and fixed location could lead to over-utilization of surrounding trees by monkeys, significantly increasing tree mortality (Yang et al., 2023). What is concerning is that this provisioning pattern is also applied to the ecotourism of rhesus

Figure 1 Damage to plants caused by rhesus macaques' activities at a tourist park

A: Branches of *Pterocarpus indicus* broken by rhesus macaques while feeding on its flowers, the flowers on the ground were dropped naturally; B: One branch of palm shattered by a group of frolicking juvenile rhesus macaques; C: Bamboo shoots shattered by rhesus macaques while racing and feeding. Photo by Cheng-Feng Wu.

macaques. Areas where rhesus macaques were concentratedly provisioned had significantly lower grass coverage and plant species richness compared to non-concentrated areas in Guizhou Qianlingshan Park of China (Zhu et al., 2019). In Takasakiyama of Japan, the high-density population of Japanese macaques has led to soil compaction from excessive trampling, which prevented the growth of plant seedlings and roots (Yokota & Nagaoka, 1998).

In conclusion, provisioning hinders the rhesus macaque's role as a seed disperser by limiting its access to natural food plants and confining its foraging range. Furthermore, the increased macaque population resulting from provisioning will lead to enhanced exploitation of natural vegetation and subsequent risk of disruption of plant communities, particularly when artificial food supply is discontinued, as in the case of population management for Japanese macaques in Takasakiyama (Kurita et al., 2008). Additionally, the high-density activities of the macaques near provisioning sites can directly result in damage to plant branches and surrounding land.

Greater pressure on prey animals

As generalist omnivores, macaques may include various small animals in their diet. Rhesus macaques in Sundarban mangrove swamps of India have been observed feeding on fish (Majumder et al., 2012). Long-tailed macaques in southern Thailand could even utilize stone tools to harvest seafood (Gumert & Malaivijitnond, 2012; Malaivijitnond et al., 2007). The utilization of stones by the macaques as tools for consuming shellfish has resulted in a reduced size of shellfish in Khao Sam Roi Yot National Park in Thailand. It might be considered as evidence of over-predation (Luncz et al., 2017). Provisioning could not only promote population growth, but also hasten the occurrence of innovative new behaviors such as stone tool use (Leca et al., 2008; Sugiyama, 2015). Both could result in high predation pressure on prey animals.

Many macaques exhibited some nest predation behavior so that it might be a primary cause of breeding failure in many bird species. Japanese macaques destroyed 85% of artificial nests simulating the Northern Bobwhite (*Colinus virginianus*) within a three-day experiment (Feild et al., 1997). Pig-tailed macaques (*M. nemestrina*) preyed upon nests of bulbuls and coucals in Thailand (Pobprasert & Pierce, 2010; Tokue, 2007), accounting for 43.7% of nest predation incidents in some areas (Pierce & Pobprasert, 2013). Similar behaviors were also observed for Northern pig-tailed macaques (Khamcha et al., 2018), lion-tailed macaques (*M. silenus*) (Balakrishnan, 2010) and long-tailed macaques (Safford, 1997).

Although the relationships between native populations of rhesus macaques and birds in natural environment might be in a dynamic balance, studies of introduced populations of rhesus macaques have implied that they could have negative impacts on local bird species. Artificial nests were more likely to be predated when located in areas with a relatively high macaque abundance in introduced areas (Anderson et al., 2016). As noted by a government report from the United States Commonwealth of Puerto Rico, introduced rhesus macaque population has led to the disappearance of all seabird species on Desecheo Island. They consumed 200 to 300 bird eggs per week in 1969 and made the hatching success rate of red-footed boobies and brown boobies on the island zero in 1987 (USDA, 2021). However, little is known about the impact of a booming local population of rhesus macaque population resulting from human provisioning on local bird species (Figure 2).

Greater pressure on competitors

Introduced or provisioned populations of rhesus macaques might exert negative impacts on other local species with similar ecological niches. In India, some rhesus macaques have been translocated from urban sites to rural sites to mitigate human-monkey conflicts (Imam et al., 2002). However, due to their larger body size as well as greater aggression relative to bonnet macaques, rhesus macaques have such a significant advantage of interspecific competition as to completely replace local bonnet populations in some introduced areas (Kumar et al., 2011). Even in their native habitats, due to their high adaptability to human disturbance and high reproductive potential, rhesus macaque could recover and thrive more quickly than other more sensitive species (Garrott et al., 2003). A recent Chinese study focused upon a conflict event between rhesus macaque and Hainan gibbon (*Nomascus hainanus*), one of the most endangered primates in the world (Cai et al., 2024). This case has highlighted the necessity of paying greater attention to the impact of rapidly booming rhesus macaque populations on other sympatric endangered species.

Disease transmission

Many human infectious diseases, such as acquired immunodeficiency syndrome (AIDS) and yellow fever, originate in non-human primates (Wolfe et al., 2007), possibly due to the genetic, physiological and social similarities (Davies & Pedersen, 2008). There is convincing evidence for parasitic exchange between humans and macaques, such as malaria (Chapman et al., 2005; Pedersen & Davies, 2009). For disease propagating through a direct contact, transmission is assumed to be density-dependent so that any increase in hosts elevates the overall level of transmission (Best et al., 2012). Therefore, the growing macaque population and extensive human-macaque interaction at ecotourism areas might facilitate the transmission of diseases and parasites among humans, macaques and other wildlife (Becker & Hall, 2014; Parmar et al., 2012; Simonetti, 1995). A recent review inventoried 183 zoonotic pathogens in wild Asian primates, including 63 helminthic gastrointestinal parasites, two blood-borne parasites, 42 protozoa, 45 viruses, 30 bacteria and one fungus (Patouillat et al., 2024). In rhesus macaques of Bangladesh, parasitic richness was elevated in large macaque groups interacting with human communities and livestock. And almost all parasitic taxa identified were of zoonotic clinical significance (Islam et al., 2022). And in Nepal, most methicillin-resistant *Staphylococcus aureus* strains from rhesus macaques around temple areas could be associated with humans (Roberts et al., 2018, 2020). As a result, recent publications on viruses, parasites or other pathogens carried by macaques have attracted growing attention to the risk of disease transmission in contact with wild macaques (Adhikari et al., 2023; Sawaswong et al., 2019; Yu et al., 2023). Thus, it is imperative to pay greater attention to the potential risks of zoonotic transmission and limit contacts with wild rhesus macaques.

MEASURES OF MANAGING MACAQUE POPULATIONS

The formation of human-induced high-density macaque populations disrupts the natural balance, potentially exerting pronounced negative effects on various sympatric animals and vegetation, while also exacerbating conflicts between humans and macaques. Therefore counter-measures should be taken to manage the macaque populations exceeding the carrying capacity of environment (Barfield et al., 2006).

Culling problematic populations

The most direct means of population management involves directly culling individuals to reduce population size (Knight, 2017). In mid-1990s, Japanese government began culling Japanese macaques to mitigate the damage of farmland. For a long time, this method effectively curtained agricultural losses and the number of culled Japanese macaques rapidly spiked to over 20000 in 2011, leading to the disappearance of Japanese macaque populations in many areas (Enari, 2021). However, with widespread ethical considerations and the concept of humane treatment of animals deeply ingrained in public consciousness, humans are seeking more reasonable and animal welfare-friendly ways of addressing this issue (Oogjes, 1997).

Sterilization

Sterilization is currently considered as an acceptable method for managing the populations of rhesus macaque. It refers to artificially disrupting the breeding process and shrinking population size by reducing the number of offspring. Hormone control for females and vasectomy for males have been widely applied (Martelli et al., 2020; Shek & Cheng, 2010; Yu et al., 2015) without any negative impact on their behaviors and health (Wolfe et al., 1991). In recent years, Hong Kong has started implementing sterilization measures to control the populations of rhesus macaque. Since 2002, over 1500 macaques have undergone sterilization in Hong Kong, resulting in a declining trend in overall birth rate of the population, reaffirming the preliminary effectiveness of the program (Shek& Cheng, 2010; Wong & Chow, 2004).

However, Hong Kong might be the only place where sterilization was effective to manage wild macaque populations. It remains rather problematic to determine the actual efficacy of sterilization under field conditions (Mikail et al., 2023). Furthermore, manpower, resources and time required for sterilizing wild rhesus macaques cannot be ignored. And programs should be optimized for maximizing the benefit-cost ratio to ensure long-term sustainability (Kirkpatrick, 2007). For example, birth rates and population growth of rhesus macaque are more limited by the number of fertile females so that sterilizing females is more cost-effective than sterilizing males (Martelli et al., 2020).

Feeding ban

A combination of feeding bans and sterilization proved to be an efficient way of managing wild primate populations (Dittus et al., 2019; Shek & Cheng, 2010). In fact, all the above-mentioned methods of culling or sterilization are impractical if provisioning continued to sustain high birth rates, survival rates and growth rates in rhesus macaque populations. To resolve the dilemma of rapid growth of macaque populations in human-disturbed environment, it is imperative to implement the laws and regulations to discourage and control human provisioning behavior. However, currently no national law has been enacted for forbidding feeding wild animals in China. In many areas, local managers can only discourage or dissuade the feeding of wild rhesus macaques in no vein (Zhang et al., 2018). Furthermore, some ecotourism parks promote the purchase of monkey food for tourists to feed wild macaques to generate revenue (Zhang et al., 2018). These feeding practices have become widespread among tourists, further

Figure 2 Rhesus macaque eating a raw chicken egg snatched from tourists at a tourism park
Photo by Cheng-Feng Wu.

complicating efforts to restrict feeding. Taking Singapore as an example, half of long-tailed macaque population in Singapore accepted human provisioning, leading to heightened human-macaque conflict (Sha et al., 2009). To tackle this and other problems related to feeding of wildlife, Singapore amended the WILDLIFE ACT to prohibit arbitrary feeding of wild animals in 2020, imposing a maximum fine of $5000 for first-time offenders. It is worth noting the impact of the law on human provisioning behavior and local long-tailed macaque populations deserves attention. Such a feeding ban has proven efficient in reducing human-monkey conflicts at Polonnaruwa (Dittus et al., 2019).

For a certain high-density population of rhesus macaque, ceasing feeding might result in the dispersal of macaques to adjacent areas in search of natural food to meet their energy requirements, potentially damaging the surrounding plant communities (Yokota & Nagaoka, 1998; Yokota & Ono, 1993). Therefore, feeding ban is primarily a preventive measure. It is best applied in conjunction with other population management measures.

Protecting endangered native macaques

Although rhesus macaques thrive in some areas due to human provisioning, others still face threats to their survival in China (Li et al., 2020a). Currently, over 94% of potential macaque habitats are not covered by China's protected areas (Wang et al., 2024). Although some macaque groups in Taihang Mountains have spiked rapidly due to human provisioning (Chai, 2014), the whole population in this area with high ecological vulnerability has high genomic vulnerability with inbreeding and low heterozygosity, putting them under a high risk of extinction under climate changes (Wu et al., 2023). Similar inbreeding risk was also noted for the population in Shangchuan Island, Guangdong (Gu & Liu, 2024). Therefore, more localized measures should be implemented for managing the expanding rhesus macaque populations due to human disturbance. Also, we are obliged to protect other natural native populations at a risk of decline to achieve a better survival of this species in China.

SUMMARY

As a generalist omnivore species with diverse diets and relatively high reproductive potential, rhesus macaque has adapted well to human disturbance environment. At the same time, human activities have eliminated the macaque's natural predators. Development of ecotourism has promoted the provisioning of rhesus macaques. An artificial introduction of them into new habitats might further contribute to the prosperity of macaque populations in these human-disturbed areas. However, traditional studies of these human-disturbed populations have focused largely upon the changes in macaque behavior and their interactions with humans (Hill, 1999; Pragatheesh, 2011; Sengupta & Radhakrishna, 2018; Southwick et al., 1976). Few studies have examined the effects of these high-density populations on other local flora and fauna communities. Through summarizing the existing studies, we concluded that populations growth and changes in behavior patterns in provisioned populations of rhesus macaque might compromise their capability of seed dispersal, exert additional pressure on their preferred food plants and prey animals, crowd out the living space for other species and elevate the risk of disease transmission in surrounding areas. This could become a serious problem for some ecotourism areas, such as Qianlingshan Park, Guizhou, China (Zhu et al., 2019). To prevent similar incidents, the relevant laws should be formulated to strictly control human provisioning for wild rhesus macaques and other wild animals. And more robust studies are required for clarifying the inter-species relations of rhesus macaques in these areas. We also emphasize the need to protect other non-provisioned native populations at a risk of decline. Future studies should appreciate the differences among macaque populations in different environments and devise targeted conservation or management strategies to achieve harmonious coexistence between humans and rhesus macaques, as well as other animal and plant communities.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests

AUTHORS' CONTRIBUTIONS

P.F.F. and C.F.W. contributed to conception and design of this manuscript. C.F.W., P.Z.X., Y.X.F. and Z.H.X. participated in the collection and organization of documents and data. And C.F.W. and P.Z.X. composed the manuscript. All authors read and approved the final version of the manuscript.

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