

Cognitive adaptations in two sympatric mouse lemur species occupying different ecological niches

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Summary

Cognition describes an individual's abilities to perceive, process, and act on information of the abiotic and biotic environment. The investigation of cognitive variation between individuals and species has been of interest for many decades and several hypotheses have been proposed to explain the evolution of cognition. Sizes of certain brain areas covary with the cognitive abilities they process, and socio-ecological factors have been related to various brain size measures. However, covariations of phenotypic cognitive performances with socio-ecological factors are essential to understand the adaptive value of cognitive abilities. While links with social factors have been the focus of comparative studies, which and how cognitive abilities and ecological factors link with each other, has been less systematically investigated. Precisely, it is assumed, that ecological generalists consistently outperform ecological specialists in cognitive challenges, but a respective link lacks systematic empirical evidence.

In my first theoretic approach, I reviewed the literature for comparative studies that experimentally assessed cognitive performances among at least two species of the same phylogenetic order. I found that cognitive variation can be related to species-specific dietary preferences, related foraging behaviors, migratory behavior, or habitat complexity. However, other ecological factors, such as the synecology with predators or parasites, or the degree of ecological specialization, have largely been disregarded to be linked with cognitive performances. Only a subset of the reviewed studies specifically mentioned the degree of ecological specialization of the species in comparison. After complementing the respective information using additional literature, I applied a sign-test to estimate whether the degree of dietary or habitat specialization consistently covaries with cognitive performances. Across a total of 34 comparisons, $N = 26$ cognitive performances differed between the species in comparison. In 62% of these comparisons, the dietary generalist achieved higher performance scores than the relative dietary specialist. Habitat generalists achieved higher scores than relative habitat specialists in 72% of the comparisons. However, ecological generalism was not significantly associated with higher performances that go beyond innovative and flexible learning abilities. It

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remains therefore questionable, whether generalist species consistently outperform more specialist species across a broader range of cognitive abilities.

In my second empirical approach, I applied a conclusive cognitive test battery to two wild primate sister species. The gray and the Madame Berthe's mouse lemur possess a comparable social system, occur in sympatry at the chosen study site, but are differentially adapted to ecological factors. Essentially, the gray mouse lemur is a dietary and habitat generalist, while the Madame Berthe's mouse lemur is more specialized along these ecological niche axes. Occupying different ecological niches, while experiencing similar ecological challenges, assumes complex evolutionary processes for ecological adaptations that may be linked to cortical development, and may covary with cognition. Following the *Opportunistic Intelligence Hypothesis*, the generalist gray mouse lemur should consistently outperform the specialist Madame Berthe's mouse lemur across the various cognitive tests. Alternatively, species-specific performance levels could covary with specific ecological adaptations. For instance, gray mouse lemurs feed more on gum, a characteristic that has been associated with better self-control. Madame Berthe's mouse lemurs have larger home ranges and feed mostly on spatially clumped homopteran secretions, which may covary with spatial abilities. In summary, the two species differed in about two third of the assessed performance scores. Gray mouse lemurs were more innovative, which may provide them the advantage to adaptively respond to variable environmental conditions. However, they did not consistently outperform Madame Berthe's mouse lemurs, which were more active and learned visual and spatial reward contingencies faster.

Hence, the experimental results in mouse lemurs parallel the theoretic findings of the reviewed literature, in that generalist species do not outperform specialist species *per se*. Despite the apparent superposition of generalists with respect to innovative problem-solving, they do not consistently outperform specialists in other cognitive tasks. Rather, performances are better linked to other ecological factors, which might be more accurately disentangled in future studies using metric estimates instead of the categoric classification of ecological specialization. Nevertheless, as the first large scale comparative approach within this exciting research field, the results of my thesis offer substantial insight into the link between cognitive test performances and ecological factors.

Zusammenfassung

Mit kognitiven Fähigkeiten können Tiere Informationen aus der abiotischen und biotischen Umwelt wahrnehmen, verarbeiten und auf diese Informationen in einem angemessenen Umfang reagieren. Die Untersuchung kognitiver Variabilität zwischen Individuen und Arten ist von großem wissenschaftlichem Interesse, das zur Formulierung mehrerer Hypothesen zur Erklärung kognitiver Evolution geführt hat. Hirnareale können in Größe und Entwicklung mit kognitiven Fähigkeiten, die sie verarbeiten korrelieren, und sozio-ökologische Faktoren wurden mit verschiedenen Maßen zur kognitiven Entwicklung in Verbindung gebracht. Um den adaptiven Wert kognitiver Fähigkeiten zu verstehen, sind jedoch Kovariationen zwischen phänotypischen kognitiven Leistungen und sozio-ökologischen Faktoren ausschlaggebend. Während die Untersuchung entsprechender Zusammenhänge mit sozialen Faktoren im Fokus vergleichender Studien standen, wurde weniger systematisch untersucht, inwiefern kognitive Fähigkeiten mit welchen ökologischen Faktoren verknüpft sind. So wird zwar vermutet, dass ökologische Generalisten ökologische Spezialisten bei kognitiven Herausforderungen konsequent übertreffen, ein entsprechender Zusammenhang ist jedoch empirisch nicht systematisch belegt.

In dem ersten theoretischen Ansatz meiner Dissertationsarbeit, habe ich bisherige vergleichende Studien untersucht, in denen kognitive Leistungen zwischen mindestens zwei Arten der gleichen phylogenetischen Ordnung experimentell verglichen wurden. Diese Studien belegen, dass kognitive Variationen mit artspezifischen Nahrungspräferenzen, damit im Zusammenhang stehenden Futtersuchverhalten, sowie der Anpassung zur Migration oder der Komplexität des Lebensraums zusammenhängen können. Andere ökologische Faktoren, wie beispielsweise eine Synökologie mit Raubtieren oder Parasiten, oder der Grad der ökologischen Spezialisierung, wurden jedoch nur gelegentlich mit kognitiven Leistungen in Verbindung gebracht. Nur ein Teil der untersuchten Studien erwähnte ausdrücklich den Grad der ökologischen Spezialisierung der verglichenen Arten. Nachdem ich die entsprechenden Informationen durch das Heranziehen zusätzlicher Literatur ergänzt hatte, verwendete ich einen Vorzeichentest, um abzuschätzen, ob der Grad der Nahrungs- oder

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Habitatspezialisierung konsistent mit kognitiven Leistungen kovariiert. In insgesamt 26 von 34 Vergleichen unterschieden sich die untersuchten Arten in ihren kognitiven Leistungen. In 62% dieser Vergleiche erzielte der Nahrungsgeneralist höhere Leistungswerte als der relative Nahrungsspezialist. Habitatgeneralisten erzielten in 72% der Vergleiche höhere Werte als relative Habitatspezialisten. Allerdings war die Ausprägung zum ökologischen Generalisten nicht signifikant mit höheren Leistungswerten verbunden, vor allem, wenn andere kognitive Fähigkeiten als innovative und flexible Lernfähigkeiten untersucht wurden. Es bleibt daher fraglich, ob Generalisten über ein breiteres Spektrum kognitiver Fähigkeiten hinweg generell besser abschneiden als spezialisiertere Arten.

In dem zweiten empirischen Ansatz meiner Dissertationsarbeit, habe ich zwei wildlebende Primatenarten in einer umfangreichen kognitiven Testbatterie getestet. Die beiden Schwesterarten, der Graue und der Madame Berthe-Mausmaki besitzen ein vergleichbares Sozialsystem, sind im gewählten Studienort zeitgleich vorzufinden, sind dort aber unterschiedlich an ökologische Faktoren angepasst. Im Wesentlichen ist der Graue Mausmaki ein Nahrungs- und Habitatgeneralist, während der Madame Berthe-Mausmaki entlang dieser Achsen ihrer ökologischen Nische stärker spezialisiert ist. Das Besetzen unterschiedlicher ökologischer Nischen bei ähnlichen ökologischen Herausforderungen steht mit komplexen evolutionären Prozessen für ökologische Anpassungen in Zusammenhang, die mit der kortikalen Entwicklung verbunden sein und mit kognitiven Fähigkeiten kovariieren können. Entsprechend der Hypothese zur Opportunistischen Intelligenz, sollte der generalistische Graue Mausmaki den spezialisierten Madame Berthe-Mausmaki durchwegs in kognitiven Tests übertreffen. Alternativ dazu könnten artspezifische Leistungsniveaus mit artspezifischen ökologischen Anpassungen kovariieren. Zum Beispiel fressen Graue Mausmakis mehr Baumharz, eine Eigenschaft, die mit besserer Selbstkontrolle in Verbindung gebracht wurde. Madame Berthe-Mausmakis bewegen sich über größere Aktionsräume und ernähren sich hauptsächlich von ungleichmäßig verteilten Insektensekreten, was mit räumlichen Fähigkeiten kovariieren könnte. Letztendlich haben sich die beiden Arten in etwa zwei Dritteln der untersuchten kognitiven Leistungswerte unterschieden. Graue Mausmakis waren dabei innovativer, was ihnen den Vorteil verschaffen könnte, adaptiv

auf variable Umweltbedingungen zu reagieren. Jedoch übertrafen sie die Madame Berthe-Mausmakis nicht durchgehend. Diese waren beispielsweise aktiver und konnten visuelle und räumliche Zusammenhänge mit einer Futterbelohnung schneller erlernen.

Meine experimentellen Ergebnisse der Mausmakis decken sich also mit den theoretischen Erkenntnissen der untersuchten Literatur, indem Generalisten Spezialisten nicht *per se* in kognitiven Experimenten übertreffen. Trotz der scheinbaren Überlegenheit von Generalisten in Bezug auf innovatives Problemlösen, sind sie Spezialisten in anderen kognitiven Aufgaben nicht durchweg überlegen. Vielmehr sind kognitive Leistungen besser mit anderen ökologischen Faktoren verknüpft, die in zukünftigen Studien detaillierter entschlüsselt werden könnten, wenn anstelle der kategorischen Klassifizierung der ökologischen Nische eher metrische Variablen gemessen würden. Nichtsdestotrotz geben die Ergebnisse meiner Arbeit als erster groß angelegter vergleichender Ansatz in diesem spannenden Forschungsfeld einen wesentlichen Einblick in den Zusammenhang zwischen testbaren kognitiven Fähigkeiten und ökologischen Faktoren.

Chapter I: General introduction

Cognition – *“The word seems straightforward, yet it is often a cause of debate in the psychological and neuroscience fields, particularly about whether a behavior of an animal that happens not to be human is truly “cognitive”, in a similar sense to human cognition.”*
– Geoffrey North (in Bayne et al. 2019, p R608)

In non-human animals, we consider cognition as all cognitive traits, that provide an individual the abilities to “acquire, process, store and act on information from the environment” (Shettleworth 2009). Cognitive traits vary between individuals, as well as between species. Due to the neurological nature of cognition, it is assumed that cognitive abilities covary with neuronal structures, such as the development of certain brain areas. Consequently, the *Social Intelligence Hypothesis* (Humphrey 1976; Whiten and Byrne 1988) and the *Ecological Intelligence Hypothesis* (Parker and Gibson 1977; Milton 1988) suggest that brain size varies with social or ecological factors. While these hypotheses have been posited to be exclusive, more recent studies support a rather complementary influence of social and ecological factors on cognitive evolution (Emery and Clayton 2004; Lefebvre and Sol 2008; Reader et al. 2011; MacLean et al. 2012; Rosati 2017a). A respective link between social complexity and cognitive abilities finds broad support (Bond et al. 2003; Bond et al. 2007; MacLean et al. 2008; Amici et al. 2008; Byrne and Bates 2010; MacLean et al. 2013; Perry et al. 2017; Ashton et al. 2018b; Amici et al. 2018). However, which specific ecological factors covary with which cognitive abilities has rarely been empirically investigated across the animal kingdom.

To better understand the ecological nature of cognitive variation and, therefore, the adaptive value of certain cognitive abilities, potential links between ecological factors and cognitive abilities need to be systematically investigated. By comparing individuals of different species that exhibit different ecological adaptations while possessing comparable social organizations, the coevolution of cognitive traits and adaptations to ecological conditions may be better understood. With my thesis, I contribute to this endeavor by investigating cognitive variation among two closely related and sympatric primate species that are differently adapted to ecological conditions but are socially similarly organized.

Chapter I: General introduction

In the following, I explain the principles of cognitive variation in response to socio-ecological factors. Thereby, I wrap-up the most prominent hypotheses that have been proposed to understand the evolution of brain size and correlating cognitive abilities. Further, I provide a brief overview of common links, as well as mixed patterns of previous investigations on cognitive variation in relation to socio-ecological factors. Subsequently, I describe the concept of niche theory with the classification of ecological specialization and respective adaptive responses to habitat and dietary breadth. Then, I introduce two mouse lemur species which I tested for this thesis by also giving an overview of prior investigations in this genus. Finally, I outline the specific aims of my thesis and provide an overview of the content of the next chapters.

1 Towards understanding variation in brain size and cognitive abilities

As Thorndike emphasized in the 18th century, it is “[associations], and not instinct, [that] make the animal use the best feeding grounds, sleep in the same lair, avoid new dangers and profit by new changes in nature” (Thorndike 1898). An essential prerequisite for associative learning abilities, as for cognitive traits in general, are neuronal structures. However, the more complex the neuronal structures and the larger the metabolically expensive brain, the more energy must be consumed (Rumbaugh and Washburn 2003; Roth and Dicke 2005). Therefore, larger brains should only evolve when their benefits exceed their high metabolic costs (Laughlin et al. 1998; Lennie 2003). Essentially, such benefits can be related to an animal’s socio-ecological conditions. Hence, different hypotheses have been proposed to explain variation in brain size and subsequently variation in cognitive abilities.

1.1 Principles of cognitive variation in response to socio-ecological factors

According to the *Social Intelligence Hypothesis* (SIH), it is suggested, that brain size covaries with social factors (Humphrey 1976; Whiten and Byrne 1988; Dunbar 1998; Dunbar et al.

2007). Specifically, social complexity seems to be associated with brain size (Jolly 1966; Barton 1996; Kudo and Dunbar 2001; Byrne and Bates 2010). More socially complex species are those that live in larger groups instead of smaller pair-bonds or that spend most of their active time solitary. Subsequently, they experience more complex social challenges that require specific social skills, like managing group dynamics, or effectively communicating and coordinating with group members (Dunbar et al. 2007; Kappeler 2019; Peckre et al. 2019). In support for the SIH, primates, bats, and specifically insectivores that live in larger groups developed larger brains than species living in smaller groups (Barton 1996; Dunbar 1998; Kudo and Dunbar 2001; Byrne and Bates 2010; MacLean et al. 2013; Todorov et al. 2019). However, this correlation is debated in carnivores and ungulates (Shultz and Dunbar 2006; Dunbar and Shultz 2007; Shultz and Dunbar 2007; Holekamp et al. 2007; Pérez-Barbería et al. 2007; Finarelli and Flynn 2009), and seems to be absent in birds (Beauchamp and Fernández-Juricic 2004; Iwaniuk and Arnold 2004). Additionally, recent comparative analyses indicate that brain size is better predicted by ecological than social factors (DeCasien et al. 2017; Powell et al. 2017; DeCasien and Higham 2019).

Following the *Ecological Intelligence Hypothesis* (EIH), larger brains allow animals to develop better cognitive abilities to cope with ecological challenges (Parker and Gibson 1977; Milton 1988). Evidence for the EIH has been reported in many animals, including birds and primates (Harvey et al. 1980; MacLean et al. 2009; DeCasien et al. 2017; Powell et al. 2017). Specifically, birds that rely on food-caching or food-hoarding develop larger hippocampi, the brain area which is associated with spatial processing and memory (Krebs 1990; Sherry et al. 1992; Clayton 1998). This relation parallels with spatial abilities in mammals, with species feeding on spatiotemporally distributed fruits having larger brains than more folivorous species (Clutton-Brock and Harvey 1980; MacLean et al. 2009; Mace et al. 2009; Rosati et al. 2014). In primates, specific manipulation skills, such as extractive foraging techniques, covary with neocortex size (Heldstab et al. 2016). Nocturnal or cathemeral lemurs have larger relative brain sizes than diurnal species (MacLean et al. 2009).

Additionally, the *Cognitive Buffer Hypothesis* (Deaner et al. 2003) posits that a larger brain specifically buffers challenges that come along with variable environmental conditions, as it allows for more adaptive behavioral flexibility. Therefore, generalists,

which face more variable conditions, might have evolved larger brains than more specialized species (Reader 2003; Lefebvre et al. 2004; Sol et al. 2005b; Ducatez et al. 2015).

1.2 (Co-)Variation of cognitive abilities

Despite an apparent covariation of cognitive abilities with brain size or brain structure (Clutton-Brock and Harvey 1980; Barton and Harvey 2000; Kudo and Dunbar 2001; Deaner et al. 2007; Chittka and Niven 2009; Dicke and Roth 2016), the suggested hypotheses do not consider a direct relationship of social or ecological factors with cognitive abilities. However, when investigating variation in cognitive abilities in animals, we mostly rely on the behavioral phenotype that can be observed while solving problems (Shettleworth 2009). Thus, cognitive abilities have been operationalized using performance scores in artificial experimental set-ups (Ramsey et al. 2007; Healy et al. 2009; Pritchard et al. 2016; Shaw and Schmelz 2017).

Yet, such empirical studies report evidence for a covariation with social, as well as ecological factors and a link with the size of specific cortical areas. For instance, social complexity correlated positively with performance scores of inhibitory control, transitive inference, or flexible learning abilities in primates and birds (Bond et al. 2003; Bond et al. 2007; MacLean et al. 2008; Amici et al. 2008; Ashton et al. 2018a; Amici et al. 2018; Miller et al. 2019; Ashton et al. 2019). Inhibitory control is also enhanced in more frugivorous or gum-feeding primates, as compared to rather folivorous primates or primates that predominantly feed on mobile insects, and inhibitory control further correlates with brain size (Stevens et al. 2005; MacLean et al. 2014). Migratory or food-storing birds and mammals experience better spatial abilities than residential or non-storing species and develop larger hippocampi (Shettleworth et al. 1990; Clayton and Krebs 1994a; Cristol et al. 2003; Emery and Clayton 2004; Barkley and Jacobs 2007). Spatial abilities are also enhanced in species living in more complex habitats, or species that feed on more stable rather than mobile food items (Pleskacheva et al. 2000; White and Brown 2015a; Trapanese et al. 2019; Teichroeb and Vining 2019). More actively foraging species are more flexible learners than sit-and-wait predators (Day et al. 1999a). Flexible learning and related innovative propensities are also enhanced in species or individuals, that experience

harsher environmental conditions, more urban environments or seasonal changes in food availability (van Woerden et al. 2012; Tebbich et al. 2016; Sayol et al. 2016; Preiszner et al. 2017; Chow et al. 2021). Further, learning abilities have been related to both ecological factors and brain morphology in fish (White and Brown 2015a; White and Brown 2015b; Pike et al. 2018). However, some studies report no difference in cognitive performances in relation to socio-ecological factors or brain size measures (Healy and Suhonen 1996; Bond et al. 2007; Clarin et al. 2013; Hernández-Montero et al. 2020; Pladevall et al. 2020).

Additionally, it is questioned if cognitive abilities emerge in a convergent manner or rather in concordance with a mosaic brain evolution (Barton and Harvey 2000). Functionally different brain areas vary in size in relation to cognitive and sensory specializations to respective ecological adaptations and, therefore, cognitive abilities would vary between cognitive domains (Cosmides and Tooby 1994; Domain-Specific Hypothesis; Barton 1996; Striedter 2006). For example, olfactory cortical structures are larger in nocturnal than in diurnal primates, which have larger visual cortexes (Barton et al. 1995). Further, both of these brain regions are enlarged in primates with high-quality diets or group-living species, while brain regions that are related to spatial processing are enlarged in primates with low-quality diets or solitary species (DeCasien and Higham 2019).

Alternatively, according to the *Domain-General Hypothesis* or the congruent *General Intelligence Hypothesis*, cognitive abilities covary across cognitive domains and correlate onto a common psychometric *g*-factor (Spearman 1904; Humphreys 1979; Jensen 1985; Deaner et al. 2006). In WEIRD (western, educated, industrialized, rich, and democratic) people, a higher-level *g*-factor even provides advantages in several decision-making processes (Gottfredson 1997; Henrich et al. 2010). In non-human animals, a *g*-factor has been reported for rodents, dogs, birds, and non-human primates (Anderson 1993; Herndon et al. 1997; Galsworthy et al. 2002; Matzel et al. 2003; Banerjee et al. 2009; Keagy et al. 2011; Reader et al. 2011; Isden et al. 2013; Hopkins et al. 2014; Matzel et al. 2011; Woodley of Menie et al. 2015; Shaw et al. 2015; Arden and Adams 2016; Ashton et al. 2018a; Damerius et al. 2019). However, other studies on rodents, birds, as well as non-human primates reject the *Domain-General Hypothesis* (Locurto et al. 2003; Locurto et al. 2006;

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Herrmann et al. 2007; Boogert et al. 2011; Herrmann and Call 2012; Amici et al. 2012; Anderson et al. 2017; Huebner et al. 2018).

Therefore, common patterns of (co)variation of cognitive abilities are not yet completely understood across the animal kingdom. Cognitive abilities may correlate within, and partly also between cognitive domains. Further, cognitive abilities can covary with certain social, as well as ecological factors. The investigation of a respective link with sociality has received great interest in previous studies (Bond et al. 2003; Bond et al. 2007; MacLean et al. 2008; Amici et al. 2008; Byrne and Bates 2010; Ashton et al. 2018b; Amici et al. 2018). The link between cognitive variation and ecological factors remains biased towards innovative and spatial abilities, and towards a species diet, invasion potential, or migratory behavior (Pleskacheva et al. 2000; Day et al. 2003; Cristol et al. 2003; Stevens et al. 2005; Bond et al. 2007; MacLean et al. 2009; White and Brown 2015a; Rosati 2017b; Trapanese et al. 2019; Teichroeb and Vining 2019). Specifically, a covariation between cognitive abilities and the degree of ecological specialization has been rarely investigated.

1.3 Niche theory and the classification of ecological specialization

The degree of ecological specialization aims to characterize an animal's ecological niche, i.e., a multidimensional space comprising all ecological factors to which the animal has evolved adaptive phenotypic traits. Species that experience a broad habitat or dietary breadth are classified as ecological generalists, while species with more specialized preferences are classified as ecological specialists (Hutchinson 1953; MacArthur 1957; Hutchinson 1957; Roughgarden 1972; Sargeant 2007). Adaptive phenotypic traits can be either specific morphological structures or behavioral tactics to explore and exploit specific habitats and food patches most efficiently, or more general and flexible behaviors to be able to explore and exploit various habitats and food types. For example, nectivorous hummingbirds (Trochilidae) or bats (e.g., *Leptonycteris* spp.) have evolved specialized rostra, such as elongated and thinner beaks or tongues and snouts, with which they can more efficiently exploit flowers that are specifically rich in nectar (Hoffmeister 1957; Temeles et al. 2002; Rico-Guevara et al. 2019). In line with these morphological adaptations, these species have evolved behavioral adaptations which allows them to

better profit from their specialized lifestyle. Nectivorous Saussure's long-nosed bats (*L. yerbabuena*), for example, have more pronounced spatial skills compared to Palla's long-tongued bats (*Glossophaga soricina*), which additionally feed on fruits and insects (Henry and Stoner 2011). In contrast, generalists do not possess such specialized adaptations, but are more likely to innovate and they are more flexible learners than specialists (Daly et al. 1982; Overington et al. 2011; Mettke-Hofmann 2014; Ducatez et al. 2015). This provides the generalist with the advantage to flexibly respond to variable environmental conditions, whereas specialists experience advantages over generalists in more stable environments (Lahann et al. 2006; Dewar and Richard 2007; Wilson and Yoshimura 2008). Specifically, specialists may exhibit better long-term memory which allows to use and improve specific routes during habitat exploration, and to discriminate between and relocate former food patches (Mettke-Hofmann 2014).

Despite suggestive covariations between cognitive abilities and the degree of ecological specialization, respective empirical studies have rarely been conducted. Instead, it remains hypothesized that generalist species exhibit better cognitive abilities *per se* (Parker 1978). Supporting this, generalists are more likely to innovate, and innovative propensity has been reported to correlate with general intelligence and, further, with brain size measures (Reader 2003; Reader et al. 2011; Ducatez et al. 2015). Additionally, self-control is enhanced in dietary generalist primates and dietary generalist birds and primates developed larger brains than dietary specialists (Reader 2003; Lefebvre et al. 2004; Sol et al. 2005b; MacLean et al. 2014; Ducatez et al. 2015).



Yet, for an overall conclusion, we lack systematic investigations across a broader variety of cognitive abilities. Therefore, in the scope of my thesis, I reviewed the literature on comparative approaches that experimentally assessed interspecific variation in cognitive abilities in relation to ecological factors. With this basis of previously reported common links across studies, I empirically investigated interspecific variation across various cognitive abilities with the use of a comprehensive cognitive test battery applied to wild non-human primates. As study species served two sympatric species of mouse lemurs that experience similar environmental conditions and possess comparable social systems, while exhibiting different adaptations to ecological factors, including different degrees of ecological specialization.

2 Studying mouse lemurs

Studying non-human primates is specifically of broad interest, due to their close relatedness to us humans. Researchers hope to shed light on our distinctiveness to non-human animals and on the evolutionary success of our own species. In the scope of the present topic to investigate variation in cognitive abilities in relation to ecological factors, mouse lemurs (*Microcebus* spp.) represent a suitable study organism. These small (appr. 31 – 100 g), nocturnal, and primarily solitary lemurs encompass 25 described species that are endemic to Madagascar but occupy different ecological niches (Yoder et al. 2000; Mittermeier et al. 2008; Schüßler et al. 2020). Adaptations to ecological conditions can even differ across populations of one species that are exposed to different environments (Ganzhorn and Schmid 1998; Lahann et al. 2006; Schülke and Ostner 2007; Zimmermann and Radespiel 2014). In several regions, at least two mouse lemur species occur in sympatry, usually with one species being more ecologically specialized than the other (Schmid and Kappeler 1994; Rakotondravony and Radespiel 2009; Rakotondranary and Ganzhorn 2012). In central Western Madagascar, the generalist gray mouse lemur (*M. murinus*) and the more specialized Madame Berthe's mouse lemur (*M. berthae*) occur in sympatry in parts of the remaining dry-deciduous lowland forests, as at my study site in Kirindy forest (Schwab and Ganzhorn 2004).

The larger gray mouse lemur (60 g) is a habitat and dietary generalist, occurring across various habitat types (Lahann et al. 2006; Mittermeier et al. 2010), including highly degraded forest fragments (Ganzhorn and Schmid 1998; Ganzhorn et al. 2012), and experiencing a broad dietary breadth (Dammhahn and Kappeler 2008a). The World's smallest primate, the Madame Berthe's mouse lemur (31 g) is a habitat and dietary specialist, occurring only in dry-deciduous lowland forest in central Western Madagascar (Rasoloarison et al. 2000; Schäffler and Kappeler 2014), and experiencing a narrower dietary breadth (Dammhahn and Kappeler 2008a). In Table 1.1, I summarize the main species-specific characteristics concerning socio-ecological factors, as well as prior research efforts in the broad context of cognition and the currently assigned IUCN states. In summary, the two species differ in various ecological adaptations, while social characteristics are largely comparable. As they occur in sympatry at my study site in Kirindy forest, they experience similar environmental characteristics. The fact that they,

Table 1.1 Main socio-ecological characteristics of gray and Madame Berthe’s mouse lemurs, as well as IUCN state and cognitive research effort. Dietary breadth (B) based on Levin’s standardized index (Krebs 1989)

		
	Gray mouse lemur	Mme Berthe’s mouse lemur
mean body mass ^{1,2}	60 g	31 g
distribution ^{1,2}	throughout western Madagascar	central western Madagascar
occurrence	diverse: evergreen littoral forest, dry-deciduous forest, primary and secondary forest, degraded forest fragments ³	specific: dry-deciduous lowland forest, primary forest only ⁴
diet		
- dietary breadth ⁵	- broad (B = 0.63)	- narrow (B = 0.12)
- composition ⁶	- patchy homopteran secretions (59%), abundant animal matter (17%), stationary fruits/flowers (9%), patchy/stationary gum (9%), others (6%)	- patchy homopteran secretions (82%), mobile insects (11%), stationary fruits/flowers (2%), patchy/stationary gum (0.2%), others (5%)
ecological specialization ^{4,6}	habitat generalist	habitat specialist
energy saving strategies ⁷	dietary generalist	dietary specialist
- males	- short-term torpor	- short-term torpor
- females	- short- & long-term torpor	- short-term torpor
home range size ⁸		
- males	- 2.8 ha	- 4.9 ha
- females	- 1.7 ha	- 2.4 ha
sleeping sites	mainly tree holes ⁹	mainly leave nests ⁸
sociality	solitary forager, formation of sleeping groups, cooperative breeder ¹⁰	solitary forager, solitary resting, formation of sleeping groups ⁸
mating season	October – November ¹¹	November ⁸
cognition research	diverse: captivity & wild, social & physical abilities, personality, aging effects ¹²	wild only, innovation, personality ¹³
IUCN state	least concern ¹⁴	critically endangered ¹⁵

¹Schmid and Kappeler 1994; Rasoloarison et al. 2000; ²Mittermeier et al. 2010; ³Ganzhorn and Schmid 1998; Lahann et al. 2006; ⁴Schäffler and Kappeler 2014; ⁵Dammhahn and Kappeler 2008a; ⁶Dammhahn and Kappeler 2008b; ⁷Schmid 1999; Schmid et al. 2000; Dammhahn and Kappeler 2012; ⁸Dammhahn and Kappeler 2005; ⁹Schmid 1998; ¹⁰Eberle and Kappeler 2006; ¹¹Eberle and Kappeler 2004a; ¹²Schilling 1979; Joly et al. 2004; Picq 2007; Dammhahn 2012; Joly et al. 2014b; Huebner et al. 2018; ¹³Henke-von der Malsburg and Fichtel 2018; ¹⁴Reuter et al. 2020; ¹⁵Markolf et al. 2020

Chapter I: General introduction

nevertheless, occupy different ecological niches, assumes complex evolutionary processes for ecological adaptations that may be linked to cortical development, and may covary with cognition. Hence, they are suitable study species to investigate patterns of covariation of interspecific differences in cognitive abilities and adaptations to ecological factors in the wild.

Assuming, that social factors cannot solely explain variation in cognition (Rosati 2017a), I expected interspecific variation in cognitive performances in relation to the species' adaptations to ecological conditions. Specifically, according to the *Opportunistic Intelligence Hypothesis*, the generalist gray mouse lemur should consistently outperform the specialist Madame Berthe's mouse lemur. Alternatively, species-specific ecological characteristics, irrespective of the degree of ecological specialization, should covary with specific cognitive performances. For instance, since Madame Berthe's mouse lemurs inhabit larger home ranges and feed on more stationary food items (Dammhahn and Kappeler 2008b), they should exhibit better spatial abilities. Instead, gray mouse lemurs feeding more on fruits and flowers (Dammhahn and Kappeler 2008b), should exhibit better causal understanding.

Finally, by studying Madame Berthe's mouse lemurs' various cognitive abilities, I extend our overall knowledge of cognition in non-human primates. Cognitive abilities of gray mouse lemurs have been studied to a large extent in previous studies, both in captivity and in the wild (Lührs et al. 2009; Dammhahn 2012; Schilling 2012; Joly et al. 2014; Huebner et al. 2018; Kittler et al. 2018; Schmidtke et al. 2018; Henke-von der Malsburg and Fichtel 2018; Fichtel et al. 2020). Using a great variety of experimental tasks, we already have knowledge about cognitive abilities in the social and the physical domain, about personality traits, sensory predispositions, as well as aging effects and links with fitness parameters (Jolly 1964; Schilling 1979; Santos et al. 2005; Bons et al. 2006; Joly et al. 2004; Picq 2007; Siemers et al. 2007; Lührs et al. 2009; Dammhahn and Almeling 2012; Languille et al. 2012; Schilling 2012; Huebner et al. 2018; Kittler et al. 2018; Fichtel et al. 2020). Additionally, both species habituate easily to short-term captivity, they are trap happy and their populations have been monitored for over 25 years in Kirindy forest (Eberle and Kappeler 2002; Kraus et al. 2008; Hämäläinen et al. 2014b; Huebner et al. 2018; Henke-von der Malsburg and Fichtel 2018). Thus, wild populations of mouse lemurs at

this study site are particularly suited to examine their cognitive skills using a comprehensive test battery that requires many experimental sessions and, accordingly, the chance to repeatedly recapture single individuals.

3 This study

The specific aim for my thesis was to broaden our understanding of cognitive evolution in relation to ecological factors. Therefore, I empirically investigated patterns of covariation between cognitive performances and species-specific adaptations to ecological conditions, specifically the degree of ecological specialization.

Specifically, I answered the questions (1) how ecological factors, including the degree of ecological specialization, covary with cognitive performances across various species of the animal kingdom (**Chapter II**), (2) whether the generalist gray mouse lemur consistently outperforms the specialist Madame Berthe's mouse lemur in cognitive performances (**Chapter III**), (3) to which extent cognitive abilities can covary with ecological factors (**Chapter III**) and (4) whether cognitive performances in mouse lemurs correlate to general intelligence (*g*-factor) which further correlates across species (*G*-factor; **Chapter III**). For this, I reviewed the literature by selecting experimental comparative studies that investigated variation in cognition in relation to ecological adaptation. To add experimental data to this theoretic approach, and to test formulated hypotheses concerning the evolution of cognition, I conducted a comprehensive cognitive test battery on wild populations of the sympatric gray and Madame Berthe's mouse lemurs, which differ in their degree of ecological specialization.

In **Chapter II** of my thesis, I start with a summary of proposed hypotheses aiming to explain the evolution of cognition and provide an overview of covariations with brain size, sociality, and ecology. I continue evaluating the results of my literature survey on experimental comparative studies investigating covariations of cognitive performances with ecological factors in non-human animals. Finally, I estimate general patterns of covariation between cognitive performances and the degree of habitat and dietary specialization, the social group size, as well as the brain size.

Chapter I: General introduction

In **Chapter III**, I first introduce the topic of interspecific variation in cognitive abilities across non-human animals and in relation to socio-ecological factors. Then, I describe the species-specific socio-ecological factors characterizing gray and Madame Berthe's mouse lemurs in more detail. For this experimental approach, I applied a test battery comprising several cognitive tasks to investigate innovative problem-solving abilities, persistence, associative and reversal learning abilities, spatial abilities, inhibitory control, means-end understanding, and goal directedness. I included two additional personality tests to measure the individuals' explorative and neophilic tendencies which might confound cognitive test performances. In addition to the investigation of interspecific variation in cognitive abilities, I estimate the probability of general intelligence in mouse lemurs.

In **Chapter IV**, I summarize and connect the main aspects of the results reported in **Chapter II** and **III**. Additionally, I evaluate the gained knowledge in terms of how it helps to understand cognitive evolution and provide ideas of how this data can be used for future studies extending this exciting field of research.

Chapter II: Literature review

Linking ecology and cognition: does ecological specialization predict cognitive test performance?

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JHM, PMK and CF wrote the manuscript.

Note: The original publication has been requested for correction. Here, I include the corrected version.

Abstract

Variation in cognitive abilities is thought to be linked to variation in brain size, which varies across species with either social factors (*Social Intelligence Hypothesis*) or ecological challenges (*Ecological Intelligence Hypothesis*). However, the nature of the ecological processes invoked by the *Ecological Intelligence Hypothesis*, like adaptations to certain habitat characteristics or dietary requirements, remains relatively poorly known. Here, we review comparative studies that experimentally investigated interspecific variation in cognitive performance in relation to a species' degree of ecological specialization. Overall, the relevant literature was biased towards studies of mammals and birds as well as studies focusing on ecological challenges related to diet. We separated ecological challenges into those related to searching for food, accessing a food item, and memorizing food locations. We found interspecific variation in cognitive performance that can be explained by adaptations to different foraging styles. Species-specific adaptations to certain ecological conditions, like food patch distribution, characteristics of food items or seasonality also broadly predicted variation in cognitive abilities. A species' innovative problem-solving and spatial processing ability, for example, could be explained by its use of specific foraging techniques or search strategies, respectively. Further, habitat generalists tended to outperform habitat specialists. Hence, we found evidence that ecological adaptations and cognitive performance are linked, but that the classification concept of ecological specialization cannot sufficiently explain variation in cognitive performance.

Keywords

cognition, ecological adaptation, foraging style, habitat complexity, *Ecological Intelligence Hypothesis*, brain size

1 Introduction

Cognition can be defined as the ability to perceive, memorize and process information from an individual's social as well as ecological environment (Shettleworth 2009), and variation in this ability is thought to be positively correlated with brain size. Relative brain

size varies considerably among species (e.g., Sol et al. 2008; Mace et al. 2009) and is indeed associated with variation in average species-typical cognitive performance (Deaner et al. 2006; Reader et al. 2011). Several hypotheses have been proposed to explain this link between interspecific variation in brain size and the associated cognitive abilities. The most prominent hypotheses are the *Social Intelligence Hypothesis* (SIH; Humphrey 1976) and the *Ecological Intelligence Hypothesis* (EIH; Parker and Gibson 1977; Milton 1988), which have been subsequently refined as the *Domain-General Hypothesis* (Deaner et al. 2006), *Domain-Specific Hypothesis* (Whiten and Byrne 1988), *Adaptive Intelligence Hypothesis* (Tooby and Cosmides 2003), *Machiavellian Intelligence Hypothesis* (Whiten and Byrne 1988), *Cultural Intelligence Hypothesis* (Herrmann et al. 2007; van Schaik and Burkart 2011), *Social Brain Hypothesis* (Dunbar 1998; Dunbar et al. 2007) and *Cognitive Buffer Hypothesis* (CBH; Deaner et al. 2003) (see Fig. 2.1).

The SIH suggests that bigger brains co-evolved with increasing social complexity, i.e., cognitive challenges to manage social relationships, which, in turn, have evolved as means of solving ecological problems (Jolly 1966; Humphrey 1976; Whiten and Byrne

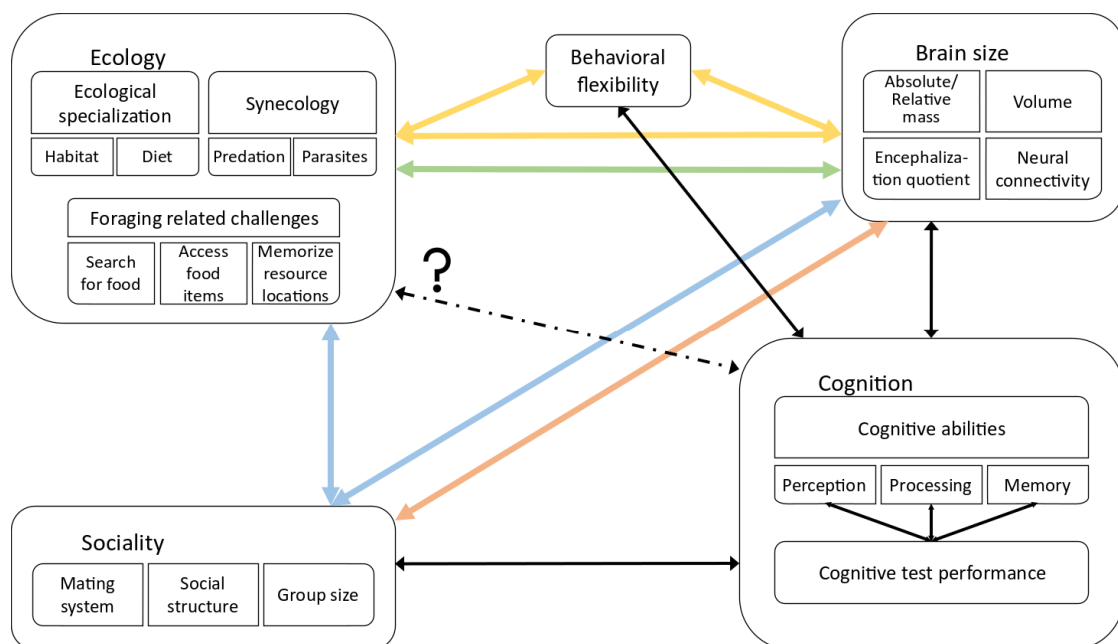


Fig. 2.1 Relationships between ecology, sociality, brain size measures and cognitive abilities. Main hypotheses related to particular links are represented with colored thick lines: red for the *Social Intelligence Hypothesis* (challenges related to sociality drive brain development; Humphrey 1976), green for the *Ecological Intelligence Hypothesis* (challenges related to ecology drive brain evolution; Parker and Gibson 1977), blue for the *Social Brain Hypothesis* (ecological challenges predict sociality which drives brain size; Dunbar 1998; Dunbar and Shultz 2017), and yellow for the *Cognitive Buffer Hypothesis* (environmental variation drives brain size which favours adaptive behavioural flexibility; Deaner et al. 2003). Thinner black lines represent previously reported relationships between cognitive abilities and sociality, behavioral flexibility, and brain size. The dashed line represents the relationship between cognitive abilities and ecology discussed in this paper

Chapter II: Literature review

1988; Barton 1996; Dunbar 1998; Kudo and Dunbar 2001; Dunbar et al. 2007; Byrne and Bates 2010). In contrast, the EIH posits that ecological challenges in food acquisition, including spatial or spatio-temporal processes to memorize seasonally available food or manipulative skills for extractive foraging, have ultimately selected for larger brains (e.g., Clutton-Brock and Harvey 1980; Heldstab et al. 2016; DeCasien et al. 2017; Powell et al. 2017). At the end of the day, brains evolve within species, where environmentally induced changes in physiological traits, such as glucose concentrations and hormone levels, impact cognitive performance (Roth et al. 2010; Thornton and Lukas 2012; Maille and Schradin 2016a).

Comparative studies investigating the link between measures of brain size and socio-ecological factors revealed inconsistent results, finding either a positive relationship between measures of brain size and sociality in primates and ungulates (Dunbar 1998; Pérez-Barbería et al. 2007; Dunbar and Bever 2010) or equivocal support in carnivores (Holekamp et al. 2007; Pérez-Barbería et al. 2007; Finarelli and Flynn 2009), for instance. Among primates, the most recent comparative analyses indicated that brain size is better predicted by ecological than social factors (DeCasien et al. 2017; Powell et al. 2017). However, compared to social factors (Ashton et al. 2018b), less is known about the extent to which variation in specific ecological factors predicts cognitive performance (Fig. 2.1). Here, we therefore explore the question whether ecological adaptations can explain interspecific variation in cognitive abilities by first briefly summarizing hypotheses about the evolution of cognitive abilities addressing potential links between cognition and brain size, sociality, as well as ecology, respectively. Second, we provide a summary of comparative studies relating interspecific variation in cognitive performance with ecology, specifically the degree of ecological specialization. Using these studies, we also explore the relative impact of sociality and brain size on variation in cognitive performance. Finally, we discuss the effects of the degree of ecological specialization, potentially confounding factors in experimental studies, and limitations of this review that may inform future research on this topic.

1.1 The link between cognition and brain size

Some comparative studies have suggested that measures of brain size co-vary positively with performance in cognitive tests (see Appendix 1, Table S1-1 for explanations of cognitive terms), such as performance in inhibitory control across vertebrates (MacLean et al. 2012), a general intelligence (*g*-factor) extracted from performance in innovation, social learning, tool use, extractive foraging and tactical deception (Reader and Laland 2002; Reader et al. 2011), a *g*-factor extracted from performance in tests on spatial and causal understanding, reversal learning and delayed response (Deaner et al. 2006, 2007), or performance in problem-solving (Benson-Amram et al. 2016). In addition, guppies (*Poecilia reticulata*) selected for larger brains outperformed those with smaller brains in a numerical learning assay (Kotrschal et al. 2013), demonstrating this link also at the intra-specific level.

However, it is questionable whether simple measures of brain size can be used to infer its impact on the solution of a specific problem (Healy and Rowe 2007). In addition, different neuroanatomical measures of brain size have been combined with inconsistently labelled methods and various cognitive response measures (Healy and Rowe 2007). To circumvent these problems, some studies extracted a general intelligence factor, which is a statistical value derived from correlating performance in several cognitive tasks (Spearman 1904; Jensen 1985). In primates (Reader and Laland 2002; Deaner et al. 2006; Deaner et al. 2007; Reader et al. 2011), the *g*-factor co-varied positively with brain size. Although some other studies provided evidence for a *g*-factor in humans (Jensen 1985), non-human primates (Fernandes et al. 2014; Damerius et al. 2019), rodents, rabbits, cats, dogs (Galsworthy et al. 2014), and birds (Sol et al. 2005a; Ducatez et al. 2015), we lack validation that this correlation factor represents general intelligence (Burkart et al. 2017). In fact, it can simply reflect the selection of cognitive tasks that tap into similar cognitive domains, which would not necessarily validate the notion of general intelligence (Shaw and Schmelz 2017; Bräuer et al. 2020).

Alternatively, domain-specific cognition might support the notion of mosaic brain evolution (Barton and Harvey 2000). The vertebrate brain consists of several functionally different structures, of which many vary in size within and between clades (Striedter 2006). Differences in the relative size of different brain regions are thought to reflect both

Chapter II: Literature review

neurodevelopmental/functional size changes and selection for ecologically relevant cognitive and sensory specialization (Barton 1996). For example, food-caching birds have relatively, but not absolutely larger hippocampi (Krebs 1990), and brain regions associated with spatial processing are enlarged in species with better spatial abilities (Sherry et al. 1992; Clayton 1998). Moreover, group-living primates with high-quality diets have larger brain regions for olfactory or visual processing, whereas solitary species or those with low-quality diets have larger brain regions for processing spatial memory (DeCasien and Higham 2019). Finally, the number of neurons in the mammalian cerebral cortex, or in the bird pallium, appear to be good predictors of inhibitory control (Herculano-Houzel 2017). Hence, specific neuroanatomical measures can be broadly associated with variation in cognitive performance.

1.2 The link between cognition and sociality

Cognitive abilities have been linked to traits associated with variation in social factors. Variation in sociality is often operationalized in terms of group size (Lukas and Clutton-Brock 2013; Kappeler 2019), which varies from solitary individuals and small pair-bonded units to large aggregations. The need for several social skills, like effective communication or coordination with other group members, requires specific neural structures (Dunbar and Shultz 2007; Peckre et al. 2019). Thus, group size or group dynamics are contributing to the complex social challenges an animal faces (Kappeler 2019).

Accordingly, primates living in dynamic fission-fusion systems (Aureli et al. 2008) performed better in inhibitory control tasks than those living in more stable groups, suggesting that the former exhibit greater behavioral flexibility (Amici et al. 2008; Amici et al. 2018). In lemurs and birds, species organized into more complex social groups outperformed others in transitive inference tasks (Bond et al. 2003; MacLean et al. 2008). A similar inter-specific difference was found in birds subjected to a reversal-learning task (Bond et al. 2007). Moreover, within species, Australian magpies (*Gymnorhina tibicen dorsalis*) living in larger groups performed better in several cognitive tests (inhibitory control, associative and reversal learning abilities, spatial memory and innovation) than those living in smaller groups (Ashton et al. 2018a, 2019). Since traits such as inhibitory

control and (reversal) learning abilities reflect behavioral flexibility, the underlying variation in cognition can be related to variation in sociality.

1.3 The link between cognition and ecology

Ecological challenges, such as variable schedules of resource availability, habitat complexity, predation risk or parasite exposure, may have contributed to cognitive evolution (Garamszegi et al. 2007; Lefebvre and Sol 2008; Shumway 2008; Soler et al. 2012; Morand-Ferron et al. 2016; Sayol et al. 2016). With respect to resource variation, the CBH posits that larger brains evolved to allow species to adjust their behavior adaptively in response to variable environmental conditions (Deaner et al. 2003). For instance, frugivorous species, which have on average larger brains than folivorous species, rely more on resources that vary in their spatiotemporal distribution than folivorous species (Clutton-Brock and Harvey 1980; Mace et al. 2009). Moreover, birds and Old World primates exposed to seasonal changes in food availability tend to have larger brains than species living in non-seasonal habitats (van Woerden et al. 2012; Sayol et al. 2016). Innovativeness, which is adaptive in variable environmental conditions, correlates positively with brain size in primates and birds (Reader and Laland 2002; Lefebvre et al. 2004; Overington et al. 2009), but it also correlates positively with parasitism and immunocompetence in birds (Møller et al. 2005; Garamszegi et al. 2007; Vas et al. 2011), though the link between innovation and the transmission mode of parasite types is not obvious (Ducatez et al. 2020a). Finally, in line with the EIH, brain size was best predicted by diet or home range size in primates (DeCasien et al. 2017; Powell et al. 2017).

Comparisons within species also revealed evidence that variation in cognitive abilities is associated with parasitism (Dunn et al. 2011; Bókony et al. 2014), predation (Brown and Braithwaite 2005; Park et al. 2008; Ferrari 2014), habitat complexity (Roth et al. 2010; Tebbich and Teschke 2014; Croston et al. 2017; Morand-Ferron et al. 2019), or foraging behavior (Mazza et al. 2019; Sonnenberg et al. 2019). However, only a few comparative studies explicitly explored which cognitive skills might be associated with which species-specific ecological challenges. In birds, innovation was positively correlated with parasitism (Garamszegi et al. 2007; Vas et al. 2011; Soler et al. 2012) or habitat breadth

Chapter II: Literature review

(Overington et al. 2011), but not with predation (Overington et al. 2011). In primates, abundance of socially transmitted parasites were positively associated with rates of social learning, and environmentally transmitted parasites were positively associated with rates of exploration (McCabe et al. 2015). Habitat complexity was positively correlated with spatial cognition and brain size in rodents (Mackay and Pillay 2017) and fish (White and Brown 2015a). Hence, some results point towards an association between cognitive performance and ecological adaptations and a systematic summary of respective associations across species may contribute to a better understanding of potential causalities and their relative effect sizes.

The required assessment of a species' ecological adaptation can be based on a characterization of its niche, which is a multidimensional space comprising all ecological factors that determine species viability (Hutchinson 1953; MacArthur 1957). Specialization and generalization represent the extremes of the continuous variation along each of the dimensions (Sargeant 2007). Utilizing this niche concept, however, involves some difficulties. First, it is important to differentiate between intrinsic specializations due to evolutionary adaptations (i.e., an individual's genetics describing its fundamental niche) and extrinsic specializations due to interspecific competition over resources (i.e., the observed realized niche), for instance (Hutchinson 1957; Devictor et al. 2010). Second, niche breadth can be defined by the diversity of resources used by a species, or by its overlap, measured as the deviation from other species' resource values (Sargeant 2007). Considering niche breadth, a specialist would then be a species consistently using a narrower niche than other species (Roughgarden 1972; Bolnick et al. 2003). Considering niche overlap, however, a specialist would use items/tactics that are rarely used within other species' niches (Bolnick et al. 2002). Moreover, classifications refer to only one niche axis (Futuyma and Moreno 1988), leading to species that can be highly specialized along one ecological gradient while being a generalist along another ecological gradient. It has therefore been proposed to use species co-occurrence as a measure of habitat breadth (Ducatez et al. 2014b). Finally, different studies use different terms for similar concepts without stating their definition, or they ignore differences between niche breadth and niche overlap, hampering broader comparisons (Colwell and Futuyma 1971; Devictor et al. 2010).

We, thus, use the concept of ecological specialization as formalized by Hutchinson (Hutchinson 1957) and similarly to Hughes (Hughes 2000). Accordingly, we consider a dietary specialist as a species consuming a lower variety of food types and a habitat specialist as a species occurring in a lower variety of habitat types than a dietary generalist or habitat generalist, respectively. We use this distinction always relative to the species in comparison, not as an absolute attribute. Since animals are expected to have evolved cognitive adaptations to exploit these respective conditions as efficiently as possible (Mettke-Hofmann 2014), generalists and specialists are expected to vary in their performances across cognitive tasks, but also in some personality traits. Hence, generalists have been suggested to be more explorative, to have better working memory, to learn faster, to exhibit greater behavioral flexibility and to have a higher innovative potential than specialists. Specialists are instead expected to exhibit better long-term memory, despite smaller brains, than generalists (Reader 2003; Mettke-Hofmann 2014).

Below, we review relevant studies that explicitly investigated inter-specific variation in cognitive performance posed by problems that are related to species-specific adaptations to factors reflecting the degree of ecological specialization. Using the search query “(ecolog* or general* or speciali* or “lifestyle” or opportunist*) and (cogniti* or learn* or memory) and animal” in “topic” (including titles, abstracts, keywords, and keywords plus) in the Web of Science [<https://apps.webofknowledge.com/>, accessed on 2019-07-14] and complementing the collection with other relevant studies via cross-references, we found a total of N = 25 studies, that fit our criteria.

All selected studies (1) experimentally compared (2) cognitive abilities between (3) at least two species with the aim to investigate (4) different ecological adaptations with a focus on the degree of ecological specialization. We controlled for potential phylogenetic effects by excluding studies comparing species across taxonomic classes. The remaining studies either compared species within the same genus (40%), family (48%), or order (12%). Most of the studies compared wild-caught or semi-free ranging (72%) individuals in mammals (56%) or birds (24%) (N = 2 for each in reptiles and fish, N = 1 for invertebrates). The investigated ecological adaptations were mostly related to dietary challenges and variation in habitat complexity (Table 2.1). As studies of cognitive performance often differ in experimental conditions (animal housing, feeding regimes,

Table 2.1 Table of studies comparing cognitive abilities between at least two species within the same phylogenetic class expressing different ecological adaptations

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Habitat exploration while searching and finding food					
Clarín et al. 2013	Long-fingered bat (<i>Myotis capaccinii</i>)	Same genus	Wild-caught	Spatial discrimination (plus maze)	no difference between <i>M. capaccinii</i> (open water forager), <i>M. myotis</i> (passive listening gleaner) & <i>M. emarginatus</i> (clutter specialist)
	Greater mouse-eared bat (<i>M. myotis</i>)				
	Geoffroy's bat (<i>M. emarginatus</i>)				
Clarín et al. 2013	Long-fingered bat (<i>M. capaccinii</i>)	Same genus	Wild-caught	Spatial reversal learning (plus maze)	<i>M. myotis</i> (passive listening gleaner) & <i>M. emarginatus</i> (clutter specialist)
	Greater mouse-eared bat (<i>M. myotis</i>)				
	Geoffroy's bat (<i>M. emarginatus</i>)				
Day et al. 1999	Long-fingered bat (<i>M. capaccinii</i>)	Same genus	Wild-caught	Complex spatial discrimination (extended plus maze)	<i>M. myotis</i> (passive listening gleaner) & <i>M. emarginatus</i> (clutter specialist)
	Greater mouse-eared bat (<i>M. myotis</i>)				
	Geoffroy's bat (<i>M. emarginatus</i>)				
Day et al. 1999	Nidua fringe-toed lizard (<i>Acanthodactylus scutellatus</i>)	Same genus	Wild-caught	Visual discrimination (color/shape/pattern discrimination)	no difference between <i>A. scutellatus</i> (sit-and-wait predator) and <i>A. boskianus</i> (active forager)
	Bosc's fringe-toed lizard (<i>A. boskianus</i>)				
	Nidua fringe-toed lizard (<i>A. scutellatus</i>)	Same genus	Wild-caught	Behavioral flexibility (color/shape/pattern reversal learning)	<i>A. boskianus</i> (active forager)
Gingins & Bshary 2016	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	Same family	Wild-caught	Spatial discrimination (association of food source with location)	no difference between 6 labrid species due to ecological irrelevance of the task
	other labrids (<i>Halichoeres melanurus</i> , <i>Hemigymmus melapterus</i> , <i>Labrichthys unilineatus</i> , <i>Pseudocheilinus hexataenia</i> , <i>Thalassoma lunare</i>)				
	Common vole (<i>Microtus arvalis</i>)	Same family	Captivity	Spatial reference memory (operant home cage)	<i>M. glareolus</i> (more complex habitat, omnivorous)
Haupt et al. 2010	Bank vole (<i>Myodes glareolus</i>)	Same family	Captivity	Spatial working memory (win-shift task)	<i>M. glareolus</i> (more complex habitat, omnivorous)
	Common vole (<i>M. arvalis</i>)	Same family	Captivity		

Table 2.1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Henry & Stoner 2011	Saussure's long-nosed bat (<i>Leptonycteris yerbabuena</i>) Palla's long-tongued bat (<i>Glossophaga soricina</i>)	Same family	Wild-caught	Spatial working memory (foraging task)	<i>L. yerbabuena</i> (dietary specialist)
Jones et al. 2017	Sprague Dawley rat (<i>Rattus norvegicus</i>) D57BL/6J mouse (<i>Mus musculus</i>)	Same family	Laboratory	Learning (Go/NoGo judgement bias task)	differential learning: <i>R. norvegicus</i> (opportunistically omnivorous, moving food) learn NoGo-condition, <i>M. musculus</i> (largely herbivorous, active predators, static food) learn Go-condition
Mackay & Pillay 2018	Three striped mice (<i>Rhabdomys pumilio</i> , <i>R. bechuanae</i> , <i>R. dilectus</i>)	Same genus	Wild-caught	Spatial learning (Barne's maze)	no difference between <i>R. pumilio</i> (low scrubby bushes, open habitat), <i>R. bechuanae</i> (grassy cover, savanna) & <i>R. dilectus</i> (grassy cover, mosaic forest)
Pleskacheva et al. 2000	Bank vole (<i>Myodes glareolus</i>) Root vole (<i>Microtus oeconomus</i>)	Same family	Wild-caught	Spatial search (Morris water test)	<i>M. glareolus</i> (more complex habitat, dispersed seeds)
Szabo & Whiting 2020	Sleepy lizard (<i>Tiliqua rugosa asper</i>) Eastern blue-tongue skink (<i>T. scincoides</i>)	Same genus	Wild-caught	Visual discrimination (color/pattern discrimination)	no difference between <i>T. r. asper</i> (rural habitat) and <i>T. s. scincoides</i> (urban habitat)
Szabo & Whiting 2020	Sleepy lizard (<i>Tiliqua rugosa asper</i>) Eastern blue-tongue skink (<i>T. scincoides</i>)	Same genus	Wild-caught	Behavioral flexibility (color/pattern reversal learning)	<i>T. r. asper</i> (rural habitat)
Teichroeb & Vining 2019	Grey mouse lemur (<i>M. murinus</i>) Fat-tailed dwarf lemur (<i>Cheirogaleus medius</i>) Aye-aye (<i>Daubentonia madagascariensis</i>)	Same order	Captivity	Spatial navigation (multi-destination array with six feeding platforms)	<i>C. medius</i> (stationary food) > <i>M. murinus</i> (stationary & mobile/ephemeral food)

Table 2.1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Bond et al. 2007	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Same family	Wild-caught	Spatial discrimination (two-choice task)	<i>N. columbiana</i> (highly dependent on food-caching)
Bond et al. 2007	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Same family	Wild-caught	Behavioral flexibility (color/spatial reversal learning)	<i>G. cyanocephalus</i> (less dependent on food-caching)
Cristol et al. 2003	Two dark-eyed juncos (<i>Junco hyemalis hyemalis</i> , <i>J. h. carolinensis</i>)	Different subspecies	Wild-caught	Spatial memory accuracy (one-trial associative memory test)	<i>J. h. hyemalis</i> (migratory)
Gibson & Kamil 2005	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Same family	Wild-caught	Spatial discrimination (landmark distance discrimination)	<i>A. californica</i> (not dependent on food caching; pilfer caches of conspecifics) and <i>G. cyanocephalus</i> (highly dependent on food caching; pilfer caches of conspecifics)
Healy & Suhonen 1996	Willow tit (<i>Poecile montanus</i>) marsh tit (<i>P. palustris</i>)	Same genus	Wild-caught	Food retrieval performance (retrieving stored food after delays)	no difference between <i>P. montanus</i> (store food for a several weeks) and <i>P. palustris</i> (store food for a few hours/days)
Platt et al. 1996	Wied's marmoset (<i>Callithrix kuhlii</i>) Golden lion tamarin (<i>Leontopithecus rosalia</i>)	Same family	Captivity	Spatial memory retention (radial maze, delayed matching-to-sample task; short retrieval intervals)	<i>C. kuhlii</i> (revisit food patches several times a day)
Platt et al. 1996	Wied's marmoset (<i>C. kuhlii</i>) Golden lion tamarin (<i>L. rosalia</i>)	Same family	Captivity	Spatial memory retention (radial maze, delayed matching-to-sample task; long retrieval intervals)	<i>L. rosalia</i> (revisit food patches several times a week)

Table 2.1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Trapanese et al. 2019	Tonkean macaque (<i>Macaca tonkeana</i>)	Same order	Semi-free ranging	Foraging decision & goal-directed travel (feeding boxes)	<i>M. tonkeana</i> (most frugivory)
	Long-tailed macaque (<i>M. fascicularis</i>)				
	Capuchin monkey (<i>Sapajus apella</i>)				
White & Brown 2015	Cocos frillgoby (<i>Bathygobius cocosensis</i>)	Same family	Wild-caught	Spatial learning (T-maze)	<i>B. cocosensis</i> & <i>B. krefftii</i> (more complex habitat)
	Krefft's goby (<i>B. krefftii</i>)				
Eastern long finned goby (<i>Favonigobius lentiginosus</i>)					
	Hoese's sandgoby (<i>Istigobius hoesei</i>)				
Accessing food sources					
Day et al. 2003	Lion tamarin (<i>Leontopithecus</i> spp.)	Same family	Captivity	Innovative abilities (novel extractive foraging tasks)	<i>Leontopithecus</i> spp. (manipulative extractive foraging) > <i>Callithrix</i> spp. (extractive foraging)
	Tamarin (<i>Saguinus</i> spp.)				
Griffin & Diquelou 2015	Marmoset (<i>Callithrix</i> spp.)				
	Indian myna (<i>Acridotheres tristis</i>)	Same order	Wild-caught	Innovative abilities (novel foraging tasks)	<i>A. tristis</i> (opportunistic niche occupation, introduced species)
Henke-von der Malsburg & Fichtel 2018	Noisy myner (<i>Manorina melanoccephala</i>)				
	Grey mouse lemur (<i>Microcebus murinus</i>)	Same genus	Wild-caught	Innovative abilities (novel food extraction task)	<i>M. berthae</i> (diet & habitat specialist)
	Mime Berthe's mouse lemur (<i>M. berthae</i>)				
Memorizing (previous) resource locations					
Barkley & Jacobs 2007	Merriam's kangaroo rat (<i>Dipodomys merriami</i>)	Same genus	Wild-caught	Spatial memory accuracy (cache simulation task)	<i>D. merriami</i> (intensive scatter hoarder)
	Great Basin kangaroo rat (<i>D. microps</i>)				
Bond et al. 2007	Pinyon jay (<i>Gymnorhinus cyanocephalus</i>)	Same family	Wild-caught	Visual discrimination (color discrimination)	no difference between <i>N. columbiana</i> (highly dependent on food-caching), <i>G. cyanocephalus</i> (less dependent on food-caching) and <i>A. californica</i> (not dependent on food-caching)
	Clark's nutcracker (<i>Nucifraga columbiana</i>)				
	Western scrub jay (<i>Aphelocoma californica</i>)				

Table 2.1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Rosati & Hare 2012	Chimpanzee (<i>Pan troglodytes</i>) Bonobo (<i>P. paniscus</i>)	Same genus	Semi-free ranging	Spatial working memory (foraging task)	<i>P. troglodytes</i> (dependence on patchily distributed food)
Rosati et al. 2014	Ruffed lemur (<i>Varecia</i> spp.) Ring-tailed lemur (<i>Lemur catta</i>) Mongoose lemur (<i>Eulemur mongoz</i>) Coquerel's sifaka (<i>Propithecus coquereli</i>)	Same family	Captivity	Spatial memory (food retrieval tasks)	<i>Varecia</i> spp. (most frugivorous diet)
Other challenges					
Bednekoff & Balda 1996	Clark's nutcracker (<i>N. columbiana</i>) Mexican jay (<i>Aphelocoma ultramarina</i>)	Same family	Wild-caught	Observational spatial memory (pair cache/recovery tasks)	<i>A. ultramarina</i> (non-specialized cacher)
Day et al. 1999	Nidua fringe-toed lizard (<i>A. scutellatus</i>) Bosc's fringe-toed lizard (<i>A. boskianus</i>)	Same genus	Wild-caught	Spatial memory accuracy (Barne's maze, local cue version)	no difference between <i>A. scutellatus</i> (distributed mobile prey) and <i>A. boskianus</i> (clumped sedentary prey)
Hoedjes et al. 2012	3 wasps (<i>Nasonia vitripennis</i> , <i>N. longicornis</i> , <i>N. giraulti</i>)	Same genus	Laboratory	Olfactory memory (T-maze olfactometer)	<i>N. vitripennis</i> (host generalist), <i>N. longicornis</i> (lesser host generalist)

Criteria for selection were that (1) at least two study species (2) within the same phylogenetic class were compared in (3) at least one cognitive ability using an experimental approach (4) taking some kind of ecological difference into account

environmental conditions, local and temporal conditions, experimental task and procedure, role of experimenter, etc.), measurement of cognitive performance and analysis in interspecific comparisons, we focused on explicitly comparative studies. Since only a few species were explicitly labelled as either generalist or specialist in the original studies, we assessed the relative degrees of habitat and/or dietary specialization between the species investigated using additional literature. Similarly, if not mentioned in the original study, we gleaned information on group and brain size or proxies for brain size by consulting additional literature (Table 2.2).

2 Cognitive performance and ecological specialization

Ecological challenges are of various nature, including the avoidance of predators and parasites and securing access to shelter or resources. However, most existing studies investigated variation in cognitive performance related to experienced foraging challenges. In the following, we distinguish among challenges related to habitat exploration while searching and finding food, accessing food items, and memorizing previous resource locations, and summarize their associations with the degree of ecological specialization.

2.1 Habitat exploration while searching and finding food

Exploring different habitat types while searching for food may require different foraging techniques. More complex habitats with variable and unpredictable environments may require superior spatial learning abilities, allowing animals to flexibly adjust to these variable environments. Bats have been widely studied across habitats since their echolocation varies with landscape features (Schnitzler et al. 2003). Geoffroy's bats (*Myotis emarginatus*) and greater mouse-eared bats (*M. myotis*), which forage in more complex and less stable habitats, learned a complex spatial discrimination faster and showed more flexibility when reward contingencies changed, than long-fingered bats (*M. capaccinii*), which forage in simpler and more stable open water habitats (Clarín et al. 2013). Similarly, Cocos frillgobies (*Bathygobius cocosensis*) and Krefft's gobies (*B. krefftii*) that occur in

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spatially complex rock pool habitats performed better in a spatial learning test than Eastern long finned gobies (*Favonigobius lentiginosus*) and Hoese's sandgobies (*Istigobius hoesei*) occurring in homogenous sandy shores (White and Brown 2015). Also bank voles (*Myodes glareolus*), which occur in more complex habitats, exhibited better spatial search behavior than root voles (*Microtus oeconomus*), which occur in more open habitats (Pleskacheva et al. 2000). Moreover, omnivorous bank voles and herbivorous common voles (*M. arvalis*) were similar in their efficiency of exploiting stable habitats, but the omnivorous bank voles were more efficient in exploiting habitats with temporally changing food locations (Haupt et al. 2019). However, striped mice (*Rhabdomy pumillo*, *R. bechuanae*, *R. dilectus*) occurring in habitats of different complexity did not differ in spatial learning abilities, possibly due to phylogenetic constraints (Mackay and Pillay 2017). Finally, adapting to and persisting in urban landscapes have been suggested to be associated with behavioral flexibility in several species (Sih 2013; Sol et al. 2013; Ducatez et al. 2020b). However, Eastern blue-tongue skinks (*Tiliqua scincoides scincoides*) originating from urbanized areas did not perform better in a reversal learning task than sleepy lizards (*T. rugosa asper*) originating from rural areas (Szabo and Whiting 2020). Hence, variation in habitat complexity seems to covary with learning abilities in most cases, in particular spatial learning abilities and decision-making.

Regarding the search for food, animals use specific ranging behavior to track the spatio-temporal distribution of dietary items. By using specific navigational heuristics, i.e., decision rules applied to certain situations (Gigerenzer 2008), animals can improve their exploitation of the environment while reducing cognitive effort and energy expenditure. The use of such heuristics varies with the distribution of food items or the mobility of preferred food items. In primates, the more frugivorous Tonkean macaques (*Macaca tonkeana*) exhibited more goal directed search strategies while foraging than the less frugivorous long-tailed macaques (*M. fascicularis*) or capuchin monkeys (*Sapajus apella*; Trapanese et al. 2019). The mobility of food items also influenced search strategies in three lemur species (Teichroeb and Vining 2019). Fat-tailed dwarf lemurs (*Cheirogaleus medius*), which are specialized on stationary fruits, performed best in a multi-destination array with several feeding platforms. Their superiority was explained by efficient use of specific heuristics for exploration and feeder exploitation. In comparison, dietary generalist grey

mouse lemurs (*Microcebus murinus*), which feed on stationary food items like flowers and gum but also on mobile food items such as insects, used fewer heuristics. Aye-ayes (*Daubentonia madagascariensis*), which are specialized on mobile and ephemeral insect larvae, used basically no heuristics at all, resulting in greater explorative effort and lower cognitive task performance. Similarly, Saussure's long-nosed bats (*Leptonycteris yerbabuena*), which are specialized on nectar, foraged more efficiently in a feeder set-up with artificial flowers by revisiting the feeders less often and depleting them more than long-tongued bats (*Glossophaga soricina*), who complement their nectar and pollen diet additionally with fruits and insects according to seasonal availability (Henry and Stoner 2011). Thus, the reliance on more mobile food items seems to increase exploration, which results in lower task performance in spatial cognition tests.

Variation in cognitive performance is also associated with foraging style. In rodents, faster exploring mice (*Mus musculus*) learned contingencies between an auditory cue and a food reward or punishment differently than slower exploring rats (*Rattus norvegicus*). Both rodents could learn either of the reward contingency, i.e., to stay in the initial compartment or move to a second compartment, to receive a food reward. However, they were unable to overcome their baseline activity tendencies to avoid a punishment: the more active mice only reached the learning criterion when they had to move to the second compartment, while rats only reached the learning criterion when they had to stay in the initial compartment to avoid punishment (Jones et al. 2017). In reptiles, the actively foraging Bosc's fringe-toed lizard (*Acanthodactylus boskianus*) learned a visual reversal learning paradigm faster than the Nidua fringe-toed lizard (*A. scutellatus*), which is a sit-and-wait predator (Day et al. 1999a). Thus, a more proactive foraging style is consistently associated with superior performance in various cognitive tests.

2.2 Accessing food items

Once an animal has solved the problem of locating a given food patch, it encounters the next challenge: the extraction of the actual food item. Depending on the item's characteristics, superior sensorimotor coordination or manipulative skills, including extractive foraging techniques or tool use, are beneficial but also energetically more costly,

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and ultimately require a larger brain (Parker and Gibson 1977; Heldstab et al. 2016). Sensorimotor control and extractive foraging abilities seem to be especially helpful for solving innovative problems, and the majority of innovative behaviors has indeed been recorded in the foraging domain (Reader and Laland 2002). Indian mynas (*Acridotheres tristis*) which exhibited greater diversity in motor behaviors, were more innovative than noisy miners (*Manorina melanocephala*) (Griffin and Diquelou 2015). Madame Berthe's mouse lemurs (*Microcebus berthae*) that expressed better motor control than grey mouse lemurs, subsequently learned a modified innovative problem faster (Henke-von der Malsburg and Fichtel 2018). In seven species of callitrichid monkeys, the existence of extractive foraging techniques predicted innovative abilities, with lion tamarins (*Leontopithecus* spp.), which are manipulative extractive foragers with a higher innovative potential, exceeding the gum-specialized, extractive foraging marmosets (*Callithrix* spp.) and the non-extractive, but only visually foraging tamarins (*Saguinus* spp.) (Day et al. 2003). These examples suggests that efficient access to food sources can vary with cognitive abilities such as innovative behaviors, which also seemed to be influenced by motor coordination.

2.3 Memorizing previous resource locations

When animals are highly reliant on cached food or when they migrate to other habitats, usually due to seasonal food shortage (Wall and Stephen 1990; Dingle 2014), they require well developed spatial cognitive abilities. In both cases, animals with good spatial processing abilities are better at memorizing locations of food patches than animals with no or only basic spatial processing abilities (Shettleworth 1990; Sherry et al. 1992). For example, compared to non-migratory dark-eyed juncos (*Junco hyemalis carolinensis*), migratory dark-eyed juncos (*J. h. hyemalis*) showed greater accuracy in remembering feeder locations that have been visited only once before a certain retrieval interval (Cristol et al. 2003). Moreover, Merriam's kangaroo rats (*Dipodomys merriami*), intensive scatter hoarders, showed better spatial memory accuracy in a cache simulation task than Great Basin kangaroo rats (*D. microps*), leaf-eating specialists that do not rely on scatter-hoarding (Barkley and Jacobs 2007). Furthermore, food caching Clark's nutcrackers (*Nucifraga co-*

lumbiana) performed better in an initial spatial discrimination task than less food caching pinyon (*Gymnorhinus cyanocephalus*) and non-food caching Western scrub jays (*Aphelocoma californica*). Pinyon jays, however, performed better than the other two corvid species in serial reversal learning tasks (Bond et al. 2007) and Western scrub jays performed better in a distance discrimination task (Gibson and Kamil 2005). Thus, the reliance on food caching can co-vary with spatial memory, but not necessarily with other cognitive abilities.

Although primates do not rely on food-caching, spatial memory abilities can be beneficial for relocating a certain food patch. Indeed, chimpanzees (*Pan troglodytes*) that feed on more patchy distributed foods than bonobos (*P. paniscus*) exhibited better retrieval performance when food items were hidden by a human demonstrator (Rosati and Hare 2012). Similarly, lemurs varied in performance in spatial memory tasks according to their diet. The most frugivorous ruffed lemurs (*Varecia* spp.) showed better spatial memory than ring-tailed lemurs (*Lemur catta*), mongoose lemurs (*Eulemur mongoz*) and Coquerel's sifakas (*Propithecus coquereli*); the latter being the most folivorous species (Rosati et al. 2014). Wied's marmosets (*Callithrix kuhlii*) performed better than golden lion tamarins (*Leontopithecus rosalia*) in spatial memory experiments with relatively short retention intervals (5 or 30 min). However, they performed poorly after longer retention intervals (24 or 48 h), while the tamarins could maintain their performance level (Platt et al. 1996). Again, the observed interspecific differences match the species' foraging strategies: while marmosets revisit single food patches several times per day (Rylands 1989), tamarins do so only every three days (Peres 1989). Hence, spatial memory abilities also vary in accordance with a species-typical foraging ecology.

3 Ecological generalism versus ecological specialization

Empirical comparisons of cognitive performance between generalists and specialists have either investigated effective habitat exploration in, for instance, spatial memory tasks (Pleskacheva et al. 2000; Haupt et al. 2010), or specific foraging abilities like innovative propensities (Day et al. 2003; Overington et al. 2009; Overington et al. 2011; Griffin and Diquelou 2015; Henke-von der Malsburg and Fichtel 2018), associative learning (Hoedjes

Table 2.2 Overview of studies comparing cognitive abilities under certain ecological relevance, indicating the degree of ecological specialization (habitat/dietary) of the best performing species, as well as its group size as indicator for sociality and an indicator for brain size, each as relative measure to the species in comparison

Reference	Species	Best performance			Brain size
		Cognitive measure	Primary ecological relevance	Species	
Habitat exploration					
Bond et al. 2007	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Spatial discrimination	Habitat exploration: locating food patch	<i>N. columbiana</i> Habitat specialist Dietary specialist	Smaller (solitary/pair-living) ¹ <i>G. cyanocephalus</i> , smaller than <i>A. californica</i> (relative hippocampal volume to body mass) ²
sign - - - - 0/-					
Clarín et al. 2013	Long-fingered bat (<i>M. capaccinii</i>) Greater mouse-eared bat (<i>M. myotis</i>) Geoffroy's bat (<i>M. emarginatus</i>)	Spatial discrimination	Habitat exploration: locating food patch	No difference <i>M. capaccinii</i> : Habitat specialist Dietary generalist ³ <i>M. myotis</i> : Habitat generalist Dietary generalist ³ <i>M. emarginatus</i> : Habitat generalist Dietary specialist ³	Similar (males roost singly or in small colonies) Relative skull length: <i>M. capaccinii</i> < <i>M. emarginatus</i> < <i>M. myotis</i>
sign - - - - 0					
Clarín et al. 2013	Long-fingered bat (<i>M. capaccinii</i>) Greater mouse-eared bat (<i>M. myotis</i>) Geoffroy's bat (<i>M. emarginatus</i>)	Spatial reversal learning	Habitat exploration: modified food patch location	<i>M. myotis</i> <i>M. emarginatus</i> Habitat generalist Dietary generalist ³ <i>M. emarginatus</i> : Habitat generalist Dietary generalist ³	Not assigned (no difference in cognitive performance) Similar (males roost singly or in small colonies) Potentially larger (relative skull length)
sign + + + + 0					

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Clarín et al. 2013	Long-fingered bat (<i>M. capaccinii</i>)	Complex spatial discrimination	Habitat exploration: locating food patch	<i>M. myotis</i>	<i>M. myotis</i> : Habitat generalist Dietary generalist ³	Similar (males roost singly or in small colonies)	Potentially larger (relative skull length)
	Greater mouse-eared bat (<i>M. myotis</i>)			<i>M. emarginatus</i>	<i>M. emarginatus</i> : Habitat generalist Dietary generalist ³		
	Geoffroy's bat (<i>M. emarginatus</i>)						
Cristol et al. 2003	Two dark-eyed juncos (<i>J. h. hyemalis</i> , <i>J. h. carolinensis</i>)	Spatial memory accuracy	Habitat exploration: locating previous food items	<i>J. h. hyemalis</i>	Similar habitat/dietary specialization	Similar (group-living)	Smaller (fixed brain mass, telencephalon volume)
					sign + + + 0	0	+
Day et al. 1999	Nidua fringe-toed lizard (<i>A. scutellatus</i>)	Spatial memory accuracy	Habitat exploration: locating preferable sites	No difference (ecological irrelevance of the task)	Similar habitat/dietary specialization ^{4,5}	Similar (solitary)	Difference in relative medial/dorsal cortex volume ⁶
	Bosc's fringe-toed lizard (<i>A. boskianus</i>)				sign 0 0 0	0	-
Gibson & Kamil 2005	Pinyon jay (<i>G. cyanocephalus</i>)	Spatial discrimination	Habitat exploration: locating preferable sites	<i>G. cyanocephalus</i>	<i>G. cyanocephalus</i> : Habitat generalist Dietary generalist	Larger (flocks) ⁷	Similar for <i>G. cyanocephalus</i> , larger for <i>A. californica</i> (relative hippocampal volume to body mass) ²
	Clark's nutcracker (<i>N. columbiana</i>)			<i>A. californica</i>	<i>A. californica</i> : Habitat generalist Dietary generalist		
	Western scrub jay (<i>A. californica</i>)						
					sign + + +	+	0/+

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Gingins & Bshary 2016	Bluestreak cleaner wrasse (<i>L. dimidiatus</i>) other labrids (<i>P. hexataenia</i> , <i>H. melanurus</i> , <i>T. lunare</i> , <i>H. melapterus</i> , <i>L. unilineatus</i>)	Spatial discrimination	Habitat exploration: locating preferable sites	No difference (ecological irrelevance of the task)	<i>L. dimidiatus</i> : Dietary specialist Others: Dietary generalist	NA NA	NA
Haupt et al. 2010	Common vole (<i>M. arvalis</i>) Bank vole (<i>M. glareolus</i>)	Spatial memory	Habitat exploration: locating food patches	<i>M. glareolus</i>	Habitat generalist Dietary generalist	Smaller (solitary) ^{8,9}	NA
Haupt et al. 2010	Common vole (<i>M. arvalis</i>) Bank vole (<i>M. glareolus</i>)	Spatial memory	Habitat exploration: locating food patches	<i>M. glareolus</i>	Habitat generalist Dietary generalist	Smaller (solitary) ^{8,9}	NA
Jones et al. 2017	Sprague Dawley rat (<i>R. norvegicus</i>) D57BL/6j mouse (<i>M. musculus</i>)	Go/NoGo-Learning	Habitat exploration: locating preferable sites	Go-learning: <i>M. musculus</i> D57BL/6j NoGo-learning: <i>R. norvegicus</i>	NA NA	NA	NA

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Mackay & Pillay 2018	Three striped mice	Spatial learning	Habitat exploration: locating food patches	No difference (phylogenetically constrained)	Different ecological characteristics ¹⁰⁻¹²	<i>R. pumilio</i> : group-living ¹³ <i>R. bechuanae</i> : solitary <i>R. dilectus</i> : solitary ¹⁴	NA
	<i>R. pumilio</i>						
	<i>R. bechuanae</i>						
Pleskacheva et al. 2000	Bank vole	Spatial search	Habitat exploration: locating preferable sites	<i>M. glareolus</i>	Habitat generalist	Similar (solitary) ^{8,15}	Larger (relative brain mass, mossy fiber projection)
	<i>(M. glareolus)</i>						
	Root vole						
Teichroeb & Vining 2019	Grey mouse lemur	Spatial navigation	Habitat exploration: locating food patches	<i>C. medius</i>	Habitat generalist	Similar (solitary)	Smaller (relative brain mass to body mass) ¹⁶
	<i>(M. murinus)</i>						
	Fat-tailed dwarf lemur						
Trapanese et al. 2019	Aye-aye	Decision-making	Habitat exploration: choosing food patches	<i>(D. madagascariensis)</i>	Dietary specialist		
	Tonkean macaque						
	<i>(Macaca tonkeana)</i>						
Trapanese et al. 2019	Long-tailed macaque	Decision-making	Habitat exploration: choosing food patches	<i>M. fascicularis</i>	Habitat generalist to <i>S. apella</i> ^{17,18}	Larger	Larger (endocranial volume) ²⁰
	<i>(M. fascicularis)</i>						
	Capuchin monkey						
Trapanese et al. 2019	<i>(Sapajus apella)</i>						

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance				
				Species	Ecological lifestyle	Social organization	Brain size	
White & Brown 2015	Cocos frillgoby (<i>B. cocosensis</i>) Kreffft's goby (<i>B. krefftii</i>) Eastern long finned goby (<i>F. lentiginosus</i>) Hoesé's sandgoby (<i>I. hoesei</i>)	Spatial learning	Habitat exploration: locating food patches	<i>B. cocosensis</i> <i>B. krefftii</i>	NA NA	NA NA	Larger (relative telencephalon volume) ²¹	
Foraging								
Barkley & Jacobs 2007	Merriam's kangaroo rat (<i>D. merriami</i>) Great Basin kangaroo rat (<i>D. microps</i>)	Spatial memory accuracy	Foraging: food-caching	<i>D. merriami</i>	Similar habitat specialization Dietary specialist ^{22,23}	Similar (solitary) ²⁴	Larger (encephalization quotient) ²⁵	
Bednekoff & Balda 1996	Clark's nutcracker (<i>N. columbiana</i>) Mexican jay (<i>A. ultramarina</i>)	Observational spatial memory	Foraging: food-caching	<i>A. ultramarina</i>	Habitat generalist Dietary generalist ^{7,26}	Larger (flocks of several dozen)	NA	
				sign	0	-	0	+
				sign	+	+	+	NA

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance		
				Species	Ecological lifestyle	Social organization
Bond et al. 2007	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Visual discrimination	Foraging: identifying food item	No difference	<i>G. cyanocephalus</i> : Habitat generalist Dietary generalist <i>N. columbiana</i> : solitary/pair-living <i>A. californica</i> : Habitat specialist Dietary specialist <i>A. californica</i> : Habitat generalist Dietary generalist	<i>G. cyanocephalus</i> = <i>N. columbiana</i> < <i>A. californica</i> (relative hippocampal volume to body mass) ²
Bond et al. 2007	Pinyon jay (<i>G. cyanocephalus</i>) Clark's nutcracker (<i>N. columbiana</i>) Western scrub jay (<i>A. californica</i>)	Behavioral flexibility	Foraging: identifying food item	sign <i>G. cyanocephalus</i>	Not assigned (no difference in cognitive performance) Similar habitat/dietary specialization to <i>A. californica</i> <i>A. californica</i> Habitat generalist Dietary generalist to <i>N. columbiana</i>	Similar to <i>A. californica</i> , larger than <i>N. columbiana</i> , smaller than <i>A. californica</i> (relative hippocampal volume to body mass) ²
Day et al. 1999	Nidua fringe-toed lizard (<i>A. scutellatus</i>) Bosc's fringe-toed lizard (<i>A. boskianus</i>)	Visual discrimination	Foraging: identifying food item	No difference	sign 0/+ 0/+ 0/+ 0/+ 0/+	Difference in relative medial/dorsal cortex volume ⁶

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Day et al. 1999	Nidua fringe-toed lizard (<i>A. scutellatus</i>) Bosc's fringe-toed lizard (<i>A. boskianus</i>)	Behavioral flexibility	Foraging: identifying food item	<i>A. scutellatus</i>	Similar habitat/dietary specialization ^{4,5}	Similar (solitary)	Larger (relative medial/dorsal cortex volume) ⁶
Day et al. 2003	Lion tamarin (<i>Leontopithecus</i> spp.) Tamarin (<i>Saguinus</i> spp.) Marmoset (<i>Callithrix</i> spp.)	Innovative problem-solving	Foraging: food extraction	<i>Leontopithecus</i> spp.	Habitat specialist Dietary generalist	Intermediate (group-living)	Intermediate (encephalization quotient) ²⁷
Griffin & Diquelou 2015	Indian myna (<i>A. tristis</i>) Noisy myner (<i>M. melanocephala</i>)	Innovative problem-solving	Foraging: food extraction	<i>A. tristis</i>	Habitat generalist Dietary generalist	Smaller (pair-living)	Smaller (lower positive residuals of brain size)
Healy & Suhonen 1996	Willow tit (<i>P. montanus</i>) marsh tit (<i>P. palustris</i>)	Food retrieval performance	Foraging: food-caching	No difference (unsuitable study design)	Similar habitat/dietary specialization ^{28,29}	Similar (pair-living) ^{28,29}	Relative hippocampal formation volume larger in <i>P. palustris</i> than <i>P. montanus</i> ³⁰
				sign	0	0	+
				sign	-	+	0
				sign	+	+	-
				sign	+	-	-
				sign	Not assigned (no difference in cognitive performance)		

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Henke-von der Malsburg & Fichtel 2018	Grey mouse lemur (<i>M. murinus</i>) Mme Berthe's mouse lemur (<i>M. berthae</i>)	Innovative problem-solving	Foraging: food extraction	<i>M. berthae</i>	Habitat specialist Dietary specialist	Similar (solitary) ³¹	NA
Henry & Stoner 2011	Saussure's long-nosed bat (<i>L. yerbabuena</i>) Palla's long-tongued bat (<i>G. soricina</i>)	Spatial working memory	Foraging: exploiting food patches	<i>L. yerbabuena</i>	Habitat generalist Dietary specialist ^{32,33}	Larger (colonies of up to tens of thousands)	NA
Hoedjes et al. 2012	3 wasps (<i>N. vitripennis</i> , <i>N. longicornis</i> , <i>N. giraulti</i>)	Olfactory memory	Foraging: memorizing food patch (here: host)	<i>N. vitripennis</i>	Host generalist	NA	NA
Platt et al. 1996	Wied's marmoset (<i>C. kuhlii</i>) Golden lion tamarin (<i>L. rosalia</i>)	Spatial memory retention	Foraging: food retrieval after a relatively short period (5 or 30 min)	<i>C. kuhlii</i>	Habitat generalist Dietary specialist ³⁴	Smaller ³⁴	Potentially smaller (encephalization quotient) ²⁷
				sign	+	+	-

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Platt et al. 1996	Wied's marmoset (<i>C. kuhlii</i>)	Spatial memory	Foraging: food retrieval after a relatively long period (24 or 48 h)	<i>L. rosalia</i>	Habitat specialist Dietary generalist ³⁴	Larger ³⁴	Potentially larger (encephalization quotient) ²⁷
	Golden lion tamarin (<i>L. rosalia</i>)	retention					
Rosati & Hare 2012	Chimpanzee (<i>P. troglodytes</i>)	Spatial working memory	Foraging: food retrieval	<i>P. troglodytes</i>	Similar habitat/dietary specialization ³⁵	Similar (group-living) ³⁵	Larger hippocampus, greater connection with other brain regions ³⁵
	Bonobo (<i>P. paniscus</i>)	memory					
Rosati et al. 2014	Ruffed lemur (<i>Varecia</i> spp.)	Spatial memory	Foraging: food retrieval	<i>Varecia</i> spp.	Dietary specialist (note: another dietary specialist performed the worst, two dietary generalist species performed on an intermediate level)	Medium	Smaller (relative brain mass to body mass) ¹⁶
	Ring-tailed lemur (<i>L. catta</i>)	retention					
	Mongoose lemur (<i>E. mongoz</i>)						
	Coquerel's sifaka (<i>P. coquereli</i>)						
				sign	0	0	0
				sign	NA	-	0
				sign	NA	0	-

Table 2.2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance			
				Species	Ecological lifestyle	Social organization	Brain size
Szabo & Whiting 2020	Sleepy lizard (<i>T. r. asper</i>) Eastern blue-tongue skink (<i>T. s. scincooides</i>)	Visual discrimination	Foraging: identifying food patch	No difference	<i>T. r. asper</i> : Habitat generalist Dietary generalist <i>T. s. scincooides</i> : Habitat specialist Dietary specialist	<i>T. r. asper</i> : pair-living <i>T. s. scincooides</i> : solitary	NA
				sign	Not assigned (no difference in cognitive performance)		
Szabo & Whiting 2020	Sleepy lizard (<i>T. r. asper</i>) Eastern blue-tongue skink (<i>T. s. scincooides</i>)	Behavioral flexibility	Foraging: identifying food patch	<i>T. r. asper</i>	Habitat generalist Dietary generalist	Larger (pair-living)	NA
				sign	+	+	+

Studies are grouped after the ecological relevance of the task being rather linked to habitat exploration or foraging. The type of specialization crucial for the ecological relevance is underlined. Below each study, the respective sign used in the sign-test is given, where a plus (+) means that the best performing species is relatively more habitat (left) and/or dietary (right) generalist, lives in relatively larger groups or has a relatively bigger brain (or higher value in the according brain size measure) and vice versa for a minus (-). In case the specie was intermediate, or the compared species do not differ in these variables, we assigned a zero (0). Superscript numbers link to references used to complement the respective variables. NA indicates not available data

¹Clary and Kelly 2011; ²Pravosudov and De Kort 2005; ³Dietz and Kiefer 2016; ⁴Aicha et al. 2017; ⁵Roobas and Feulner 2013; ⁶Day et al. 1999b; ⁷Bond et al. 2007; ⁸Lundrigan and Mueller 2003; ⁹Noble 2017; ¹⁰Meynard et al. 2012; ¹¹Du Toit et al. 2016a; ¹²Ganem et al. 2020; ¹³Schradin and Pillay 2004; ¹⁴Ganem et al. 2012; ¹⁵Bieberich 2007; ¹⁶MacLean et al. 2009; ¹⁷Boubli et al. 2020; ¹⁸Riley et al. 2020; ¹⁹Eudey et al. 2020; ²⁰Heldstab et al. 2016; ²¹White and Brown 2015b; ²²Timm et al. 2016; ²³Cassola 2016; ²⁴Howard 1994; ²⁵Hafner and Hafner 1984; ²⁶McCormack and Smith 2008; ²⁷Hartwig et al. 2011; ²⁸BirdLife International 2017; ²⁹BirdLife International 2019; ³⁰Lucas et al. 2004; ³¹Dammhahn and Kappeler 2005; ³²Cole and Wilson 2006; ³³Alvarez et al. 1991; ³⁴Day et al. 2003; ³⁵Rosati 2017b

et al. 2012), or behavioral flexibility (Day et al. 1999a), using a variety of problem-solving experiments, including food extraction tasks, visual or olfactory discriminations, or reversal learning tasks.

3.1 Habitat exploration and the degree of habitat specialization

Occurring across larger and more complex areas, habitat generalists would benefit from advanced navigational strategies to efficiently explore these areas, specifically when they feed on patchy distributed but potentially predictable food sources. The habitat generalist bank vole, for instance, showed increased spatial memory compared to the more specialized root vole (Pleskacheva et al. 2000). In lemurs, the species with greater habitat specialization performed better in the spatial memory task due to more efficient use of navigational heuristics (Teichroeb and Vining 2019). In bats, Saussure's long-nosed bats, a relative habitat generalist, exhibited more efficient feeder exploitation than the sympatric but more specialized long-tongued bats (Henry and Stoner 2011). Similarly, the relative habitat generalists, the greater mouse-eared and Geoffroy's bats, learned a complex visual discrimination faster and were more flexible in a reversal learning task than the most specialized long-fingered bat (Clarín et al. 2013).

Migratory vertebrates tend to be more habitat specialists than generalists, possibly because they need to disperse further to find a habitat patch with suitable conditions (Martin and Fahrig 2018). In a comparative study on spatial memory accuracy in two junco subspecies (Cristol et al. 2003), the migratory subspecies performed better than the residential subspecies. However, since both subspecies rely on comparable diets and occur in similar habitats throughout the year, and due to a lack of data on population densities and different habitat types, it is neither possible to calculate a species specialization index (Martin and Fahrig 2018), nor to classify the migratory subspecies as more specialized than the residential one. Overall, one may argue, however, that the degree of habitat specialization tends to covary with spatial memory accuracy, learning flexibility and decision-making.

3.2 Foraging and the degree of dietary specialization

Food storing or caching can be considered as a behavioral adaptation to variable resource abundance. While a positive link between these behaviors and spatial memory abilities has been reported (Clayton and Krebs 1994a, b; Bednekoff et al. 1997), it is not clear how the degree of ecological generalism may fit into this relationship. The aforementioned example on spatial memory accuracy in a cache simulation task reported the better performing kangaroo rat to be a leaf-eating specialist (Barkley and Jacobs 2007), but others classified them as less specialized because they also, although more rarely, feed on seeds like other kangaroo rats (Cassola 2016; Timm et al. 2016), indicating that the classification into generalists and specialists is not always straightforward.

The degree of dietary breadth was related to discriminative learning abilities in a comparative study of parasitic wasps. The more dietary generalists (*Nasonia vitripennis*, *N. longicornis*) learned an association between an odor and a rewarding host better than the more specialized *N. giraulti* (Hoedjes et al. 2012). Also, the dietary generalist bank vole performed better in a spatial learning task with temporally changing food locations than the more dietary specialist common vole (Haupt et al. 2010). Hence, dietary generalism seems to covary with discriminative and spatial learning abilities.

Individuals with greater innovative abilities are also expected to deal more efficiently with changing environmental conditions, including diet (Sol et al. 2005a). Since generalist species are by definition exposed to more variable conditions, they are suggested to express greater behavioral flexibility and greater innovative propensities than specialists (Ducatez et al. 2015; Navarrete et al. 2016). Among birds, habitat generalist species have indeed higher innovation rates than habitat specialists (Overington et al. 2011). Moreover, the omnivorous Indian myna showed a higher innovative propensity than the noisy miner, which is specialized on honey (Griffin and Diquelou 2015). In contrast, the more dietary and habitat specialized Madame Berthe's mouse lemur outperformed the sympatric generalist gray mouse lemur in innovative extractive foraging tasks with variable difficulties (Henke-von der Malsburg and Fichtel 2018). The better performance of the specialist might have been a result of enhanced executive control enabling individuals to inhibit the use of a previously learned problem-solving technique and to develop an adjusted solution to a modified problem, indicating that other factors

Chapter II: Literature review

than ecological specialization may explain variation in performance. Across primates, however, performance in inhibitory control tests was best predicted by absolute brain size and dietary breadth, suggesting that species differences in dietary specialization might indeed be related to levels of self-control (MacLean et al. 2014). Hence, dietary specialization seems to covary with learning ability, spatial learning, and inhibitory control.

In general, cognitive performance can be related to the degree of ecological specialization. Eighteen of the interspecific comparisons reviewed here report cognitive differences between species expressing a different degree of habitat specialization, while five do not (sign-test: $p = 0.011$). By trend, habitat generalists ($N = 13$) were more likely to outperform habitat specialists ($N = 5$; sign-test: $p = 0.064$). Twenty-one of the comparisons report cognitive differences between species expressing a different degree of dietary specialization while three do not (sign-test: $p < 0.001$). However, the degree of dietary specialization could not explain interspecific variation in cognitive performance (sign-test: $N_{\text{generalist}} = 13$, $N_{\text{specialist}} = 8$, $p = 0.383$).

4 Variation in cognitive performance in relation to group size

Because performance in cognitive tests in these studies might be explained by consistent differences in sociality, we scored the species included in this review with respect to their group size to index their social complexity (Table 2.2). While half of the comparisons ($N = 12$) controlled for group size effects, the other half ($N = 12$) compared species living in differently sized groups, which also exhibit interspecific cognitive variation. However, we do not find species living in larger groups to generally perform better than those living in smaller groups, which might also be due to our small sample size (sign-test: $N_{\text{larger}} = 7$, $N_{\text{smaller}} = 5$, $p = 0.774$).

Five studies supported a positive link between group size and cognitive performance: Mexican pinyon, as well as Western scrub jays, which live in larger flocks, performed better in spatial learning paradigms than Clark's nutcrackers (Bednekoff and Balda 1996; Gibson and Kamil 2005), Saussure's long-nosed bats, which form larger

colonies, performed better in a spatial working paradigm than Palla's long-tongued bats (Henry and Stoner 2011), pair-living sleepy lizards were more behaviorally flexible in a visual reversal learning task than solitary Eastern blue-tongue skinks (Szabo and Whiting 2020), and golden lion tamarins, which live in relatively larger groups, showed better memory retention for longer retention intervals than Wied's marmosets (Platt et al. 1996). However, Wied's marmosets outperformed golden lion tamarins in the same task using a shorter retrieval period (Platt et al. 1996). In lemurs, performance in a spatial memory task was not linearly related to group size across four species (Rosati et al. 2014). Moreover, in innovative problem-solving paradigms, primates living in intermediate-sized (Day et al. 2003) or birds living in smaller groups (Griffin and Diquelou 2015) outperformed the respective species living in relatively larger groups.

Based on the currently available evidence, it is therefore not possible to determine whether sociality covaries with cognitive performance scores in these studies. First, we set the focus on studies comparing species with variation in ecological adaptations, which were not designed to compare species with different group size. Second, we indexed sociality in terms of group size, but disregarded group composition, stability, cohesion, or hierarchy. Finally, most of the cognitive tests were not explicitly designed to have any functional relevance in terms of sociality or variation in social traits, so that a correlation with performance scores is unlikely. Hence, to address the relative importance of either ecological or social factors driving the evolution of brain size, comprehensive cognitive test batteries addressing both sets of factors are required (Shaw and Schmelz 2017; Völter et al. 2018; Fichtel et al. 2020).

5 Variation in cognitive performance in relation to brain size

Brain size can be assessed via absolute or relative brain mass or volume, via an encephalization quotient (Jerison 1973; Hartwig et al. 2011), or neural connectivity, for instance. Since the studies included in this review were not designed to compare potential effects of a certain brain size measure, we had to find comparable measures or proxies elsewhere (Table 2.2). With this information, we did not find evidence for a link between experimental cognitive performance and brain size in this sample (sign-test: $N_{\text{bigger}} = 10$,

$N_{\text{smaller}} = 7$, $p = 0.629$). Since the available brain size measures differed between these relatively few studies, the observed lack of an effect of brain size on cognitive performance might reflect this methodological shortcoming.

6 Discussion

In this review, we summarized comparative research investigating variation in cognitive performance in relation to specific adaptations to ecological factors animals are exposed to in their daily life. Although these ecological factors can vary greatly among species in the same taxonomic group, studies systematically investigating the relationship between ecological factors and cognitive performance are still rare. Most studies reported a predicted relationship between the measured cognitive performance and an ecological factor differentiating the study species (Table 2.1), but we cannot know whether this pattern is affected by a publication bias against studies reporting no effect. Our rough control indicated that phylogeny as well as group and brain size did not have pervasive effects on the observed pattern. Nonetheless, some studies failed to find an effect of ecology, perhaps due to unsuitable study designs (Bednekoff and Balda 1996; Healy and Suhonen 1996) and/or ecological irrelevance of the respective cognitive ability tested (Day et al. 1999a; Gingins and Bshary 2016). Below, we discuss the main correlates of interspecific variation in cognitive performance in terms of flexible foraging strategies, spatiotemporal habitat exploration and food patch exploitation, as well as the degree of ecological specialization. Further, we highlight the importance of considering potentially confounding factors when designing a study appropriate for the investigation of species-specific ecological adaptations (Shaw and Schmelz 2017; Schubiger et al. 2020).

6.1 Adaptations to ecological factors correlate with cognitive performance

6.1.1 Flexible foraging strategies

Interspecific differences in cognitive performance have been reported as a function of variation in ranging behavior and search strategies (Trapanese et al. 2019; Teichroeb and

Vining 2019), foraging activity (Day et al. 1999a; Day et al. 2003; Jones et al. 2017), foraging techniques (Day et al. 2003), characteristics of preferred dietary items (Pleskacheva et al. 2000; Henry and Stoner 2011; Teichroeb and Vining 2019), adaptations to habitat complexity (Pleskacheva et al. 2000; Clarin et al. 2013; White and Brown 2015a), or adaptations to seasonality (Cristol et al. 2003; Barkley and Jacobs 2007; Henry and Stoner 2011) (Fig. 2.2). Active or manipulative extractive foragers have been reported to learn more flexibly (Day et al. 1999a) or to be more innovative (Day et al. 2003), respectively. Flexible learning and innovative abilities can be linked in innovators that possess the ability to invent a new behavior or to modify an existing behavior (Reader and Laland 2003) and to incorporate these into the behavioral repertoire via flexible learning

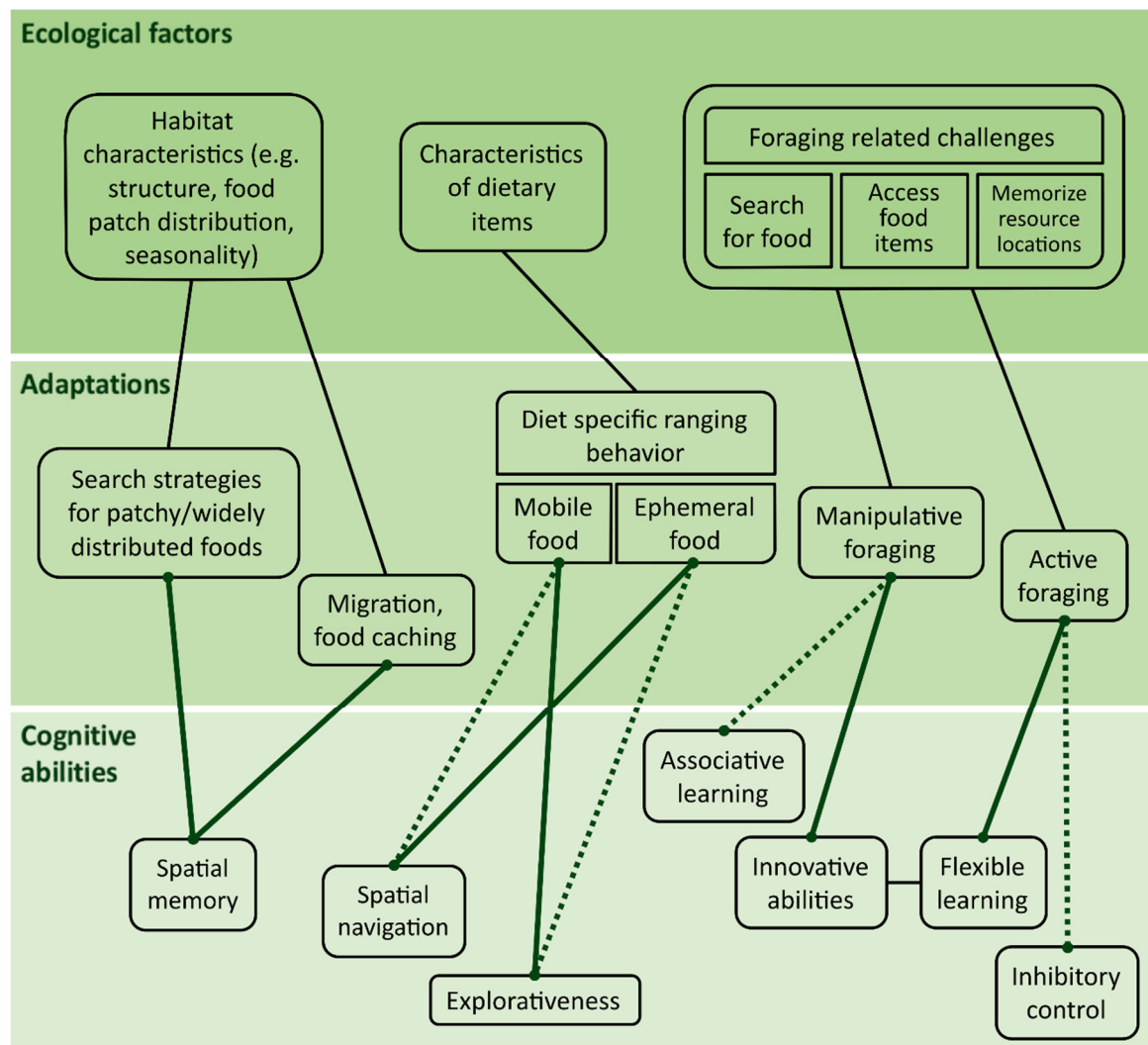


Fig. 2.2 Links between ecology and cognition. We identified several links (thick lines) between cognitive abilities and adaptations to ecological factors (thin lines) such as certain habitat characteristics, characteristics of dietary items or ecological challenges related to the foraging process (including the search for food, access to food items and memorizing resource locations). Positive relationships between specific adaptations and cognitive abilities are represented with thick solid lines while negative relationships are represented with dashed lines

mechanisms (Dukas and Ratcliffe 2009). In contrast to sit-and-wait predators, active foragers need to rapidly adjust the current foraging strategy to the behavior of the prey of interest as well as to the environment while searching and hunting for prey. They would specifically benefit by learning the association of a certain stimulus with a reward (i.e., the prey) and to flexibly update such associations whenever the stimulus or other conditions change. This underlying behavioral flexibility is then an advantageous characteristic when environmental conditions change (Lee 2003; Lefebvre et al. 2004). Further, innovations appear predominantly in the foraging context (Reader and MacDonald 2003), favoring a link with a species' foraging ecology rather than with its sociality.

6.1.2 Spatiotemporal habitat exploration and food patch exploitation

When searching for food, animals always need to deal with the trade-off between habitat exploration and food patch exploitation (Hills et al. 2015). The decision of when to switch from one to the other varies with the spatiotemporal distribution of food items since this determines the energetic costs of habitat exploration and energy intake during patch exploitation. Habitat exploration is particularly costly when food items are sparse or patchy distributed or when food abundance is (seasonally) low. Using specific navigational heuristics or investment in spatial memory can reduce foraging costs under these conditions. However, the underlying capacities are energetically constrained and should, therefore, evolve in species that feed on stationary rather than mobile food items, on dispersed rather than highly abundant items, or in species, that are exposed to harsh environments (Roth and Pravosudov 2009).

Also, when relocating a certain food patch, irrespective of the length of a retrieval interval, the energetic investment in spatial memory capacities can be beneficial. At least in birds, rodents, and primates, there is evidence that the evolution of spatial memory abilities parallels a species-specific foraging ecology. Better spatial cognition has been reported for species feeding on dispersed items of rather unpredictable abundance (Platt et al. 1996; Pleskacheva et al. 2000; Rosati and Hare 2012; Clarin et al. 2013), frugivorous species (Rosati et al. 2014; Trapanese et al. 2019; Teichroeb and Vining 2019), scatter hoarders (Barkley and Jacobs 2007) or migrating species (Cristol et al. 2003). In such cases,

better-adapted species evolve greater hippocampi as an adaptation to the highly demanding ecological challenge of memorizing previous food locations or caches.

6.1.3 Other ecological adaptations

Evidence for a general association between cognitive performance and ecological factors might be biased since most studies measuring interspecific variation conducted experiments on only a few cognitive skills such as spatial processing, flexible learning or innovative problem-solving. It remains to be investigated, however, whether other cognitive tasks, such as those estimating the ability of causal reasoning or numerical understanding, or a combination of different tasks in a valid test battery can also be linked to ecological factors (Shaw and Schmelz 2017). Also, the potential effects of other ecological factors, such as predation and parasite risk, on relevant cognitive abilities remains largely unstudied (Garamszegi et al. 2007; Soler et al. 2012). Thus, there is a need for additional studies to obtain a more comprehensive understanding of the ecology-cognition link.

6.2 How does cognitive performance correlate with the degree of ecological specialization?

In several studies we found the degree of ecological specialization to be correlated with variation in certain cognitive abilities (Platt et al. 1996; Pleskacheva et al. 2000; Day et al. 2003; Barkley and Jacobs 2007; Haupt et al. 2010; Henry and Stoner 2011; Hoedjes et al. 2012; Rosati et al. 2014; Griffin and Diquelou 2015; Henke-von der Malsburg and Fichtel 2018). We found that habitat generalists were likely to outperform habitat specialists, but this relation was not significant and the degree of dietary specialization did not consistently covary with cognitive performance. Given, that habitat generalists regularly face more challenges by exploring a broader, more variable habitat than specialists, they might specifically exhibit better spatial processing abilities and more behavioral flexibility (Overington et al. 2011); at least in the sense of 'behavioral flexibility' allowing for adaptations to variable environments (Lea et al. 2020). However, behavioral flexibility

does not necessarily result in better cognitive performance *per se* because less behaviorally flexible species, as specialists, may instead possess other behavioral characteristics that promote better performance in certain cognitive skills (Henke-von der Malsburg and Fichtel 2018). In studies reporting the more specialized species to exhibit better performance than the generalist (e.g. Teichroeb and Vining 2019), better performance was linked to specific adaptations for habitat exploration or exploitation. In this context, efficiency can be of various nature: to not use certain paths multiple times while foraging, to deplete a certain food patch to a certain extent varying with search decision rules (Wilke et al. 2009), or to not use ineffective solutions but to inhibit the execution of related behaviors. Greater efficiency might be more likely to vary with specific adaptations to certain ecological challenges than to the degree of ecological specialization *per se* and would require a more detailed investigation than the currently available evidence allows.

6.3 Confounding factors and limitations of the review

Several factors may confound a putative relationship between a particular ecological factor and a corresponding cognitive ability. First, the cognitive trait under study must have ecological relevance. This problem becomes apparent for example in a study designed to compare cognitive abilities in an ecologically non-relevant context, i.e., spatial discrimination abilities across six species of labrid fishes (Gingins and Bshary 2016). Because these cleaner fish do not rely on advanced spatial abilities, as they do not actively search for food patches but are visited by parasitized client fish, it is not surprising that they exhibited similar performances when associating a food source with a location.

Second, social factors that differ systematically between species may obscure the effects of ecological factors on cognitive abilities. For example, more social Mexican jays performed better than food-caching Clark's nutcrackers in a spatial memory task in which the birds' recovery performance of food caches made by conspecifics was measured (Bednekoff and Balda 1996). Similarly, of three corvid species, pinyon jays, who live in the most socially complex environment, performed better in a reversal learning task than Clark's nutcrackers and Mexican jays with a more generalist ecology (Bond et al. 2007).

Finally, given the currently available sample size of studies meeting our criteria, the purported link between ecological specialization and cognitive performance might reflect a publication bias. Comparisons of mostly mammals (especially primates) and birds, and the focus on ecological challenges related to foraging may also create a bias. Nonetheless, we hope that the present review will stimulate more comparative research regarding this interesting topic, using additional taxa and, most importantly, a wider range of ecologically relevant cognitive traits to draw firm conclusions about the relative importance of various ecological factors in shaping cognitive abilities.

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Appendix 1

Table S1-1 Definitions and explanations of cognitive terms.

General terms	
Cognitive ability	Ability to perceive, process and memorize information from the environment or other individuals.
Decision-making	Determination of an action considering environmental cues and experience.
Learning	Any change in behavior as result of experience; operationalized by an increase in performance.
Cognitive task performance	Operationalization for an individual's learning abilities, often measured as success latency or ratio to solve a problem.
Problem-solving ability	Ability to solve problems incorporating objects (i.e., inanimate objects, food), e.g., puzzle box, object manipulation test.
General intelligence (<i>g-factor</i>)	Composite factor derived from correlating cognitive performances across various cognitive tasks.
Cognitive test battery	Array of at least two different cognitive tasks; often conducted to investigate correlations between cognitive abilities.
Cognitive abilities related to perception	
Discrimination learning	Learning contingencies between events via conditioning. In a visual discrimination learning task, usually objects differing in shape, color, pattern, and/or location serve as stimuli, of which only one is associated with a reward. Performance is measured as trials or time until a specified learning criterion is reached.
Reversal learning	Reversed learning after an initial discrimination learning with the previously rewarded stimulus becoming unrewarded.
Numerical learning	Learning of contingencies in relation with numbers, e.g., the ability to discriminate between quantities.
Cognitive abilities related to processing	
Behavioral flexibility	Ability to flexibly adjust the behavior according to the actual circumstances.
Innovation	Solution to a novel problem or novel solution to a modified problem; operationalized using problem-solving tasks.
Causal reasoning	Cognitive ability to relate two events with each other using causal understanding instead of arbitrary contingencies like space or time; operationalized using, e.g., a string-pulling task where pulling a string should be related to getting access to an attached reward.
Tool use	Behavior in which an animal uses a secondary object as a specific tool to solve a given problem.

Table S1-1 (continued)

Cognitive abilities related to memory	
Shor-term memory	Holding information that is currently being processed, e.g., the memorization of a certain learning contingency from one experimental session to the other.
Long-term memory	Relatively persistent storing of information; can be manifested via several repetitions.
Spatial memory	Holding specifically spatial information; operationalized, e.g., using a maze with several end locations of which only one holds the rewarded stimulus, or using a cache simulation task, where the subject can relocate a hidden food reward after a certain retention interval.
Cognitive abilities in social contexts	
Social learning	Changes in an individual's behavior resulting from attending to another individual's behavior or its products.
Recognition memory	Memory capacities to recognize other individuals.
Transitive inference	Deductive reasoning allowing to derive a relation between items or individuals that have not been explicitly compared before. I.e., if A is related to B and B is related to C, then A must also be related to C.
Tactical deception	Usage of a behavior in an unusual context that is likely to be misinterpreted by other individuals.
Individual characteristics that could affect problem-solving performance	
Personality trait	Behavior that is consistent across time and space. E.g., exploration as the tendency to explore an unknown arena over a short time interval.
Persistence	Perseverance of a certain behavior despite its inefficiency; often operationalized by measuring the manipulative effort towards a puzzle box with a blocked opening mechanism.
Executive/Inhibitory /Self-control	Ability to inhibit a prepotent behavior due to its (temporary) inefficiency; operationalized using, for example, a detour reaching task with a transparent cylinder.

Electronic supplementary material

The online version contains the literature search records as supplementary material and is available at <https://doi.org/10.1007/s00265-020-02923-z>

Chapter III: Empirical study

Linking cognition to ecology in wild sympatric mouse lemur species

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Abstract

Cognitive abilities covary with both social and ecological factors across animal taxa. Ecological generalists have been attributed with enhanced cognitive abilities, but which specific ecological factors may have shaped the evolution of which specific cognitive abilities remains poorly known. To explore these links, we applied a cognitive test battery (two personality, ten cognitive tests; N = 1,104 tests) to wild individuals of two sympatric mouse lemur species (N = 120 *Microcebus murinus*, N = 34 *M. berthae*) varying in ecological adaptations but sharing key features of their social systems. The habitat and dietary generalist gray mouse lemurs were more innovative and exhibited better spatial learning abilities; a cognitive advantage in responding adaptively to dynamic environmental conditions. The more specialized Madame Berthe's mouse lemurs were faster in learning associative reward contingencies; providing relative advantages in stable environmental conditions. Hence, our study revealed key cognitive correlates of ecological adaptations and indicates potential cognitive constraints of specialists that may help explain why they face a greater extinction risk in face of current environmental changes.

1 Background

The evolution of cognitive abilities has been linked to variation in brain size, which covaries across species with social factors (*Social Intelligence Hypothesis*; Humphrey 1976) and/or ecological challenges (*Ecological Intelligence Hypothesis*; Parker and Gibson 1977). Recent comparative analyses across primates suggested that evolutionary variation in brain size is better predicted by ecological than social factors (DeCasien et al. 2017). Yet, little is known about whether and how these factors are linked to performance in cognitive tests in primates, but also across other taxonomic groups (Ashton et al. 2018b; Henke-von der Malsburg et al. 2020). Hence, to better understand the evolution of cognitive abilities and the underlying variation in brain size, studies of how variation in specific ecological or social factors are linked to performance in cognitive tests across taxa are required.

In this context, the degree of ecological specialization has been suggested to covary with cognitive abilities (*Opportunistic Intelligence Hypothesis*; Parker 1978). This notion builds upon the idea of characterizing a species' ecological niche as a multidimensional

space that combines all adaptations to ecological conditions that contribute to its evolutionary success (Hutchinson 1953). Accordingly, an ecological generalist experiences a wider niche breadth than a specialist (Sargeant 2007).

Generalist species are assumed to be better and more flexible learners than specialists (Overington et al. 2011; Mettke-Hofmann 2014). Since generalists should be exposed to a greater variety of ecological conditions, they may also face a greater variety of ecological problems. Hence, they may have evolved specific innovative problem-solving abilities to overcome various problems. Similarly, the diverse ecological conditions may create a need for greater behavioral flexibility, especially, when conditions change unexpectedly (Lea 2020). Hence, species that experience harsher or more dynamic environmental conditions are more flexible or more innovative than others (Tebbich et al. 2016). Innovative abilities and flexibility, therefore, appear to be tightly linked (Griffin 2016). Furthermore, innovation appears to be positively correlated with other cognitive abilities (Reader et al. 2011). In addition, more innovative or behaviorally flexible species experience greater colonization success (Sol et al. 2002) or a greater diversification potential (Nicolakakis et al. 2003). Both evolutionary processes have been linked to the evolution of larger brains, especially when colonizing seasonal regions (Ducatez et al. 2020b). Finally, dietary generalists have indeed larger brains than dietary specialists (Lefebvre et al. 2004; Sol et al. 2005b; MacLean et al. 2014). Despite these suggestive links, generalists, do not consistently perform better in cognitive tests than specialists, however (Henke-von der Malsburg et al. 2020).

To systematically examine covariation between cognitive abilities and the degree of ecological specialization, we applied a comprehensive cognitive test battery to wild individuals of two mouse lemur species (*Microcebus* spp.) that vary in some of their ecological adaptations but share key features of their social systems. Gray (*M. murinus*, GML) and Madame Berthe's mouse lemurs (*M. berthae*, MBML) represent separate lineages within the genus *Microcebus* that shared a common ancestor as long as 9-10 MA ago (Yoder et al. 2016). The comparison of these two species is informative because they are both nocturnal solitary foragers that are syntopic, and therefore experience identical current environmental conditions, but MBML is ecologically more specialized (Dammhahn and Kappeler 2005; Dammhahn and Kappeler 2008b). Such direct

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comparisons of cognitive performance in pairs of sympatric sister species can help to reveal the role of ecological factors in the evolution of cognition.

GML inhabit various habitat types across Western Madagascar, occur in primary as well as secondary forests, and even in highly degraded forest fragments (Lahann et al. 2006; Andriatsitohaina et al. 2020), making them habitat generalists. Their feeding niche breadth, based on Levin's standardized index, has been estimated as 0.63 (Dammhahn and Kappeler 2008b), supporting this classification. MBML occur only in a few km² of seasonally dry deciduous lowland forests (Schäffler and Kappeler 2014) and have an annual feeding niche breadth of 0.12 (Dammhahn and Kappeler 2008b), qualifying them as habitat specialists. As the smallest living primates, they are also more sensitive to natural and anthropogenic habitat modifications (Schäffler and Kappeler 2014), markedly decreasing their population size in recent years (Schäffler et al. 2021), and justifying their classification as "Critically Endangered" (Markolf et al. 2020).

Using a comprehensive test battery with ten cognitive tests and two standard personality tests, we compared cognitive abilities of these two species. In a total of 1,104 tests, we tested $N = 120$ GML and $N = 34$ MBML. As ecologically relevant abilities, we chose variation in exploration and neophilia, innovative propensities, persistence, learning abilities regarding associative and flexible learning using visual and spatial cues, and spatial memory. To also examine cognitive performances in tasks without obvious ecological relevance (Henke-von der Malsburg et al. 2020), i.e., cognitive abilities that are not expected to covary with the degree of ecological specialization, we assessed variation in inhibitory control, means-end understanding and goal directedness (see Appendix 2 for justification and predictions, Fig. 3.1). Finally, we examined whether cognitive performance across tests loads onto one common general intelligence (G/g -)factor (Humphreys 1979; Deaner et al. 2006).

2 Materials and Methods

2.1 Study site and study period

We conducted this study in Kirindy Forest, a dry deciduous lowland forest in central western Madagascar within a 12,500 ha forest concession operated by the Centre National

de Formation, d'Études et de Recherche en Environnement et Foresterie (CNFEREF) Morondava. Mouse lemurs at Kirindy Forest have been captured on a monthly basis as part of an ongoing long-term project (Dammhahn and Kappeler 2005; Kraus et al. 2008). We captured GML (N = 120) in a population that has been regularly monitored since 1993 (Eberle and Kappeler 2002) and MBML (N = 34) in another population that has been monitored since 2002 (Dammhahn and Kappeler 2005) (see Appendix 2 for the details of the capture procedure). Between 2017 and 2019, we conducted experiments with wild animals in temporary short-term captivity across three field seasons covering the transitions from the wet to the dry season (March – May/June) and the transitions from the dry to the wet season (August – October/November), respectively.

2.2 Study animals: Housing and experimental test battery

In the following, we briefly describe the experimental procedure and the general statistical analyses. Detailed information about sample sizes, experimental set-ups, statistical analyses and repeatability analyses are provided in the Appendix 2.

At the field station, individually marked mouse lemurs were housed in cages of 80 cm x 80 cm x 80 cm equipped with a nest box, several branches, an experimental platform, and *ad libitum* access to water. We kept animals for a maximum of three (N = 488; in 65 cases four, in 17 cases five) nights, after which they were released at dusk at their site of capture. In total, we tested up to 150 mouse lemurs per task in a total of 1,104 tests. Sample sizes differ between tasks as it was not possible to recapture all individuals until they have participated in all tasks of the test battery (Appendix 2: Table S2-1).

Testing started between 18:00 and 19:00h under red light conditions, when subjects were active and motivated, and ended when the motivation of the animals decreased. The experimental test battery comprised two personality tests, an open field test and a novel object test, and ten cognitive tests (food extraction task, persistence test, discrimination and reversal learning paradigms with visual discrimination, visual reversal learning, spatial discrimination, and spatial reversal learning, plus maze, cylinder test, two string-pulling tasks), for which we used small pieces of banana as food rewards (Appendix 2: Table S2-1; Fig. 3.1).

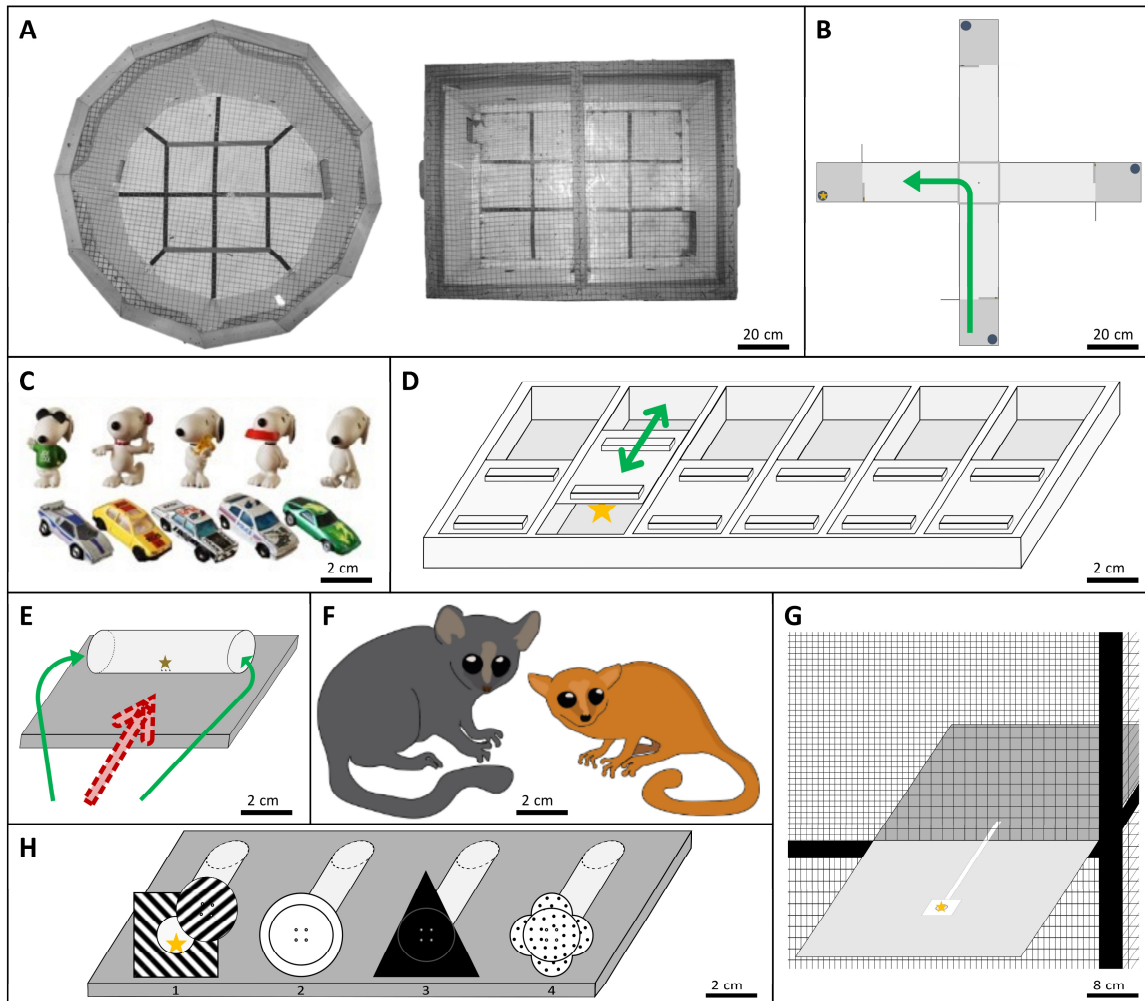


Fig. 3.1 Experimental test battery and mouse lemurs. **A)** Arenas used in the open field test. **B)** Plus maze. **C)** Objects used in the novel object test. **D)** Food extraction task and persistence test. **E)** Cylinder test. **F)** Left: gray mouse lemur, right: Madame Berthe’s mouse lemur; scaled to size differences. **G)** String-pulling task, single-string set-up. **H)** Apparatus used for the visual and spatial discrimination and reversal learning paradigm; numbers indicate the position of the forms. Green filled arrows indicate correct routes. Red striped arrows indicate incorrect routes. Yellow stars represent a food reward.

2.2.1 Personality tests

We assessed an individual’s explorative tendencies in an unknown environment, using an open field test (Fig. 3.1A). After subjects entered the arena voluntarily, they were observed for 5 min exploring the arena. We used the duration the subjects spent locomoting as measure for *exploration* (Appendix 2: Table S2-2). To assess an individual’s neophilic tendencies, we introduced a novel object (Fig. 3.1C) directly after each open field test into the arena. We counted the number of contacts over the course of a 5 min test duration and used this contact frequency as our measure for *neophilia*.

2.2.2 Food extraction task

To assess *innovative propensities*, individuals could extract up to six food rewards from a problem-solving box with six uniform wells (Fig. 3.1D) within a test duration of 20 min. As initial *innovation speed*, we measured the success latency as the time span between the response (i.e., entering the experimental platform and visualizing the task) and the first success (i.e., extracting the 1st piece of banana; solver). In case an individual did not succeed at all (non-solver), we set its success latency to 20 min as the maximum test duration. Additionally, we counted the number of successes as measure for repeated *innovative propensity*.

2.2.3 Persistence test

To assess an individual's *persistence* in manipulating an object with potential access to food, we modified the problem-solving box, in that five of the six lids were blocked and only one of the six rewards could be extracted. We calculated an individual's *persistence* rate by dividing the duration manipulating the box by the duration being in contact with the box and noted whether an individual opened the well (solver) or not (non-solver).

2.2.4 Visual and spatial discrimination and repeated reversal learning paradigm

To assess an individual's *associative and flexible learning abilities*, we used a repeated discrimination and reversal learning paradigm with four separate tasks. On a plate, we positioned four tubes that only differed in shape and pattern of a form at the front part (Fig. 3.1H). Attached to the form was a lid that could be easily rotated to obtain access to the food reward in case of the S⁺. For the first task, the visual discrimination, and the second task, the visual reversal, the shape and pattern of the form served as cue to locate the S⁺. In the third task, the spatial discrimination, and the fourth task, the spatial reversal, the shape and pattern became irrelevant, and the position of the form served as S⁺. Across sessions of 15 trials, we counted the number of correct trials (i.e., manipulating only the S⁺ form and extracting the food reward) which we used as measure for *associative learning*

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abilities. After the subject had correctly chosen the S⁺-form for at least 24 out of 30 trials (80%-learning criterion over two consecutive sessions), we proceeded with the next experimental task and used the total number of trials to reach this learning criterion as measure for the *overall performance* per task. As measure of *flexibility*, we calculated a transfer index (TI, Equation 1) for the transitions with changing reward contingencies (i.e., from the visual discrimination to the visual reversal, from the visual reversal to the spatial discrimination, and from the spatial discrimination to the spatial reversal).

$$\text{Equation 1} \quad \text{TI} = \frac{\text{post-reversal performance}}{\text{pre-reversal performance}}$$

2.2.5 Plus maze

To assess an individual's *spatial learning abilities* and *spatial memory*, we set up a plus maze with four arms leading to four terminal boxes (Fig. 3.1B), of which only one was baited (goal box). We counted how often a subject entered the wrong arm and/or box per trial and summed it up to an error score per trial, which we defined as *spatial learning performance*. For the *overall spatial performance*, we used the mean sum of errors throughout one session of 15 trials.

2.2.6 Cylinder test

To assess an individual's *inhibitory control*, we conducted a detour-reaching task using the cylinder test design (MacLean et al. 2014) (Fig. 3.1E). After an initial training session with an opaque cylinder (see Appendix 2), we conducted the experimental session using a transparent cylinder. Throughout one session of ten trials, we counted the number of incorrect trials, i.e., when the subject did not take the detour as a first response to get access to the food reward in the center of the transparent cylinder.

2.2.7 String-pulling task, single-string set-up

To assess an individual's *means-end understanding*, we conducted a string-pulling task in the single-string set-up (Fig. 3.1G). Within a 20 min test duration, the subject could pull a cable tie to access the food reward at the outer end of the cable tie. We measured the success latency as timespan between the response and reaching the reward. For subjects that did not succeed (non-solver), we set the success latency to the maximum time of the trial (20 min) plus the response latency. We used this success latency as proxy for *means-end understanding*.

2.2.8 String-pulling task, perpendicular strings set-up

To assess an individual's *goal directedness*, we conducted a string-pulling task with a perpendicular strings set-up, as modification of the single-string set-up, where a second, non-baited cable tie was presented. In a session of ten trials, we counted the number of incorrect trials, i.e., the subject did not succeed, or it manipulated the incorrect string, which we used as proxy for *goal directedness*.

2.3 Statistical analyses

2.3.1 Variation in cognitive performances

We conducted all statistical analyses in R (version 4.0.0, R Core Team, 2020), using multivariate (mixed) models to examine interspecific and intraspecific variation in performances (gaussian linear models (LM), gaussian linear mixed models (LMM), negative binomial models (NBM), negative binomial mixed models (NBMM), zero-inflated negative binomial models (0-infl NBM), cox-proportional hazards models (cox PHM), poisson models (PM)), and factor analytical approaches to examine general intelligence factors. Since there is no sexual dimorphism in either species, but body mass changes occur as a result of sex-specific energy strategies, as well as with hormonally induced somatic changes (Eberle and Kappeler 2002; Dammhahn and Kappeler 2005), we controlled for sex and body condition using the body mass index (BMI) as a proxy. In addition, we controlled for stable individual differences in behavior, i.e., personality traits,

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since an individual's exploration level or neophilic tendencies can potentially influence its engagement in experimental tasks and, subsequently, its performance level. In principle, we examined interspecific variation in performances by setting species, sex, and age (log-transformed) as fixed factors. To examine intraspecific variation in performance, we set sex, season, BMI (log-transformed) and personality factors as fixed factors. We tested for interactions of species and sex with other fixed factors but included the interaction only if the model significantly differed from the model without interactions. To test the significance of the predictors as a whole, we compared all full models with the respective null model comprising only the intercept and potential random factors (see Appendix 2; Forstmeier and Schielzeth 2011).

2.3.2 General intelligence

Finally, we investigated general intelligence across, as well as within species. For the interspecific *G*-factor, we calculated two principal axis factor analyses, using the function 'fa' with the argument 'fm' set to 'pa' ('psych' package). The first PAF contained performance scores of individuals that completed all tests (N = 20 GML, N = 9 MBML). For the second PAF, we used performance scores of individuals that completed all tests, except for the discrimination and reversal learning paradigm, resulting in a larger sample size (N = 76 GML, N = 19 MBML). We controlled for sphericity by applying the Bartlett's test and for sampling adequacy by applying the KMO.

For the intraspecific *g*-factor, we used the same (log-transformed) performance scores as for the *G*-factor. For each species separately, we calculated two PCAs per species. The first PCA per species contained the performance scores of all tests excluding the spatial discrimination and the spatial reversal, which reduced the data sets to N = 21 GML and N = 9 MBML. For the second PCA per species, we excluded all performance scores of the repeated discrimination and reversal learning paradigm, achieving a sample size of N = 76 GML and N = 19 MBML. For each PCA, we controlled for sphericity by applying the Bartlett's test and for sampling adequacy by applying the KMO.

3 Results

3.1 Interspecific comparisons

3.1.1 Personality: open field and novel object test

Since locomotion loaded most strongly on the first principal component and was most repeatable (Appendix 2: Table S2-4), we retained this variable as personality trait *exploration*. Variation in *exploration* was predicted by an interaction between species and sex (LM: $p = 0.018$; Appendix 2: Table S2-5, model: a). Female MBML were more explorative than males as well as GML (Fig. 3.2A). Age did not predict variation in *exploration*.

In the novel object test, approach speed and contact frequency were poorly repeatable (approach speed: $ICC = 0.158$; contact frequency: $ICC = 0.106$). Since approach speed was skewed towards individuals that did not contact the novel object, we retained contact frequency as a measure of *neophilia*. About one third of the individuals of both species ($N = 28$ out of 90 GML and $N = 8$ out of 24 MBML) did not contact the novel object. The full model estimating variation in *neophilia* did not significantly differ from the null model (0-infl NBM: $p = 0.073$, Appendix 2: Table S2-5, model: b). Thus, variation in *neophilia* was predicted by neither species ($p = 0.489$), sex ($p = 0.791$), nor age ($p = 0.621$).

3.1.2 Food extraction task: problem solving

Variation in *innovation speed* (latency to 1st success) differed between species (cox PHM: $p = 0.013$) and sexes ($p = 0.044$; Appendix 2: Table S2-6, model: a). GML were faster to extract the first food reward than MBML, and males of both species were faster than females. Age did not predict *innovation speed* ($p = 0.209$).

Variation in *innovative propensity* (N opened wells) differed between species (Appendix 2: Table S2-6, model: b). GML opened more wells than MBML (PM: $p = 0.006$, Fig. 3.2B). Sex ($p = 0.670$) and age ($p = 0.874$) did not predict *innovative propensity* in either species. Both measures were repeatable (*innovation speed*: $ICC = 0.605$, *innovative propensities*: $ICC = 0.405$; $N = 21$ individuals: 15 GML and 6 MBML).

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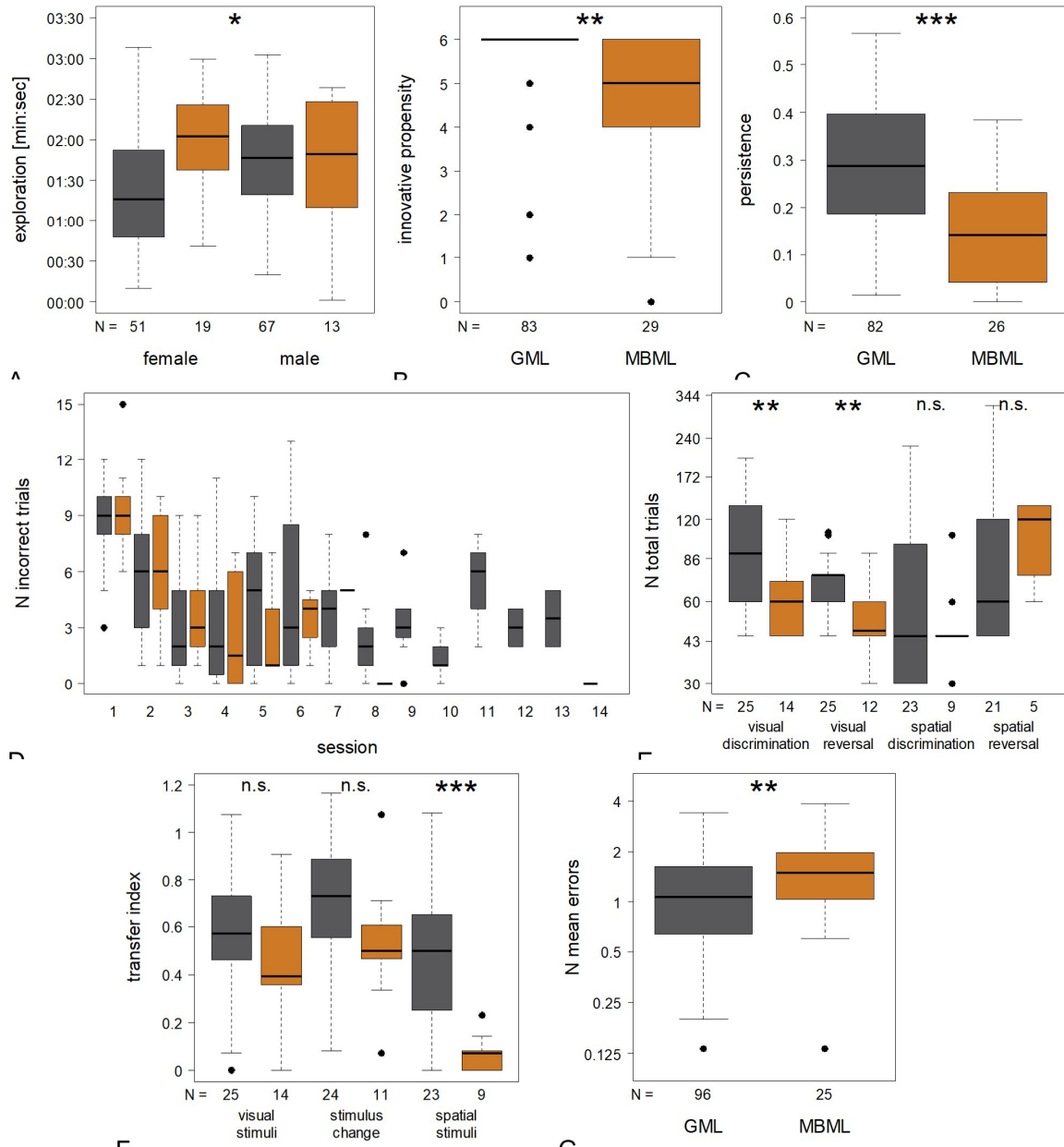


Fig. 3.2 **A)** Open field test: time spent exploring for females and males. **B)** Food extraction task: innovative propensity (N opened wells) per species. **C)** Persistence test: duration spent manipulating the box as a rate to the duration spent in contact with the box per species. **D)** Visual discrimination learning across sessions per species ($p < 0.05$). **E)** Visual discrimination and reversal learning paradigm: overall performances within tasks. **F)** Visual discrimination and reversal learning paradigm: flexible learning between tasks. **G)** Plus maze: spatial memory performance per species. Sample sizes (N) are given below each boxplot. Gray: GML, orange: MBML. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

3.1.3 Persistence test

Variation in *persistence* was predicted by species (LM: $p < 0.001$; Appendix 2: Table S2-7, model: a). GML were more persistent than MBML (Fig. 3.2C). Sex ($p = 0.198$) and age ($p = 0.090$) did not predict *persistence* in either species. Persistence was repeatable

(ICC=0.725, N = 15 individuals, 9 GML and 6 MBML). Persistence across the two food extraction tests correlated positively (Spearman rho = 0.382, $p < 0.001$, N = 108) and was repeatable (ICC=0.394).

3.1.4 Visual discrimination

Variation in *visual discrimination learning* was predicted by species in an interaction with session (NBMM: $p = 0.020$) and age ($p = 0.015$; Appendix 2: Table S2-8, model: a). Both species decreased the number of incorrect trials across sessions, but this decrease was less pronounced in GML than in MBML (Fig. 3.2D). In both species, older individuals had more incorrect trials across sessions than younger individuals. Sex did not predict variation in *visual discrimination learning* across sessions ($p = 0.102$). Variation in the *overall visual discrimination performance* was predicted by species (LM: $p = 0.009$; Appendix 2: Table S2-8, model: b; Fig. 3.2E) and age ($p = 0.008$). GML and older individuals reached the learning criterion after more trials than MBML and younger individuals, respectively. Sex did not predict variation in *visual discrimination performance* ($p = 0.458$).

3.1.5 Visual reversal learning

Variation in *visual reversal learning* was predicted by species (NBMM: $p = 0.001$), session ($p < 0.001$) and age ($p = 0.018$, Appendix 2: Table S2-9, model: a). Both species decreased the number of incorrect trials across sessions. However, this decrease was less pronounced in GML than in MBML. Older individuals had fewer incorrect trials across sessions than younger individuals. Sex did not predict variation in *visual reversal learning* across sessions ($p = 0.758$). Variation in the *overall visual reversal performance* was predicted by species (LM: $p = 0.011$, Appendix 2: Table S2-9, model: b; Fig. 3.2E). GML reached the learning criterion after more trials than MBML ($p = 0.003$). Sex ($p = 0.614$) and age ($p = 0.186$) did not predict variation in the *visual reversal performance*.

Neither species (LM: $p = 0.310$; Fig. 3.2F), sex ($p = 0.192$), nor age ($p = 0.054$; Appendix 2: Table S2-9, model: c) had a significant effect on the transfer index (TI), i.e., *flexible learning* from visual discrimination to visual reversal learning. The TI did not

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correlate with the number of trials to reach the learning criterion in the visual reversal learning (Spearman $\rho = 0.006$, $p = 0.974$, $N = 36$) or with the *innovative propensity* (Spearman $\rho = 0.144$, $p = 0.401$, $N = 36$).

3.1.6 Spatial discrimination

Variation in *spatial discrimination learning* was predicted by species in an interaction with session (NBMM: $p = 0.002$), sex in an interaction with session ($p = 0.001$), age in an interaction with species ($p = 0.005$), and by the position of the rewarded tube S^+ ($p < 0.001$, Appendix 2: Table S2-10, model: a). Both species and sexes decreased the number of incorrect trials across sessions. However, in GML and females this decrease was less pronounced than in MBML and males, respectively. While older GML had more incorrect trials across sessions than younger individuals, older MBML had fewer incorrect trials than younger ones. Mouse lemurs that learned to associate position 1 (S^+) with the food reward had fewer incorrect trials than individuals learning the positions 2, 3 or 4. Variation in *spatial discrimination performance* was predicted by species (Fig. 3.2E) in an interaction with age (LM: $p = 0.043$), and by the S^+ ($p = 0.002$, Appendix 2: Table S2-10, model: b). While older GML reached the learning criterion after more trials than younger individuals, the effect was reversed for MBML. Position 1 was learned after fewer trials than the other three positions. Sex ($p = 0.931$) did not predict variation in *spatial discrimination performance*.

The TI from visual reversal learning to spatial discrimination was predicted by sex (LM: $p = 0.014$), with males achieving a higher TI than females, but not by species ($p = 0.066$; Fig. 3.2F) and age ($p = 0.680$; Appendix 2: Table S2-10, model: c) The TI correlated negatively with the number of trials to reach learning criterion in the spatial discrimination task (Spearman $\rho = -0.463$, $p = 0.008$, $N = 32$). Hence, initially more flexible individuals (higher TI) were faster learners (fewer trials to reach the learning criterion). However, TI did not correlate with *innovative propensity* (Spearman $\rho = 0.039$, $p = 0.831$, $N = 33$).

3.1.7 Spatial reversal learning

Variation in spatial reversal learning was predicted by species in interaction with session (NBMM: $p = 0.004$), sex ($p = 0.034$), and by the S^+ ($p = 0.041$, Appendix 2: Table S2-11, model: a). In both species, the number of incorrect trials decreased across sessions. However, in GLM this decrease was less pronounced than in MBML. Females had fewer incorrect trials across sessions than males. Mouse lemurs that learned to associate position 1 with the food reward ($N = 7$), had fewer incorrect trials than others (position 2: $N = 5$, position 3: $N = 6$, position 4: $N = 8$). Age did not predict variation in *spatial reversal learning* ($p = 0.931$). Variation in the *overall spatial reversal performance* was predicted by sex in interaction with the S^+ (LM: $p = 0.012$, Appendix 2: Table S2-11, model: b). Male mouse lemurs that learned to associate position 3 with the food reward ($N = 3$), reached the learning criterion after more trials than the others. Species ($p = 0.267$; Fig. 3.2E) and age ($p = 0.122$) did not predict variation in the *spatial reversal performance*.

The TI from spatial discrimination to spatial reversal learning was predicted by species (LM: $p < 0.001$), with GML achieving a higher TI than MBML (Appendix 2: Table S2-11, model: c; Fig. 3.2F). Sex ($p = 0.168$) and age ($p = 0.492$) did not predict variation in *flexible learning*. TI correlated negatively with the number of trials to reach the learning criterion in the spatial reversal learning task (Spearman $\rho = -0.522$, $p = 0.006$, $N = 26$). Hence, initially more flexible individuals (higher TI) were faster learners (fewer trials to reach the learning criterion). However, TI did not correlate with *innovative propensity* (Spearman $\rho = 0.112$, $p = 0.549$, $N = 31$). Since we only tested one to two GML repeatedly in 2-4 of the tasks, we could not estimate repeatability of the performance scores in this experiment.

3.1.8 Plus maze: spatial memory

Variation in *spatial learning* was predicted by species in an interaction with trial (NBMM: $p = 0.005$) and by the goal box ($p < 0.001$; Appendix 2: Table S2-12, models: a). Both species made fewer errors across trials, and mouse lemurs assigned to the straight goal box ($N = 22$) made fewer errors across trials than those assigned to the left ($N = 52$) or right

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goal box (N = 47). Sex ($p = 0.254$) and age ($p = 0.537$) did not predict variation in *spatial learning* across trials.

Variation in *spatial memory* was predicted by species (LM: $p = 0.003$) and by the goal box ($p < 0.001$, Appendix 2: Table S2-12, model: b). GML made fewer errors than MBML (Fig. 3.2G). Mouse lemurs assigned to the left or right goal box made more errors than those assigned to the straight goal box. Sex ($p = 0.361$) and age ($p = 0.429$) did not predict variation in *spatial memory*. *Spatial memory* was repeatable ICC=0.412 (N = 21 individuals, 15 GML and six MBML).

3.1.9 Cylinder test: inhibitory control

In the inhibitory control task, individuals that needed more trials to reach the learning criterion prior to testing made more errors during the testing session (NBM: $p = 0.005$). Variation in *inhibitory control* was not predicted by either species ($p = 0.126$), sex ($p = 0.783$), or age ($p = 0.319$; Appendix 2: Table S2-13, model: b).

Inhibitory control did not correlate with *innovative propensity* (Spearman $\rho = -0.152$, $p = 0.121$, N = 105), *flexible learning* (TI from visual reversal learning: Spearman $\rho = -0.096$, $p = 0.576$, N = 36; TI visual reversal to spatial discrimination learning: Spearman $\rho = -0.030$, $p = 0.869$, N = 36; TI from spatial reversal learning: Spearman $\rho = -0.026$, $p = 0.891$, N = 33) or *overall learning performances* (visual discrimination: Spearman $\rho = -0.133$, $p = 0.439$, N = 36; visual reversal: Spearman $\rho = -0.007$, $p = 0.970$, N = 34; spatial discrimination: Spearman $\rho = 0.008$, $p = 0.966$, N = 31; spatial reversal: Spearman $\rho = 0.078$, $p = 0.713$, N = 25). The number of training trials (ICC=0.556) were repeatable, but the number incorrect test trials were only poorly repeatable (ICC=0.141).

3.1.10 String pulling task: means-end understanding and goal directedness

Performance in the *means-end understanding* (cox PHM: $p = 0.600$) and *goal directedness* (PM: $p = 0.874$) was not predicted by any of the investigated factors (Appendix 2: Table S2-14,

model: a, b). We estimated the repeatability for $N = 11$ individuals (7 GML and 4 MBML) that repeated this test (response latency: $ICC = -0.137$, success latency: $ICC = -0.192$).

3.2 General intelligence

We did not find evidence for an interspecific G -factor in either mouse lemur species. The performance scores did not load similarly onto the first component of the PAF, including data from the larger sample size (including tests on problem solving, spatial memory, means-end understanding, goal directedness, inhibitory control), and Bartlett's tests of sphericity was non-significant, indicating a generally low correlation across performance scores (Appendix 2: Table S2-15). The results were similar for the reduced PAF (including tests on visual and spatial discrimination as well as reversal learning, Appendix 2: Table S2-16).

3.3 Intra-specific variation in performance in personality and cognitive tests

We also investigated whether intra-specific performance in these tests was influenced by sex, age, body mass index, or in case of cognitive tests, also by variation in personality traits. In both species, variation in performance scores was only occasionally explained by these individual characteristics, with no systematic variation within species. We also did not find evidence for an intraspecific g -factor. The complete results and the discussion thereof can be found in the Appendix 2 (GML: Table S2-17, MBML: Table S2-18).

4 Discussion

Gray and Madame Berthe's mouse lemurs differed in 13 of 21 performance measures (Table 3.1), which were moderately repeatable in the majority of tests and, hence, consistent within individuals (Appendix 2: Table S2-2). Overall, the ecological generalist GML were more innovative, more persistent, showed better spatial learning and memory, and greater flexibility when spatial stimulus-reward contingencies were changed. The

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ecologically more specialized MBML were more explorative and learned visual and spatial reward contingencies faster, achieving better total performances in visual association learning. However, the two species did not differ in neophilia, inhibitory control, means-end understanding or goal directedness. Moreover, we did not find evidence for an interspecific *G*- or intraspecific *g*-factor. In summary, our study provides support for domain-specific cognitive co-evolution with ecological factors, and a particular advantage of generalists in confronting novel challenges with a greater innovative potential and greater flexibility when confronted with changing spatial stimuli.

Table 3.1 Overview of species differences in performance across tasks. (↑) indicates better and (↓) indicates worse performance, whereas (-) indicates no difference in performance.

Task	GML	MBML	Age	Sex
Activity	-	-	-	↓ GML: females
Neophilia	-	-	-	↓ males
Innovation:				
speed	↑	↓	-	↑ males
propensity	↑	↓	-	-
persistence	↑	↓	-	-
Visual discrimination:				
learning	↓	↑	↓ old	-
performance	↓	↑	↓ old	-
Visual reversal:				
learning	↓	↑	↑ old	-
performance	↓	↑	-	-
Spatial discrimination:				
learning	↓	↑	↓ old GML, ↑ old MBML	↑ males
performance	-	-	↓ old GML, ↑ old MBML	-
Spatial reversal:				
learning	↓	↑	-	↓ males
performance	-	-	-	↓ males: position 3
Flexibility (TI)				
visual	-	-	-	-
visual - spatial	-	-	-	↑ males
spatial	↑	↓	-	-
Spatial memory:				
learning	↑	↓	-	-
performance	↑	↓	-	-
Inhibitory control	-	-	-	-
Means-end understanding	-	-	-	-
Goal directedness	-	-	-	-

In both species, performance in personality and cognitive tests was weakly and inconsistently influenced by individual characteristics and moderately repeatable, reflecting general patterns on intra-individual consistency in cognitive performances in animals (Cauchoix et al. 2018). Regarding personality traits, both species did not differ in exploration. However, female MBML were more explorative than males in comparison to GML. In addition, the two species did not differ in their neophilic response, supporting neither the *Dangerous-Niche Hypothesis* (i.e., generalists should be more neophobic as they may encounter more dangerous situations) nor the *Neophobia Threshold Hypothesis* (i.e., generalists should be less neophobic as they may have more diverse prior experiences; Greenberg 1983; Greenberg 2003).

Concerning cognitive performance, GML were indeed more innovative and achieved higher flexibility scores, at least under changing spatial stimuli. These abilities may allow them to respond more adaptively to dynamically changing habitats and anthropogenic influences (Schäffler and Kappeler 2014; Rakotoniaina et al. 2016). In our study region, the abundance of GML is generally higher than that of MBML, especially in habitats with anthropogenic influence, such as edge habitats (Schäffler and Kappeler 2014; Rakotoniaina et al. 2016). Similarly, in Northern Madagascar, GML were largely unaffected by habitat fragmentation, while the abundance of the sympatric but ecologically more specialized golden-brown mouse lemurs (*M. ravelobensis*) decreased with increasing habitat fragmentation (Andriatsitohaina et al. 2020). Increasing anthropogenic activities, such as deforestation or habitat fragmentation contribute to an alarming species loss in Madagascar (Schwitzer et al. 2014a). Such environmental changes may eventually promote a species turnover towards ecological generalists, whereas more specialized species may suffer from decreased population size (Irwin et al. 2010; Markolf et al. 2020). Our study therefore indicates potential cognitive constraints of ecological specialization that may help to explain why some species experience a higher extinction risk in the face of ongoing environmental changes.

MBML learned the associative reward contingencies faster; a characteristic that allows specialists to experience advantages over generalists in stable environmental conditions (Wilson and Yoshimura 2008). Specifically, MBML's better motor control to abandon previously successful behaviors (Henke-von der Malsburg and Fichtel 2018) and

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their lower persistence to produce a behavior that does not lead to success (this study), may have contributed to their superior performance, at least in visual associative learning experiments. GML feed relatively more often on tree gum, a foraging strategy associated with enhanced inhibitory control (Stevens et al. 2005). However, the two species did not differ in inhibitory control, suggesting that the fact that they feed on gum rather than the relative frequency of this foraging behavior is associated with superior inhibitory control. Both inhibitory control and reversal learning abilities reflect behavioral flexibility (MacLean et al. 2014; Beran 2015). However, these measures did not correlate with each other, suggesting that they reflect different aspects of cognitive flexibility in mouse lemurs. The TI is a standard proxy for flexible learning abilities, reflecting the potential to switch between tactics when conditions change, i.e., in the context of a first response to a modified reward contingency (Rumbaugh et al. 1972). However, it does not indicate how well the old tactic will be abandoned in favor of the new tactic. This might be better reflected by the number of trials until criterion after reversal or the number of perseverative errors across sessions, because these measures better reflect how quickly individuals may overcome the previously learned reward contingency and, therefore, how flexible an animal switches between strategies (Hauser 1999). The TI and the number of trials to reach the criterion after reversal correlated negatively with each other in the transfer from the visual to spatial stimuli and in the spatial reversal learning, indicating that individuals that responded more flexibly to the reversed reward contingency learned this reward contingency faster in spatial learning. Hence, with regard to spatial stimuli, which might be ecologically more relevant than abstract forms as in the visual reversal paradigm, mouse lemurs were able to switch flexibly between strategies, and GML were more flexible when confronted with changing spatial stimuli than MBML.

The plus maze assays spatial learning and memory that is essential for effective spatial navigation. GML learned this task faster than MBML, supporting earlier results on their spatial learning and high travel efficiency (Lührs et al. 2009). Although MBML have larger home ranges and should therefore have better spatial abilities, the ability to adapt to different habitat types may require more flexible spatial learning abilities and may therefore better explain from an evolutionary perspective why GML performed better in

this task and also why they responded more flexibly when spatial stimulus-reward contingencies changed.

In tasks with little ecological relevance, where species differences in cognitive performance were not predicted regarding the degree of ecological specialization, such as inhibitory control, means-end understanding or goal directedness, both species performed on par, suggesting that they did not differ *per se* in cognitive performance. These results also support our interpretation of the adaptive nature of the observed differences as being driven by different ecological factors.

In humans, cognition has evolved towards positively correlating generally high-level cognitive abilities (Herrmann et al. 2007; Burkart et al. 2017). However, a general correlation between cognitive abilities and brain size has received mixed support in comparative studies of animals (Burkart et al. 2017). In mouse lemurs, we did not find evidence for general intelligence, neither on the interspecific, nor on the intraspecific level. Our results rather support the *Domain-Specific Hypothesis* (Cosmides and Tooby 1994), which postulates enhanced abilities in only some cognitive domains, whereas abilities in others remain on more basic performance levels (Poirier et al. 2020).

Finally, this study raises new questions about the evolutionary mechanisms driving cognitive adaptations to environmental features. From a phylogenetic perspective, the split between the basic lineages to which these two species belong occurred about 8-10 million years ago. Phylogenetic reconstructions of the speciation patterns in mouse lemurs suggests that the longitudinal dispersal along the west coast of Madagascar by GML was achieved with relative ease throughout the Pleistocene (Yoder et al. 2016). However, habitat fragmentation via Holocene droughts may have erected natural barriers such as rivers, creating several centers of endemism (Wilmé et al. 2006), isolating some species, such as MBML, in small ranges. Thus, gray mouse lemurs actually had more time available to evolve cognitive and ecological adaptations to the habitat in which they now co-occur, but they appear to have retained cognitive abilities that may provide ecological advantages across their entire range. Genetic studies investigating patterns of gene flow and heritability in different cognitive abilities are now indicated to begin exploring the evolutionary mechanisms shaping the links between ecological adaptations and cognitive constraints.

5 Conclusions

We show that direct comparisons of cognitive performances between sympatric sister-species with a similar social system can help to unfold the role of ecological factors in the evolution of cognition. Species-specific ecological adaptations covary with cognitive abilities. The ecologically more generalist species was particularly more innovative, persistent, exhibited better spatial learning abilities, spatial memory, as well as spatial flexibility than the specialist, affording them with the behavioral flexibility to respond adaptively to rapidly changing habitats and anthropogenic disturbances. How these differences in cognitive abilities have been maintained over millions of generations in local sympatry requires further study.

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Ethical approval

This study was conducted in accordance with the German and Malagasy (Commission Tripartite CAFF) legal and ethical requirements of appropriate animal procedures. Research protocols and experimental procedures were approved by the Bundesamt für Naturschutz (BfN) in Germany and by the Ministère de l'Environnement et des Eaux et Forêts in Madagascar (MINEEF). Research in Kirindy was authorized by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) Morondava.

Appendix 2

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Predictions

Regarding variation in personality, we predicted that Madame Berthe’s mouse lemurs (MBML), which have larger home ranges, are more explorative than gray mouse lemurs (GML). In line with the *Dangerous-Niche Hypothesis*, high neophobia may protect individuals from potentially dangerous situations (Greenberg 2003). As GML may encounter more dangerous situations, we predicted them to be more neophobic than MBML. Alternatively, as the ecological generalist encounters a greater variety of habitat and/or food types, it should have more diverse prior experiences against which it can rate novelty (*Neophobia Threshold Hypothesis* (Greenberg 1983)). Accordingly, the GML should be less neophobic than MBML.

Regarding variation in cognitive abilities, we predicted that the generalist GML exhibit greater innovative potential and greater flexible learning abilities than the ecologically more specialized sister-species. Since MBML live in less variable environments, we predicted that they learn associated reward contingencies faster. We also predicted that they have better spatial memory because they feed preferentially on spatially clumped resources, whereas GML feed on more abundant and mobile food items (Dammhahn and Kappeler 2008a). Moreover, because MBML were more flexible in solving a more complex food extraction task, as they had better inhibitory motor control than GML (Henke-von der Malsburg and Fichtel 2018), we predicted GML to be more persistent. Self-control is generally associated with dietary breadth across 36 primates (MacLean et al. 2014), suggesting that dietary generalists should have better self-control than dietary specialists. Since both species do not feed on dietary items requiring specific extractive foraging techniques, we did not predict significant interspecific

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differences regarding means-end understanding or goal directedness. We nonetheless included these tests to also examine cognitive performances in tasks without obvious ecological relevance(Henke-von der Malsburg et al. 2020), in which differences in performance are not predicted by the degree of ecological specialization. Finally, given the contrasting predictions across the various cognitive abilities, we did not expect variation in performance across tasks to be correlated and to load onto one common general intelligence (*G/g*-)factor(Humphreys 1979; Deaner et al. 2006). Rather, we expected both species to have evolved domain-specific cognitive abilities (*Domain-Specific Hypothesis*(Cosmides and Tooby 1994)).

Supplemental methods

Study animals: Capture and housing

We baited Sherman live traps with a slice of banana, set them at dusk at trail intersections and collected them at dawn. Captured mouse lemurs were brought to the near-by field station and individually identified. All individuals were weighted. If they were newly captured, they were briefly restrained with 0.6 μ l ketamine (50 mg/ml) per 1 g body mass to mark them individually with a subdermal microtransponder (Trovan, Usling, Germany). If they were captured for the first time, we also took several standard morphologic measures(Eberle and Kappeler 2002). We calculated an individual's current body mass index (BMI) by dividing its bizygomatic head breadth [mm] by the individual's current body mass [g]. We estimated an individual's age by determining the number of days between birth and the date of the respective experimental test. We set an individual's birth date to the modal birth date 1 January of the year of its first capture(Eberle and Kappeler 2002). The individuals' ages ranged from 0.26 to 8.58 yrs. (mean = 1.21 ± 1.40) in GML and from 0.33 to 5.35 yrs. (mean = 1.20 ± 1.17) in MBML.

At the field station, mouse lemurs were housed in cages of 80 cm x 80 cm x 80 cm equipped with a nest box, several branches, an experimental platform, and *ad libitum* access to water. We kept animals for a maximum of three ($N = 488$; in 65 cases four, in 17 cases five) nights, after which they were released at dusk at their site of capture. Since the complete experimental test battery was usually not completed during one test session

comprising three nights, we selectively recaptured subjects after they had spent at least three nights in the forest. The animals usually exhibited great trap happiness, with some individuals entering traps more than 100 times (Eberle and Kappeler 2002). Testing started each evening between 0600 and 0700 pm under red light conditions, which wavelengths is not visible for the dichromatic mouse lemurs (Peichl et al. 2019), and ended when the motivation of the animals decreased, usually around midnight. When a mouse lemur voluntarily left its nest box, the nest box was closed to facilitate later testing. Throughout the night, it could hide between branches and rest at any time. The mouse lemurs were fed after testing with cockroaches, moths and pieces of banana. In total, we tested up to 150 mouse lemurs per test in a total of 1,104 tests (Table S2-1).

General experimental procedure

The experimental test battery comprised two personality tests, an open field test and a novel object test, and ten cognitive tests (food extraction task, persistence test, discrimination and reversal learning paradigms with visual discrimination, visual reversal learning, spatial discrimination, and spatial reversal learning, plus maze, cylinder test, two string-pulling tasks; Table S2-1; Fig. 3.1). The order of the tests was randomized and counterbalanced between subjects. All subjects were naïve to experimental conditions, unless otherwise stated ($N = 20$; Table S2-1). Subjects were captured on average 2.39 ± 1.68 times. To complete the relatively time-consuming discrimination and reversal learning paradigm, subjects were tested on average in 3.00 ± 1.26 test sessions (i.e., time periods of three nights), resulting in smaller sample sizes in these tests (Table S2-1). The remaining tests could be completed on average in 2.07 ± 0.80 test sessions.

We started with the experiments only when subjects were active and motivated, i.e., when they were actively moving around and could be easily lured with a stick covered with banana to the start position at the opposite end of the experimental platform. We used small pieces of banana as food rewards. Before any experimental session, we cleaned the experimental platform, the test apparatus, or the respective arena for the open field test and plus maze with 70%-ethanol to remove any odor cues. In experiments comprising

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several trials, we repeated the cleaning procedure throughout the trials as stated in the respective test section.

Each experimental test session was videotaped (Sony HDR-CX 240) and later analyzed using BORIS (Friard and Gamba 2016). For each test, 10% of the videos were double-coded by a second observer naïve to the research question, resulting in a mean interobserver reliability of 96.0% (min.: 80.2%, max.: 100%; Table S2-2).

General statistical analyses

We conducted all statistical analyses in R (version 4.0.0, R Core Team, 2020), using multivariate (mixed) models to examine interspecific and intraspecific variation in performances (gaussian linear models (LM), gaussian linear mixed models (LMM), negative binomial models (NBM), negative binomial mixed models (NBMM), zero-inflated negative binomial models (0-infl NBM), cox-proportional hazards models (cox PHM), poisson models (PM)), and factor analytical approaches to examine general intelligence factors. Since there is no general sexual dimorphism in either species, but body mass changes occur as a result of sex-specific energetic strategies, as well as with hormonally induced somatic changes (Eberle and Kappeler 2002; Dammhahn and Kappeler 2005), we controlled for sex and body condition using BMI as a proxy. In addition, we controlled for stable individual differences in behavior, i.e., personality traits, since an individual's exploration level or neophilic tendencies can potentially influence its engagement in experimental tasks and, subsequently, its performance level.

We examined interspecific variation in performances by setting species, sex, and age (log-transformed) as fixed factors. To examine intraspecific variation in performance, we set sex, season, BMI (log-transformed) and personality factors as fixed factors. For models including data of a smaller sample size, we calculated several reduced models by retaining only a maximum of $N = 10$ data points for fixed factors each. We scaled covariates to a mean of zero and a standard deviation of one to obtain comparable estimates and to achieve more easily interpretable coefficients. If a continuous variable was not symmetrically distributed (visual inspection), we log-transformed it before scaling.

We tested for interactions of species and sex with other fixed factors but included the interaction only if the model significantly differed from the model without interactions. We first tested the overall effect of the fixed factors by comparing the selected full model's deviance with that of its null model comprising only the intercepts (and random factors, if applicable). These tests of significance were based on an analysis of variance (ANOVA) with F-test for gaussian linear models, Wald-test for cox-proportional hazards models, or likelihood ratio test (LRT) for other models. For the individual predictors, we derived respective test-statistics and p-values using the function 'drop1', which compares the deviance of the full model with that of the reduced model, lacking the respective individual predictor. For all tests, we used a significance level of 0.05. We extracted sample size adjusted effect sizes (R^2) directly from the summary output for linear models. For other models, we calculated Nagelkerke's R^2 . We checked various diagnostics of model validity and stability (Cook's distance using the function 'cooks.distance'; DFBetas using the function 'dfbeta'; DFFits using the function 'dffits'; overdispersion; variance inflation factors using the function 'vif' ('car' package(Fox and Weisberg 2011)) applied to standard linear models without any random factors; normality and homogeneity of residuals by plotting a qq-plot for the residuals and a scatterplot between residuals and fitted values), which never indicated obvious influential cases, nor obvious deviations from the respective model assumptions.

Additionally, we tested the repeatability of the measured performances, as well as the interobserver reliability of video codes using the intraclass correlation coefficient (ICC; 'ICCest' function, 'ICC' package(Wolak 2015)).

Task-specific experimental procedure and statistical analyses

Open field test: Experimental set up

We assessed an individual's explorative tendencies in an unknown environment, using either a rectangular (80 cm x 60 cm x 60 cm) or cylindrical wooden arena (\varnothing 80 cm x 80 cm; Fig. 3.1A). To avoid potential influences on the personality measures arising from initial neophobic responses due to the new housing conditions, we conducted this test only after subjects got used to the new housing condition, i.e., after the first night being in camp.

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After subjects entered the arena voluntarily, they were observed for 5 min exploring the arena. To measure the repeatability of personality traits, we subjected individuals repeatedly to the open field test, using the two arenas alternately. The first repetition was usually conducted when subjects were captured for the second time (number of days between tests: mean = 81.38 ± 88.02). Further repetitions were conducted each time when we re-captured the subject until it had accomplished the complete test battery, but for a maximum of two times per field season (days between test 2 and 3: mean = 130.14 ± 122.12 ; days between test 3 and 4: mean = 66.14 ± 76.32). We tested 118 GML and 32 MBML at least once and one third of all individuals up to three times (Table S2-3). Only a small subset was tested in a fourth ($N = 29$), fifth ($N = 8$), sixth ($N = 4$) or seventh ($N = 1$) open field test. $N = 16$ individuals were tested in the rectangular arena in previous studies conducted 11 – 47 months before (mean = 25.12 ± 15.75 ; Table S2-1 (Huebner et al. 2018; Henke-von der Malsburg and Fichtel 2018)). Based on video-recordings, we measured time spent locomoting and exploratory tendencies of subjects (Table S2-2).

Open field test: Statistical analyses

We visually inspected whether the variables of the first open field test were symmetrically distributed and applied a log-transformation to achieve a more symmetric distribution if necessary. We checked the correlation matrix of symmetrically distributed (log-transformed) variables using the function 'rcorr' ('Hmisc' package (Harrell 2021)) and controlled for sphericity by applying Bartlett's test (function 'cortest.bartlett', 'psych' package (Revelle 2020)), which was significant ($X^2 = 203.51$, $df = 10$, $p < 0.001$). Then, we conducted a principal component analysis (PCA) using the 'pca' function ('psych' package) with the standard varimax rotation. The Kaiser-Meyer-Olkin index (KMO; 'KMO' function, 'psych' package (Morton and Altschul 2019)) revealed good sampling adequacy with a value of 0.56. We retained two components as suggested by the function 'fa.parallel' ('psych' package). The first component explained an individual's active exploration, with locomotion and cells traversed loading positively and the latency enter (log-transformed) loading negatively. The second component explained an individual's

more passive, stationary exploration, with rears, i.e., standing on hindlegs, (log-transformed) and dips, i.e., inserting head into blind holes or closed doors of the open field, (log-transformed) loading positively (Table S2-4).

To estimate variation in *exploration*, we used a linear model with gaussian error distribution ('lm' function) with the duration subjects spent locomoting as response variable. In the interspecific model (Table S2-5, model: a), we used species in interaction with sex, and age (log-transformed) as fixed factors. In the intraspecific models (Table S2-17, Table S2-18, models: a), we used sex, season, and BMI (log-transformed) as fixed factors.

Novel object test: Experimental set-up

To assess an individual's neophilic tendencies, we introduced a novel object (either a plastic snooply or a metallic toy car; Fig. 3.1C) directly after each open field test into the arena. Out of the 150 individuals, only one was tested with a similar novel object in a previous study 11 months earlier (Table S2-1; (Henke-von der Malsburg and Fichtel 2018).)

We measured an individual's latency to approach the novel object by one grid cell (approach latency), to contact the novel object (contact latency), and the number of contacts over the course of a 5 min test duration (contact frequency). With the two latencies, we calculated the approach speed by subtracting the contact latency from the approach latency. If an individual did not contact the novel object, we set the approach speed to the sum of contact latency (which was set to the 5 min test duration) and the respective approach latency (which was also set to 5 min in case the individual did not approach the object). We chose the contact frequency as our measure for *neophilia*, as the other variables were highly skewed towards individuals that did not contact the object.

Novel object test: Statistical analyses

To estimate variation in *neophilia*, we used a zero-inflated negative binomial model with logit-link error function (function 'zeroinfl' with the argument 'dist' set to 'negbin'; 'pscl' package (Jackman et al. 2020)) and the number of contacts with the novel object as response

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variable. In the interspecific model (Table S2-5, model: b), we used species, sex, and age (log-transformed) as fixed factors in the count part and set sex as fixed factor in the zero part. In the intraspecific models (Table S2-17, Table S2-18, models: b), we used sex, season, and BMI (log-transformed) as fixed factors in the count part and set sex as fixed factor in the zero part.

Food extraction task: Experimental set-up

To assess an individual's *innovative propensities*, we presented a problem-solving box (6 cm x 12 cm; Fig. 3.1D). Each of the six uniform wells (5 cm x 4.5 cm) was baited with a small piece of banana, which could be extracted by sliding a lid open. After the box was introduced onto the experimental platform within the subject's cage, the animals had 20 min to extract the six rewards. We tested a total of $N = 112$ individuals (83 GML and 29 MBML). $N = 5$ individuals were subjected to this task in a previous study 11 – 53 months earlier (mean = 34.30 ± 15.31 ; (Huebner et al. 2018)).

We measured an individual's response latency from the start of the test, when the box was deposited on the experimental platform, to its approach to the experimental platform, visualizing the task. As initial *innovation speed*, we measured the success latency as time span between the response latency and the first success (i.e., extracting the 1st piece of banana; solver). In case an individual did not succeed at all (non-solver), we set its success latency to 20 min as the maximum test duration. Additionally, we counted the number of successes as measure for repeated *innovative propensity*. We estimated the repeatability of the variables by calculating the ICC for $N = 21$ individuals (15 GML and six MBML), that repeated this test (response latency: ICC = -0.050, success latency: ICC = 0.605, success number: ICC = 0.405).

Food extraction task: Statistical analyses, *innovation speed*

To investigate interspecific variation in *innovation speed* (Table S2-6, model: a), we calculated a cox-proportional-hazards model (function 'coxph', 'survival' package (Therneau et al. 2020)) with the function Surv(success latency (log-

transformed) | solver) as proportional hazard and species, sex, and age (log-transformed) as fixed factors. In the model for GML (Table S2-17, model: c), we used sex, season, BMI (log-transformed), activity, and neophilia as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: c) according to the small sample size. We set sex and season, sex, and BMI (log-transformed), sex in interaction with activity, and sex and neophilia as fixed factors, respectively.

Food extraction task: Statistical analyses, *innovation propensity*

To investigate interspecific variation in *innovative propensity* (Table S2-6, model: b), we calculated a poisson model with log link error function (function 'glm', family = 'poisson') with the number of successes as response and species, sex, and age (log-transformed) as fixed factors. In the intraspecific model for GML (Table S2-17, model: d), we used sex, season, BMI (log-transformed), activity, and neophilia as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: d) adapted to the low sample size in this species. We set sex and season, sex and BMI (log-transformed), sex and activity, and sex and neophilia as fixed factors, respectively.

Persistence test: Experimental set-up

To assess an individual's *persistence* in manipulating an object with potential access to food, we modified the problem-solving box, in that five of the six lids were blocked and only one of the six rewards could be extracted. Therefore, the persistence test always followed the food extraction test. If an individual did not open all the six wells during the food extraction test, we performed an additional training session prior to the persistence test ($N = 17$). This training session was similar to the food extraction test, with the only modification that all lids were opened by 5 mm.

The persistence test lasted 20 min and was extended by 10 min in case the individual was still manipulating the box after 20 min ($N = 6$). We calculated an individual's *persistence* as the duration manipulating the box in relation to the duration being in contact with the box and noted whether an individual opened the well (solver) or

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not (non-solver). We tested a total of $N = 108$ (82 GML and 26 MBML). We estimated the repeatability of the variables by calculating the ICC for $N = 15$ individuals (nine GML and six MBML), that repeated this test (manipulation: ICC = 0.570, contact: ICC = -0.147, persistence: ICC = 0.725). Additionally, we estimated the repeatability of *persistence* across tasks by calculating the ICC across the food extraction task and the persistence test for $N = 108$ individuals (82 GML and 26 MBML).

Persistence test: Statistical analyses

To investigate variation in *persistence*, we calculated a linear model with gaussian error distribution. We used *persistence* as response variable and species, sex, and age (log-transformed) as fixed factors in the interspecific model (Table S2-7, model: a). Running the same model excluding the $N = 17$ individuals that received additional training, did not affect the results (Table S2-7, model: b). In the intraspecific model for GML (Table S2-17, model: e), we used sex, season, BMI (log-transformed), activity, and neophilia as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: e) due to the low sample size for this species. We set sex and season, sex in interaction with BMI (log-transformed), sex and activity, and sex and neophilia as fixed factors, respectively.

Visual and spatial discrimination and repeated reversal learning paradigm: Experimental set-up

To assess an individual's *associative and flexible learning abilities*, we used a repeated discrimination and reversal learning paradigm with four individual tasks. On a plate, we positioned four tubes that only differed in shape and pattern at the front part (Fig. 3.1H). Tubes were fixed with clips on the plate, so that we could easily exchange the position between trials. The tube opening was surrounded of a plate in the form of either a square (pattern: black-white striped), a circle (pattern: white), a triangle (pattern: black), or flower (pattern: white with black dots). In front of each plate, we attached a lid that could be easily rotated to access a small piece of banana. As an odor control for non-rewarded

tubes, we placed a piece of banana in the center of each tube, which, however, was not accessible to the subjects.

Before the first testing session, we conducted a familiarization session. In this session, the order of the tubes was always the same across the subjects (square – circle – triangle – flower) and each tube opening was baited with a food reward. We removed the lids, so that the animals could easily access the food reward in each of the tubes. A trial started when the apparatus was fully introduced on the experimental platform within the subject's cage and lasted a maximum of 10 min, or until the subject retrieved all four food rewards. After the subject had retrieved all four food rewards in six familiarization trials, we started with the actual experiment.

In the first experimental task, the visual discrimination, we randomly selected one of the four forms serving as S^+ , containing the food reward. Across sessions of 15 trials, we randomized the position of the S^+ -form across the four positions in a counterbalanced order between the left (position 1 and 2) and right side (position 3 and 4) of the plate (Fig. 3.1H). The S^+ -form was never presented on the same position for more than two times in a row. We additionally cleaned the apparatus after every third trial. The time-interval between trials within a session was 10-30 s, depending on how fast the experimenter could re-bait the tube, change the tube positions and clean the apparatus, as well as how easily the subject was lured back to the starting position. We defined a trial as correct, if the subject extracted the food reward by only manipulating the S^+ -form. If it manipulated an incorrect form, we noted the trial as incorrect and let the subject continue to explore the apparatus until it retrieved the reward or a maximum of 10 min. Depending on the subject's motivation (i.e., actively moving around and easily lured to the start position), we conducted two sessions in a row with a short break of 5 min between sessions and a break of at least 30 min to a third session. We conducted a total of four to five sessions per individual and night, always taking the subject's motivation into account. After the subject had correctly chosen the S^+ -form for at least 24 out of 30 trials (80%-criterion over two consecutive sessions), we proceeded with the next experimental task, the visual reversal learning.

For the visual reversal learning, the former S^+ -form became unrewarded, and we chose one of the other three forms as new S^+ . We started with the first session of this part

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in the same testing period as the last visual discrimination session. The rest of the testing procedure remained the same as in the visual discrimination until the 80%-learning criterion was reached.

As the third experimental task, we conducted a spatial discrimination test. In this task, the shape and pattern of the forms became irrelevant, but only the position of the tube served as S^+ . We conducted the first session in the night following the last visual reversal learning session, which could be either during the same testing period, or when we recaptured the individual (days between tests: mean = 6.88 ± 7.99 , max = 27). As in the visual tasks, we removed odor cues from the apparatus after every third trial. Additionally, we cleaned the tube opening, the frontal form, and the lid after each trial to remove any remainder of the food reward from the previous trial, if this specific tube was not positioned at the S^+ -position in the subsequent trial. The rest of the testing procedure remained the same until the 80%-learning criterion was reached.

Finally, we conducted a spatial reversal learning test, with the former S^+ -position becoming non-rewarded and another position becoming the new S^+ . We chose a position on the other side of the plate to avoid a potential side preference. If, for example, the S^+ -position in the spatial discrimination was position 1, we chose the S^+ -position in the spatial reversal learning as either position 3 or 4. As for the visual reversal learning, we conducted the first spatial reversal session in the same testing period as the last spatial discrimination session. The rest of the testing procedure remained the same as in the spatial discrimination until the 80%-learning criterion was achieved.

For each trial, we measured the response latency and success latency similarly to the other experiments. For each session, we counted the number of correct and incorrect trials (errors) and calculated the mean response latency and the mean success latency. We used the number of errors across sessions as proxy for *associative learning abilities* in each task. For the *overall performance* per task, we used the total number of trials until the learning criterion was reached. As measure of *flexibility*, we calculated a transfer index (TI, Equation 1; (Rumbaugh and Pate 1984)) for the transitions with changing reward contingencies (i.e., from the visual discrimination to the visual reversal, from the visual reversal to the spatial discrimination, and from the spatial discrimination to the spatial reversal). Therefore, we used the last 15 trials of the previous task (pre-reversal

performance) and the trial 2 to 15 of the following task (post-reversal performance). The first trial of the post-reversal session was excluded, since it primarily served as a cue that the initial reward contingency has changed.

$$\text{Equation 2} \quad \text{TI} = \frac{\text{post-reversal performance}}{\text{pre-reversal performance}}$$

The sample sizes slightly decreased over the experimental tasks (Table S2-1), since we failed to recapture some individuals before they completed the repeated discrimination and reversal learning paradigm. Only $N = 1$ individual failed to learn the reward contingency in the spatial discrimination. For $N = 2$ individuals, we erroneously continued with the subsequent experimental task before the previous reward contingency was learned, and they were subsequently excluded from the analyses.

Discrimination and reversal learning paradigm: Statistical analyses, learning across sessions

To assess differences in *associative learning abilities* within each task, we used negative binomial mixed models with log link error function (function 'glmer.nb', 'MASS' package(23)) with the number of incorrect trials per session as response. For all the interspecific models, we set subject ID and session ID as random factors. We controlled for a possible influence of performance of the S^+ but did not include this variable as fixed factor if it did not affect the performance in the respective task. For the visual discrimination model (Table S2-8, model: a), we set species in interaction with session, sex, and age (log-transformed) as fixed factors. For the visual reversal learning model (Table S2-9, model: a), we set species, sex, age (log-transformed) and session as fixed factors. For the spatial discrimination model (Table S2-10, model: a), we set species in interaction with age (log-transformed), species in interaction with session, sex in interaction with session, and the S^+ as fixed factors. Since this model did not converge with standard settings, we set the optimizer to "bobyqa" and the maximum likelihood estimation to 100,000 iterations. For the spatial reversal learning model (Table S2-11, model: a), we set species in interaction with session, sex, age (log-transformed), and the S^+ as fixed factors. Since

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this model also did not converge with standard settings, we set the optimizer to “bobyqa” and the maximum likelihood estimation to 100,000 iterations.

Discrimination and reversal learning paradigm: Statistical analyses, *performance within tasks*

To assess variation in the *overall performance* within each task, we used linear gaussian models with the total number of trials (log-transformed) as response. For the interspecific models of the visual tasks (Table S2-8, Table S2-9, models: b), we set species, sex, and the mean age (log-transformed) between the first and the last session as fixed factors. For the spatial discrimination model (Table S2-10, model: b), we set species in interaction with the mean age (log-transformed), sex, and the S⁺ as fixed factors. For the spatial reversal learning model (Table S2-11, model: b), we set species, sex in interaction with the S⁺, and the mean age (log-transformed) as fixed factors. Due to small sample sizes, we calculated four less complex models per task for GML to model intraspecific variation in associative learning performances (Table S2-17, models: f, g, i, k). Therefore, we set sex and mean BMI (log-transformed) between the first and last session, sex and activity, sex and neophilia, and sex and the S⁺ as respective fixed factors. For MBML, we calculated five models per task, reducing the number of fixed factors to one (Table S2-18, models: f, g, i, k).

Discrimination and reversal learning paradigm: Statistical analyses, *flexible learning between tasks: transfer index*

To assess variation in *flexible learning* between tasks, we modelled the TI using linear gaussian models with species, sex, and the mean age (log-transformed) as fixed factors (Table S2-9 – Table S2-11, models: c). Due to small sample sizes, we calculated three less complex models per task for GML to model intraspecific variation in flexible learning (Table S2-17, models: h, j, l). Therefore, we set sex and mean BMI (log-transformed) between the last pre-reversal and the first post-reversal session, sex and activity, and sex and neophilia as respective fixed factors. For MBML, we calculated four models per task, reducing the number of fixed factors to one (Table S2-18, models: h, j, l).

Additionally, we calculated Spearman rank correlations between the TIs and the number of trials to reach the posterior learning criteria, as well as the *innovative propensity* to estimate potential covariations between these flexible learning proxies.

Plus maze: Experimental set-up

To assess an individual's *spatial learning abilities* and *spatial memory*, we set up a plus maze with four arms (40 cm x 17 cm x 17 cm) leading to four terminal boxes (20 cm x 17 cm x 17 cm; Fig. 3.1B). Each terminal box contained a plastic lid in its back at the opposite side of its door, in which we placed a small piece of banana in case of the rewarding location. For an initial familiarization trial, we baited three terminal boxes and released the subject at the fourth box at the start arm. The familiarization trial started when we opened the door of the start box and ended either when the subject had eaten all the three food rewards or after a maximum of 15 min. In the latter case, we repeated the familiarization trial either at the same or the following testing night when the individual showed higher motivation to participate in the task. After the subject had eaten the third reward, we distracted it briefly with a stick smeared with banana at the backside of the box, closed the door and released it again at the start box for the next trial or in its home cage when the test was done.

For the actual test session (15 successive trials), only one terminal box (= goal box) was baited. As goal box, we chose the box in which we caught the animal during the familiarization trial ($N_{\text{straight}} = 22$, $N_{\text{right}} = 47$, $N_{\text{left}} = 52$). Since only the goal box was baited during the test session, we placed on top of each terminal box a piece of banana peel that was out of reach for the subject to control for olfactory stimuli. Similar to the familiarization trial, a test trial started when we opened the door of the start box and ended as soon as the subject had retrieved the food reward in the goal box. However, we stopped a trial after 10 min, when the subject did not succeed. We stopped a session if the subject did not exit the start box within 10 min and continued the session either later in the night or in the following night. We additionally cleaned the maze after every third trial. We

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rotated the terminal boxes throughout the session to prevent the subject to follow potential odor cues left inside the goal box.

We counted how often a subject entered the wrong arm and/or box and summed it up to an error score per trial, which we defined as *spatial learning performance*. For the *overall spatial performance*, we used the mean sum of errors throughout the 15 trials. We tested a total of $N = 121$ (96 GML and 25 MBML). We estimated the repeatability of the mean sum of errors by calculating the ICC for $N = 21$ individuals (15 GML and six MBML), that repeated this test (ICC = 0.412). $N = 5$ individuals were subjected to this task in a previous study 11 – 53 months earlier (mean = 33.23 ± 15.80 ; (Huebner et al. 2018)).

Plus maze: Statistical analyses, spatial learning across trials

To investigate variation in *spatial learning*, we modelled the sum of errors per trial in a negative binomial mixed model with log link error function (function 'glmer.nb', 'MASS' package (Brian et al. 2021)). Since the model did not converge with standard settings, we set the optimizer to "bobyqa" and the maximum likelihood estimation to 100,000 iterations. We set species in interaction with trial, sex and the goal box as fixed factors and subject ID and trial ID as random factors (Table S2-12, model: a).

Plus maze: Statistical analyses, spatial memory

To investigate variation in *spatial memory*, we modelled the mean sum of errors across the 15 trials (log-transformed) in a gaussian linear model. For the interspecific model, we set species, sex, age (log-transformed), and the goal box as fixed factors (Table S2-12, model: b). In the intraspecific model for GML (Table S2-17, model: m), we set sex, season, BMI (log-transformed), activity, neophilia and the goal box as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: m) due to the small sample size in this species. We set sex and season, sex and BMI (log-transformed), sex and activity, sex and neophilia, and sex and the goal box as respective fixed factors.

Cylinder test: Experimental set-up

To assess an individual's *inhibitory control*, we conducted a detour-reaching task using the cylinder test design (MacLean et al. 2014; Kabadayi et al. 2018). Prior to testing, we conducted a training session with an opaque cylinder. The food reward was placed in the center of the cylinder, invisible for the subject during its approach. To reach the reward, the subject had to take a detour and enter the cylinder by one of the open sides which were set in an 90° angle from the approach direction onto the experimental platform within the subject's cage. We additionally removed odor cues after every fifth trial. We counted the number of correct and incorrect trials until a learning criterion was met that was defined as five consecutive trials taking the detour as a first response without prior touching or sniffing at the cylinder (MacLean et al. 2014). In some cases ($N = 23$, 18.9%), we only noticed during the video analysis that this criterion was not entirely met. $N = 15$ individuals did not reach the criterion in the conducted trials. $N = 8$ individuals already reached the criterion earlier, but some more trials were conducted. This erroneous evaluation happened when an individual approached very quickly without directly touching the cylinder but sniffing at its very edge. In these cases, it could be difficult to directly classify the sniffing as happening only from the side, i.e., the entrance of the cylinder (correct) or as happening from the front (incorrect). However, whether the learning criterion was achieved or not did not affect performance in the subsequent testing session indicated by a model excluding these individuals (Table S2-13, model: a).

For the actual testing session of ten trials, we changed the cylinder to a transparent cylinder and repeated the cleaning every third trial, the rest of the experimental set-up was the same as in the training (Fig. 3.1E). Using a transparent cylinder, the subject could see the charcoal-colored piece of banana, while approaching the task. It could also smell the banana from the front through little holes in the center of the cylinder. Nevertheless, it had to inhibit an initial response to reach directly through the transparent barrier. Instead, it had to take a detour to one of the open sides to enter the cylinder and reach the reward, as in the training. We used the number of incorrect trials as proxy for *inhibitory control*. We tested a total of $N = 110$ individuals (83 GML and 27 MBML). We estimated the repeatability of the used variables by calculating the ICC for $N = 12$ individuals (seven GML and five MBML), that repeated this test (number training trials: ICC = 0.556,

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number incorrect test trials: ICC = 0.141). $N = 2$ individuals were subjected to this task in a previous study 34 – 41 months ago (mean = 37.61 ± 3.91 ; (Huebner et al. 2018)).

Cylinder test: Statistical analyses

To investigate variation in *inhibitory control*, we calculated a negative binomial model with log link error function (function 'glm.nb', 'MASS' package(Brian et al. 2021)). We set the number of incorrect trials during the testing session as response, and species, sex, age (log-transformed) and the number of training trials as fixed factors in the interspecific model (Table S2-13, model: b). In the intraspecific model for GML (Table S2-17, model: n), we set sex, season, BMI (log-transformed), activity and neophilia as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: n) due to the low sample size for this species. We set sex and season, sex and BMI (log-transformed), sex and activity, and sex and neophilia as fixed factors, respectively.

Additionally, we calculated Spearman rank correlations between inhibitory control and the TIs, the number of trials to reach the learning criteria in the discrimination and reversal learning paradigm, as well as the *innovative propensity* to investigate potential covariations between these proxies for flexible learning abilities.

String-pulling task: Experimental set-up, *single-string set-up*

To assess an individual's *means-end understanding*, we conducted a string-pulling task in the single-string set-up(Jacobs and Osvath 2015). As string served a cable tie that was placed onto an external platform attached to the subject's cage just in front of the experimental platform within the cage. At the far end of the cable tie, we attached a piece of banana onto a small plate. The inner end of the cable tie reached 5 cm into the cage (Fig. 3.1G). Just before we placed the cable tie at its position, we lured the subject to the top wire in the center of the experimental platform. After positioning the cable tie, the subject had 20 min time to pull the end of the cable tie into reach to access the reward. We measured the response latency as duration from positioning the cable tie until the subject's approach and calculated the success latency as timespan between the response and reaching the

reward. For subjects that did not succeed (non-solver), we set the success latency to the maximum time of the trial (20 min) plus the response latency. We used this success latency as proxy for *means-end understanding*. We tested a total of $N = 114$ individuals (86 GML and 28 MBML). We estimated the repeatability of the variables by calculating the ICC for $N = 11$ individuals (seven GML and four MGML), that repeated this test (response latency: ICC = -0.137, success latency: ICC = -0.192). $N = 5$ individuals were subjected to this task in a previous study 11 – 53 months ago (mean = 34.36 ± 15.31 ; (Huebner 2020)).

String-pulling task: Experimental set-up, *perpendicular strings set-up*

To assess an individual's *goal directedness*, we conducted a string-pulling task with a perpendicular strings set-up (Jacobs and Osvath 2015). To ensure that the animal had sufficient understanding of the string-pulling task itself, we conducted a training prior to testing. This training consisted of the means-end understanding test, that was repeated until the subject successfully pulled the string three times. If it continuously failed to pull the cable tie for three trials, we moved the cable tie 2 cm further into the cage and decreased the maximum trial length to 10 min ($N = 11$). If the subject failed to pull the cable tie for another three trials, we moved the cable tie another 2 cm further into the cage. We continued with this procedure until the subject succeeded. In the subsequent trials, we changed the set-up to the original one, with the cable tie reaching 5 cm into the cage. For the actual goal directedness task, we positioned two identical cable ties with four grid cells distance (about 6 cm) at the center of the platform. The food reward was only attached to one cable tie (correct string), but we attached a plate at the outer end of both cable ties. The position of the correct string (left or right) was randomly assigned but counterbalanced across a session of ten trials and changed every second to third trial. The trials started when the two cable ties were fully introduced and ended when the subject reached the reward or after a maximum of 10 min. When the subject pulled the incorrect string first, we did not stop the trial, but allowed it to further explore the task until it pulled the correct string and reached the reward within the maximum trial duration. After each trial, we removed potential odor cues with 70%-ethanol.

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In the goal directedness task, we counted the number of correct and incorrect trials across one session of ten trials. We considered a trial as correct if the subject did only manipulate the correct string and reached the reward. We considered a trial as incorrect if the subject did not succeed, or if it manipulated the incorrect string. We used the number of incorrect trials as proxy for *goal directedness*. We tested a total of $N = 105$ individuals (83 GML and 22 MBML). We estimated the repeatability of the number of incorrect trials by calculating the ICC for $N = 8$ individuals (six GML and two MBML), that repeated this test (ICC = 0.119).

String pulling task: Statistical analyses, *means-end understanding*

To investigate interspecific variation in *means-end understanding*, we calculated a cox proportional-hazards model with the function `Surv(success latency | solver)` as proportional hazard and species, sex, and age (log-transformed) as fixed factors (Table S2-14, model: a). In the intraspecific model for GML (Table S2-17, model: o), we set sex in interaction with neophilia, season, BMI (log-transformed) and activity as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: o) because of the low sample size in this species. We set sex and season, sex and BMI (log-transformed), sex and activity, and sex and neophilia as fixed factors, respectively.

String pulling task: Statistical analyses, *goal-directedness*

To investigate variation in *goal directedness*, we calculated a poisson model with log link error function. In the interspecific model (Table S2-14, model: b), we set the number of incorrect trials as response and species, sex, and age (log-transformed) as fixed factors. In the intraspecific model for GML (Table S2-17, model: p), we set sex, season, BMI (log-transformed), activity and neophilia as fixed factors. For MBML, we calculated four less complex models (Table S2-18, model: p) due to the low sample size for this species. We set sex and season, sex and BMI (log-transformed), sex and activity, and sex and neophilia as fixed factors, respectively.

General intelligence

Finally, we investigated general intelligence across, as well as within species. For the interspecific *G*-factor, we calculated two principal axis factor analyses, using the function 'fa' with the argument 'fm' set to 'pa' ('psych' package). The first PAF contained the performance scores of individuals that completed all tests (excluding the spatial discrimination and the spatial reversal due to very low sample sizes in these tasks; $N = 21$ GML, $N = 9$ MBML). For the second PAF, we used the performance scores of individuals that completed all tests, except for the discrimination and reversal learning paradigm ($N = 76$ GML, $N = 19$ MBML). We controlled for sphericity by applying Bartlett's test and for sampling adequacy by applying KMO.

For the intraspecific *g*-factor, we used the same (log-transformed) performance scores as for the *G*-factor. For each species separately, we calculated two PCAs per species. The first PCA per species contained the performance scores of all tests (excluding the spatial discrimination and the spatial reversal due to very low sample sizes in these tasks), which resulted in a data set of $N = 23$ GML and $N = 9$ MBML. For the second PCA per species, we excluded all performance scores of the repeated discrimination and reversal learning paradigm, obtaining a sample size of $N = 76$ GML and $N = 19$ MBML. For each PCA, we controlled for sphericity by applying Bartlett's test and for sampling adequacy by applying KMO.

Supplemental results and discussion

Interspecific comparisons

We report the statistic results of the models estimating interspecific variation in personality traits (Table S2-5) and cognitive abilities (Table S2-6 – Table S2-14), as well as the results of the factor analytical approach to estimate a *G/g*-factor (Table S2-15 – Table S2-16).

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Intraspecific variation in performance in personality and cognitive tests

Since we did not find systematic variation among sex or age within species performance, we briefly summarize only significant differences below. The complete results are presented for GML in Table S2-17, and for MBML in Table S2-18.

Gray mouse lemurs

Briefly, performance in the food extraction and persistence task, the visual discrimination and reversal learning paradigm, spatial discrimination, plus maze, cylinder test, and string-pulling task was not influenced by sex, BMI, or personality factors (Table S2-17).

In the open field test, male GML were more explorative than females (LM: $p = 0.009$, Table S2-17, model: a) and individuals in less good body condition were slightly more neophilic than individuals with higher BMI ($p = 0.041$, Table S2-17, model: b). Variation in the *spatial reversal performance* (Table S2-17, model: k) was explained by sex (LM: $p = 0.002$) and body condition ($p = 0.026$). Males reached the learning criterion after more trials than females. GML in worse body condition reached the learning criterion after more trials than those in better body condition. Variation in *flexible learning* from the visual reversal learning to the spatial discrimination (Table S2-17, model: j) was explained by sex (LM: $p = 0.049$), with males reaching a higher TI than females. Variation in *flexible learning* from the spatial discrimination to the spatial reversal learning (Table S2-17, model: l) was explained by sex in interaction with neophilia (LM: $p = 0.022$), with more neophilic females achieving lower TIs than less neophilic females, whereas this effect was reversed for males.

Madame Berthe's mouse lemurs

Performance in the personality tests, food extraction task, visual discrimination and visual reversal performance, spatial discrimination and spatial reversal performance, flexible learning from the visual reversal learning to the spatial discrimination and from the spatial discrimination to the spatial reversal learning, plus maze, cylinder test, and goal directedness was not influenced by sex, BMI, or personality factors (Table S2-18).

Variation in *persistence* (Table S2-18, model: e) was explained by sex in interaction with BMI (LM: $p = 0.011$). Females in better body condition were less persistent than those in worse body condition and for males, this effect was reversed. Variation in flexible learning from the visual discrimination to the visual reversal learning (Table S2-18, model: h) was explained by sex (LM: $p = 0.029$), with males achieving lower TIs than females. Variation in *means-end understanding* (Table S2-18, model: o) was predicted by BMI (cox PHM: $p = 0.016$), with MBML in better body condition solving the string-pulling task in the single-string set-up faster than those in worse body condition.

Discussion: Intra-specific variation in performance in personality and cognitive tests

Concerning individual characteristics influencing performance in personality and cognitive tests, we found minor and inconsistent sex or age effects across tasks. First, males and females differed only in four out of 22 performance measures (in two cognitive tests and in two personality tests). Second, we controlled for potential effects of motivational state to participate in tests by estimating an individual's BMI (Sol et al. 2012; Cauchoux et al. 2020), but BMI was positively correlated with cognitive performance in only two out of 22 performance measures, suggesting no systematic link between test performance and an individual's current motivational state. Third, learning abilities partially covaried with age but not consistently across tasks and species. In our study, we mainly tested rather young individuals of a limited age range, with only 10 individuals being 4 yrs. or older (mean age = 1.21 ± 1.34 yrs.). Previous studies reported a positive correlation between age and learning abilities, and an increased impairment of cognitive abilities in elderly individuals (Bonté et al. 2014; Franks and Thorogood 2018; Hopkins et al. 2020). However, previous studies on mouse lemurs were conducted on captive individuals of larger age ranges (up to 13 yrs.) with a categorization of "elderly" or "aged" individuals starting at an age of five or six years (Languille et al. 2012). Compared to younger individuals, aged mouse lemurs express deficits in memory, flexible learning, and spatial abilities, while simple associative abilities seem to be preserved (Trouche et al. 2010; Picq et al. 2012). Wild mouse lemurs have a relatively short modal life expectancy of about three years and have been previously reported to not exhibit functional senescence, unlike their captive

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conspecifics(Hämäläinen et al. 2014a). Thus, potential age effects in cognitive performance might be difficult to demonstrate in wild mouse lemurs and the here reported correlations do not allow for firm conclusions about a relationship between an individual’s age and its cognitive performance.

Regarding the personality traits, neither neophilia, nor activity covaried with cognitive performance levels in either GML or MBML. In several prior studies, performance scores were confounded by variation in personality traits(Tebbich et al. 2012; Guenther et al. 2014). However, these links are by far not consistent across studies, emphasizing the importance to control for such non-cognitive factors(Ducatez et al. 2014a; Griffin et al. 2015; Guillette et al. 2015; Logan 2016; Huebner et al. 2018; Henke-von der Malsburg and Fichtel 2018; Rasolofoniaina et al. 2020; Schubiger et al. 2020).

Supplemental tables

Table S2-1 Sample sizes per species and sex for the single tasks, as well as the measured personality or cognitive trait, and the number of individuals that were not naïve to the respective experimental task. Sample sizes differ between tasks as it was not possible to recapture all individuals until they had completed all tasks of the test battery

task	measured trait	GML		not naïve	MBML		not naïve	total
		F	M		F	M		
open field test	activity	51	67	15	19	13	1	150
novel object test	neophilia	51	67	0	19	13	1	150
food extraction task	innovative	36	47	5	18	11	0	112
	propensity							
persistence test	persistence	35	47	0	17	9	0	108
visual	associative	14	11	0	8	6	0	39
discrimination	learning							
visual reversal	associative/ flexible learning	14	11	0	7	5	0	37
spatial	associative/ flexible learning	12	11	0	4	5	0	32
discrimination	flexible learning							
spatial reversal	associative/ flexible learning	11	10	0	2	3	0	26
plus maze	spatial memory	39	57	5	15	10	0	121
cylinder test	inhibitory	37	46	2	17	10	0	110
	control							
string-pulling task	means-end understanding	37	49	5	17	11	0	114
perpendicular strings	goal	36	47	0	15	7	0	105
	directedness							

Table S2-2 Intraclass correlation coefficients (ICC) estimating the interobserver reliability of the measured behaviors for 10% of the analyzed videos per task

measured behavior	ICC per behavior	ICC per test
open field test		0.989
latency enter	>0.999	
stationary	0.831	
locomotion	0.866	
cells traversed	0.990	
latency grid	0.918	
grid cell changes	0.995	
jumps	0.914	
rears	0.778	
dips	0.396	
novel object test		0.905
approach latency	0.971	
contact latency	0.974	
approach speed	0.862	
contact frequency	0.910	
food extraction task		>0.999
response latency	>0.999	
success latency	>0.999	
number of successes	0.837	
persistence test		0.957
duration in contact	0.906	
duration manipulating	0.992	
solver	1.000	
repeated discrimination and reversal learning paradigm		0.999
response latency	>0.999	
success latency	0.997	
number of incorrect trials	0.937	
plus maze		0.986
latency to enter correct arm per trial	0.984	
sum of errors per trial	0.877	
mean sum of errors per session	0.961	
cylinder test		0.802
number of incorrect trials	0.802	
string-pulling task single-string set-up		>0.999
response latency	>0.999	
success latency	>0.999	
string-pulling task perpendicular strings set-up		1.000
number of incorrect trials	1.000	

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Table S2-3 Repeatability of the personality tests. Intraclass correlation coefficients were calculated between the first and second test, between the first, second, and third test, and between the first, second, third, and fourth test. Sample sizes are given in parentheses

behavior	test 1-2 (N = 104)	test 1-3 (N = 52)	test 1-4 (N = 29)
latency enter*	-0.103	-0.040	-0.061
locomotion	0.343	0.409	0.415
cells traversed	0.381	0.423	0.358
rears*	0.365	0.275	0.269
dips*	0.132	0.059	0.076
contact latency	0.022	-0.046	0.017
approach speed	0.158	0.044	0.073
contact frequency	0.106	0.002	0.036

*log-transformed variables

Table S2-4 Loadings of the principal component analyses (varimax rotation) of the first and second open field test, including eigenvalues and explained variances per rotated component (RC), as well as the Kaiser-Meyer-Olkin factor (KMO) and statistics of the Bartlett's test of sphericity

behavior	test 1		test 2	
	RC1	RC2	RC1	RC2
latency enter*	-0.486	-0.028	-0.424	-0.142
locomotion	0.898	0.056	0.916	0.042
cells traversed	0.904	0.138	0.912	0.107
rears*	0.260	0.773	0.306	0.787
dips*	-0.073	0.868	-0.018	0.892
eigenvalue	1.93	1.37	1.95	1.45
explained variance	0.58	0.42	0.57	0.43
KMO	0.555		0.547	
Bartlett's test	X ² = 203.509 df = 10 p<0.001		X ² = 151.463 df = 10 p<0.001	

*log-transformed variables

Table S2-5 Personality traits. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>activity</i>		3.99	0.004	4	0.074
	species * sex	GML: -38.45 ± 10.90 M: -18.26 ± 14.58 GML:M: 39.35 ± 16.41	5.75	0.018		
	age	-2.22 ± 3.34	0.44	0.509		
b)	<i>neophilia</i>		8.56	0.073	4	0.056
	species	GML: 0.11 ± 0.16	0.69	0.489		
	sex	M: 0.04 ± 0.14	0.27	0.791		
	age	-0.03 ± 0.07	-0.49	0.621		
	zero-part: sex	F: -0.93 ± 0.32 M: -1.49 ± 0.71	-2.87	0.004		

Table S2-6 Foraging extraction task. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>innovation speed</i>					
	Surv(success latency solver)		11.37	0.010	3	0.102
	species	GML: 0.61 ± 0.24	2.49	0.013		
	sex	M: 0.41 ± 0.20	2.02	0.044		
	age	0.13 ± 0.10	1.26	0.209		
b)	<i>innovation propensity</i>					
	N opened wells		8.39	0.039	3	0.073
	species	GML: 0.28 ± 0.10	7.64	0.006		
	sex	M: 0.04 ± 0.08	0.181	0.670		
	age	0.01 ± 0.04	0.03	0.874		

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Table S2-7 Persistence, a) total sample size, **b)** excluding N = 17 individuals that received additional training. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R²), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate ± SE	ts	p	df	R ²
a)	<i>persistence</i>, N = 108		9.47	<0.001	3	0.192
	species	GML: 0.15 ± 0.03	25.56	<0.001		
	sex	M: -0.03 ± 0.03	1.68	0.198		
	age	-0.02 ± 0.01	2.92	0.090		
b)	<i>persistence</i>, N = 91		6.36	<0.001	3	0.152
	species	GML: 0.15 ± 0.04	16.52	<0.001		
	sex	M: -0.04 ± 0.03	1.98	0.163		
	age	-0.02 ± 0.01	2.39	0.126		

Table S2-8 Visual discrimination. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R²), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate ± SE	ts	p	df	R ²
a)	<i>visual discrimination learning</i>					
	N incorrect trials		20.99	<0.001	5	0.088
	species * session	GML: -0.29 ± 0.19	5.46	0.020		
		session: -0.25 ± 0.07				
		session:GML: 0.14 ± 0.06				
	sex	M: 0.18 ± 0.11	2.68	0.102		
	age	0.14 ± 0.06	5.97	0.015		
b)	<i>visual discrimination performance</i>					
	N total trials		5.16	0.005	3	0.247
	species	GML: 0.36 ± 0.13	7.70	0.009		
	sex	M: 0.10 ± 0.13	0.56	0.458		
	age	0.18 ± 0.07	7.81	0.008		

Table S2-9 Visual reversal and flexible learning. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>visual reversal learning</i>					
	N incorrect trials		41.57	<0.001	4	0.234
	species	GML: 0.42 ± 0.12	10.31	0.001		
	sex	M: 0.04 ± 0.11	0.10	0.758		
	age	-0.14 ± 0.06	5.61	0.018		
	session	-0.38 ± 0.03	24.75	<0.001		
b)	<i>visual reversal performance</i>					
	N total trials		4.30	0.011	3	0.216
	species	GML: 0.31 ± 0.10	10.29	0.003		
	sex	M: 0.05 ± 0.10	0.26	0.614		
	age	-0.07 ± 0.05	1.83	0.186		
c)	<i>flexible learning (visual cues)</i>					
	TI		2.87	0.050	3	0.128
	species	GML: 0.09 ± 0.09	1.06	0.310		
	sex	M: -0.12 ± 0.09	1.77	0.192		
	age	0.08 ± 0.04	3.96	0.054		

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Table S2-10 Spatial discrimination and flexible learning. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R²), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate ± SE	ts	p	df	R ²
a)	<i>spatial discrimination learning</i>					
	N incorrect trials		73.17	<0.001	10	0.412
	species * session	GML: -0.58 ± 0.25 session: -0.33 ± 0.07 session:GML: 0.21 ± 0.07	10.02	0.002		
	sex * session	M: 0.14 ± 0.23 session:M: -0.17 ± 0.05	10.71	0.001		
	species * age	age: -0.57 ± 0.20 age:GML: 0.68 ± 0.24	7.83	0.005		
	S [±]	position 2: 1.47 ± 0.33 position 3: 1.56 ± 0.28 position 4: 1.34 ± 0.26	27.91	<0.001		
b)	<i>spatial discrimination performance</i>					
	N total trials		3.48	0.010	7	0.359
	species * age	GML: 0.05 ± 0.18 age: -0.30 ± 0.16 age:GML: 0.44 ± 0.20	4.58	0.043		
	sex	M: -0.02 ± 0.19	0.01	0.931		
	S [±]	position 2: 0.96 ± 0.29 position 3: 0.93 ± 0.24 position 4: 0.74 ± 0.23	6.42	0.002		
	c)	<i>flexible learning (cue change)</i>				
TI			3.50	0.027	3	0.181
species		GML: 0.16 ± 0.09	3.64	0.066		
sex		M: 0.22 ± 0.08	6.71	0.014		
	age	0.02 ± 0.04	0.17	0.680		

Table S2-11 Spatial reversal and flexible learning. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>spatial reversal learning</i>					
	N incorrect trials		41.78	<0.001	10	0.220
	species *	GML: -0.86 ± 0.27	8.10	0.004		
	session	session: -0.19 ± 0.05				
		session:GML: 0.13 ± 0.05				
	sex	M: 0.35 ± 0.16	4.51	0.034		
	age	0.006 ± 0.07	0.01	0.931		
b)	<i>spatial reversal performance</i>					
	N total trials		6.19	<0.001	9	0.651
	species	GML: -0.24 ± 0.21	1.33	0.267		
	sex * S $^{\pm}$	M: 0.53 ± 0.29	5.05	0.012		
		position 2: 0.61 ± 0.42				
		position 2:M: -0.42 ± 0.53				
		position 3: 0.23 ± 0.26				
	position 3:M: 0.95 ± 0.40					
	position 4: 0.45 ± 0.5					
	position 4:M: -0.58 ± 0.38					
age	-0.14 ± 0.09	2.66	0.122			
c)	<i>flexible learning (spatial cues)</i>					
	TI		6.90	0.001	3	0.364
	species	GML: 0.39 ± 0.10	16.18	<0.001		
	sex	M: -0.13 ± 0.09	2.01	0.168		
age	0.03 ± 0.05	0.49	0.492			

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Table S2-12 Spatial memory. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>spatial learning</i>					
	N errors		73.77	<0.001	7	0.042
	species * trial	GML: -0.15 ± 0.21 trial: -0.12 ± 0.02 trial:GML: -0.06 ± 0.02	7.88	0.005		
	sex	M: -0.14 ± 0.13	1.18	0.277		
	goal box	right: 0.26 ± 0.14 straight: -0.45 ± 0.18	14.54	<0.001		
	age	0.03 ± 0.05	0.38	0.537		
b)	<i>spatial memory</i>					
	N mean errors		5.11	<0.001	5	0.146
	species	GML: -0.47 ± 0.15	9.47	0.003		
	sex	M: -0.11 ± 0.12	0.84	0.361		
	age	0.05 ± 0.06	0.63	0.429		
	goal box	right: 0.24 ± 0.14 straight: -0.46 ± 0.17	8.10	<0.001		

Table S2-13 Inhibitory control, a) excluding N = 21 individuals that did not meet the learning criterion in the prior training session, b) total sample size. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>inhibitory control, N = 87</i>					
	N incorrect trials		8.22	0.084	4	0.081
	species	GML: -0.16 ± 0.17	0.85	0.356		
	sex	M: -0.09 ± 0.14	0.38	0.538		
	age	-0.04 ± 0.07	0.27	0.598		
	N trials training	0.02 ± 0.01	6.85	0.009		
b)	<i>inhibitory control, N = 110</i>					
	N incorrect trials		10.34	0.035	4	0.082
	species	GML: -0.21 ± 0.14	2.34	0.126		
	sex	M: 0.03 ± 0.12	0.08	0.783		
	age	-0.06 ± 0.06	0.99	0.319		
	N trials training	0.02 ± 0.01	7.98	0.005		

Table S2-14 Means-end understanding and goal directedness. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. GML: gray mouse lemur, M: male

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>means-end understanding</i>					
	Surv(success latency solver)		1.98	0.600	3	0.018
	species	GML: 0.33 ± 0.24	2.01	0.156		
	sex	M: 0.01 ± 0.20	0.00	0.986		
	age	0.01 ± 0.09	0.01	0.942		
b)	<i>goal directedness</i>					
	N incorrect trials		0.67	0.874	3	0.006
	species	GML: -0.05 ± 0.10	0.25	0.621		
	sex	M: 0.06 ± 0.09	0.44	0.508		
	age	0.01 ± 0.04	0.10	0.747		

Table S2-15 General intelligence on reduced set of tests. Interspecific G loadings of the PAF, as well as intraspecific g loadings for gray mouse lemurs (GML) and Madame Berthe's mouse lemurs (MBML). For each factor and component, the squared factor (SS) loadings or eigenvalue, and the proportion of explained variance are given. For each analysis, the sample size (N), the Kaiser-Meyer-Olkin (KMO) index, and the statistics for the Bartlett's test of sphericity are given

cognitive performance	G loadings	g loadings	g loadings
	($N_{GML} = 76, N_{MBML} = 19$)	GML ($N = 76$)	MBML ($N = 19$)
FE: success latency	0.54	-0.57	-0.31
FEP: persistence	-0.02	-0.43	0.47
CT: N incorrect trials	-0.02	0.07	0.21
SP1: success latency	-0.22	0.29	0.53
SP2: N incorrect trials	-0.07	0.21	-0.26
PM: N mean errors	0.50	-0.60	-0.54
SS loadings	0.60		
eigenvalue		1.18	1.45
explained variance	0.10	0.23	0.37
KMO	0.45	0.45	0.55
Bartlett's test	$\chi^2 = 19.51$	$\chi^2 = 18.95$	$\chi^2 = 19.95$
	df = 15	df = 15	df = 15
	p = 0.192	p = 0.216	p = 0.174

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Table S2-16 General intelligence including all cognitive performance measures. Interspecific G loadings of the PAF, as well as intraspecific g loadings for gray mouse lemurs (GML) and Madame Berthe's mouse lemurs (MBML). For each factor and component, the squared factor (SS) loadings or eigenvalue, and the proportion of explained variance are given. For each analysis, the sample size (N), the Kaiser-Meyer-Olkin (KMO) index, and the statistics for the Bartlett's test of sphericity are given

cognitive performance	G loadings (N _{GML} = 21, N _{MBML} = 9)	g loadings GML (N = 21)	g loadings MBML (N = 9)
FE: success latency	0.47	-0.40	0.50
FEP: persistence	0.03	-0.15	-0.26
CT: N incorrect trials	0.29	0.06	0.36
SP1: success latency	-0.45	0.17	-0.41
SP2: N incorrect trials	-0.01	-0.43	-0.39
PM: N mean errors	0.74	-0.54	0.27
Dv: N trials	-0.20	-0.36	0.13
Rv: N trials	-0.08	-0.43	-0.39
SS loadings	1.11		
eigenvalue		1.43	1.67
explained variance	0.14	0.20	0.35
KMO	0.49	0.32	0.21
Bartlett's test	$\chi^2 = 24.71$ df = 28 $p = 0.644$	$\chi^2 = 36.60$ df = 45 $p = 0.810$	$\chi^2 = 26.26$ df = 28 $p = 0.559$

Table S2-17 Gray mouse lemurs, all statistic models. Given are test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. M: male; visual stimuli: DF: dotted flower, SS: striped square, WC: black triangle

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>activity</i>		3.00	0.034	3	0.049
	sex	M: 20.43 \pm 7.71	7.03	0.009		
	season	dry-wet: 4.49 \pm 8.64	0.27	0.604		
	BMI	-0.192 \pm 3.92	0.24	0.625		
b)	<i>neophilia</i>		10.65	0.031	4	0.088
	sex	M: -0.04 \pm 0.16	-0.25	0.806		
	season	dry-wet: -0.10 \pm 0.17	-0.58	0.561		
	BMI	-0.157 \pm 0.08	-2.05	0.041		
	zero-part: sex	F: -0.83 \pm 0.35 M: -1.53 \pm 0.73	-2.34 -2.10	0.019 0.035		
c)	<i>innovation speed</i>					
	Surv(success latency solver)		9.29	0.100	5	0.110
	sex	M: 0.34 \pm 0.24	2.04	0.153		
	season	dry-wet: 0.43 \pm 0.24	3.34	0.067		
	BMI	0.22 \pm 0.14	2.58	0.108		
	activity	0.11 \pm 0.13	0.75	0.388		
d)	<i>innovation propensity</i>					
	N successes		0.48	0.993	5	0.006
	sex	M: 0.03 \pm 0.10	0.09	0.771		
	season	dry-wet: 0.04 \pm 0.09	0.20	0.654		
	BMI	-0.02 \pm 0.05	0.09	0.763		
	activity	0.01 \pm 0.05	0.07	0.795		
e)	<i>persistence</i>		1.92	0.100	5	0.054
	sex	M: -0.04 \pm 0.03	1.91	0.171		
	season	dry-wet: -0.03 \pm 0.03	0.99	0.323		
	BMI	-0.02 \pm 0.02	1.49	0.226		
	activity	0.05 \pm 0.02	7.36	0.008		
f)	<i>visual discrimination</i>					
	N total trials		2.34	0.120	2	0.100
	sex	M: 0.11 \pm 0.19	0.36	0.552		
	BMI	0.21 \pm 0.10	4.66	0.042		
	N total trials		0.66	0.528	2	-0.029
	sex	M: -0.04 \pm 0.20	0.03	0.857		
	activity	0.12 \pm 0.10	1.30	0.267		
	N total trials		0.47	0.631	2	-0.046
sex	M: 0.00 \pm 0.20	0.00	0.995			
neophilia	0.10 \pm 0.10	0.93	0.347			

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	N total trials		0.95	0.458	4	-0.009
	sex	M: -0.03 ± 0.22	0.02	0.899		
	S±	DF: 0.34 ± 0.30	1.26	0.317		
		SS: -0.08 ± 0.27				
		WC: 0.31 ± 0.32				
g)	<i>visual reversal</i>					
	N total trials		1.89	0.153	4	0.129
	sex	M: 0.10 ± 0.10	0.94	0.344		
	S±	DF: -0.17 ± 0.15	2.43	0.096		
		SS: -0.20 ± 0.14				
		WC: 0.12 ± 0.13				
	N total trials		0.74	0.491	2	-0.023
	sex	M: 0.05 ± 0.11	0.25	0.620		
	BMI	-0.06 ± 0.05	1.25	0.276		
	N total trials		0.23	0.793	2	-0.068
	sex	M: 0.03 ± 0.11	0.10	0.760		
	activity	0.03 ± 0.06	0.25	0.619		
	N total trials		0.11	0.898	2	-0.080
	sex	M: 0.05 ± 0.11	0.20	0.660		
	neophilia	0.00 ± 0.06	0.01	0.937		
h)	<i>flexible learning (visual cues)</i>					
	TI		1.61	0.224	2	0.048
	sex	M: -0.12 ± 0.13	0.93	0.346		
	BMI	0.10 ± 0.06	2.39	0.134		
	TI		0.58	0.569	2	-0.036
	sex	M: -0.14 ± 0.14	1.01	0.325		
	activity	0.04 ± 0.07	0.41	0.530		
	TI		0.39	0.681	2	-0.053
	sex	M: -0.12 ± 0.13	0.77	0.389		
	neophilia	0.01 ± 0.07	0.04	0.837		
i)	<i>spatial discrimination</i>					
	N total trials		4.20	0.014	4	0.368
	sex	M: -0.08 ± 0.22	0.14	0.714		
	S±	position 2: 0.89 ± 0.32	4.93	0.011		
		position 3: 0.94 ± 0.28				
		position 4: 0.69 ± 0.28				
	N total trials		2.38	0.118	2	0.111
	sex	M: -0.30 ± 0.25	1.50	0.235		
	BMI	0.23 ± 0.13	3.34	0.083		
	N total trials		0.61	0.554	2	-0.037
	sex	M: -0.29 ± 0.27	1.12	0.303		
	activity	-0.00 ± 0.14	0.00	0.978		
	N total trials		1.14	0.340	2	0.012
	sex	M: -0.27 ± 0.26	1.11	0.304		
	neophilia	-0.13 ± 0.13	1.00	0.329		

j)	<i>flexible learning (cue change)</i>					
	TI		4.22	0.029	2	0.219
	sex	M: 0.19 ± 0.09	4.33	0.049		
	BMI	-0.09 ± 0.05	4.09	0.056		
	TI		2.33	0.122	2	0.103
	sex	M: 0.16 ± 0.10	2.47	0.131		
	activity	0.05 ± 0.05	0.85	0.366		
	TI		1.90	0.174	2	0.073
	sex	M: 0.20 ± 0.10	3.79	0.065		
neophilia	-0.02 ± 0.05	0.13	0.722			
k)	<i>spatial reversal</i>					
	N total trials		9.65	0.001	2	0.464
	sex	M: 0.73 ± 0.20	13.75	0.002		
	BMI	-0.24 ± 0.10	5.90	0.026		
	N total trials		6.03	0.004	4	0.501
	sex	M: 0.66 ± 0.20	11.00	0.004		
	S±	position 2: 0.15 ± 0.29 position 3: 0.72 ± 0.24 position 4: 0.20 ± 0.27	3.23	0.050		
	N total trials		6.04	0.010	2	0.335
	sex	M: 0.66 ± 0.22	8.60	0.009		
	activity	0.13 ± 0.11	1.27	0.275		
	N total trials		5.34	0.015	2	0.303
	sex	M: 0.70 ± 0.22	0.97	0.006		
neophilia	0.07 ± 0.12	0.37	0.549			
l)	<i>flexible learning (spatial cues)</i>					
	TI		4.42	0.016	3	0.318
	sex * neophilia	M: -0.17 ± 0.10 neophilia: -0.20 ± 0.06 neophilia:M: 0.26 ± 0.11	6.17	0.022		
	TI		2.03	0.158	2	0.085
	sex	M: -0.18 ± 0.11	2.39	0.138		
	BMI	0.08 ± 0.06	1.66	0.212		
	TI		1.87	0.180	2	0.073
sex	M: -0.21 ± 0.12	3.20	0.089			
activity	0.07 ± 0.06	1.38	0.253			
m)	<i>spatial memory</i>					
	N mean errors		3.01	0.007	7	0.129
	sex	M: -0.18 ± 0.14	1.64	0.203		
	season	dry-wet: 0.06 ± 0.14	0.17	0.685		
	BMI	0.12 ± 0.07	3.02	0.086		
	activity	0.09 ± 0.07	1.64	0.204		
	neophilia	-0.02 ± 0.07	0.06	0.805		
	goal box	right: 0.30 ± 0.15 straight: -0.44 ± 0.20	7.22	0.001		

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n)	<i>inhibitory control</i>					
	N incorrect trials		9.76	0.135	6	0.100
	sex	M: -0.15 ± 0.15	0.95	0.331		
	season	dry-wet: -0.16 ± 0.14	1.34	0.247		
	BMI	-0.06 ± 0.07	0.81	0.367		
	activity	0.15 ± 0.08	3.59	0.058		
o)	<i>means-end understanding</i>					
	Surv(success latency solver)		10.29	0.113	6	0.110
	sex * neophilia	M: 0.19 ± 0.26	6.80	0.009		
		neophilia:F: -0.19 ± 0.18				
		neophilia:M: 0.67 ± 1.96				
	season	dry-wet: 0.29 ± 0.24	1.41	0.236		
p)	<i>goal directedness</i>					
	N incorrect trials		1.79	0.877	5	0.021
	sex	M: 0.02 ± 0.10	0.03	0.865		
	season	dry-wet: -0.01 ± 0.10	0.01	0.918		
	BMI	-0.05 ± 0.05	1.11	0.292		
	activity	0.03 ± 0.05	0.40	0.529		
	neophilia	-0.05 ± 0.05	0.89	0.346		

Table S2-18 Madame Berthe's mouse lemurs, all statistic models. Given are estimates, test-statistics (ts), p-value and degrees of freedom (df) of the full-null-model comparison (bold), effect sizes (R^2), as well as estimates and standard errors (SE), test-statistics and p-values of the individual predictors. M: male; visual stimuli: DF: dotted flower, SS: striped square, WC: black triangle

model ID	response fixed factors	estimate \pm SE	ts	p	df	R^2
a)	<i>activity</i>		1.27	0.303	3	0.026
	sex	M: -13.00 ± 15.51	0.70	0.409		
	season	dry-wet: -12.23 ± 16.83	0.53	0.473		
	BMI	11.40 ± 7.67	2.21	0.148		
b)	<i>neophilia</i>		1.71	0.789	4	0.053
	sex	M: 0.19 ± 0.28	0.67	0.501		
	season	dry-wet: -0.06 ± 0.31	-0.21	0.835		
	BMI	0.08 ± 0.15	0.55	0.581		
	zero-part: sex	F: -1.07 ± 0.64	-1.68	0.093		
		M: -1.01 ± 1.31	-0.77	0.439		
c)	<i>innovation speed</i>					
	Surv(success latency solver)		6.87	0.080	3	0.235
	sex * activity	M: 0.52 ± 0.43	6.38	0.012		
		activity:F: -0.65 ± 0.52				
		activity:M: 1.33 ± 0.55				

	Surv(success latency solver)	1.62	0.400	2	0.033
	sex M: 0.52 ± 0.45	1.16	0.247		
	season dry-wet: -0.41 ± 0.45	-0.90	0.366		
	Surv(success latency solver)	0.94	0.600	2	0.059
	sex M: 0.36 ± 0.42	0.85	0.396		
	BMI -0.08 ± 0.20	-0.37	0.713		
	Surv(success latency solver)	1.99	0.400	2	0.076
	sex M: 0.61 ± 0.8	1.29	0.200		
	neophilia -0.30 ± 0.27	-1.12	0.261		
d)	<i>innovation propensity</i>				
	N successes	1.39	0.500	2	0.051
	sex M: 0.11 ± 0.19	0.34	0.560		
	BMI 0.10 ± 0.09	1.18	0.278		
	N successes	0.76	0.682	2	0.028
	sex M: 0.05 ± 0.19	0.08	0.772		
	season dry-wet: 0.14 ± 0.19	0.56	0.455		
	N successes	1.15	0.562	2	0.042
	sex M: 0.06 ± 0.19	0.09	0.759		
	activity -0.09 ± 0.09	0.94	0.331		
	N successes	0.34	0.844	2	0.013
	sex M: 0.07 ± 0.19	0.12	0.725		
	neophilia 0.03 ± 0.09	0.13	0.717		
e)	<i>persistence</i>	5.97	0.004	3	0.374
	sex * BMI M: -0.05 ± 0.04	7.61	0.011		
	BMI: -0.08 ± 0.02				
	BMI:M: 0.11 ± 0.04				
	<i>persistence</i>	1.06	0.363	2	0.005
	sex M: -0.06 ± 0.05	1.39	0.250		
	season dry-wet: 0.05 ± 0.05	1.04	0.318		
	<i>persistence</i>	1.39	0.270	2	0.030
	sex M: -0.06 ± 0.05	1.67	0.209		
	activity -0.03 ± 0.02	1.67	0.210		
	<i>persistence</i>	1.16	0.324	2	0.015
	sex M: -0.03 ± 0.05	0.54	0.468		
	neophilia -0.03 ± 0.02	1.28	0.270		
f)	<i>visual discrimination</i>				
	N total trials	1.02	0.332	1	0.002
	activity -0.08 ± 0.08	1.023	0.332		
	N total trials	0.01	0.927	1	-0.083
	sex M: -0.02 ± 0.16	0.01	0.927		
	N total trials	0.59	0.456	1	-0.032
	BMI -0.06 ± 0.08	0.59	0.456		
	N total trials	0.44	0.522	1	-0.045
	neophilia 0.05 ± 0.08	0.44	0.522		

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	N total trials		1.22	0.353	3	0.048
	S ⁺	DF: 0.31 ± 0.21 SS: -0.01 ± 0.23 WC: 0.04 ± 0.23	1.22	0.353		
g)	<i>visual reversal</i>					
	N total trials		2.22	0.164	3	0.249
	S ⁺	DF: 0.04 ± 0.23 SS: 0.42 ± 0.24 WC: -0.11 ± 0.24	2.22	0.164		
	N total trials		0.83	0.384	1	-0.016
	sex	M: 0.17 ± 0.18	0.83	0.384		
	N total trials		0.55	0.476	1	-0.043
	BMI	0.07 ± 0.09	0.55	0.476		
	N total trials		0.51	0.493	1	-0.047
	activity	-0.07 ± 0.10	0.51	0.493		
	N total trials		0.16	0.700	1	-0.083
	neophilia	-0.04 ± 0.10	0.16	0.700		
h)	<i>flexible learning (visual cues)</i>					
	TI		6.15	0.029	1	0.284
	sex	M: -0.25 ± 0.10	6.15	0.029		
	TI		0.53	0.481	1	-0.038
	BMI	0.05 ± 0.06	0.53	0.481		
	TI		1.85	0.198	1	0.062
	activity	0.08 ± 0.06	1.85	0.198		
	TI		3.75	0.077	1	0.175
	neophilia	0.11 ± 0.06	3.75	0.077		
i)	<i>spatial discrimination</i>					
	N total trials		1.74	0.229	1	0.085
	sex	M: -0.32 ± 0.24	1.74	0.229		
	N total trials		0.21	0.661	1	-0.110
	BMI	-0.09 ± 0.20	0.21	0.661		
	N total trials		0.28	0.611	1	-0.098
	activity	0.08 ± 0.15	0.28	0.611		
	N total trials		1.27	0.298	1	0.032
	neophilia	-0.15 ± 0.13	1.27	0.298		
	N total trials		0.94	0.489	3	-0.025
	S ⁺	position 2: 0.10 ± 0.41 position 3: 0.10 ± 0.41 position 4: 0.53 ± 0.32	0.94	0.489		
j)	<i>flexible learning (cue change)</i>					
	TI		2.97	0.119	1	0.164
	sex	M: 0.24 ± 0.14	2.97	0.119		
	TI		0.10	0.756	1	-0.099
	BMI	-0.03 ± 0.08	0.10	0.756		
	TI		2.82	0.128	1	0.154
	activity	-0.12 ± 0.07	2.82	0.128		

	TI		0.20	0.663	1	-0.087
	neophilia	0.04 ± 0.08	0.20	0.663		
k)	<i>spatial reversal</i>					
	N total trials		6.00	0.092	1	0.556
	activity	-0.31 ± 0.12	6.00	0.092		
	N total trials		0.55	0.512	1	-0.126
	sex	M: 0.27 ± 0.36	0.55	0.512		
	N total trials		3.31	0.167	1	0.366
	BMI	-0.27 ± 0.15	3.31	0.167		
	N total trials		4.75	0.118	1	0.484
	neophilia	-0.29 ± 0.13	4.75	0.118		
	N total trials		0.78	0.442	1	-0.058
	S ⁺	position 4: -0.38 ± 0.43	0.78	0.442		
l)	<i>flexible learning (spatial cues)</i>					
	TI		0.90	0.375	1	-0.013
	sex	-0.05 ± 0.05	0.90	0.375		
	TI		0.72	0.423	1	-0.036
	BMI	-0.02 ± 0.03	0.72	0.423		
	TI		0.00	0.959	1	-0.142
	activity	0.00 ± 0.03	0.00	0.959		
	TI		0.73	0.422	1	-0.035
	neophilia	-0.02 ± 0.03	0.73	0.422		
m)	<i>spatial memory</i>					
	N mean errors		1.13	0.342	2	0.011
	sex	M: 0.17 ± 0.29	0.32	0.575		
	BMI	0.21 ± 0.15	2.06	0.165		
	N mean errors		0.42	0.665	2	-0.051
	sex	M: 0.09 ± 0.31	0.08	0.778		
	season	dry-wet: 0.25 ± 0.31	0.65	0.429		
	N mean errors		1.05	0.366	2	0.004
	sex	M: 0.19 ± 0.30	0.40	0.533		
	activity	0.21 ± 0.15	1.91	0.181		
	N mean errors		0.96	0.399	2	-0.004
	sex	M: 0.20 ± 0.30	0.45	0.509		
	neophilia	-0.20 ± 0.15	1.73	0.202		
	N mean errors		0.81	0.501	3	-0.024
	sex	M: 0.06 ± 0.31	0.04	0.847		
	goal box	right: 0.01 ± 0.38 straight: -0.49 ± 0.35	1.13	0.343		
n)	<i>inhibitory control</i>					
	N incorrect trials		0.34	0.844	2	0.013
	sex	M: -0.04 ± 0.24	0.03	0.859		
	activity	-0.07 ± 0.12	0.34	0.559		
	N incorrect trials		0.14	0.934	2	0.005
	sex	M: 0.01 ± 0.23	0.00	0.954		
	season	dry-wet: -0.09 ± 0.23	0.14	0.713		

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	N incorrect trials		0.07	0.966	2	0.003
	sex	M: -0.01 ± 0.23	0.00	0.952		
	BMI	-0.03 ± 0.11	0.07	0.791		
	N incorrect trials		0.06	0.969	2	0.002
	sex	M: 0.01 ± 0.23	0.00	0.961		
	neophilia	-0.03 ± 0.11	0.06	0.802		
o)	<i>means-end understanding</i>					
	Surv(success latency solver)		6.35	0.040	2	0.216
	sex	M: -0.36 ± 0.43	-0.82	0.410		
	BMI	0.58 ± 0.24	2.42	0.016		
	Surv(success latency solver)		1.72	0.400	2	0.064
	sex	M: -0.38 ± 0.44	-0.87	0.382		
	season	dry-wet: 0.49 ± 0.45	1.08	0.279		
	Surv(success latency solver)		1.42	0.500	2	0.052
	sex	M: -0.33 ± 0.43	-0.78	0.438		
	activity	-0.21 ± 0.22	-0.95	0.345		
	Surv(success latency solver)		2.80	0.200	2	0.094
	sex	M: -0.58 ± 0.46	-1.24	0.216		
	neophilia	0.32 ± 0.21	1.48	0.138		
p)	<i>goal directedness</i>					
	N incorrect trials		1.85	0.396	2	0.082
	sex	M: 0.27 ± 0.20	1.82	0.178		
	activity	0.05 ± 0.10	0.25	0.617		
	N incorrect trials		1.63	0.444	2	0.073
	sex	M: 0.24 ± 0.20	1.32	0.250		
	season	dry-wet: 0.03 ± 0.21	0.02	0.877		
	N incorrect trials		1.63	0.443	2	0.073
	sex	M: 0.25 ± 0.19	1.61	0.204		
	BMI	0.02 ± 0.10	0.03	0.869		
	N incorrect trials		1.84	0.399	2	0.082
	sex	M: 0.24 ± 0.19	1.48	0.223		
	neophilia	0.04 ± 0.09	0.24	0.627		

Chapter IV: General discussion

The objective of my thesis was to broaden our understanding of cognitive evolution in relation to ecological factors, with a specific focus on the degree of ecological specialization. The specific aims were to summarize common links of variation in cognitive test performances with ecological factors across the animal kingdom (**Chapter II**), and to link cognitive performances across a broad range of cognitive abilities with the degree of ecological specialization and species-specific ecological adaptations (**Chapter III**). To this end, I systematically investigated patterns of (co)variation between cognitive performances and species-specific ecological adaptations across the animal kingdom, and empirically assessed cognitive performances in two sympatric mouse lemur species, that differ in their degree of ecological specialization. In my first theoretic approach, I found that cognitive performances have been associated with ecological factors, such as food patch distribution, characteristics of food items, habitat complexity or seasonality. Other ecological factors, such as the synecology with predators or parasites remain largely understudied. Also, a covariation of cognitive performances with the degree of ecological specialization has rarely been explicitly investigated. By classifying the species in comparison in their degree of dietary and habitat specialization, I found that this categorical proxy for a species-specific ecological niche does not consistently correlate with cognitive performances (**Chapter II**). In my second experimental approach, I found that the generalist gray mouse lemur does not consistently outperform the more specialized and sympatric Madame Berthe's mouse lemur across a broad range of cognitive abilities. The gray mouse lemur was more innovative and showed greater persistence, whereas the Madame Berthe's mouse lemur was more active and learned associative reward contingencies faster. The two species did not differ in inhibitory control, means-end understanding, or goal directedness (**Chapter III**). These experimental results parallel the theoretic findings of the reviewed literature, in that generalist species do not outperform specialist species *per se*. Instead, generalists are specifically more innovative, which may provide them the adaptive advantage to better cope with rapidly changing environmental conditions. Other cognitive abilities, however, may rather covary with other ecological adaptations, such as species-specific ranging behavior or foraging

strategies, or social factors that are unrelated to the degree of dietary and habitat specialization.

In this last chapter, I evaluate the compiled results by integrating them into the theory of cognitive variation and evolutionary development. Additionally, I discuss how my results can be useful for future studies on cognition within the animal kingdom.

1 The generalist's advantage?

Studies examining innovative problem-solving, reversal learning abilities or inhibitory control, aim to investigate an individual's behavioral flexibility (Amici et al. 2008; Griffin and Guez 2014; Beran 2015; Griffin 2016). Having the potential to behave flexibly, allows an individual to better adapt to variable conditions (Lee 2003; Lefebvre et al. 2004; Sol et al. 2005a; Lea et al. 2020). Generalists are exposed to more variable conditions, i.e., a greater range of habitat types or a broader dietary niche. Thus, they presumably face a greater variety of ecological challenges in their natural habitats, which might explain their advantageous ability to invent novel or modified solutions to occurring problems (Reader and Laland 2003; Sol et al. 2005a). In fact, large literature reviews on innovation counts report generalist birds and primates to be more innovative than more specialized species (Overington et al. 2011; Ducatez et al. 2015). Similarly, dietary generalist primates possess better inhibitory control than more specialized primates (MacLean et al. 2014). Additionally, most of the here reviewed experimental studies reported generalists to outperform more specialized species in innovative problem-solving or reversal learning tasks (Day et al. 1999a; Day et al. 2003; Bond et al. 2007; Griffin and Diquelou 2015; Szabo and Whiting 2020). In mouse lemurs, I could replicate the correlation regarding innovative potential, with the generalist gray mouse lemurs performing better in the innovative problem-solving task. However, the more specialized Madame Berthe's mouse lemur learned reversed reward contingencies faster, while the two species only partly differed in their degree of an initial flexible response (transfer index) and did not differ in their inhibitory control. Additionally, innovative propensity and inhibitory control did not correlate with each other, with the transfer indices or the discrimination and reversal

learning performances. Hence, these proxies may capture different aspects of flexibility in mouse lemurs.

In a previous study comparing innovative abilities in the same species, the more specialized Madame Berthe's mouse lemur outperformed the generalist gray mouse lemur in a modified version of the presented problem-solving task (Henke-von der Malsburg and Fichtel 2018). In that study, gray mouse lemurs persisted to use a previously successful solving technique, while Madame Berthe's mouse lemurs were less conservative and, thus, better able to adjust their behavior to a more efficient solution (Henke-von der Malsburg and Fichtel 2018). Persistence reflects task-directed motivation and seems to be specifically important for innovative problem-solving using novel extractive foraging tasks (Benson-Amram and Holekamp 2012; Thornton and Samson 2012; Huebner and Fichtel 2015; Chow et al. 2016; Guez and Griffin 2016). However, persistence can hinder efficient problem-solving, when individuals conservatively use previous solving techniques which result in a high number of perseverative errors (Hauser 1999). In general, conservatism may prevent generalists to encounter potentially dangerous situations, such as the production of more costly and/or less efficient novel or modified behaviors (*Omnivore's paradox*; Rozin 1976). This conservatism can be specifically favored over a more flexible response, when animals face more complex modifications (Chow et al. 2016; Davis et al. 2019; Lea et al. 2020), as it may have been the case in the previous study (Henke-von der Malsburg and Fichtel 2018) and in the here presented reversal learning paradigm.

This challenges the notion of the generalist's advantage to respond flexibly to changing environmental conditions, which, amongst others, come along with the current climatic change or anthropogenic disturbances (Sol et al. 2002; Schuck-Paim et al. 2008; Wilson and Yoshimura 2008; Wright et al. 2010).

1.1 Insufficient explanatory potential of the categorical system of niche theory

Despite the apparent superposition of generalists with respect to innovative problem-solving, they do not consistently outperform specialists in other cognitive tasks. Thus,

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categorizing species into generalists and specialists cannot sufficiently explain species-specific cognitive adaptations. As with any categorical system, the degree of ecological specialization captures only a subset of an animal's ecological adaptations (Hutchinson 1957; Devictor et al. 2010). Moreover, an animal can be a generalist regarding one niche dimension, while being more specialized within another dimension (Futuyma and Moreno 1988). For example, golden lion tamarins (*Leontopithecus rosalia*) are omnivorous, while being restricted to the tropical rain forest in south-eastern Brazil (Day et al. 2003). They are, thus, categorized as dietary generalists and habitat specialists. Additionally, the classification can either be based on the relative comparison to other species, or on an estimate, such as Levin's standardized index which measures dietary breadth (Krebs 1989). For instance, the fat-tailed dwarf lemur (*Cheirogaleus medius*) is broadly described as omnivorous, but prefers a frugivorous diet, which leads to a more specialized classification (Lahann 2007; Teichroeb and Vining 2019). Similarly, the gray mouse lemur has a broad dietary breadth (Levin's standardized index $B = 0.63$) and adjusts its diet flexibly to seasonal food availabilities throughout the year in dry-deciduous forests. However, in the same area, at the onset of the dry season they feed on a large proportion on homopteran secretions (>60%) which is mostly complemented with animal matter (Dammhahn and Kappeler 2008a; Dammhahn and Kappeler 2008b). Whereas in rain forests, they are mainly frugivorous year-round (Atsalis 1999; Lahann 2007). Thus, regarding its dietary preferences and depending on season and region, the gray mouse lemur maybe categorized as generalist or as more specialized when their mean dietary breadth throughout the year is not estimated using a metric index.

While providing a ubiquitous scaling system, niche breadth estimates are rarely used to classify a species ecological niche in cognitive studies. These studies rather provide a descriptive overview of a species' preferences which then are correlated with cognitive performances (Henry and Stoner 2011; Teichroeb and Vining 2019). Additionally, studies systematically estimating a species ecological niche, are only available for a subset of species, making it difficult to compare interspecific variation across studies. Similarly, a numeric degree of ecological specialization, which should categorize a certain ecological niche (Hutchinson 1953), is sparsely available across species and can be differently defined and measured. When defining the ecological specialization as niche breadth, the diversity

of resources a species uses would be measured (Roughgarden 1972; Bolnick et al. 2003). Accordingly, a specialist would use a narrower niche than a generalist. Alternatively, the ecological specialization can be defined as niche overlap. Here, the deviation of used resources in comparison to another species would be measured and a species would be categorized as specialist if it uses resources which are only rarely used by other species (Bolnick et al. 2002). Consequently, the interspecific comparison of cognitive abilities in relation to the species' degree of ecological specialization can be already confounded by methodological issues.

1.2 Factors explaining interspecific variation in cognitive abilities

1.2.1 Social and cultural intelligence

Social factors can covary with both, social and non-social cognition (Whiten and van Schaik 2007). For instance, social group size correlated positively with performances in reversal learning paradigms in birds on the species and the individual level (Bond et al. 2007; Ashton et al. 2018a; Ashton et al. 2019). Social group size and dominance hierarchies, as well as dynamics in fission-fusion systems correlated positively with performances on transitive inference and inhibitory control in primates and birds (MacLean et al. 2008; Amici et al. 2008; Miller et al. 2019).

Consequently, supporters of the *Social Intelligence Hypothesis* (Humphrey 1976; Whiten and Byrne 1988) or the related *Cultural Intelligence Hypothesis* (Whiten and van Schaik 2007; Herrmann et al. 2007; Street et al. 2017) suggest that social complexity broadly covaries with various cognitive abilities, not only within the social domain. These ideas are based on human evolution where humans have evolved outstanding cognitive abilities, specifically in western, educated, industrialized, rich, and democratic (WEIRD) communities. The formation of cultural structures thereby seems to evoke an immense selection pressure towards better cognitive abilities and ultimately to enlarged brains (Jerison 1973; Harvey et al. 1980; Herrmann et al. 2007; Street et al. 2017). Cultural structures are considered to include a sophisticated vocal communication, and physical cognition that is transmitted and spread via forms of social learning (Galef 1992; Boyd and Richerson 1996; De Waal 1999). Traits that are also apparent in non-human animals.

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Consequently, recent research investigated cultural formation also in non-human primates, birds, or cetaceans that live in well-organized social groups, communicate vocally (e.g., bird songs), possess well-developed physical cognition (e.g., tool-use), as well as forms of social learning (e.g., motor imitation) (Whiten 2000; Rendell and Whitehead 2001; Whiten 2017; Aplin 2019). The *Cultural Intelligence Hypothesis* found, for instance, support in non-human primates, when great apes were reported to possess better cognitive abilities than monkeys and prosimians in terms of tool-use (Kittler et al. 2018), flexible learning (Rumbaugh and Gill 1973), or social learning (Reader and Laland 2002).

However, the great ape's superposition is not consistent across studies and cognitive traits (Deaner et al. 2006; Herrmann et al. 2007; Reader et al. 2011; Herrmann and Call 2012; Amici et al. 2012), contradicting the *General Intelligence Hypothesis*, which posits the convergent evolution of cognitive abilities within and across cognitive domains (Spearman 1904; Humphreys 1979). Instead, cognitive abilities may evolve in a rather domain-specific way, which is supported by the mixed evidence for general intelligence in other non-human animals (Cosmides and Tooby 1994; reviewed in Burkart et al. 2017), including mouse lemurs, both, on the species-level and on the individual-level (Kittler 2017; Huebner 2020). Hence, different cognitive abilities may be differently selected for, leading to a more modular representation of cognitive abilities (Amici et al. 2012; DeCasien and Higham 2019).

1.2.2 Ecological intelligence

Cognitive abilities can covary with ecological factors when they provide benefits for daily challenges, such as efficient habitat exploration and exploitation (Dukas 1998; Dukas 2004). In this respect, the assessment of spatial abilities receives great scientific attention, as spatial cognitive traits can be advantageous for solving various ecological problems, such as to efficiently navigate through large home ranges or complex habitats, or to (re-)locate previous, stationary or distributed food patches. Thus, spatial abilities covary broadly with a species diet (e.g., frugivory) or a migratory lifestyle (Platt et al. 1996; Pleskacheva et al. 2000; Cristol et al. 2003; Barkley and Jacobs 2007; Bond et al. 2007; Haupt

et al. 2010; Henry and Stoner 2011; Rosati and Hare 2012; Clarin et al. 2013; Rosati et al. 2014; White and Brown 2015a; Trapanese et al. 2019; Teichroeb and Vining 2019).

Moreover, in most of the reviewed studies investigating variation in spatial abilities, the more generalist species outperformed the more specialized species. This parallels the experimental finding in mouse lemurs, with the gray mouse lemur achieving higher performance scores than the Madame Berthe's mouse lemur in the plus maze. However, this result was unexpected, since Madame Berthe's mouse lemurs have larger home ranges and rely more on stationary food resources (Dammhahn and Kappeler 2005; Dammhahn and Kappeler 2008b) for which they would benefit from enhanced spatial abilities. However, their spatial performance may be confounded by individual characteristics, or methodological factors, that I discuss below.

Another frequently examined ecological factor covarying with cognitive variation, is a species' diet and related foraging behaviors. According to its diet, a species has evolved specific foraging strategies that can involve certain cognitive abilities. For instance, the dependence on scatter hoarding or food-caching requires spatial memory abilities to relocate the cached food items (Clayton and Krebs 1994a). Consequently, species that are more dependent on these foraging strategies, perform better in spatial memory tasks (Cristol et al. 2003; Barkley and Jacobs 2007; Bond et al. 2007). However, food-caching Clark's nutcrackers performed worse than non-caching Mexican jays in a spatial memory task, where they were supposed to recover food caches made by conspecifics (Bednekoff and Balda 1996). In that study, the unexpected species difference with regard to a correlation with ecological adaptations, was explained by social factors, since Mexican jays experience more complex social organizations than Clark's nutcrackers (Bednekoff and Balda 1996). Thus, potential interactions between ecological and social factors must be considered when designing experimental tasks.

Species feeding predominantly on embedded or cryptic food items, benefit from cognitive abilities that facilitate the detection and extraction of these food items (Parker and Gibson 1977; Vitale et al. 1990). For instance, in order to extract concealed prey, lion tamarins (*Leontopithecus* spp.) have not only evolved specialized morphological structures, i.e., elongated fingers, but also extractive manipulative techniques (Dietz et al. 1997). In

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comparison to other callitrichids, that are less extractive or visual foraging, they, subsequently perform better in extractive problem-solving tasks (Day et al. 2003).

Additionally, discriminative abilities allow to detect and discriminate between food items with higher nutritional value from food items with lower nutritional value or even detrimental food items which becomes specifically important for species feeding on ephemeral or cryptic prey (Shettleworth 2001; Dukas 2004). However, in my literature survey I did not detect comparative studies that investigated discriminative abilities between species within the same order that differed in this specific foraging ecology. Nevertheless, when primates that do not choose between ephemeral and resident food items on a regular basis, were compared to cleaner fish that prefer to clean and feed on ephemeral clients, cleaner fish performed better in a respective dichotomous choice task (Salwiczek et al. 2012; Prétôt et al. 2016). However, given the great phylogenetic distance between fish and primates, the different task performance might also result from other factors, such as adjusted experimental designs or species-specific solving strategies.

In mouse lemurs, I found Madame Berthe's mouse lemurs to learn visual and spatial reward associations faster than gray mouse lemurs. However, Madame Berthe's mouse lemurs feed predominantly on homopteran secretions (Dammhahn and Kappeler 2008b) which does not imply an apparent need for specific discrimination abilities. Thus, the interspecific variation in discrimination learning performance might be explained by other factors that do not necessarily relate to their foraging ecology. Specifically, as the presented artificial stimuli did not relate to any naturalistic stimulus mouse lemurs encounter in their natural habitat.

In addition to dietary or habitat characteristics, ecological factors related to a synecology with predators or parasites might also covary with certain cognitive abilities. However, factors related to a species-specific synecology have rarely been associated with cognitive abilities. One example is provided by an intraspecific comparison in guppies (*Poecilia reticulata*), where predation risk was related to spatial memory performance (Burns and Rodd 2008). When compared to the population in the low-predation regime, the population in the high-predation regime was described as less hasty and tended to have larger telencephalons, which would provide greater cognitive capacity to process spatial information. Yet, the two populations did not differ in their spatial memory

performance (Burns and Rodd 2008). Concerning a potential link between cognitive performance and parasitism, a conclusive review on birds suggests that intraspecific variation in cognition covaries with exposure to parasites, as well as metabolic and energetic influences by the parasite on the host (Ducatez et al. 2020a). However, respective patterns seem to be mixed across species and do not yet allow for general conclusions. Respective interspecific comparisons have rarely been conducted, but suggest a positive correlation between innovation rates and parasite load in birds (Garamszegi et al. 2007; Vas et al. 2011; Soler et al. 2012).

In summary, cognitive abilities in non-human animals coevolve with social and ecological factors, but not consistently with the degree of ecological specialization. While species-specific foraging behavior, habitat complexity, or responses to seasonal variability have been linked with innovative propensities, flexible problem-solving performances, or spatial memory abilities, potential patterns of covariation with the predator regime or parasite abundances require further systematic investigations.

2 Coevolution with brain size and fitness implications

Explaining variation in cognitive abilities with socio-ecological factors constitutes one step towards an understanding of how cognition evolves. However, in order to fully understand the evolution of cognition, we need to elucidate the benefits of cognitive abilities that are genetically inherited and ultimately lead to a greater fitness (Dukas 2004; Thornton and Lukas 2012; Thornton et al. 2014).

2.1 Linking cognition with brain size proxies

The fundamental structural variation of the brain underlies a cost-benefit trade-off with energetic requirements, and it is phylogenetically constrained (Laughlin et al. 1998; Lennie 2003; Kotrschal et al. 2013; Logan et al. 2018). Various proxies of cortical development have been linked to cognitive abilities (Jerison 1973; Healy and Rowe 2007; Kotrschal et al. 2013; Logan et al. 2018). Such proxies can be measures of absolute or relative brain size, as well as assessments of cortical development by determining neuron density or connectivity or

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by ascertaining volume or density of gray and white matter. Which proxy is subsequently used to explain cognitive abilities, differs across studies and, more importantly, affects patterns of covariation (Deaner et al. 2000; Deaner et al. 2007; Healy and Rowe 2007). Additionally, data acquisition on brain structures can be complicated or even impossible in some species due to methodological or ethical issues. It is, therefore, difficult to reliably relate cognitive performance measures with structural variations of the brain across a broad range of species within the animal kingdom.

In the scope of my thesis, I did not find a consistent covariation of cognitive abilities with cortical measures, which were mostly extracted from secondary literature (**Chapter II**). In the subjected wild mouse lemurs (**Chapter III**), it was ethically not justifiable to euthanize single individuals with the purpose to measure brain sizes. Instead, a rough estimation of head volumes based on head width, indicates that gray mouse lemurs have, on average, slightly larger absolute and relative brain sizes than Madame Berthe's mouse lemurs (absolute: gray mouse lemur: $4.88 \pm 0.96 \text{ cm}^3$, Madame Berthe's mouse lemur: $3.50 \pm 1.12 \text{ cm}^3$; relative: gray mouse lemur: $55.45 \pm 9.53 \text{ mm}^3$, Madame Berthe's mouse lemur: $47.14 \pm 12.63 \text{ mm}^3$; Appendix 3, Table S3-1). Additionally, systematic prior investigations reported that dietary generalist birds and primates developed larger brains than dietary specialist species (Reader 2003; Lefebvre et al. 2004; Sol et al. 2005b; Ducatez et al. 2015). Thus, if brain size was a reliable predictor for cognitive abilities, gray mouse lemurs should consistently outperform Madame Berthe's mouse lemurs. Since that was not the case, I cannot conclude that the size of the whole brain covaries with all cognitive abilities in mouse lemurs. Instead, brain size may correlate with innovative propensities, as suggested by previous studies (Reader and Laland 2002; Ratcliffe et al. 2006; Sayol et al. 2016; Buechel et al. 2018; Ducatez et al. 2020b), while other cognitive abilities may better correlate with the size or structure of single brain areas that I could not estimate in wild mouse lemurs.

2.2 Adaptive advantage of enhanced cognitive abilities

Developing a larger brain and/or enhanced cognitive abilities can have fitness implications. This relationship is important as it builds the basis for natural selection on

heritable variations. Investigating effects of cognitive variation on individual fitness can, thus, elucidate the adaptive value of cognitive abilities, as well as of cortical development (Thornton et al. 2014). For example, innovative propensities relate with greater invasion success and a greater diversification potential (Sol and Lefebvre 2000; Sol et al. 2002; Nicolakakis et al. 2003; Sol et al. 2005c; Griffin and Diquelou 2015; Reader et al. 2016). More accurate spatial memory or problem-solving performance were linked with male mating success or reproductive success in birds (Keagy et al. 2009; Cole et al. 2012; Cauchard et al. 2017; Wetzel 2017; Shaw et al. 2019; Sonnenberg et al. 2019). Faster responses to predation stimuli or better spatial memory increased survival in rodents (Maille and Schradin 2016b). However, survival was not linked to spatial memory or problem-solving performance in gray mouse lemurs (Huebner et al. 2018). Thus, enhanced cognitive abilities may provide adaptive fitness advantages. However, this research field has not yet received great empirical interest and needs further exploration to allow broad and general conclusions across the animal kingdom.

Overall, cognitive abilities evolve in covariation with social and ecological factors, can covary with cortical development and can provide fitness benefits (Thornton et al. 2014). However, cortical development also has fitness costs, due to a high energy consumption (Laughlin et al. 1998; Lennie 2003; Kotrschal et al. 2013). Additionally, as social and ecological factors are likely to interact with each other, it is difficult to disentangle their exclusive impact on the evolution of cognition. Similarly, occupying different ecological niches, while experiencing similar ecological challenges, assumes complex evolutionary processes for ecological adaptations that require systematic and more in-depth future investigations.

3 Limitations and future implications

With the present study, I provide a broad overview of how cognitive abilities can vary with species-specific ecological adaptations. By investigating patterns of covariation between cognitive task performances and the degree of ecological specialization, I broaden our understanding of how cognitive abilities link with a species ecological niche. However, this niche concept is only a categorical estimation of species-specific ecological

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adaptations. To further understand to which extent certain ecological factors relate with certain cognitive abilities, future studies might profit from focusing on metric ecological variables. Specifically, niche breadth can be assessed by behavioral observations in combination with fecal analyses or environmental characteristics, resulting in a metric standardized index (Colwell and Futuyma 1971; Krebs 1989), which could be related to cognitive performance measures.

Further, my thesis stresses the importance to consider several methodological aspects of testing animals, especially in the wild. Experimental approaches must be properly designed to match a species' morphological possibilities, but also to reduce potential internal (e.g., motivational aspects, personality traits) or external influences (e.g., distractions by other organisms, distracting interactions with human experimenters) to a minimum, or to be able to adequately control for such potential influences (Barrett 2014; Rowe and Healy 2014; Thornton 2014; Schubiger et al. 2020). First, considering the here conducted plus maze, the spatial learning score was confounded by species-specific avoidance behavior. Although neophilia scores did not correlate with spatial learning scores, it is likely that other individual characteristics, such as boldness impacted individual's behaviors in this relatively open arena. Indeed, bolder individuals explore their environment more actively which can influence learning performances (Sih et al. 2004; Verdolin and Harper 2013; Guenther et al. 2014; Liedtke and Fromhage 2019). It is therefore important to consider and control for various non-cognitive traits (Thornton and Lukas 2012; Griffin and Guez 2014; Griffin et al. 2015; Dougherty et al. 2018).

Second, automatic testing procedures reduce distracting interactions with the human experimenter and facilitate the execution of cognitive tasks that require multiple trials (Wild et al. 2008; Fagot and Bonté 2010; McBride et al. 2016; Wither et al. 2020). However, to date most available automatic testing apparatuses are not yet well adapted to field studies, as they require stable set-ups and constant energy supply, and cannot sustain high temperatures, humidity, or relatively dusty environments.

Third, in experimental tasks, researcher usually use stimuli that might not be relevant in the natural environment of an animal (Lahti 2015). On purpose, rather artificial stimuli are chosen with the aim to solely measure specific behavioral traits instead of a behavioral response towards a potentially familiar stimulus that would influence the

measured performance score by experience (Rowe and Healy 2014; Shaw and Schmelz 2017). However, when these artificial stimuli do not have any relevance for the study subject, there might simply be no need for the animal to learn an association or to explore the presented stimulus/task, resulting in relatively low performances and rather arbitrary patterns of variation that do not match the species-specific ecological relevance (Rowe and Healy 2014; Gingsins and Bshary 2016; van Horik and Madden 2016; Farashahi et al. 2020). Additionally, a defined “better” cognitive performance depends on the researchers understanding of how a given task is designed to be solved. However, the subjected animal may perceive the presented problem differently and approach the task in a different manner than expected. This can result in “lower” performance scores which do not necessarily reflect the actual cognitive ability (Byrne and Bates 2006; Bayne et al. 2019).

Finally, despite increasing efforts, cognitive testing and the use of comprehensive test batteries remain rare in wild animals (Halsey et al. 2006; Benson-Amram and Holekamp 2012; Thornton and Samson 2012; Shaw et al. 2015; Cauchoix et al. 2017; Huebner et al. 2018; Audet et al. 2018; Henke-von der Malsburg and Fichtel 2018; Kumpan et al. 2020). However, to better understand, which ecological factors covary with cognitive performances and to disentangle social and ecological influences on cognitive variation, we need to test individuals in their natural ecological environment rather than under controlled conditions in captivity and to compare sympatric species differing in their socio-ecological adaptations (Domjan and Galef 1983; Pritchard et al. 2016). The thereby accumulated information could further impact future conservation efforts (Greggor et al. 2014; Ratsimbazafy et al. 2016; Dinnen and Ware 2020), which would be desirable for many endangered species (Schwitzer et al. 2014b; Schwitzer et al. 2014a; Estrada et al. 2017).

4 Conclusions

As the first large scale comparative approach to assess cognitive variation among species differing in their degree of ecological specialization, the results of my thesis offer substantial insight into the link between cognition and ecological factors, as well as the evolution of cognitive abilities on the species-level. The results of my literature review and

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my empirical cognitive test battery show, that generalist species do not outperform more specialized species *per se*. Nevertheless, their greater innovative potential may allow for more adaptive responses towards changing environmental conditions. Other cognitive abilities, however, can be better explained by species-specific foraging or ranging behavior that do not necessarily correlate with the degree of ecological specialization. Additionally, cognitive abilities may rather evolve in a domain-specific way, as I did not find evidence for a general intelligence factor in mouse lemurs which parallels other studies on non-human animals. Essentially, cognitive performances covary with a complex of several ecological and social factors, as well as individual characteristics. To disentangle single relationships, it is advisable to investigate patterns of covariation between different cognitive performances and measurable socio-ecological factors that go beyond species-specific foraging behavior or social group size, and to include various species across the animal kingdom.

Appendix 3

Table S3-1 Head volumes for a total of 422 gray mouse lemurs (N = 145 females, N = 277 males; Mmu) and 42 Madame Berthe's mouse lemurs (N = 23 females, N = 19 males; Mbe) that were captured between April 2013 and November 2019. The total data set of 865 measures for Mmu and 106 measures for Mbe includes repeated measures (mean = 3.04 ± 1.57 times) for 223 Mmu and 26 Mbe. Absolute head volumes were estimated using the formula $\frac{4}{3} \pi r^3$, with r being half of the head width [mm]. Relative head volumes were related to the individuals' body length [mm]. Given are mean \pm standard deviation (SD), minimum and maximum values

species	sex	absolute [cm ³]			relative [mm ³]		
		mean \pm SD	min	max	mean \pm SD	min	max
Mmu	combined	4.88 \pm 0.96	2.57	18.48	55.45 \pm 9.53	8.94	205.30
	female	4.97 \pm 1.27	2.57	18.48	55.70 \pm 12.81	8.94	205.30
	male	4.83 \pm 0.70	3.11	14.00	55.30 \pm 6.82	38.82	147.33
Mbe	combined	3.50 \pm 1.12	2.15	14.00	47.14 \pm 12.63	30.62	164.66
	female	3.65 \pm 1.42	2.31	14.00	48.14 \pm 16.01	34.57	164.66
	male	3.28 \pm 0.36	2.15	4.00	45.76 \pm 4.99	30.62	53.37

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Curriculum Vitae

Personal information

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Born May 31st, 1993 in Gräfelfing (Germany)

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Scientific education and research experience

- 04/2017 – 05/2021 **Ph. D. in Behavior and Cognition**
 Behavioral Ecology and Sociobiology Unit, German Primate Center & Georg-August-University Göttingen, Germany
 Project: Cognition in two sympatric mouse lemur species, the Grey mouse lemur (*M. murinus*) and the Madame Berthe's mouse lemur (*M. berthae*)
 03/2017 – 11/2019 (1.5 years) Field experience: data collection, Kirindy forest, Morondava (Madagascar)
 2020 Mentee in the Dorothea Schlözer mentoring program of the Georg-August-University Göttingen, Germany
- 12/2016 – 05/2017 **Research assistant:** Statistic analyses, experiments on cognition in lemurs
 Behavioral Ecology and Sociobiology Unit, German Primate Center
- 10/2014 – 01/2017 **M. Sc. Developmental, Neural and Behavioral Biology**
 Georg-August-University Göttingen, Germany
 Thesis: Innovation in two sympatric mouse lemurs (*M. murinus* and *M. berthae*)
 09/2015 – 10/2015 Field experience: lab course, Kirindy forest, Morondava (Madagascar)
 08/2016 – 10/2016 Field experience: data collection for master's thesis, Kirindy forest, Morondava (Madagascar)
- 10/2011 – 09/2014 **B. Sc. Biology**
 University of Hamburg, Germany
 Thesis: Populationsgenetik des Graubraunen Mausmakis (*M. griseorufus*) im Nationalpark Tsimanampetsotsa, Madagaskar [Population genetics of the grey-brown mouse lemur (*M. griseorufus*) in the national park Tsimanampetsotsa, Madagascar]
 09/2013 – 02/2014 Study abroad: Grado Biología at Universidad de La Laguna, San Cristóbal de La Laguna (Tenerife, Spain)

Scientific grants and awards

- 2019 **Diverse Intelligence Summer Institute**
Templeton World Charity Foundation, St Andrews, Scotland, June 30 – July 20
- 2019 **GfP-Award for best poster**
16th Conference of the Gesellschaft für Primatologie e.V., Göttingen (Germany),
February 13–15
- 2017 **GfP-Award for master's Thesis**
Gesellschaft für Primatologie e.V.
- 2016 **PROMOS: Master's Thesis in Kirindy Forest (Madagascar)**
Data collection of cognitive experiments on wild living mouse lemurs
- 2015 **PROMOS: lab course in Kirindy Forest (Madagascar) within M. Sc.**
Project: Reversal learning in two sympatric mouse lemurs (*Microcebus murinus* and
M. berthae)
- 2013 **ERASMUS: study abroad at Universidad de La Laguna (San Cristóbal de La
Laguna, Tenerife, Spain): Grado Biología**

Publications and conference contributions

- In prep **Article: Henke-von der Malsburg J., Fichtel C.** Memory retention in relation to
differential activity patterns over a hibernation period in gray mouse
lemurs.
- In prep **Article: Henke-von der Malsburg J., Fichtel C.** On the investigation of
interspecific variation in cognition and the potential link with ecological
factors.
- 2020 **Article: Henke-von der Malsburg J., Kappeler P. M., Fichtel C.** Linking ecology
and cognition: does ecological specialization predict cognitive test
performance?
Behavioral Ecology and Sociobiology, 74:154. DOI 10.1007/s00265-020-02923-z
- 2019 **Presentation: Innovation in two sympatric mouse lemurs (*Microcebus murinus*,
M. berthae)**
16th Conference of the Gesellschaft für Primatologie e.V., Göttingen, February 13–15
- 2019 **Poster: Do generalists and specialists differ in cognitive abilities? Award for
best poster**
16th Conference of the Gesellschaft für Primatologie e.V., Göttingen, February 13–15
- 2018 **Article: Henke-von der Malsburg J., Fichtel C.** Are generalists more innovative
than specialists? A comparison of innovative abilities in two wild
sympatric mouse lemur species.
Royal Society Open Science, 4, 180-480. DOI 10.1098/rsos.180480
- 2017 **Poster: Behavioral Flexibility in problem-solving abilities in a generalist and
specialist species, the grey mouse lemur and Madame Berthe's mouse
lemur.**
50th Anniversary of the Primatological Society of Great Britain, London (UK),
November 28–29

- 2017 **Poster:** Duel of mouse lemurs: Comparing innovative abilities in two sympatric mouse lemur species (*Microcebus murinus* & *Microcebus berthae*).
12th Conference of the Ethologische Gesellschaft e.V., Bonn (Germany), February 22–24
- 2017 **Poster:** Innovation in two sympatric mouse lemur species (*Microcebus murinus* & *M. berthae*).
15th Conference of the Gesellschaft für Primatologie e.V., Zurich (Switzerland), February 15–17
- 2015 **Article:** Scheel B. M., **Henke-von der Malsburg J.**, Giertz P., Rakotondranary S. J., Hausdorf B., & Ganzhorn J. U. Testing the influence of habitat structure and geographic distance on the genetic differentiation of mouse lemurs (*Microcebus*) in Madagascar.
International Journal of Primatology, 36(4), 823-838. DOI 10.1007/s10764-015-9855-z
- 2015 **Poster:** Population genetics of the reddish-grey mouse lemur (*Microcebus griseorufus*) in Tsimanampetsotsa National Park, Madagascar.
14th Conference of the Gesellschaft für Primatologie e.V., Leipzig (Germany), February 25–27

Declaration

I hereby declare that all parts of my thesis titled “Cognitive adaptations in two sympatric mouse lemur species occupying different ecological niches” were written by myself. Assistance of third parties was only accepted if scientifically justifiable and acceptable in regard to the examination regulations. Assistance or contributions to the individual chapters are indicated and all sources have been quoted.

Göttingen, 21.04.2021

Johanna Henke-von der Malsburg