

Evaluating Cognitive Flexibility in Non-Human Primates under Ongoing Anthropogenic Environmental Changes

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Keywords: Primates, Cognitive Abilities, Adaptation, Behaviour, Protection, Environmental Changes

Abstract: This paper examines how non-human primates (NHPs) use cognitive abilities to adapt their behaviour in changing environments. It is argued that while NHPs have developed cognitive adaptations to cope with resource loss, these abilities may be insufficient to counter ongoing population declines driven by human and environmental threats, such as deforestation and climate change. Simians, which are more social and active during the day, show a high level of cognitive flexibility, allowing them to respond to changes in food sources, seasonal shifts, and social interactions. Prosimians, on the other hand, tend to be nocturnal and solitary, relying more on biological traits such as enhanced senses, flexible diets, and spatial memory to survive in areas with limited resources. Despite these adaptations, both groups face growing threats from climate change, habitat loss, and other human activities. This study also points out gaps in current research, especially on wild and prosimian populations, which limits our understanding of how cognition may help NHPs survive in changing environments. To protect vulnerable primate species and their habitats, it is crucial to prioritise research and conservation efforts. This paper concludes that while NHPs have developed ways to cope with their surroundings, these skills are likely not enough to protect them from today's fast-changing environment.

1. Introduction

Non-human primates (NHPs) are an order of mammals including simians (monkeys and apes) and prosimians (lemurs), excluding *homo sapiens*. Simians can be divided into further subgroups: Old World monkeys (long-tailed macaque and rhesus monkey), which reside in Africa and southeastern Asia, and New World monkeys (capuchin and squirrel monkey), which are found in South and Central America. They are characterised by a large and complex brain, grasp of objects using hands, reliance on vision over smell, and complex behaviour [1]. Their cognitive abilities are the skills that allow NHPs to make decisions by thinking critically and using the information they acquire [2]. Because their cognitive abilities and physiological reactions closely mirror humans compared to other animals, certain types of NHPs, such as Rhesus monkeys, have been used for research purposes. 67% of studies are for pharmaceuticals and drug safety testing [3]; however, research into the cognitive abilities of captive-bred NHPs can be used to look at how wild

populations interact and adapt to a changing environment. The environment of NHPs is undergoing significant change globally; this could be shrinkage due to deforestation, as well as rising temperatures from climate change. The drastic decline in NHP populations worldwide has been described as an “impending extinction crisis” [4]. This paper will explore whether the cognitive abilities of NHPs will help them adapt to changes in their natural environment by investigating research about NHPs in impacted areas, which may indicate any changes in population numbers.

2. Conservation Status of Primates

Asia and Madagascar had the highest proportion of threatened primate species with around 60% and 70% of species considered endangered or critically endangered respectively. The Americas and Africa had lower percentages of threatened primate species around 20% and 30% respectively (Fig.1). Overall, the evident trend of vulnerable primate populations globally indicates the urgency for evaluating their protection from extinction.

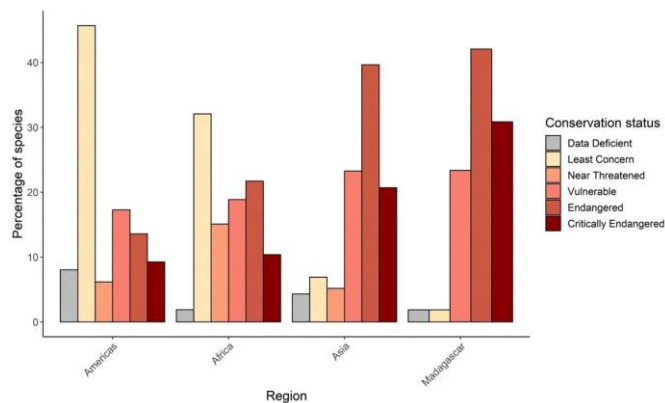


Figure 1 Conservation Status of Primates According to Region

Note. From The Current Status of the World's Primates: Mapping Threats to Understand Priorities for Primate Conservation, D. Fernández, D. Kerhoas, A. Dempsey, J. Billany, G. McCabe, E. Argirova, 2022, International Journal of Primatology, 43,15-39.[5]

The current downward trend in populations would seem to indicate that the cognitive abilities of NHPs do not compensate for the loss of resources caused by the threats to their environment. While in-situ and ex-situ adaptations can offer short-term protection, they are unlikely to prevent population declines as threats intensify. Human-related factors, including deforestation and agricultural development, and environmental threats like rising temperatures and extreme weather events pose extreme threats to the availability of resources. Some limits in current research may be due to the variety between species and ecological restraints. This likely applies particularly to prosimians, where nocturnality in most species prevents researchers from collecting comprehensive data. The geographic distribution of primates globally complicates the full impact of different factors specific to each species; overall, these concerns highlight potential gaps in the understanding of trends in primate adaptation.

3. Adaptations to Environmental Changes

3.1 Adaptations In-Situ

Many species of NHPs have demonstrated their ability to adapt to environmental changes in-situ, through changes to their foraging patterns and spending more time on the ground; however, it is unclear the extent to which these are cognitive behaviours that will allow their populations to thrive

in the long-term.

3.1.1 Ground use

One adaptation that has been seen in a number of NHPs is increased time spent on the ground; the main ecological causes of this relate to increasing temperatures, decrease in canopy cover, and in some species, dietary shift away from fruits. Descending to the ground is generally associated with greater predation risk from ‘novel predators and predation patterns’; however, predators in the same environment experience similar challenges, which are likely to impact their populations, reducing the risk to NHPs. Arboreal primates use the ground to access water sources; this behaviour is likely to be amplified by the increase in hot periods and general temperatures. However, an increase in ground use is not a cognitive adaptation, as they have already demonstrated this response — it is a proportional reaction to increasing temperatures. Even though this change is not a cognitive adaptation, the ability to forage more efficiently on the ground may require cognitive abilities. The travel paths of lowland gorillas increasing in linearity as the value of the food rewards becomes higher at target locations to minimise the time and energy [6]. The trade-off of energy for higher rewards can improve the overall net reward rate compared to the immediate smaller rewards. The evidence of foraging more efficiently on the ground, shown through the travel paths of lowland gorillas and mantled howler monkeys, demonstrates a clear cognitive adaptation. The ability to plan and make decisions about foraging strategies demonstrates advanced problem-solving skills that improve the chances of securing resources; however, while this adaptation may help them cope with short-term change, the overall improvement in survival rates could be limited due to ongoing food scarcity and continued deforestation, which could reduce the availability of even high-value food sources.

Moreover, primates may face physical challenges to their brain, which could limit their cognitive abilities and ultimately, their survival.

3.1.2 Consequences of Food Scarcity on Brain Size

The brain is what must carry out the cognitive abilities that NHPs use, making it energy-costly and “nutritionally expensive” [7]. Another consequence of fragmented forests and deforestation is a scarcity of high-value food sources and therefore, it is likely to pose a risk to the population of NHPs in affected areas. There is evidence to suggest that certain groups within NHPs may be biologically more flexible to adapt to constricted food sources than others. Since body mass is positively correlated with food mechanical properties (FMPs) due to metabolic rates, larger species of NHPs, on average, tolerate lower-quality foods than smaller species [8]. Smaller species of NHPs will undergo more pressure on their diets as food sources become more limited. Some such species have demonstrated their cognitive abilities to use energy-minimising strategies to adapt to this new restriction. These strategies include shifting their diets away from fruits to low-quality substitute [9]. The “Cognitive Buffering” and “Expensive Brain” hypotheses support the shift towards lower-quality foods and habitats as being additional constraints to brain size and cognitive abilities [7]. The continued fragmentation of forests is likely to lead to a sustained lack of high-quality food, may contribute to the shrinkage of NHPs’ brains.

3.1.3 Social and Reproductive Relationships

In the event that NHPs experience brain shrinkage as a result of the long-term scarcity of high-quality food, there may be a detrimental impact on their ability to negotiate relationships, and therefore, is likely to pose an additional risk to their population if their environment continues to change. These abilities directly correlate to health and fitness (fertility and longevity), as well as

immune function and reproductive rates [7]. The effects of brain shrinkage on NHPs that live in larger groups are especially variable: Group size is simply a proxy for this constellation of demands [7]. In larger groups, individual primates are likely to have greater pressure on their cognitive abilities to survive in social hierarchies with higher competition and manage more complex coordination within the group. Group size can act as a proxy for understanding the effects of brain shrinkage and the potential adaptations that occur as a result. NHPs' reproductive strategies are particularly significant; due to their slow life histories and low reproductive rates [10]). This makes them especially vulnerable to disruptions in breeding seasonality, as they must rely on in-situ adaptation to survive in the same location despite changing conditions. Typically, primates with more pronounced reproductive seasonality have evolved to synchronise their reproductive cycles with periods of food abundance or favourable environmental conditions [11]. This strategy allows primates to maximise the survival chances of their offspring by timing births during periods when resources are plentiful. However, the concentration of reproductive efforts in a narrow window may leave little room for adjustment if climate-induced changes alter the timing of favourable conditions. Large-scale climate phenomena have already shown negative impacts on NHP populations, including variations in abundance and vital rates; however, this is only shown in single populations and cannot certainly indicate a causal relationship. However, it is uncertain whether NHPs can actually develop this behavioural plasticity in a short period of time, rather than through generations; it is possible as primates' slow life history is a strategy for developing their cognition over their reproduction and growth [12]. Even species with developed cognitive advantages may face reproductive declines if environmental changes become too erratic or extreme, especially because most NHP species are already constrained by slow reproductive rates. Therefore, although there is a scarcity of research to say that climate-induced changes will definitively cause long-term reproductive declines, the available evidence suggests that populations with slow-life histories are extremely vulnerable to seasonal breeding changes.

The evidence suggests that many species of NHPs demonstrate the ability to adapt to some extent in-situ. However, there is insufficient conclusive evidence to be absolute that these adaptations are all due to their cognitive abilities. Additionally, specific adaptations, including efficient foraging patterns, dietary flexibility, and strategic reproductive periods are not likely to be acquired quickly nor be effective enough to sustain the populations, especially those with slow-life histories and live in large groups.

3.2 Adaptations Ex-Situ

3.2.1 Migration to Different Environments

As NHPs face significant environmental changes, more populations are likely to be observed migrating to new habitats; though, this is often a forced adaptation rather than a conscious cognitive decision. Factors that drive migration include rising global temperatures, decreased precipitation, and most significantly, human-related threats, resulting in constrained food sources and fragmented or shrunk forest spaces (Fig.2). Estrada et al. (2017) [4] suggest that NHPs have already shown the cognitive abilities to evaluate risks around fragmented forests and make cognitive decisions for the pursuit of food. Furthermore, they describe migration as a last-resort option.

The graph illustrates the different factors that contribute to the decision to migrate, differing based on geographic location. The new environments primates encounter often differ significantly from their original habitats. Several conditions that could possibly vary in new environments; these may lead to continual migration if intolerable. Despite the lack of quantitative data on NHP migration and survival, it could be inferred that there is likely a high probability of success based on their cognitive abilities to adapt using new landmarks.

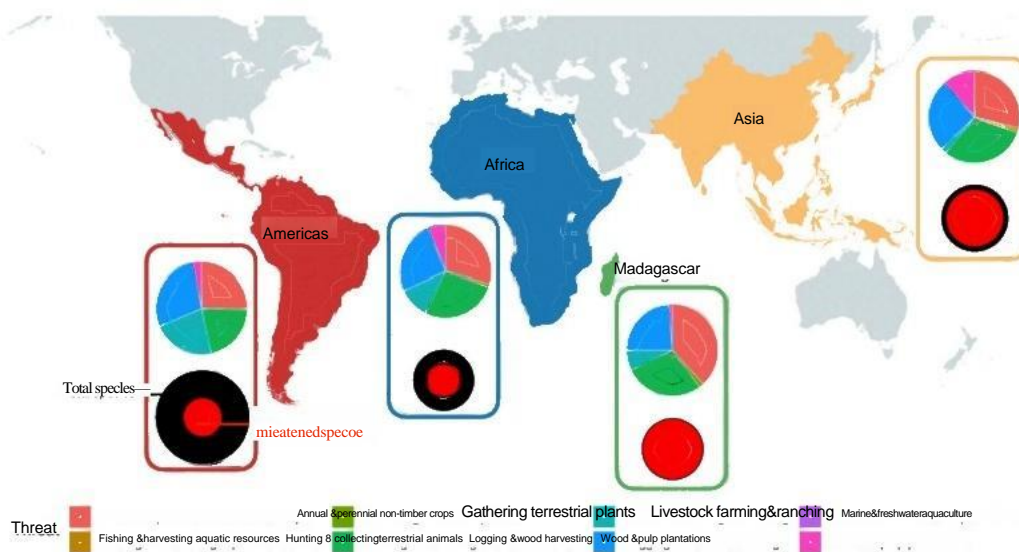


Figure 2 Human-Related Threats to Primates by Region.

Note. From *The Current Status of the World's Primates: Mapping Threats to Understand Priorities for Primate Conservation*, D. Fernández, D. Kerhoas, A. Dempsey, J. Billany, G. McCabe, E. Argirova, 2022, *International Journal of Primatology*, 43, 15–39. [5]

3.2.2 Use of Landmarks and Landmark Discrimination

Allritz et al. (2022) [13] investigated the spatial memory and cognition of chimpanzees, as well as their behaviour in entirely new virtual environments. The study revealed that the chimpanzees quickly learned to locate virtual food using a familiar landmark, such as a virtual tree, even when the food was not directly visible. This ability to associate the landmark with a reward demonstrated their capacity for spatial learning. After initially learning to locate virtual food using a familiar landmark (a virtual tree), they were introduced to a second, novel goal landmark. Some chimpanzees, such as Alex, quickly adapted by bypassing the old landmark when it was no longer baited, while others initially persisted in using the familiar landmark before adjusting to the new one. This ability to adapt to novel landmarks could be extrapolated to represent NHPs' variance in cognitive flexibility to adjust to new spatial cues. However, familiar environmental cues that aid NHPs in spatial memory may be destroyed, making it difficult for them to migrate out of their original habitat. This would ultimately cause a decline in their population numbers, as these conditions were not suitable for them in the first place. If there are no familiar landmarks ex-situ, NHPs demonstrate adaptability in spatial memory to quickly recognize new landmarks and trends.

Dolins et al. (2016) [14] supported the hypothesis that positive and negative associations with landmarks help NHPs in developing relatively efficient routes. Positive landmarks were correlated to guides that helped the chimpanzee reach the goal, while negative landmarks were correlated to distractions that led it away from the goal. The results suggested that their spatial memory could be updated dynamically as they effectively discriminate between positive and negative landmarks. Participants, including chimpanzees, reduced their latency and path length with increased familiarity with the virtual settings. In fact, one female chimpanzee was able to navigate the most complex maze route with greater accuracy compared to adult humans. The flexible memory of NHPs will likely help them learn the spatial mapping of new environments that they have migrated to. Their path length and time will also likely decrease as they use their spatial cognition to make positive and negative associations with unfamiliar landmarks.

3.2.3 Male Dominance and Decision-Making

Male NHPs have a cognitive and physical advantage in adapting ex-situ to females. Male NHPs migrating in also evaluate the relative fighting ability and potential rank in the new group, weighing potential reproductive benefits compared to the costs of injury [15]. These males demonstrate cognitive flexibility in decision-making and risk evaluation based on their benefit-cost analysis, strategically prioritising decisions for their reproductive success. In cases of temporary relocation, cortisol concentrations generally return to baseline levels upon the animal's return to its home environment. For permanent relocations, cortisol levels typically decrease to pre-move levels as the animal adapts to its new environment. However, the time course of such adaptation may vary under different conditions. [16]. It could be argued that although conditions can vary in the time taken, permanent moves made by some male NHPs during the breeding season familiarise them with the cognitive distress of migrating. A key difference between subordinate and dominant males is that in stable hierarchies, subordinate males will have higher glucocorticoid (stress) levels; in unstable hierarchies, dominant males will experience higher stress [17]. The destabilised hierarchy caused by migration is more likely to benefit subordinate males. Males then, possibly, demonstrate lower overall stress levels compared to that of their female counterparts. This adaptation ex-situ may not be considered cognitive and conscious decisions, however; males would over time, adapt lower cortisol levels to high-stress events due to biological desensitisation, or at the very least be considered a subconscious response.

3.2.4 Responses to Novel Competition

When NHPs migrate, they may encounter novel competition from species that share similar resources, such as food and water. In the case of migration, novel competition refers to new species NHPs encounter when competing for similar resources, such as food and water. To prove that one species is outcompeting another, it needs to be demonstrated that the presence of the dominant competitor is causing a negative effect on the abundance or microevolution of the other species [18]. New environments for NHPs can include a risk of novel competitors, depending highly on the migrated area, the size of the population, and the degree to which the competition is considered threatening. These factors are extremely variable across circumstances, where temperature seasonality and rainfall have been observed to drive distribution patterns. Williams (2021) [19] concluded that not any one particular set of traits drives NHPs species-environment associations due to the relative flexibility of many primate genera; however, there are several trends observed across varying group sizes, female NHPs, and behavioural adaptations. Studies show that small populations are less able to cope with environmental changes and are more vulnerable to the effects of new competitors or predators [20]. This is particularly true for female NHPs migrating to ex-situ environments, where novel competition and changing resource landscapes demand adaptation in both social and cognitive strategies. Studies indicate that ecological shifts trigger specific types of resource competition, which affect alliances and hierarchy dynamics [21]. Increased group size, seen in olive baboons, typically heightens food competition and aggression [22]. Findings on wild chimpanzee groups show that between-group competition can impact reproductive success by elongating birth intervals and reducing offspring survival when neighbour competition is high [23]. These pressures demand female NHPs to use cognitive flexibility and social skills to adapt to food constraints, maintain rank, and optimise reproductive success.

Cognitive behavioural adaptations in response to interspecific competition can include changes in foraging patterns, activity times, and even territorial behaviours to protect resources. For instance, chimpanzees exhibit flexible foraging strategies, such as altering their departure times and nest positioning based on the type and availability of fruit [24].

NHPs' cognitive and behavioural adaptations are crucial for their survival in increasingly challenging ex-situ environments. This is likely to hold true only for as long as environmental habitats are not fully destroyed and migration remains possible.

4. Prosimians: Special Considerations

Prosimians are a group of NHPs that include lemurs, lorises, galagos, and tarsiers. They are considered to have more ancestral and primitive characteristics compared to simians.

Prosimians are found in Madagascar, Africa, and Asia, and are primarily nocturnal and arboreal. The majority of research on the behaviours of prosimians in the wild is thin and vastly outdated, thus most data must be extrapolated from studies on specific species of prosimians in captivity.

4.1 Behaviour and Cognition

Prosimians typically exhibit nocturnal and solitary behaviours that offer several adaptive advantages within their ecological habitats. This would not seemingly be the case as the general impression is that these animals are less ingenious than simians [25; however, the current scarcity of published data about cognition in prosimians is still yet to be resolved to unconditionally support the hypothesis[26]. Nonetheless, compared to simians, these adaptive behaviours could likely be just as beneficial against changing environments as the cognitive abilities that simians exhibit. Prosimians reduce direct competition for resources with diurnal primates and increase predator avoidance by limiting encounters with diurnal predators. This nocturnal adaptation supports evolution in their sensory capabilities, particularly in audition and olfaction, which allow them to navigate and forage in low-light conditions effectively. Old World monkeys are sensitive to low frequencies in a way similar to humans, but their hearing extends roughly an octave higher. New World monkeys and prosimians, however, are tuned to even higher frequencies than Old World monkeys and humans. This shift likely helps smaller species with sound localization, or identifying the direction of a sound. NHPs usually depend on vision rather than olfaction for social interactions and foraging. Prosimians rely less on vision than simians and may be seen as intermediate between typical mammalian olfactory dependence and simian visual reliance [27]. Some forage alone, while others travel and gather food in groups, ranging from small family units to larger social groups with up to 27 individuals [28]. Solitary behaviour in prosimians does not necessarily conserve more energy, even though they avoid demands of social interactions common among diurnal species. This is due to the evolved beneficiary learning that highly social groups have in foraging and survival. Learning in a group supports population survival by allowing the NHPs to learn skills, such as behavioural traditions, from social partners. These traditions offer advantages for adapting to environmental changes, as they allow for variation outside of genetic changes, thereby contributing indirectly to evolution [28]. While simians are known for their advanced cognitive abilities, some prosimians have evolved specialised foraging techniques — such as gum-feeding in some species — that require distinct cognitive and motor skills specific to their nature [29]. Despite these social and cognitive adaptations, prosimians are not fully protected from rapidly changing environments. While this species' life history traits suggest it could adapt within a few generations to shifting climates, rising maximum temperatures and reduced rainfall place this population at a greater risk of collapse [30]. The case to be argued for prosimians with faster life history would be even worse, rendering most prosimians still vulnerable to environmental changes. Overall, nocturnal and solitary behaviours equip prosimians with unique survival strategies that, while not universally advantageous, are well-adapted to the specific demands of their ecological contexts. These behaviours may not be entirely preventative of the risks prosimians face from changing climates.

4.2 Diet and Water Flexibility

The dietary and water flexibility of prosimians reflects their ecological resilience in environments with fluctuating and scarce resources. Their adaptability allows species such as the red-tailed sportive lemur, primarily folivorous, to modify their leaf intake based on seasonal availability, while insectivorous species can switch prey types when necessary [29]. Biological flexibility in diet and water allows for their survival in harsh, seasonal environments without the demand for cognitive abilities; for instance, mouse lemurs can survive long dry seasons without drinking by relying on stored body water and metabolic water derived from their food [25]. Mouse lemurs and similar species would likely use these advantages to combat the effects of lack of rainfall due to climate change.

However, the main effect of rainfall is likely to be through lagged effects on food availability [29]. Recent studies on western red colobus monkeys (*Piliocolobus badius*) show dietary flexibility in more fragmented and anthropogenically pressured habitats like Cantanhez National Park; red colobus monkeys have adapted by expanding their dietary range to include cultivated foods like mango, despite being primarily folivorous. This adaptability demonstrates how species can respond to lagged food availability by adjusting their dietary choices. These biological adaptations may serve more benefits to prosimians in resource-limited environments than the higher intellectual abilities of their simian counterparts as they do not use the same energy costs as complex cognition. However, in few prosimian species, cognitive abilities are invaluable to them to carry out their evolved biological advantages. For example, aye-ayes require their specialised long fingers to tap-forage, but also require a combination of social and cognitive adapted tools, such as the ability to socially learn by observing their mothers and their ability to identify hollow cavities in wood [28]. While biological adaptations generally provide immediate survival advantages without the need for energy-intensive learning, cognitive adaptations become invaluable in social environments where food resources are difficult to access, as exemplified by aye-ayes' ability to exploit high-calorie insect larvae within wood. In short, the advantages of biological and cognitive adaptations largely depend on the species and environmental context. In stable yet resource-limited environments, biological adaptations may be more beneficial, ensuring survival through efficient resource utilisation, whereas in more dynamic or social environments and species, cognitive adaptations offer greater dietary diversity by enabling higher thinking and social learning.

4.3 Spatial Memory and Habitat Mapping

Prosimians demonstrate advanced spatial memory and habitat mapping skills. Experimental studies show that mouse lemurs can rapidly learn new spatial arrangements, adapting their foraging routes to optimise travel efficiency in search of food sources despite changes in their surroundings [31]. This mental mapping ability is essential for daily foraging and minimising exposure to predators and parasites, as well as conserving energy during travel [32]. Research on wild lemurs further investigates how their navigational strategies are tuned to cope with trade-offs in energy expense and predator avoidance, prosimians utilising their ability to plan travel routes based on both Euclidean and route-based maps [32]. This mental flexibility is important for lemurs to adjust their movements depending on seasonal changes or shifting resource availability, enhancing their survival in the increasingly competitive and harsh ecosystems of Madagascar [25]. Moreover, these spatial skills are utilised with social learning processes that enable prosimians to share knowledge about environmental resources, such as safe feeding sites or danger zones, exemplifying the social communication skills that coevolve with their cognitive strategies [32].

5. Conclusion

NHPs have a range of cognitive abilities to help them adapt both in-situ and ex-situ when environmental changes, such as habitat loss and climate change, place pressure on their habitats and resources. These skills allow many primate species, particularly simians, to cope with shifts in food sources, seasonal changes, and different social relationships. However, research is mainly focused on simian primates, leaving a significant gap in our understanding of prosimians, which tend to be nocturnal and solitary. Given the current research, prosimians seem to rely less on advanced cognitive skills for survival and more on biological adaptations, which are unlikely to fully protect them from environmental shifts. The research on NHPs is also scattered and highly specific, often limited to single or captive species, which makes it hard to extrapolate broad conclusions about how cognition applies to wild NHPs as a whole. While the studies suggest that many primates do use cognitive skills to cope with change, these abilities alone may not be enough to maintain their populations against the rapid, human-induced changes happening today. While most NHPs will likely face substantial shifts due to climate change, species in Madagascar and parts of East and Southeast Asia may be particularly vulnerable. The impacts of human-induced climate change should be prioritised in primate research and conservation efforts, especially for species already threatened by other human activities, such as forest fragmentation and hunting [33]. Given the extent of the threats of changing global environment, it is critical that human intervention prioritises both immediate and long-term conservation strategies to protect primate populations and their habitats for future generations.

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