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The Mexican Native Primates from the Comparative Psychology Point of View: State of the Art and Perspectives

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Primates have been studied extensively to understand their behavior and the mechanisms that allow information processing. However, when we closely analyze the species studied and the different projects and topics carried out with them, we found that some species have been highly studied, while others have only a few studies. These differences create a significant underrepresentation of some primate species that could be especially problematic when we use the available information to track the evolution and the diversification of behavior and the mechanisms for information processing. With this in mind, this review aims to show the state-of-the-art of different topics studied in Mexican primates and identify topics that could be studied in the future. The review also aims to demonstrate why working with native species is a path that many low- and middle-income countries like Mexico can follow to develop research programs in their homelands.

Keywords: behavior mechanism, howler monkeys, Mexican primates, native species, spider monkeys

比較心理学の観点から見たメキシコの霊長類：最先端の研究と今後の展望

霊長類は，彼らの行動と情報処理を可能にするメカニズムを理解するために，幅広く研究されてきた．しかし，これまで研究された種と，その種で実施された様々なプロジェクトや研究内容を詳細に分析すると，非常に多くの研究がなされている種がある一方で，わずかな研究しかなされていない種もあることがわかった．これらの違いは，利用可能な情報を使って，進化や行動の多様化，情報処理のメカニズムを追跡する際に特に問題となりうる，霊長類の一部の種の著しい過小評価を生み出している．このことを念頭に置いて，この総説は，メキシコの霊長類で研究されている最先端の様々な研究内容を示し，今後研究される可能性のあるテーマを明らかにすることを目的としている．また，なぜ在来種を扱うことが，メキシコのような多くの中低所得国が自国での研究プログラムを発展させることにつながっていくのかを示すことも目的としている．

キーワード：*行動メカニズム，ハウラーモンキー，メキシコの霊長類，在来種，クモザル*

Los Primates Mexicanos Nativos desde la Psicología Comparada: Estado del Arte y Perspectivas

Los primates han sido estudiados extensamente para la comprensión de su comportamiento y los mecanismos que permiten el procesamiento de la información. No obstante, cuando se hace un análisis cuidadoso de las especies estudiadas y los diferentes proyectos y estudios realizadas con ellas, se encuentra que algunas especies han sido muy estudiadas, mientras que el estudio en otras especies es limitado. Estas diferencias crean una subrepresentación significativa de algunas especies de primates, que podría ser especialmente problemática cuando se utiliza la información disponible para el rastreo de la evolución y la diversificación del comportamiento y los mecanismos para el procesamiento de la información. Teniendo en cuenta esto, la presente revisión pretende mostrar el estado del arte de diferentes temas estudiados en primates mexicanos e identificar temas que podrían estudiarse en el futuro. La revisión también pretende demostrar por qué trabajar con especies nativas es un camino que muchos países de ingresos bajos y medios como México pueden seguir para desarrollar programas de investigación en sus países de origen.

Palabras clave: mecanismos de comportamiento, monos aulladores, primates mexicanos, especies nativas, monos araña

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Comparative researchers must study different animals to develop scientific hypotheses, theories, and models to explain behavior and how their underlying mechanism abilities work and evolve; this could include general explanations that apply to many animal species or explanations for abilities only reported in one species or a group of species (Beran et al., 2014; Bernardi & Salzman, 2019; Moore, 2003; Zentall, 2018). Under these circumstances, the countries with higher biodiversity have had a greater chance to develop research projects with the native species in their territories (Abranches, 2020; Goumas et al., 2020; Nemogá-Soto et al., 2014).

The research with non-human primates (hereafter referred to as primates) plays an important role not only as a model for tracking the evolution of human behavior (Chang et al., 2013; Janmaat et al., 2021; Meunier, 2019; Weiss & Santos, 2006), but also as a group of interest themselves (Platt et al., 2016). Primates live in tropical countries, and Africa is the continent with the highest diversity of primates, with 308 species and subspecies (Madagascar contributes 112 species), followed by the Neotropical region with 221, and Asia with 196 (Estrada et al., 2017; International Union for the Conservation of Nature / Species Survival Commission [IUCN / SSC], 2023).

Despite the importance of primates in the research of behavior and the diversity of species in the different regions of the planet, only a small number of primate species have been studied intensively to track the mechanism that the animal uses to process information. In contrast, others have been studied in a few cases, particularly species from the Neotropical region. This disparity can be seen by contrasting two pairs of Old World and New World primate species and their representation in the research. A quick search in PubMed® using the tags chimpanzees (*Pan troglodytes*) and cognition shows 1,229 published research papers from 2000 to 2023. More papers are reported if we search for rhesus macaques (*Macaca mulatta*) and cognition, with 2,729 results found in the same period. In contrast, the same search, but now using the tags capuchin monkeys (*Cebus spp.* and *Sapajus spp.*) and cognition, only shows 279 published papers and is even smaller for squirrel monkeys (*Saimiri spp.*), with only 87 published papers from 2000 to 2023. The differences in the number of publications indicate a clear underrepresentation of Neotropical primate species in the field of comparative psychology.

This underrepresentation of species could be problematic, especially for those studies interested in tracking the phylogenetical roots of behavior and information processing (Heath et al., 2008; Plazzi et al., 2010; Theofanopoulou & Boeckx, 2015; Zwickl & Hillis, 2002) or for comparative studies of primates (Healy & Rowe, 2007; Nunn & Barton, 2001; Striers, 2010). Fortunately, these limitations are now discussed in the studies trying to track the phylogeny of the mechanism involved in behavior (Primates M. et al., 2020). This lack of information is an opportunity to develop research, particularly in territories and countries with native primate species like Mexico, Latin America, or Africa. To understand the areas of opportunity and future lines of research that could be developed, we need to know the state of the art, so our aim is to show the potential to develop research projects showing the different studies carried out in the three primate species that live in Mexico.

Native Potential: The Case of the Mexican Primates

Mexico is a northern country in the Neotropical region with three native species of primates: the mantled howler monkey (*Alouatta palliata*), the black howler monkey (*A. pigra*), and the spider monkey with two subspecies (*Ateles geoffroyi vellerosus* and *A. g. yucatanensis*; Calixto-Pérez et al., 2018; Vidal-García & Serio-Silva, 2011). The biological richness of primates in Mexico is very small compared with other countries in the neotropical region, like Brazil, which possesses 148 species and subspecies of primates (IUCN / SSC, 2024). However, this reduced number of species has allowed researchers to explore many characteristics and variables that affect the Mexican primate species in detail. The studies with Mexican primates have involved topics like ecology, genetics, endocrinology, behavior, nutrition, parasites, conservation, education, communitarian interaction (e.g., Amato & Righini, 2015; Arroyo-Rodríguez & Dias, 2010; Estrada, 1984; Pinto-Marroquin & Serio-Silva, 2020; Rovirosa-Hernández et al., 2021), and studies that can be tagged as cognitive.

Before continuing, it is essential to clarify the use of the term cognition in this review. Different analyses have called attention to the difficulty of defining what cognition means (Abramson, 2013; Facchin, 2023). Some definitions have proposed that cognition is how the mind works (Pinker, 2005), which is also problematic since there has yet to be a consensus on what the mind is (Bolton & Hill, 2004; Fuchs, 2002). Additionally, some authors have suggested using the word cognition as a construct or an umbrella concept that includes or covers different mechanisms or skills that animals use to process information and ultimately adapt to the environment (Andrews & Monsó, 2021). In the present review, we use the term cognition in the latter sense while using it as minimally as possible. Now that we have clarified our use of the term cognition, the following describes studies conducted with Mexican primate species.

Perception and Sensory Capabilities

One crucial aspect necessary for the adaptation and problem-solving of all animal species is the ability to perceive their world (Dominoni et al., 2020; Kelley & Kelley, 2014). Perception provides animals with information from the environment through their senses (Greggor et al., 2014; Schneeberger & Taborsky, 2020; Thiagavel et al., 2020). An important factor that drives the evolution of sensory capabilities is food, and how animals perceive different stimuli in the context of foraging behavior has been extensively studied using experiments or observations in the field. As with many animals, primates depend entirely on perceptual and sensory characteristics not only to identify the food items that compose their diets but also to learn (Addessi et al., 2004; Dominy et al., 2001), to interact with their groups (Zentall, 2012), and to determine what kind of information they must remember (Sayers & Menzel, 2012).

Vision and Color Perception

The visual system of primates is the most studied compared to other senses since they have trichromatic color vision, in contrast to the dichromacy present in most diurnal mammals. For color vision, the primates' eyes keep special cells associated with specific proteins called opsins, which are sensitive to different light wavelengths (Carvalho et al., 2017; Jacobs, 1996; Kawamura, 2016). These opsins are the short-wavelength opsin (SWS) or "blue," with a peak sensitivity between 420-430 nm; the medium-wavelength opsin (MWS) or "green," which absorbs light at approximately 530 nm, and the long-wavelength opsin (LWS) or "red" with peak sensitivity around 560 nm (Kawamura et al., 2012; Regan et al., 2001). Old World primates, humans, and the genus Alouatta from the Neotropics are the only primates with routine trichromacy (Silveira et al., 2014; Surridge et al., 2003).

The genes that code to produce opsins are located on the X chromosome (Carvalho et al., 2017; Jacobs, 1996; Kawamura, 2016). However, it was discovered that two different genetic mechanisms for distinguishing different wavelengths exist among primate species. The first is the allelic variations of the X-linked opsin gene occurring in most New World primates and lemurs (Jacobs, 2007; Jacobs et al., 2017; Kawamura et al., 2012) or by duplication of opsin genes (M/LWS) on the X chromosome (Silveira et al., 2014; Surridge et al., 2003).

New World primates and lemurs show differential capabilities to perceive colors in their environment; most species have the short-wavelength opsin (S) or "blue" and only one longer wavelength opsin (M/LWS) located on the X chromosome. This genotype produces a polymorphic visual system where all the males and homozygous females show a lack of sensitivity to colors in the middle (green) to long (red) wavelengths (dichromats) and do not possess vision based on three colors, like ours (Carvalho et al., 2017; Gerl & Morris, 2008; Jacobs, 1996; Kawamura, 2016). In these species, the heterozygous females can see in three colors (trichromats; Jacobs, 1996; Jacobs et al., 2017; Jacobs & Deegan, 2001; Kawamura, 2016; Melin et al., 2012).

Both species of Mexican howler monkeys are trichromats, and the spider monkeys possess a polymorphic color vision. Male and female mantled, and black howler monkeys possess color vision similar to humans (Matsushita et al., 2014; Melin et al., 2017). This is possible since both have the two longer-wavelength pigment genes (green and red) by duplication of the (M/LWS) opsin gene on the X chromosome, in conjunction with a gene encoding a short-wavelength pigment (blue) on a non-sex chromosome (Kawamura, 2016). Hence, males (with only one X chromosome) and females (with two X chromosomes) have the three opsin genes. In the case of spider monkeys, both subspecies are polymorphic since the same duplication event in the howlers did not occur (Jacobs, 2007; Kawamura, 2016).

The ability to perceive red is a recent event in the evolutionary history of these neotropical primates. The hypothesis that trichromacy and red color perception is an adaptation for finding reddish ripe fruits and young leaves against background leaves has received the most attention in the studies of color vision (Gerl & Morris, 2008; Melin et al., 2013). Young leaves possess a higher content of red-green pigments (Dominy et al., 2001; Dominy et al., 2002), and some studies in populations of Mexican howler monkeys have reported that these are an essential component of their diet (Reynoso-Cruz et al., 2016).

The trichromacy of howlers allows them to efficiently detect and select reddish young leaves against a background of mature leaves (Lucas et al., 1998; Melin et al., 2017). Recently, the role of trichromacy in fruit selection based on color has been evaluated in a population of mantled howler monkeys. The visual model indicated that howler monkeys are more efficient in detecting and discriminating ripe conspicuous fruits (i.e., fruits that change color during ripeness) than ripe cryptic fruits (i.e., fruits that remain green during ripening). However, howlers consumed more cryptic fruits than conspicuous ones, suggesting that trichromacy, in addition to non-visual senses, is efficient in detecting this kind of fruit (Sánchez-Solano et al., 2020).

In the case of spider monkeys, they are mainly frugivorous, and the groups are composed of individual dichromats and trichromats (Melin et al., 2012). Some authors have suggested that the trichromats should have an advantage in detecting red, orange, or yellow fruits compared to the dichromats (Regan et al., 2001; Riba-Hernández et al., 2004). The heterozygous females can easily detect ripe fruit by color, but the males and homozygous females cannot (Melin et al., 2013; Riba-Hernández et al., 2004). A study in Costa Rica, but with the same species of spider monkey inhabiting Mexico (*A. geoffroyi*), reported an advantage in the detection of fruits by the females. However, foraging is a collective behavior more than an individual activity, and other individuals could use the information detected by the trichromatic females (Riba-Hernández et al., 2004; Vellieux et al., 2016).

Primates can use other senses besides vision, like olfaction, taste, and touch, to evaluate the ripeness state or the palatability of different food items (Dominy, 2004). Fruits change their profile of nutrients, secondary compounds (Prasanna et al., 2007; Riba-Hernández et al., 2003) and volatiles (Hiramatsu et al., 2009; Nevo & Heymann, 2015; Nevo et al., 2015; Nevo et al., 2016; Rodríguez et al., 2013), and these changes give the necessary information to the primates to choose one item over the other. These senses are not only crucial for feeding; for example, the detection of aromatics also plays a role in defensive behaviors against predators (Kats & Dill, 1998), while touch could play a role in social interactions (Dunbar, 2010).

Olfaction

The role of olfaction has been widely studied in different non-human primate species. Primates generally have been classified as microsmatic (poor olfactory abilities), based on their epithelium and olfactory bulb size and also on the number of genes that code for their olfactory receptors (Rouquier et al., 2000; Smith & Bhatnagar, 2004). However, experimental evidence has shown that many primate species possess well-developed olfactory skills, reaching similar detection levels as animals considered macrosmatic (well-developed olfactory skills) like rodents (Sarrafchi et al., 2013).

Mexican spider monkeys in captivity have been tested on their olfactory abilities using a psychophysics task (Eliasson et al., 2015; Laska et al., 2003; Nevo et al., 2015). For this task, the spider monkeys were trained to sniff aromatic substances from absorbent papers, and the substances were compared against a non-odorant solvent. The monkeys needed to detect and choose the paper with the aromatic substance by opening a box that contained a food reward (Laska et al., 2003). This procedure determines which substances they can perceive and the thresholds for each substance.

Diverse studies with spider monkeys demonstrate that they can detect olfactory stimuli at lower levels, even lower than rats (Laska et al., 2004). These primates could use their olfactory skills to detect the presence of a predator by the odor (Sarrafchi et al., 2013) and to recognize artificial olfactory profiles of ripening fruits during foraging (Nevo et al., 2015). The experimental studies on olfaction have been complemented with field studies. A study published in 2015 indicates that spider monkeys tend to sniff unripe fruit with a higher frequency than ripe ones (Pablo-Rodríguez et al., 2015).

There is no experimental data for Mexican howler monkeys' detection thresholds or capabilities of detecting olfactory stimuli. However, a behavioral study in wild mantled howler monkeys has reported a higher frequency of sniffing of unripe fruits, similar to spider monkeys, mainly fruits that change color during ripening (Sánchez-Solano et al., 2022). Thus, olfaction is useful during fruit foraging for both species.

Taste

Studies of taste have been carried out using a task of preference for substances consumed. The task is based on a forced choice in which the monkeys had to drink two liquids, and after that, they could drink freely between them for a period. One of the liquids was water with a small concentration of sucrose (simple solution), and the other was a combination of water, sucrose, and a chemical compound (compound solution; Laska et al., 2000). Based on the amount of the solution consumed during the free drinking time, it is possible to establish a preference for the simple or the compound solution. By adding different chemicals at different concentrations to the compound liquid, we can change the preference and use that data to establish the detection threshold for different chemicals (Larsson et al., 2014; Laska et al., 2000).

Studies on taste capabilities have been focused on the presence of micro and macronutrients in the food (Demi et al., 2021; Huang et al., 2021), secondary compounds (Frank et al., 2022; Remis & Kerr, 2002), the physiological characteristics of the salivary (Espinosa-Gómez et al., 2020; Thamadilok et al., 2020), and digestive response (Janiak, 2016; Ueno, 2001). All these studies have provided a clear picture of the bidirectional relationship between taste perception and food's ecological and organoleptic characteristics (Hladik, 1993; Kariñho-Betancourt, 2018).

The research on Mexican primates has tested the ability to taste compounds associated with sweet, bitter, and sour flavors (Larsson et al., 2014; Laska et al., 2009; Nicklasson et al., 2017; Pereira, et al., 2021a, b; Pereira, et al., 2021). These taste perception studies have identified particular facial expressions associated with each taste (Pereira, et al., 2021b). Regarding studies on salivary response, research conducted in mantled howler monkeys (Espinosa-Gómez et al., 2015), black howler monkeys (Espinosa-Gómez et al., 2018), and spider monkeys (Ramírez-Torres et al., 2022) have given an account of protein mechanisms that could deal with secondary compounds.

In addition to these studies, research on spider monkeys has shown that they can detect the presence of ethanol in fruits (Dausch-Ibañez et al., 2019). Therefore, they could use this compound as an indicator of fruit ripeness and sugar content (Dudley, 2004; Dudley & Maro, 2021). The ability to detect ethanol has not been identified in howler monkeys. However, it is possible that howler monkeys can detect it since ethanol consumption is harmful, causing various stomach problems because howler monkeys digest food through fermentation (Milton & McBee, 1983). Most of the studies on taste have been carried out with captive individuals or free-range individuals who have been sedated to take saliva samples; only a few studies with Mexican howlers and spider monkeys have been carried out in the field. Both studies indicate that these species bite or lick fruits, suggesting that these behaviors are essential in determining the ripeness of the fruit (Pablo-Rodríguez et al., 2015; Sánchez-Solano et al., 2022).

Touch

Some characteristics associated with the sense of touch are the dexterity of limb movements, how objects in the environment are inspected and used, and the role of touch in social interaction (Jablonski, 2021; Malcolm, 2021). The anatomy of Mexican primates has evolved to allow them to live in the canopy and search for resources at high altitudes, making them highly efficient at moving through the tropical forest canopy (Fleagle, 2013; Hunt, 2016). These primates have a prehensile tail that functions as a limb that is used for locomotion, support, or feeding (Bezanson, 2017; Lemelin, 1995). In the case of spider monkeys, they have lost their thumb to allow more efficient movement through the branches (Jones, 2008; Youlatos, 2008).

Spider monkeys have been studied to establish whether they prefer using either of their hands and whether the tail shows laterality. In the case of the manual preference, this has been tested in tasks that involve retrieving a reward within tubes of different sizes. The tasks ranged between easy, intermediate, and complex, assuming that tasks with greater difficulty would force the spider monkeys to use their preferred and most dexterous hand (Motes-Rodrigo et al., 2018). The results indicate that spider monkeys have a preferred hand (for some, it was the right, and in others, the left), and this preference was maintained by most individuals regardless of the difficulty of the task (Motes-Rodrigo et al., 2018; Nelson et al., 2015).

The prehensile tail evaluations also used tasks where a reward that was in different positions had to be reached, classified into easy, intermediate, and complex difficulty. In all tasks, the individuals skewed the movement of their tail to the right or left to reach the reward, which was taken as an indicator of lateralization of the movement (Laska, 1998). Although many individuals prefer one hand, the direction in which they move their tail is not always the same; some individuals have contralateral preferences for the movement of their tail, which implies a preference for reaching objects by moving their tails from the right side, while they prefer to reach for objects using the left hand (Laska, 1998).

The laterality of mantled howler monkeys has also been evaluated from observations in natural environments, evaluating which hand they use to reach objects in their environment. Howler monkeys did not preferentially position their tails on one side during resting, nor did they show preferential use of either of their hands when they reached for objects, which is a clear difference from spider monkeys (Laska & Tutsch, 2000).

As part of motor dexterity, animals can use objects apart from their body to reach unreachable parts with their limbs alone or to solve problems associated with food, deterrents, or cleaning/grooming activities. We looked for reports of this kind of behavior in the tree species of Mexican primates. There is only one report on spider monkeys by Stacy Lindshield and Michelle Rodriguez (2009). They reported three events in which different spider monkeys used tree branches to scratch some parts of the body that they could not scratch with their limbs. This example of using branches to reach unreachable places indicates that spider monkeys could understand the relationship of objects apart from their bodies and take the necessary actions to achieve objectives, like scratching unreachable body parts.

Related to the skills of recognizing the relation between objects, one of the experiments carried out by Amici et al. (2010) is an excellent example of this ability in spider monkeys. The task was to select between two arrangements of stimuli to reach a food reward. The arrangement used two pieces of fabric, one complete and one cut in the middle, and the rewards were placed at the ends of both pieces. Pulling the complete piece of fabric was the only way to access the reward. The spider monkeys could see the differences in the arrangements and systematically selected the complete piece of fabric that gave access to the reward, indicating that they understood the relationship of objects in space and how to use them to achieve an objective.

The use of touch has been evaluated in both wild populations of spider monkeys and mantled howler monkeys in the context of food evaluation. The data indicates a higher proportion of the use of touch for fruit inspection to determine the ripeness through hardness (Pablo-Rodríguez et al., 2015; Sánchez-Solano et al., 2022). In the case of mantled howler monkeys, touch inspections were significantly higher in fruits that did not change their color during ripening, indicating that touching is an essential strategy for fruit selection (Sánchez-Solano et al., 2022).

Memory

Memory plays a role in many daily activities of animals, like foraging (Ranc et al., 2021; Suarez et al., 2019) and social interactions (Meyer & Lieberman, 2012; Tzakis & Holahan, 2019). The studies of memory from an experimental perspective have been carried out only in Mexican spider monkeys and they have mainly tested the effect of the passage of time.

One of the topics investigated in a captive population of spider monkeys (*A. g. vellerosus*) was to determine how they use their memory to make foraging decisions. Reynoso-Cruz and collaborators (2020) based their project on the temporal waiting rule, using a task where the spider monkeys had to look for food rewards in containers that emulated foraging patches (Devenport & Devenport, 1993, 1994). These data indicate that the spider monkeys could remember the spatial position of the different patches and discriminate between them based on the amount of food that was ingested in that patch, even for periods of 24 hours (Reynoso-Cruz et al., 2020).

Another study from our research group was interested in testing the recognition memory of spider monkeys. The task consisted of a serial presentation of pictures, and after a delay, the spider monkeys had to solve a matching to sample task. These results indicate that the recognition of spider monkeys falls as the delay increases. Since the presentation of the pictures was serial, primacy and recency were present (Reynoso-Cruz et al., 2021b). However, these effects have intraindividual variation modulated by the increase of the delay. Some individuals transition from the effects of primacy and recency, others transition from recency to primacy, while others never change their serial position effects as reported in other primate species (Wright, 1999; Wright et al., 1985).

The experimental studies were complemented by fMRI studies with spider monkeys in a resting state. The study indicates the presence of functional networks in the brains, previously reported in humans, that are involved in working memory and executive functions. The working memory and executive network included prefrontal areas and different areas related to olfaction (like the olfactory bulb) and areas of emotional processing (like the amygdala; Platas-Neri et al., 2019).

Finally, a test of spatial short-term memory replicates the classical result of the forgetting curve; as time passes, the information is forgotten, and the precision decreases (Murre & Dros, 2015). In 2010, a first test indicated that spider monkeys forget where a food reward was placed when they have to wait, and as time increases, the forgetting is higher (Amici et al., 2010). Our group was interested in expanding these results and testing if the forgetting interacts with the number of places where the reward could be placed. Our results indicate that having more places to hide the reward does not increase forgetting. Our results also indicate that the errors are distributed near the position of the reward when the time to wait is short, but the errors are distributed to farther positions when the time is longer (Reynoso-Cruz et al., 2021a).

Spatial Navigation

Research projects in free-living animals have focused on studying feeding routes and analyzing how monkeys move among the trees. Valero and Byrne (2007) studied the routes a group of spider monkeys used when moving to feeding sites, using GPS to track the routes. The results indicated that the individuals' movements were mainly along straight trajectories, which is considered an indicator of planning. In contrast, a route with twists and turns indicates random movement (Tommasi & Laeng, 2012). In addition to straight-line movements, the distances at which they move are beyond the observable distance, suggesting that it is necessary to plan and remember where they want to go (Valero & Byrne, 2007).

Similar studies have been done on howler monkeys, although these studies have yet to be conducted in Mexican populations. Studies on space use have highlighted that the distances traveled by mantled howler monkeys depend on the size of the group, indicating that the greater the number of individuals in a group, the greater the displacement of individuals (Fortes et al., 2015). The travels of the mantled howlers to a place indicate efficient movements with low energy expenses and moving to trees with high-quality food items. These results suggest that the howlers possessed information about food availability in an area (Hopkins, 2016).

A study of navigation carried out in Mexico indicates that mantled howler females tend to lead the movements of the groups toward feeding trees or take a position in the front of the group. This study also reported that gestating females commonly led the movements, rather than lactating and cycling females (Ceccarelli et al., 2020). Another study in the same population of mantled howlers also indicated that the movements, routes, and places where the monkeys travel were determined by the loud calls made by the group that lived nearby (Ceccarelli et al., 2019), suggesting the relevance of ecological and social factors for howler monkeys navigation.

A study under field conditions carried out with Mexican black howler monkeys has signaled an efficient use of routes by this species. The researchers compared the routes used by two groups of black howlers against simulated random walks in their home range. The black howlers used efficient routes to visit feeding trees and differed from random walks across their home range (de Guinea et al., 2021). The study also indicates that black howlers use cognitive graph maps more than topological maps to move across their home range (de Guinea et al., 2021). Topological maps consist of a representation of the places, called nodes, that are connected by a path. In contrast, cognitive graph maps incorporate topological information plus metric information, like distances, angles, etc. (see Chrastil & Warren, 2014 for an explanation of graph maps compared with cognitive maps).

Social behavior

The three species of Mexican primates live in groups, and intra- and inter-group interactions have been reported, especially in the areas of sympatry (Cortés-Ortiz et al., 2019). However, other interactions exist and are associated with recognizing predators (Asensio & Gómez-Marín, 2002) or competitors (Dzul-Cauich et al., 2018). Under these circumstances, primate species have a series of skills that allow them to confront social situations (Dunbar, 2009; Seyfarth & Cheney, 2015).

One of the skills used in social situations is gaze following. With this ability, an individual can direct their gaze toward a spatial position that another individual observes (Zuberbühler, 2008). This ability establishes a connection and identity between two individuals, demonstrating that the organisms must recognize that other individuals may be observing things that they cannot see so they can orient themselves in the direction that marks the gaze of the other (Shepherd, 2010). A group of researchers tested whether spider monkeys were able to look in the same direction where a human experimenter was looking (i.e., the ceiling under a barrier; Amici et al., 2009b). The results indicated that spider monkeys could look more frequently at the positions observed by the human experimenter than at control positions, which suggests a spontaneous following of gaze (Amici et al., 2009b).

Studies also carried out by Amici et al. (2009a) have indicated that spider monkeys are capable of tactical deception behavior. Whiten and Byrne (1988) propose that this behavior occurs when an individual can use an honest act from his usual repertoire in a different context to mislead familiar individuals. A task that consisted of two conditions was used to study this behavior in spider monkeys. In the first condition, a low-ranking spider monkey could see where a food reward was placed or learn the mechanism of recovering the food reward, after which the monkey was tested on the ability to recover the reward. In the second condition, the low-ranking monkey could see and learn the mechanism, but after this experience, a high-ranking monkey was placed in the same area. In the first condition, the low-ranking spider monkeys recovered the food. However, when the high-ranking monkey was placed in the same space, the low-ranking spider monkeys reduced the number of times they looked at the apparatus with the food or stayed far away from the container. The times the low-ranking spider monkeys interacted with the apparatus were higher when the high-ranking spider monkeys looked in other directions (Amici et al., 2009b).

One mechanism proposed to explain why spider monkeys could perform tactical deception behaviors is inhibitory control. This mechanism allows an organism to stop one behavior to display another (Tiego et al., 2018). Another example of inhibitory control could be observed when animals wait for longer delays, receiving a greater reward (Beran, 2015). A study of this mechanism in spider monkeys used two tasks, one where the individuals had to stop a behavior and the other where they had to wait for a bigger reward, indicates that this species is capable of great inhibitory control, with performances at similar levels to chimpanzees (Amici et al., 2008). The research compared the performance of different primate species, including spider monkeys, and found that fission-fusion dynamics were a good predictor of inhibitory control, which implies that this mechanism is closely related to the social dynamics of primates (Amici et al., 2008).

The fission-fusion dynamics of spider monkeys have been studied under the perspective of collective computations. This perspective implies that each individual in a group works as a unit that processes information, and their analyses could affect the dynamic of a collective (Flack, 2012). In the case of social behavior, collective computations could affect the social dynamics of a group and the integration of individuals into a group, modifying the dynamics of fission-fusion (Flack, 2012; Ramos-Fernandez et al., 2020).

A research group led by Gabriel Ramos Fernandez used data on the social dynamics of wild spider monkeys, tracking the individuals that compose different subgroups and determining whether the size and distribution of the individuals were related to the abundance of fruits as was previously suggested (Pinacho-Guendulain & Ramos-Fernández, 2017). Their analysis indicated that the composition and size of the groups are not adequately explained by the abundance of fruit in the habitat. However, the composition of the groups could be related to the presence or absence of individuals in the groups, particularly those individuals that possess precise information on the environment and the ecological dynamics tracked over the years (Briseño-Jaramillo et al., 2022; Ramos-Fernandez et al., 2020).

Another aspect of social behavior investigated is the ability to behave prosocially towards others. Prosocial behavior could be defined as any behavior emitted by an individual that benefits or alleviates another from pain (Reynoso-Cruz & Bernal-Gamboa, 2019). A study of this ability was conducted with spider monkeys using two tasks, one which required pulling platforms and the other exchanging tokens. The platform task consisted of pulling a platform that gives food to the individual or pulling another that gives food to the individual and a partner. For the token task, one token gives food only to the individual, and another gives food to the individual and a partner. The results from both tasks indicate that spider monkeys selected the options where only the individuals received a food reward, not their partner, at a more significant percentage (Amici et al., 2014).

The cultural transmission of information is another phenomenon that has been investigated, and it is one of the most complex aspects of a social group (Johnson, 2010; Schuppli & van Schaik, 2019; Whiten & van Schaik, 2007). As with humans, culture in other animal species relies on the non-genetic and non-epigenetic inheritance capacity of the organisms (Laland & Hoppitt, 2003) and could be defined as skills and knowledge transmitted by social learning (Gariépy et al., 2014; van Schaik, 2010).

Within Mexican primates, spider monkeys (Santorelli et al., 2011) and black howler monkeys (Briseño-Jaramillo et al., 2015; Brockett et al., 2005) have demonstrated behaviors that could be described as culture. In the case of spider monkeys, 22 behaviors were presented in multiple groups, with variations of these behaviors in each group (Santorelli et al., 2011). Of these cultural behaviors, nine of those were related to social interaction, and contrast with other primate species like chimpanzees (*Pan troglodytes*) and orangutans (*Pongo spp.*), where the behaviors that could be described as a culture are related mainly to foraging (Santorelli et al., 2011).

In relation to black howler monkeys, a few behaviors that could be described as culture have been reported. One of these behaviors consists of placing the hand on the face during the production of loud calls. This behavior is only present in some groups, and each group places the hand in a particular position, which generates variations in the calls (Briseño-Jaramillo et al., 2015). The use of the hand on the face during vocalization is transmitted to nearby groups since the greater the distance between groups, the greater the variations of this behavior (Briseño-Jaramillo et al., 2015). The second behavior was reported in the neighboring country of Belize and is described as a solicitation of social interaction. The behavior is described as one adult holding the hand of another adult. This interaction is usually the start of more intricate social interactions, like grooming (Brockett et al., 2005). This behavior could be considered culture since it was only described in one group and was only displayed by adults. This highlights the relevance of specific behavior in a group and the need for social learning to display this behavior (Brockett et al., 2005).

Self-recognition

The mirror test is one of the most common tests to identify self-recognition (Anderson & Gallup, 2015; Gallup et al., 2002). In this test, an individual's behavior is evaluated after having a mirror placed in front of him or her (Anderson & Gallup, 2015; Gallup et al., 2002). The analysis of the behavior exhibited can be categorized as different levels of recognition: 0 means no recognition (the individual expresses aggressive or social behavior), 1a is exploratory (the individual explores the mirror without social or aggressive behavior), 1b is connection (the individual displays repetitive behavior towards the mirror to test the relationship) and 2 is auto-exploration (the individual displays behaviors to explore his or her body and parts of their body that are inaccessible through direct vision; Murray et al., 2020).

A group of Mexican spider monkeys exposed to a mirror showed no social or aggressive behavior toward the mirror. However, they only performed behaviors of level 1a, exploring the mirror, particularly looking at the back of it (Murray et al., 2020). Their behavior did not show a significant display of repetitive behavior or exploration of their body parts, behaviors expected for levels 1b and 2, respectively, suggesting that spider monkeys do not show clear self-recognition (Murray et al., 2020). Although spider monkeys did not show self-recognition in the mirror test, this result does not indicate the lack or the absence of these skills in spider monkeys. Different studies have indicated that the mirror test has methodological problems (Wang, 2022), and animals can recognize themselves using other perceptual skills (Szabo & Ringler, 2023), or it could simply be a lack of interest in the task, which is sometimes interpreted as an absence of self-recognition (Brandl, 2018).

Discussion

The studies discussed here represent the topics studied in the primate species living in Mexico. However, we have also included studies in other countries from the same neotropical region since they were carried out with the same species inhabiting Mexico. The studies listed in this review also tried to show some of the topics that other countries with low—and middle-income, like Mexico, could explore through cognitive research using their native primate species.

Other primatologists in Latin America have been developing research about the behavior and their mechanism in their native primate species like the research project of the use of stones to open nuts with capuchin monkeys carried out in Brazil (Falótico et al., 2018) and Panama (Méndez Carvajal & Valdés Díaz, 2017), studies about memory and spatial navigation in sympatric species of spider monkeys and woolly monkeys in Ecuador (Di Fiore & Suarez, 2007), or with capuchin monkeys in Argentina (Tujague et al., 2016). More research is still needed in the neotropical region to increase the knowledge of neotropical primates' abilities and encourage scientific cooperation initiatives like the Euromammals Initiative (Urbano & Cagnacci, 2021).

Cooperation is essential for a better understanding of behavior and its mechanisms since comparisons of multiple species are needed. The comparison of species allows us to propose hypotheses about the origin and diversification of the behavior and mechanisms, letting us identify particular ecological constraints that shape species-specific adaptations (MacLean et al., 2012; Shettleworth, 1993). The Many Primates Project is another excellent example of scientific cooperation that is interested in testing multiple species of primates across different tasks that emphasize comparability between species (ManyPrimates et al., 2020). However, despite these efforts, only a few neotropical species are involved in this initiative compared to the number of Old-World primate species involved. It is important to note that thus far, no institutions from the neotropical region are involved in the Many Primates initiative, so it is still an open area for researchers in the region to join and be active collaborators in the different research projects.

Researchers in low and middle-income countries could also collaborate with zoos, private collections, and other places that keep animals under human care to establish research initiatives with those institutions. Primates and other animals in those institutions undergo training programs, frequently for medical purposes (Fernandez & Martin, 2021), so we can approach these institutions to establish research programs. Working with animals under human care benefits both scientific research and animals since the research tasks serve as enrichment, where the individuals must use abilities commonly underutilized since many needs are supplemented by the keepers (Clark, 2017; Melfi, 2013).

Primates were the example used in this paper, but the animal groups or species to be tested could be selected based on the natural biodiversity of each country. For example, Mexico is a country with a great diversity of reptiles and amphibians (Flores-Villela & García-Vázquez, 2014; Johnson et al., 2017), a group of animals that is becoming more important in comparative psychology research (de Meester & Baeckens, 2021; Matsubara et al., 2017; Roth et al., 2019). Working with different animal taxa increases our knowledge of animal behavior and its mechanisms (Beran et al., 2014; Schubiger et al., 2020) and could become an alternative for low and middle-income countries to increase their research programs.

Throughout our review, we have used the concept of cognition. As mentioned, this term can be problematic since there is a lack of agreement among the scientific community, which could cause misunderstandings and misinterpretations (Abramson, 2013; Facchin, 2023). The lack of definition does not indicate that we cannot use these concepts since, in different disciplines, we have examples of concepts with a lack of agreement, like species (Aldhebiani, 2018; Manikas et al., 2023), genes (Baverstock, 2021; El-Hani & Meyer, 2013), or even behavior (Calhoun & El Hady, 2023; Levitis et al., 2009), but scientists still use them, sometimes without defining the meaning used by the authors. Defining the problematic concepts in advance creates an agreement between the authors and the readers. However, the problem of multiple definitions still needs to be solved, and we should also look for agreement within the scientific community (see Calhoun & El Hady, 2023 and Levitis et al., 2009 for attempts at an extensive definition of behavior).

Increasing the possibility of doing research through native species is essential to maintain scientific development in countries where science is a complicated enterprise due to the lack of funding or complicated social conditions. Funding is vital to acquire essential materials, pay salaries, and other expenses associated with research. Working with native species could reduce some of those costs while also helping to increase the visibility and appreciation of the local biodiversity and improve conservation efforts through information dedicated to environmental education (Dolby, 2019). Despite all the problems that our region is facing, we must continue to work to understand the world around us and the organisms with whom we share this space.

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