



UNIVERSIDADE FEDERAL DA BAHIA - UFBA

Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores

Doutorado em Ecologia: Teoria, Aplicação e Valores

**O PAPEL DE FATORES COMPORTAMENTAIS E ECOLÓGICOS NO
AJUSTE DE MAMÍFEROS A AMBIENTES DESAFIADORES**

JULIANA LUCATELLI DÓRIA SANTANA

Salvador, Fevereiro de 2023

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**O PAPEL DE FATORES COMPORTAMENTAIS E ECOLÓGICOS NO
AJUSTE DE MAMÍFEROS A AMBIENTES DESAFIADORES**

Tese apresentada ao Programa de Pós-
Graduação em Ecologia: Teoria,
Aplicação e Valores, como parte dos
requisitos exigidos para obtenção do
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Orientador: Dr. Hilton Japyassú

Salvador, Fevereiro de 2023



PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÃO E VALORES

UNIVERSIDADE FEDERAL DA BAHIA – INSTITUTO DE BIOLOGIA

Rua Barão de Geremoabo, s/n. Ondina – Salvador – Bahia – CEP. 40.170-000



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Título do trabalho de conclusão de curso: “O papel de fatores comportamentais e ecológicos no ajuste de mamíferos a ambientes desafiadores”

Mestrando(a): **Juliana Lucatelli Dória Santana**

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De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pelo(a) professor(a) Dr(a). Hilton Ferreira Japyassú (Presidente), Dr(a). Renata Pardini, Dr(a). Briseida Dogo de Resende, Dr(a). Tiago Falótico, e Dr(a). Bruno Vilela de Moraes e Silva, às 09:13 h do dia 05 de dezembro de 2022. O (A) doutorando(a) fez a apresentação oral da dissertação durante 47 minutos. Após o encerramento das arguições, às 12:44 horas, a Comissão Examinadora pronunciou-se pela sua aprovação, conforme parecer em anexo. Esta Ata será assinada pelos membros da Comissão Examinadora e deste Colegiado de curso, para compor o processo de emissão do diploma.

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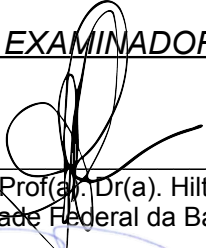



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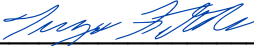
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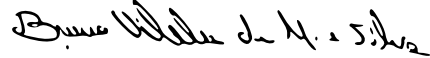
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A Comissão Examinadora considera o trabalho de conclusão de curso:

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Os itens abaixo deverão ser modificados conforme sugestão da banca:

Introdução



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Revisão Bibliográfica

Metodologia

Resultados Obtidos

Conclusões

Para assinatura do orientador **APENAS APÓS A EFETUAÇÃO DAS MODIFICAÇÕES SUGERIDAS**

Declaro, para fins de homologação, que as modificações, sugeridas pela banca examinadora, acima mencionada, foram cumpridas integralmente.

Prof.(a). Dr.(a). Hilton Ferreira Japyassú
Orientador(a)

Dedico este trabalho aos meus pais, Ana e Luiz, ao meu companheiro Gabriel e à minha amiga Caren, que acreditam mais em mim do que eu, e que me apoiaram em todos os momentos.

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O PAPEL DE FATORES COMPORTAMENTAIS E ECOLÓGICOS NO AJUSTE DE MAMÍFEROS A AMBIENTES DESAFIADORES

Juliana Lucatelli Dória Santana

As mudanças ambientais causadas pelas atividades humanas podem impactar a vida dos animais, fazendo com que alterem seus comportamentos para que consigam lidar com essas mudanças. No entanto, muitas vezes o ajuste não é possível, e espécies podem ser extintas. Dessa maneira, é importante compreendermos que fatores da história de vida, do ambiente e do comportamento dos animais podem trazer-lhes vantagens ou desvantagens nos ambientes impactados. Um exemplo de característica que pode ser importante para lidar com impactos ambientais é o quanto uma espécie é social. Alguns estudos sugerem que o grau de socialidade se associa com o quanto as espécies podem ser consideradas inteligentes, visto que espécies de vertebrados que têm grupos sociais maiores possuem também maiores tamanhos cerebrais. Estudos também apontam que maiores habilidades cognitivas podem ser importantes para lidar com impactos ambientais. Por exemplo, espécies consideradas mais inteligentes inovam mais e isso pode lhes conferir maiores chances de sobrevivência diante de desafios. No presente estudo, através de análises comparativas, avaliamos no primeiro capítulo se componentes da vida social podem influenciar no risco de espécies de mamíferos serem extintas. Também avaliamos, no segundo capítulo, se componentes sociais, dieta e longevidade estão associados às habilidades cognitivas em espécies de primatas. Nós encontramos que, para mamíferos, componentes sociais, como o cuidado da prole por ambos os pais e

o comportamento sexual promíscuo, parecem ser comportamentos que favorecem as espécies em ambientes desafiadores, pois essas espécies possuem menor risco de extinção. Já grupos sociais maiores e que possuem laços sociais e relações de dominância nos grupos parecem ser desfavorecidos, pois têm maior risco de extinção quando comparados, respectivamente, a espécies com grupos sociais menores e espécies solitárias. Em relação às habilidades cognitivas, encontramos que uma maior longevidade está associada a maiores habilidades cognitivas em primatas. No estudo, discutimos possíveis explicações para os resultados encontrados, destacamos algumas informações em falta na literatura, e também trazemos sugestões para estudos futuros.

Resumo

O contexto ambiental é determinante para a persistência das espécies. As rápidas mudanças ambientais advindas das atividades humanas, por exemplo, têm levado a alterações comportamentais de animais, que tentam se ajustar a essas mudanças, mas caso o ajuste não seja possível, populações podem declinar ou mesmo espécies podem ser extintas. Portanto, é importante identificarmos os fatores comportamentais que potencialmente favorecem ou desfavorecem as espécies diante desses impactos. Um dos fatores comportamentais que pode ser afetado pelas características ambientais é o grau de socialidade das espécies. Algumas evidências apontam que diferenças em componentes sociais estão associados a distintas habilidades cognitivas. A literatura também traz evidências de que maiores habilidades cognitivas podem ajudar a lidar com desafios ambientais. Neste contexto, temos como objetivo na presente tese avaliar o potencial papel de componentes sociais no risco de extinção de espécies de mamíferos (capítulo 1), e compreender os possíveis mecanismos envolvidos, especificamente, se as diferentes habilidades cognitivas são preditas por diferenças em componentes sociais, dieta ou longevidade de espécies de primatas (capítulo 2). Os pressupostos da relação entre socialidade e cognição são baseados em *proxies* como o tamanho do grupo e do cérebro, respectivamente, e consideramos medidas de outros aspectos sociais, bem como medidas comportamentais para testar as hipóteses de forma mais direta e completa, através de estudos comparativos com base em dados da literatura e bases de dados, considerando as filogenias. Encontramos que, de fato, características sociais são importantes para o risco de extinção de mamíferos, já que espécies com cuidado biparental e com comportamento sexual promíscuo possuem menor risco de extinção. Ademais, grupos sociais maiores e espécie com laços sociais e relações de dominância possuem maior risco de extinção que tamanhos de grupo menores e espécies solitárias, respectivamente. No entanto,

encontramos que apenas maior longevidade se associou a maiores habilidades cognitivas em primatas. Discutimos os mecanismos sociais e ecológicos que possivelmente desfavorecem a persistência das espécies, e destacamos algumas lacunas de informações na literatura relevantes para os estudos da evolução da cognição e da ecologia evolutiva e ecologia comportamental, além de trazemos sugestões para estudos futuros com base em nosso processo de pesquisa.

Palavras-chave: socialidade, impactos humanos, risco de extinção, habilidades cognitivas

Abstract

The environmental context is determinant for the persistence of species. Human induced rapid environmental changes, for example, can led to behavioral modifications in animals, which try to adjust to these changes, but if the adjustment is not possible, populations may decline or even species may become extinct. Therefore, it is important to identify the behavioral factors that potentially favor or disfavor the species in the face of these impacts. One of the behavioral factors that can be affected by environmental characteristics is the degree of sociality of species. Some evidence points out that differences in social components are associated with distinct cognitive abilities. The literature also provides evidence that greater cognitive abilities can help to deal with environmental challenges. In this context, in this thesis we aim to evaluate the potential role of social components in the risk of extinction of mammalian species (chapter 1), and to understand the possible mechanisms involved, specifically, whether different cognitive abilities are predicted by differences in social components, diet or longevity of primate species (chapter 2). The assumptions of the relationship between sociality and cognition are based on proxies such as group and brain size, respectively, and we consider measures of other social aspects as well as behavioral measures to test the hypotheses more directly

and thoroughly through comparative studies based on data from the literature and databases, considering the phylogenies. We found that, in fact, social components are relevant for the risk of extinction of mammals, since species with biparental care and with promiscuous mating behavior have a lower risk of extinction. Furthermore, larger social groups and species with social bonds and dominance relationships are at greater risk of extinction than smaller group sizes and solitary species, respectively. However, we found that only greater longevity was associated with higher cognitive abilities in primates. We discuss the social and ecological mechanisms that possibly disfavor the persistence of species, and we highlight some gaps in the literature relevant to studies of the evolution of cognition, evolutionary ecology and behavioral ecology, in addition to bringing suggestions for future studies based on our research process.

Keywords: sociality, human impacts, extinction risk, cognitive abilities

Sumário

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Estrutura da Tese

A presente tese está estruturada em dois capítulos como segue:

Capítulo I – *United will we stand? The role of sociality in extinction risks in mammals*

O artigo “United will we stand? The role of sociality in extinction risks in mammals” trata das relações entre fatores comportamentais, ecológicos e de história de vida com o risco de extinção de espécies de mamíferos.

Capítulo II – *Longevity correlates with cognitive abilities in primates*

Neste capítulo, o artigo “Longevity correlates with cognitive abilities in primates” trata da relação entre fatores sociais, ecológicos e história de vida com habilidades cognitivas em espécies de primatas.

1

2

Introdução geral

3

4 Os fatores ambientais são determinantes para a persistência das espécies.

5 Alterações ambientais causadas pelos humanos, por exemplo, como a fragmentação

6 florestal, a urbanização e a expansão agrícola, têm sido responsáveis por grandes

7 impactos levando a mudanças no comportamento animal (Mokross et al. 2014, Winandy

8 et al. 2021, Wong and Candolin 2015), declínio de populações e extinção de espécies

9 (Pievani 2014, Vitousek et al. 1997). Para lidar com as alterações e impactos ambientais,

10 habilidades cognitivas, que envolvem processos de aquisição, retenção e uso de

11 informações do ambiente (Shettleworth 2009) possivelmente auxiliam o ajuste e

12 sobrevivência dos indivíduos, através, por exemplo, da flexibilidade comportamental dos

13 animais (Ducatez et al. 2020). Inovação (Ducatez et al. 2020, Sol et al. 2005) e memória

14 (Maille and Schradin 2016) são exemplos de habilidades cognitivas que os animais

15 podem recorrer para sobreviver em ambientes desafiadores. Portanto, é possível que as

16 habilidades cognitivas e fatores aos quais estão associadas sejam relevantes para a

17 persistência das espécies em ambientes impactados. Neste caso, o reconhecimento desses

18 fatores pode trazer clareza sobre quais características das espécies devem ser foco dos

19 esforços conservacionistas.

20 Uma característica que tem sido sugerida como importante na evolução da

21 cognição é a socialidade (Humphrey 1976, Byrne and Whiten 1988, Dunbar 1992,

22 Dunbar 1998). A existência dos diferentes graus de agregação entre espécies depende dos

23 custos e benefícios associados com essas condições (Krause and Ruxton 2002). O

24 compartilhamento de espaços e recursos com coespecíficos aumenta a competição por

25 acasalamento e alimentos (Sterck et al. 1997), pode implicar na atração de predadores
26 (Botham and Krause 2005) e aumento da transmissão de parasitas (Lucatelli et al. 2021,
27 Møller et al. 2001). Por outro lado, a socialidade possibilita comportamentos
28 antipredatórios coletivos (Sorato et al. 2012), a aprendizagem social, especialmente em
29 situações em que a aprendizagem individual não é suficiente ou eficaz (Ashton et al. 2019,
30 Laland 2004), e o compartilhamento de informações sobre recursos ou diretamente de
31 recursos (Blundell 2002, Galef and Giraldeau 2001, Tennie et al. 2009). Se os benefícios
32 superam os custos, a socialidade deve prevalecer.

33 Segundo a hipótese da inteligência social (Humphrey 1976, Byrne and Whiten
34 1988, Dunbar 1992, Dunbar 1998), os desafios encontrados na vida social seriam a
35 principal pressão seletiva para evolução da cognição. Dessa maneira, variações
36 interespecíficas no grau de socialidade estariam associadas a variações nas habilidades
37 cognitivas e indivíduos de espécies mais sociais poderiam lidar melhor com desafios
38 ambientais, como os causados pelos impactos humanos. Grandes grupos apresentaram
39 menor risco de extinção que grupos pequenos de primatas (Lootvoet et al. 2015),
40 sugerindo que, de fato, possivelmente a persistência de espécies consideradas mais sociais
41 pode ser favorecida em ambientes desafiadores. Há também outras características que
42 podem favorecer o ajuste, a sobrevivência e conseqüentemente o risco de extinção das
43 espécies diante de impactos ambientais. O maior tamanho do corpo estaria associado a
44 maior risco de extinção, já que animais maiores tendem ser alvo de maior exploração
45 humana e a necessitar de mais recursos (Cardillo and Bromham 2001). Maior tamanho
46 de ninhada estaria associado a um menor risco de extinção, uma vez que pode compensar
47 uma eventual maior mortalidade (Purvis et al. 2000). Longevidade também tem sido
48 sugerida como uma característica associada a maiores habilidades cognitivas (González-
49 Lagos et al. 2010) e espécies mais longevas podem ter menor risco de extinção (Bergman

50 and Beehner 2015). Além disso, uma dieta mais ampla pode favorecer o ajuste e
51 persistência das espécies (Ducatez et al. 2020), bem como uma menor densidade
52 populacional humana tenderia a reduzir o risco de extinção (Davies et al. 2006).

53 Apesar da literatura indicar características importantes para a sobrevivência dos
54 animais não-humanos, carecemos de mais evidências de como a persistência das espécies
55 é favorecida ou desfavorecida. Portanto, é importante compreendermos quais são as
56 características que estão associadas a maiores habilidades cognitivas, potencialmente
57 essenciais para o ajuste das espécies. Além da já mencionada hipótese da inteligência
58 social, colocando a socialidade como importante pressão seletiva para evolução da
59 cognição (Humphrey 1976, Byrne and Whiten 1988, Dunbar 1992, Dunbar 1998), e da
60 indicação de que maior longevidade pode também se associar a maior cognição
61 (González-Lagos et al. 2010, Bergman and Beehner 2015), há a hipótese da inteligência
62 ecológica e suas derivadas, que colocam desafios ecológicos como pressões seletivas para
63 maiores habilidades cognitivas. Particularmente, variações referentes às dietas das
64 espécies, como a frugivoria, em que há maior imprevisibilidade quanto maior o grau de
65 frugivoria em comparação à folivoria, o que, portanto, seria mais demandante
66 cognitivamente (DeCasien et al. 2017), assim como maior amplitude da dieta poderia ser
67 um facilitador metabólico para evolução da cognição e indicar maior flexibilidade para
68 explorar recursos em condições de escassez (MacLean et al. 2014).

69 As evidências que suportam a hipótese da inteligência social e a hipótese da
70 inteligência ecológica se baseiam principalmente em medidas de tamanho de cérebro ou
71 de estruturas cerebrais, que são medidas indiretas de habilidades cognitivas (Burish et al.
72 2004, Shultz and Dunbar 2006, Pérez-Barbería et al. 2007). No entanto, o tamanho das
73 estruturas cerebrais pode refletir funções diversas e têm sido muito criticadas em relação
74 ao seu uso como representante de habilidades cognitivas (Healy and Rowe 2007, Logan

75 et al. 2018, Powell et al. 2017, Wartel et al. 2019). Portanto, é importante investigarmos
76 os fatores que se associam às habilidades cognitivas também considerando-os mais
77 diretamente, através de medidas comportamentais. Da mesma maneira, o principal
78 componente de socialidade considerado na literatura é uma medida indireta, o tamanho
79 do grupo. Mesmo sendo um componente importante da organização social, a socialidade
80 é uma característica multifacetada. O tamanho do grupo pode não capturar outros aspectos
81 da socialidade (Bergman and Beehner 2015, Kappeler 2019), e outros componentes,
82 como a estrutura social, o sistema de cuidado e o sistema de acasalamento (Kappeler
83 2019) podem se associar, inclusive de formas distintas, com habilidades cognitivas.

84 O presente trabalho visa reduzir lacunas na literatura, como a importância de
85 fatores comportamentais para persistência das espécies e, conseqüentemente, para ações
86 de conservação; e a investigação de possíveis preditores de mecanismos importantes para
87 a persistência das espécies, especificamente as habilidades cognitivas, considerando
88 medidas cognitivas comportamentais, bem como medidas sociais pouco exploradas.
89 Comumente estudos ecológicos, evolutivos e comportamentais são feitos separadamente,
90 com focos em escalas distintas, mas acreditamos que a integração de diferentes áreas do
91 conhecimento, como a ecologia comportamental, ecologia evolutiva e etologia podem
92 ajudar a elucidar problemas multiescalares e complexos, como normalmente são próprios
93 das relações biológicas.

94 Assim, no primeiro capítulo, intitulado “United will we stand? The role of
95 sociality in extinction risks in mammals”, integramos esses distintos campos para
96 investigar as características que se correlacionam ao o risco de extinção em mamíferos
97 não-humanos, incluindo componentes sociais, ecológicos e de história de vida. Nosso
98 sistema de estudo foi o grupo Mammalia, pois os mamíferos possuem alta diversidade
99 comportamental, são altamente ameaçados e possuem dados abundantes na literatura de

100 história de vida, comportamento e ecologia (Jones et al. 2009). Testamos nossas hipóteses
101 através de análises comparativas com base em dados coletados na literatura e bases de
102 dados online e incluímos dados de até 1100 espécies de mamíferos pertencentes a 27
103 ordens e 123 famílias.

104 No segundo capítulo, intitulado “Longevity correlates with cognitive abilities in
105 primates”, investigamos se componentes sociais, ecológicos e de história de vida se
106 correlacionam com as habilidades cognitivas de primatas através de análises
107 comparativas após revisão sistemática. Incluímos dados de até 81 espécies de primatas
108 pertencentes a 12 famílias. Também identificamos lacunas de informações da literatura e
109 sugerimos focos de coletas de dados, atualmente escassos, para possibilitar estudos
110 futuros ainda mais promissores. Cada capítulo foi escrito como um artigo independente.

111

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214

Capítulo I

215

Artigo submetido ao periódico *Behavioral Ecology*

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United will we stand? The role of sociality in extinction risks in mammals

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Lay Summary

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Once sociality can be associated with higher cognitive and communicational abilities, we

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explore if different aspects of social life can bring advantages to mammals' persistence

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in challenging environments. Indeed, we found that some social characteristics are

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relevant: biparental and promiscuous mammals have a lower risk of extinction. Also,

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larger group sizes, social bonds and dominance relationships species have a higher risk

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of extinction than solitary and smaller group-sized mammals.

233

Abstract

234

Human activities are driving global changes that are likely to cause a mass extinction.

235

Understanding the role of species' behavioral traits in their proneness to extinction can

236 help to build strategies to avoid it. Since variations in sociality components among species
237 can be associated with differences in cognitive and communicative abilities, and these are
238 important features to deal with environmental challenges, we tested the hypotheses that
239 extinction risk is associated with social structure, social organization, mating system and
240 care system in mammals. In addition, we included as predictor variables some life history
241 and ecological traits that are potentially associated with extinction risk, specifically, body
242 size, diet breadth, litter size, longevity and human population density. Overall, we found
243 that species with biparental care are associated with a lower extinction risk than species
244 exhibiting only maternal care. Furthermore, we found that species with a promiscuous
245 mating system have a lower risk of extinction than monogamous species. We found that
246 mammals with social bonds and a hierarchical dominance structure and species with
247 larger group sizes are at higher extinction risk than the solitary and species with smaller
248 groups. We also found positive associations between extinction risk and body size, diet
249 breadth and longevity, and a negative association with litter size. Our results stress the
250 relevance of considering multiple sociality components to identify meaningful behaviors
251 for species conservation. We discuss possible ecological and social mechanisms, such as
252 the Allee effect, information conservatism or collective dependence, disfavoring species
253 persistence, thus opening avenues for future studies.

254 **Keywords:** social structure, care system, mating system, social learning, conservation
255 status, human impact

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259 INTRODUCTION

260 Human occupation and transformation of the environment cause habitat destruction and
261 resulted in fragmented landscapes. These human-induced rapid environmental changes
262 are generally faster than those experienced by animals in wild areas (Sih et al. 2011).
263 These impacts affect the survival and reproduction of organisms, reducing populations
264 and their genetic diversity, jeopardizing species with extinction (Vitousek et al. 1997,
265 Pievani 2014). Besides the extrinsic factors affecting species, the intrinsic characteristics
266 interact to determine survival of species in these disturbed environments (Purvis et al.
267 2000, Chichorro et al. 2019). Therefore, distinct species may respond differently to
268 environmental change, and since behavior tends to play an important role in adjustments
269 to these disturbed environments (Wong and Candolin 2015) it seems relevant to identify
270 which behavioral traits could better help animals deal with human impacts (Sih et al.
271 2011, Sol et al. 2013). For instance, cognitive abilities are potentially important to cope
272 with environmental changes as demonstrated by innovation propensity's association with
273 reduced extinction risk in birds (Ducatez et al. 2020). Also, large-brained avian species
274 tend to innovate and are more likely to survive in new environments than small-brained
275 ones (Sol et al. 2005, but see Johnson-Ulrich et al. 2019). Some cognitive abilities,
276 specifically reaction time and spatial memory abilities favored survival in a mice species
277 (Maille and Schradin 2016), also suggesting the importance of variation in cognition in
278 species resistance to disturbances.

279 In turn, cognition has been considered connected to sociality accordingly to the “social
280 intelligence” or “social brain” hypothesis (Humphrey 1976, Dunbar 1992, Dunbar 1998),
281 which posits that social environment challenges are important selective forces to explain
282 relatively large brain size and/or high cognitive abilities. Some examples of social life
283 challenges include the coordination of activities within the group, the maintenance of

284 social relationships, the recognition of group members, the memory of past social
285 interactions and of the individual's own hierarchical position, as well as those of
286 conspecifics. Thus, variation within sociality components such as social structure, social
287 organization, mating and care systems (Kappeler 2019) can contribute differently to
288 cognitive processes and their role in dealing with environmental novelties (Canteloup et
289 al. 2021).

290 Notwithstanding controversies around the social intelligence hypothesis (DeCasien et al.
291 2017), some studies have identified a positive relationship between brain size and
292 sociality components (Burish et al. 2004, Shultz and Dunbar 2006, Pérez-Barbería et al.
293 2007). Furthermore, social learning in primates correlates with tool use and innovation,
294 which are measures commonly used to assess cognitive abilities (Reader and Laland
295 2002). Learning has the potential to match behavioral responses to environmental
296 changes, and social learning also enables the transmission of strategies between
297 conspecifics to cope with continued disturbances (Duboscq et al. 2016, Snijders et al.
298 2017, Canteloup et al. 2021). In this regard, Sih et al. (2011) suggest that more socially
299 complex species, for example, those that present parental care and generation overlap,
300 could better respond to human-induced rapid environmental change than less socially
301 complex species without generation overlap and parental care. Larger group sizes are
302 associated with lower extinction risk in primates (Lootvoet et al. 2015) which,
303 considering that human impact is an important cause of mass extinctions (Pievani 2014),
304 also suggests that some sociality aspects can be advantageous to survival in challenging
305 environments.

306 Communication plays an important role in mediating interactions in social life. Bird
307 songs, for instance, are involved in territorial defense by males and mate choice by
308 females, and in some groups, juveniles need to listen to their parents to learn their songs

309 (Brenowitz et al. 1997). Human impacts can alter the transmission of such
310 communicational signals possibly harming the survival and/or reproduction of animals
311 (Rabin et al. 2003). Cognitive abilities can also be required for communication, such as
312 perception in general, signal modification and potential production of new social
313 information, or association between signals and environmental context, or between
314 signals and conspecifics' identity and message content (see review in Sewall 2015). Some
315 sociality aspects have been shown to be important factors for the variation in the
316 complexity of communication. Social group size is correlated with song complexity in
317 *Poecile carolinensis* (Freeberg 2006), and hierarchically dominant individuals of *Sturnus*
318 *vulgaris* possess relatively more complex vocal repertoires (Spencer et al. 2003).
319 Additionally, song complexity is linked to the cognitive performance of males of
320 *Taeniopygia guttata*, and hence can be used as a learning ability signal for mating
321 selection by females (Boogert et al. 2008). Moreover, in a comparative study including
322 253 species, Leighton (2017) showed that cooperative breeding birds exhibit more
323 complex communication, as shown by their vocal repertoire size. And increases in vocal
324 repertoire sizes in the evolutionary history of primate species are associated with larger
325 group sizes and longer periods dedicated to social interactions (McComb and Semple
326 2005). Also, some groups considered to be very socially complex, such as corvids and
327 parrots (Burish et al. 2004), exhibit relatively more diverse vocal repertoires than other
328 bird groups' species (Schwing et al. 2012). Higher diversity in vocal repertoire can, for
329 example, enable greater flexibility to communicate with conspecifics, which could help
330 animals to deal with habitat alterations, affecting signal production, fidelity and
331 perception by conspecifics (Rosenthal and Fox 2012, Winandy et al. 2021). Thus, if
332 cognition and communication complexity are associated with variations in sociality,

333 certain group living characteristics could be favored in constantly changing
334 environments, reducing vulnerability.

335 In this context, there are social features we expect to have been more cognitively
336 demanding and, hence, could benefit and reduce the extinction risk of such species.
337 Specifically, species with biparental and alloparental care systems could require more
338 cognitive abilities to deal with larger family coordination and synchrony than maternal
339 care alone, while additional caregivers could enhance offspring survival (Whiten and
340 Waal 2017, Lukas and Clutton-Brock 2018, Kappeler 2019). Regarding mating systems,
341 promiscuous, polygynous or polyandrous species exhibit more interactions and
342 relationships to coordinate than monogamous species, however, monogamous species
343 bond maintenance requires conflict resolution, manipulation, and pair coordination,
344 activities that could also be more cognitively demanding (Schillaci 2006, Shultz and
345 Dunbar 2007). Furthermore, dominance relationships would be more cognitively
346 demanding because would favor differentiated relationships and conflict of interest
347 (Bergman and Beehner 2015, Kappeler 2019) as well as larger group sizes increase the
348 probability of more differentiated relationships and decrease stability/cohesion (Dunbar
349 1998, Bergman and Beehner 2015, Kappeler 2019).

350 Finally, some ecological and life history variables potentially correlate with extinction
351 risk, respectively, higher human population density can affect survival and reproduction
352 of other animal species (Davies et al. 2006), while bigger bodies require more resources
353 and bigger animals are more frequently explored by humans (Cardillo and Bromham
354 2001), also, a bigger litter size potentially compensate for increased mortality (Purvis et
355 al. 2000). Moreover, a longer longevity is positively associated with brain size (which
356 can be associated with cognitive abilities) and can imply more differentiated relationships
357 among individuals (which would be more cognitively demanding) (González-Lagos et al.

358 2010, Bergman and Beehner 2015), and, finally, a more diverse diet would favor survival
359 and adjustment to environmental changes (Ducatez et al. 2020).

360 Here we investigate if variation in multiple sociality components predicts extinction risk.
361 More specifically, we aim to test hypotheses regarding the relationship between
362 extinction risk and different social components: species with biparental and alloparental
363 care systems have lower extinction risk than species with only maternal care; either
364 species of the mating systems promiscuous, polygynous or polyandrous have a lower risk
365 of extinction than monogamous species or, alternatively, monogamous species have a
366 lower risk of extinction; species containing different social structures (solitary, colonial,
367 social bonds or dominance relationships) have distinct extinction risks, and dominance
368 relationships species should be associated with lower risk of extinction than solitary,
369 colonial or social bonding species; and we also predict a negative association between
370 group size and extinction risk. In addition, we test the following hypotheses focused on
371 possible confounding factors we identified: human population density and body size
372 exhibit a positive association with extinction risk; while litter size, longevity and diet
373 breadth exhibit a negative association with extinction.

374 **METHODS**

375 **Data collection**

376 We used mammals to test our hypotheses because they have high functional and
377 behavioral diversity (Jones et al. 2009) while are also highly threatened and have
378 behavioral, life history and environmental data abundant in the literature. We included
379 data from up to 1100 mammal species belonging to 27 orders and 123 families for which
380 data were available for the independent (sociality components, human impact, body size,
381 litter size, longevity and diet breadth) and dependent variables (extinction risk - Purvis et

382 al., 2000), as well as available in the source of phylogenetic information (Fritz et al.
 383 2009). Data for species' classifications on the key features of sociality components were
 384 mainly obtained from the online database Quaarvark Animal Diversity Web (Myers et
 385 al. 2021).

386 The sociality components included in the study were adapted from those considered by
 387 Kappeler (2019), which compiled distinct and complementary components of sociality,
 388 that are viable to be used in comparative studies. Thus, when considering the role of
 389 sociality on extinction risks, we analyzed care system, mating system, social structure and
 390 social organization social components, including their key features, as specified in Table
 391 1. Among the adaptations we carried out to use Kappeler's (2019) classification are the
 392 exclusion of reproductive skew as a mating system feature (for which information was
 393 not widely available in the data sources), the inclusion of the solitary species classification
 394 as one of the "Social structure" features, and the use of group size as the only feature of
 395 "Social organization".

396 **Table 1.** Sociality components and their key features included in this study, followed by
 397 the sample size (number of species, N), and their meanings, adapted from Kappeler
 398 (2019) and Kappeler and Schaik (2002).

Sociality components	Key features	Meaning
Care system: N = 648 (Categorical)	Maternal (N = 540)	The female provides the majority of parental care to the dependent offspring

	Biparental (N = 62)	Both female and male provide parental care to the dependent offspring
	Alloparental (N = 46)	Other members of the group, besides the parents, take care of the dependent offspring
<hr/>		
Mating system: N = 664 (Categorical)	Monogamous (N = 133)	A single male and female mate
	Polygynous (N = 327)	A single male mates with multiple females
	Polyandrous (N = 18)	A single female mates with multiple males
	Promiscuous (N = 186)	Males and females have several mates
<hr/>		
Social structure: N = 1100 (Ordinal variable)	Solitary (N = 408)	Individuals that spend the majority of their activity period without association with other(s) individual(s)

Colonial (N = 74) Individuals included in relatively large groups of individuals, living in close proximity, and seem not to have a clear pattern of consistent social interactions, such as predominantly affiliative or agonistic interactions

Social bonds (N = 408) Individuals that belong to cohesive social groups resulting from repeated interactions between the members, particularly with high affiliation and low agonism

Dominance relationships (N = 210) Individuals that belong to relatively more structured social groups that exhibit dominance hierarchy resulting from repeated agonistic interactions between the members. There can also be post-conflict affiliative interactions, which can enhance social complexity

Social organization	Group size	Mean social group size
(Continuous)	(N = 239)	

399

400 Social organization was represented by mean group size per species, including data from
 401 the database Pantheria (Jones et al. 2009), and from Kamilar et al. 2010 and Santana et

402 al. 2012 supplementary materials. Moreover, data about sociality components were
403 confirmed in the Quaarvark Animal Diversity Web descriptions of species behavior, or
404 in the database Pantheria (Jones et al., 2009), McDade (2005) or Long (2003) whenever
405 necessary. When the source database presented more than one key feature registered for
406 the same species, we included the most comprehensive feature recorded for each species,
407 or followed the detailed behavioral description for the species. Specifically, if solitary
408 and social bond behaviors, or if social bonds and dominance relationships, were recorded
409 as features of the same species, we considered the species feature respectively as social
410 bonds or dominance relationships. However, when social and colonial features were both
411 registered, we confirmed case by case in the species behavioral description (bat species
412 including both classifications were usually considered as colonials unless there was an
413 explicit mention of the existence of social interactions, in which case they were classified
414 in social bonds feature). Additionally, when maternal and paternal care systems were both
415 recorded, we considered maternal instead of biparental care whenever the paternal care
416 was relatively indirect, for example, involving only the protection of the group as a whole.

417 We also included in our analysis data about human impact that took place over each
418 species geographical distributions (through the mean measure of the human population
419 density per km²), the species-specific mean body size (g), the mean litter size, the
420 maximum longevity (months), and the diet breadth represented by the number of types of
421 dietary elements (1 to 8 elements, specifically, vertebrates, invertebrates, fruit,
422 flowers/pollen/nectar/gum, seeds, grass, leaves/branches/bark and roots/tubers) for each
423 species, and all obtained in the database Pantheria (Jones et al., 2009).

424 The conservation status data for the species were obtained in the IUCN Red List (2015).
425 We accessed a qualitative and ordinal classification of the vulnerability status of the
426 species (including “Least Concern - LC”, “Near Threatened - NT”, “Vulnerable - VU”,

427 “Endangered - EN” and “Critically Endangered - CR”) as a proxy to the extinction risk
428 of each species. We classified LC and NT as low extinction risk categories, and VU, EN
429 and CR as high extinction risk categories (Purvis et al. 2000).

430 **Data analyses**

431 Due to the possibility of phylogenetic dependence, we also considered the phylogenetic
432 information of the species, available in the supplementary material of Fritz et al. (2009).
433 We carried out separate phylogenetic logistic regression analysis (Ives and Garland 2010)
434 because we obtained distinct sample sizes for each social variable (Table 1), and also for
435 mean human population density (N = 878 species), mean body size (N = 950 species), ,
436 litter size (N = 861 species), longevity (N = 572 species) and diet breadth (N = 786
437 species). We also carried out the full model, containing all 9 predictor variables (N = 151
438 species), however, it’s worth noting that this implied an expressive sample loss, reducing
439 the power of the analysis; nevertheless, the full model should be informative at least for
440 exploratory purposes, in terms of the relative importance of each predictor variable.
441 Polyandry was excluded from the full model because it was too rare, with only 3 cases.
442 The classification of the extinction risk as low (LC and NT) and high (VU, EN and CR)
443 categories (Purvis et al. 2000), comprising the dependent variable extinction risk, was
444 used in the phylogenetic logistic regression analysis, which is appropriate for binary
445 dependent variables and also for both categorical discrete and/or continuous predictor
446 variables (Ives and Garland 2010). The sociality components “mating system” and “care
447 system” were included in the models as categorical variables, while the “social structure”
448 was included as an ordinal variable (Table 1), considering that its key features can express
449 growing social complexity, from solitary to dominance relationships (Kappeler, 2019).
450 Continuous predictor variables were logarithmically transformed and standardized
451 (scaled) to have a mean of zero and a standard deviation of one, the only discrete variable

452 diet breadth was standardized, and categorical variables were used as dummy variables
453 (hence, the differences between each level and the first, reference level, were tested), so
454 that the regression coefficients represent effect sizes (Ives and Garland 2010).

455 We carried out all statistical analysis in the software R (R Core Team, 2021). The
456 significance level considered in the analysis was 5%. We used the R packages: “rredlist”
457 (Chamberlain 2020) to extract IUCN data; “dplyr” (Wickham et al. 2020) to structure the
458 data when necessary; “phylolm” (Ho and Ane 2014) to carry out phylogenetic logistic
459 regression for binary dependent variables; “rr2” (Ives 2018, Ives and Li 2018) to access
460 the R^2_{lik} values, “phytools” (Revel 2012) to extract the mammal species phylogeny, in
461 newick format; “ggplot2” (Wickham 2016) to generate the plots and “rms” (Harrel Jr
462 2021) to test for collinearity in the full model.

463 **RESULTS**

464 Our detailed statistical results of the phylogenetic logistic regression models predicting
465 extinction risk are summarized in Table 2. In our full model, considering all predictor
466 variables, but with a considerable sample loss, we found that species with biparental care
467 have a lower risk of extinction than species containing maternal care (Table 2, $P = 0.040$,
468 and model's R-squared (R^2_{lik}) = 0.387, see Table 3 for variance inflation factors (VIF)
469 values, which suggest no collinearity between the predictor variables in the full model).
470 Specifically, in the models considering each predictor separately, we found significant
471 negative associations between extinction risk and both care and mating systems (Figure
472 1 a, b). Species exhibiting biparental care have a lower extinction risk than species with
473 maternal care ($P = 0.020$, $R^2_{lik} = 0.175$, Table 2). Although we didn't find any difference
474 between the extinction risk comparing species with alloparental and maternal care ($P =$
475 0.09 , Table 2), we should have caution in excluding this possibility because of our

476 reduced sample of species exhibiting alloparental care (only 7% of the species). Also,
477 species that have promiscuous mating systems have a lower extinction risk than
478 monogamous species ($P = 0.010$, $R^2_{lik} = 0.203$, Table 2). We found, however, a
479 significant positive association between extinction risk and social structure (Figure 1 c)
480 and organization (Figure 1 d): species exhibiting social bonds and dominance
481 relationships have a higher extinction risk than solitary species ($P < 0.001$ for a linear
482 increasing trend, $R^2_{lik} = 0.186$, Table 2) and larger group sizes were associated with higher
483 extinction risk (Figure 1d, $P = 0.027$, $R^2_{lik} = 0.262$, Table 2). Furthermore, we found a
484 significant association between higher extinction risk and: higher human population
485 density ($P < 0.001$, $R^2_{lik} = 0.130$, Table 2); larger body sizes ($P < 0.001$, $R^2_{lik} = 0.192$,
486 Table 2); smaller litter sizes ($P < 0.001$, $R^2_{lik} = 0.223$, Table 2); greater maximum
487 longevity ($P < 0.001$, $R^2_{lik} = 0.169$, Table 2); and finally, between higher extinction risk
488 and larger diet breadth ($P < 0.001$, $R^2_{lik} = 0.104$, Table 2). The phylogenetic correlation
489 parameter (α - which is a measure of phylogenetic signal) values of our analyses (Table
490 2) indicate moderate phylogenetic signal, since they are around the value of 0, and values
491 up to -4 indicate no signal while values bigger than 1 denote strong phylogenetic signal
492 (Ives and Garland 2010).

493 **Figure 1.** Proportions of extinction risks by care system (a), mating system (b), social
494 structure (c) key features and the number of observations of extinction risks by mean
495 group size (d), mean human population density per km² (e) and mean body size in grams
496 (f) which were both ln-transformed to better visualization, mean litter size (g), maximum
497 longevity (h) which was originally in months and was transformed in years to better
498 visualization and diet breadth (i). Sample sizes of each category are shown in parentheses.

499 a)

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501

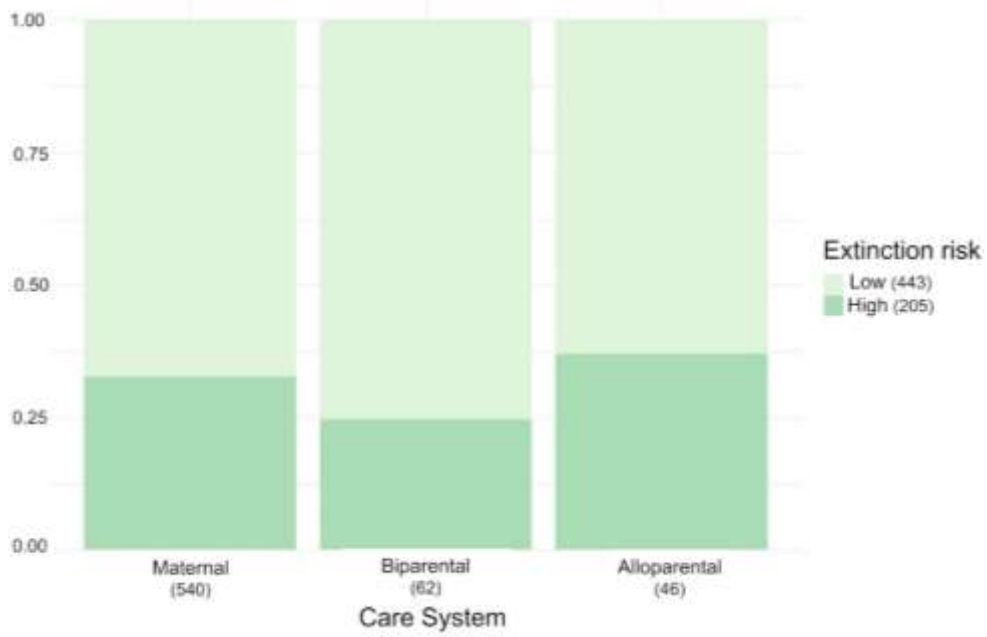
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507 b)

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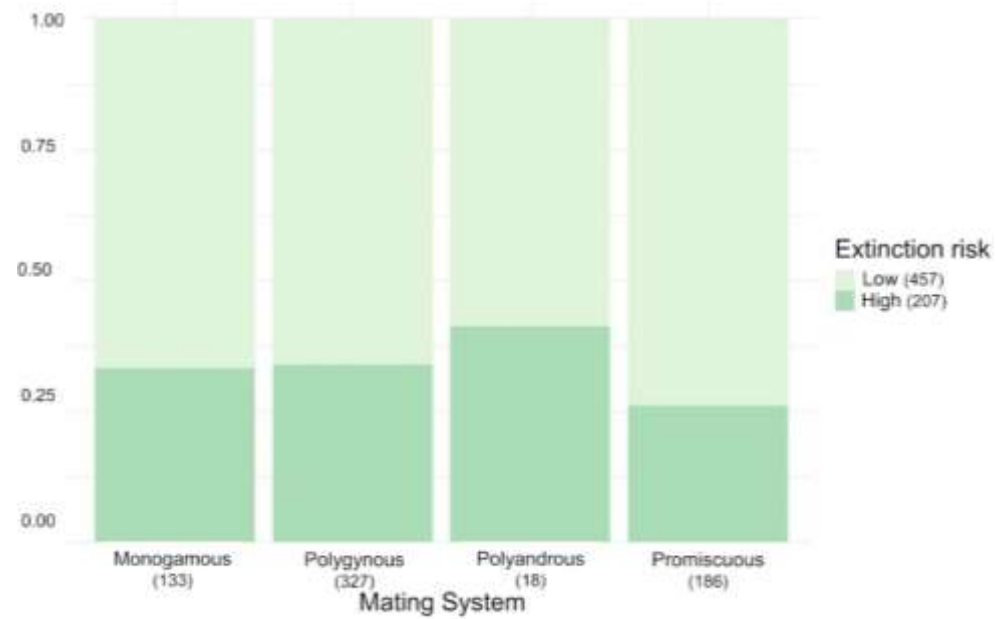
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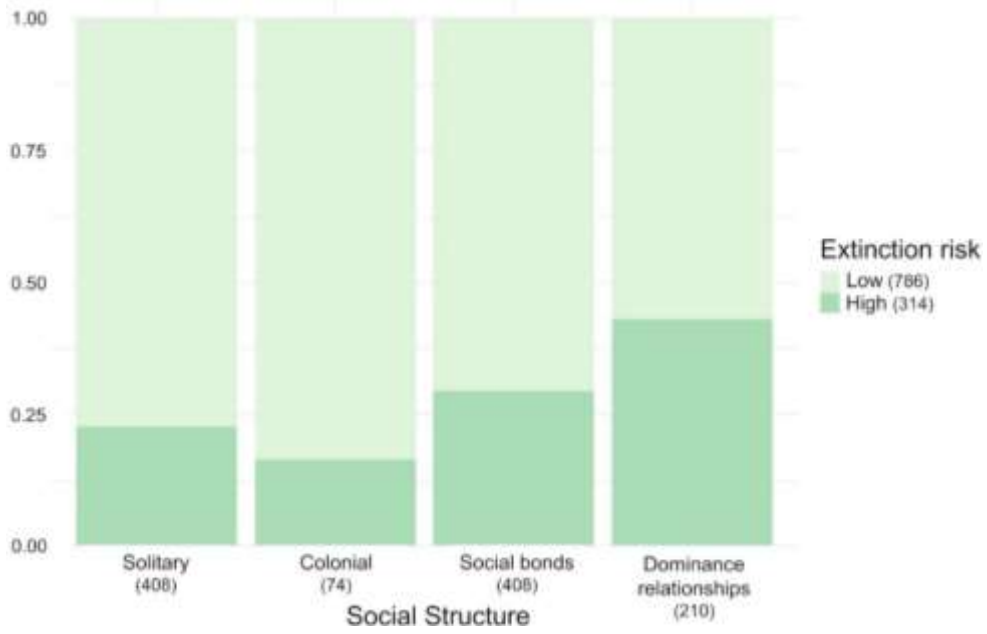
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524 d)

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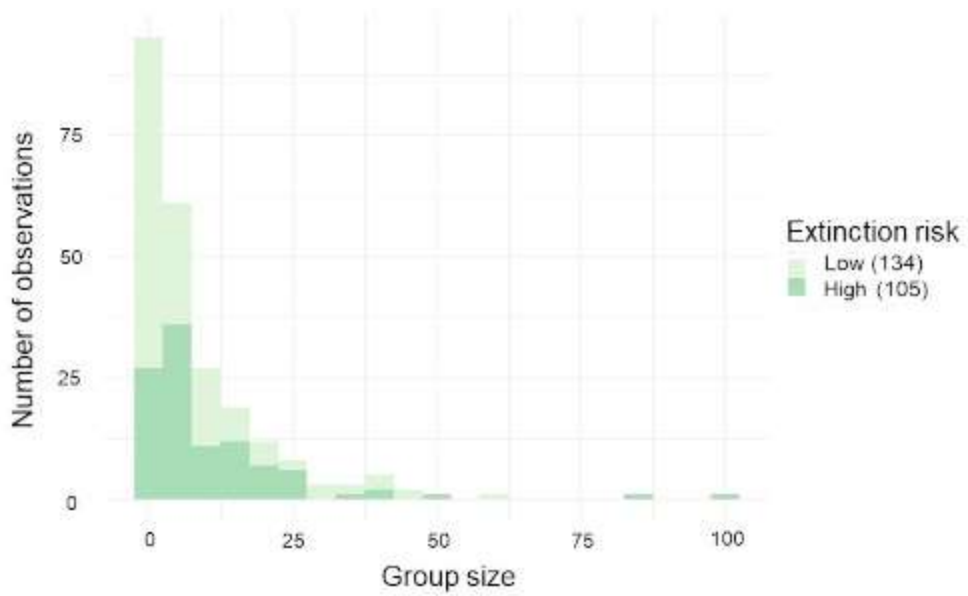
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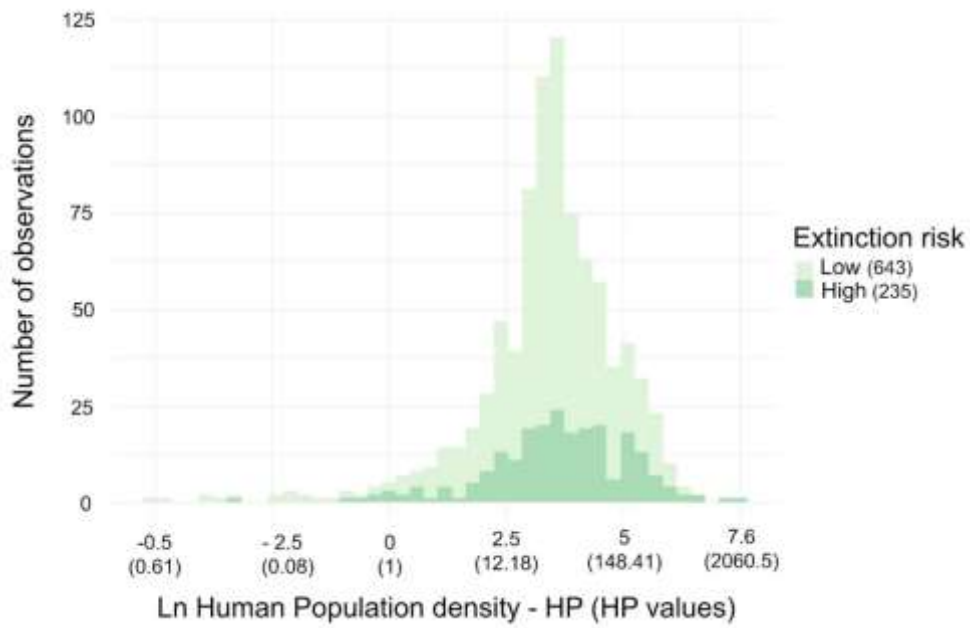
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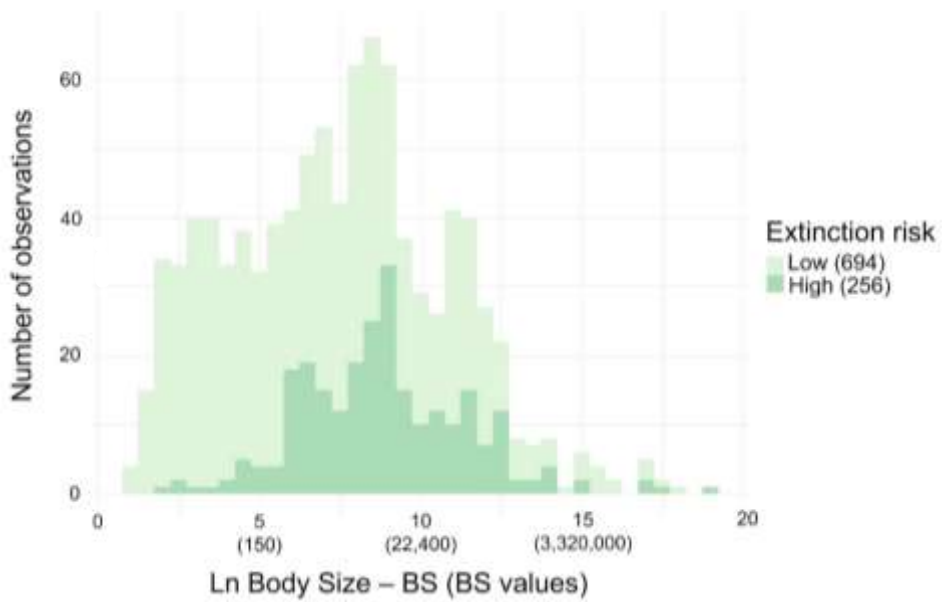
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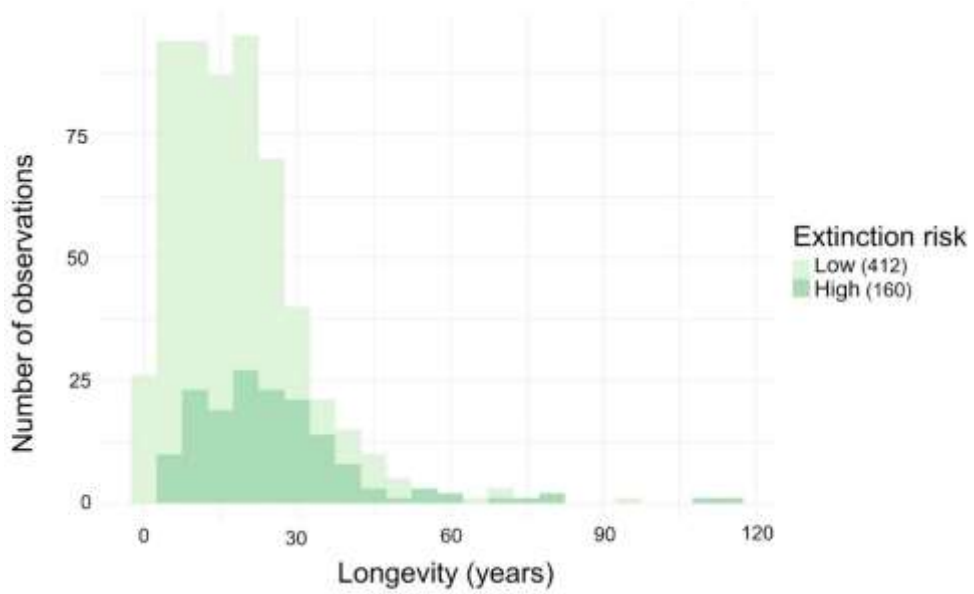
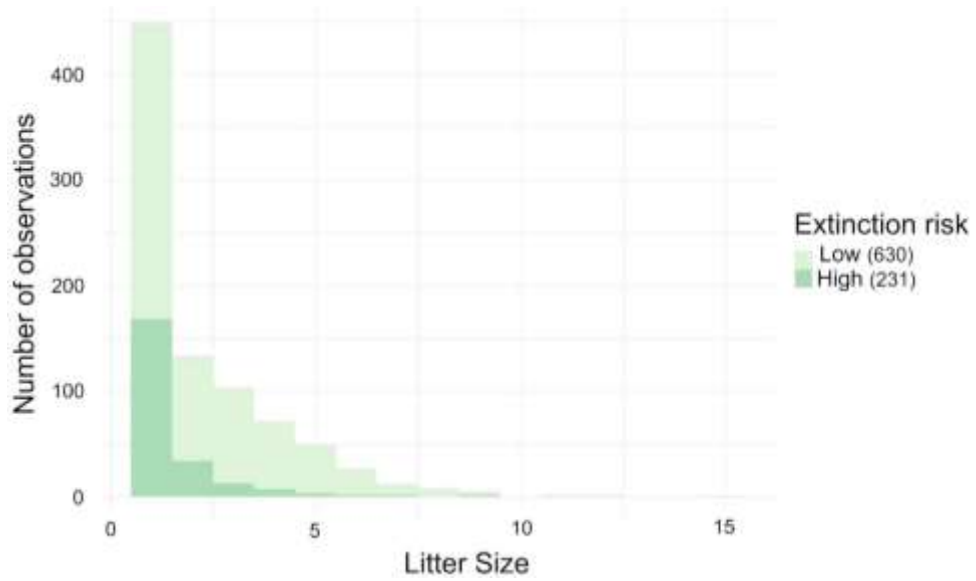
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571 i)

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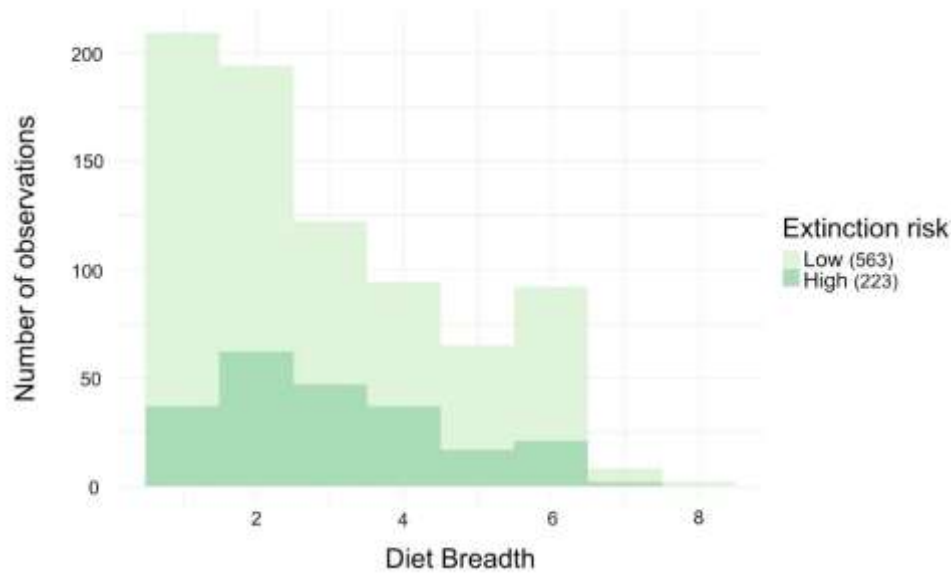
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579 **Table 2.** Summary of phylogenetic logistic regression models predicting extinction risk
 580 in 151 to 1100 mammal species (phyloglm models). For each model we show the
 581 phylogenetic correlation parameter (α), the sample size (N), coefficient estimate
 582 (Estimate), standard error (s.e.), 95% confidence interval (95% CI), Z-statistic (Z) and
 583 Wald-type p-value (p) with significant associations bold-highlighted.

Predictor	Key feature	Estimate	s.e.	Z	95% CI	P
Care system	Intercept	-0.871	0.168	-5.160	-1.175, -0.561	<0.001
	Biparental	-0.816	0.352	-2.317	-1.427, -0.097	0.020
	Alloparental	-0.604	0.367	-1.647	-1.375, 0.160	0.099
	Intercept	-0.708	0.241	-2.936	-1.123, -0.33	0.003

Mating system $\alpha = 0.033$ N = 664	Polygynous	0.005	0.213	0.023	-0.272, 0.279	0.981
	Polyandrous	0.346	0.447	0.774	-0.416, 1.499	0.438
	Promiscuous	-0.663	0.259	-2.56	-1.027, -0.284	0.010
<hr/>						
Social structure $\alpha = 0.042$ N = 1100	Intercept	-1.057	0.143	-7.38	-1.299, -0.869	<0.001
	Linear (L)	0.760	0.153	4.949	0.531, 1.044	<0.001
	Quadratic (Q)	0.282	0.191	1.471	-0.081, 0.576	0.141
	Cubic (C)	-0.240	0.222	-1.079	-0.623, 0.0913	0.280
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Social Organization						
$\alpha = 0.016$ N = 339	Intercept	0.041	0.382	0.109	-0.526, 0.630	0.912
	Group size (log10, scaled)	0.281	0.123	2.272	0.120, 0.460	0.023
<hr/>						
Human population density						
$\alpha = 0.037$ N = 878	Intercept	-1.178	0.156	-7.531	-1.399, -0.808	<0.001
	Mean human population (log10,	0.343	0.083	4.131	0.233, 0.531	<0.001

	scaled)					
Body size	Intercept	-1.190	0.136	-8.699	-1.464, -0.953	<0.001
$\alpha = 0.042$	Mean body	0.704	0.106	6.637	0.528, 0.896	< 0.001
N = 950	mass (log10, scaled)					
Litter size	Intercept	-1.408	0.210	-6.678	-1.772, -1.153	<0.001
$\alpha = 0.027$	Mean litter	-0.984	0.155	-6.348	-1.216, -0.766	< 0.001
N = 861	size (log10, scaled)					
Longevity	Intercept	-1.068	0.119	-8.929	-1.285, -0.161	<0.001
$\alpha = 0.108$	Maximum					
N = 572	longevity (log10, scaled	0.785	0.127	6.155	0.553, 1.040	< 0.001
Diet breadth	Intercept	-1.081	0.137	-7.859	-1.345, -0.853	<0.001

$\alpha = 0.045$	Number	0.255	0.080	3.160	0.135, 0.398	0.0016
N = 786	dietary items (scaled)					
Full model	Intercept	0.201	0.769	0.261	-0.440, 0.965	0.793
	Social					
$\alpha = 0.007$	Structure					
N = 151	(L)	-0.165	0.336	-0.491	-0.791, 0.412	0.623
	(Q)	0.430	0.280	1.533	-0.161, 0.913	0.125
	Biparental	-1.563	0.762	-2.051	-2.084, -0.141	0.040
	Alloparental	1.967	1.460	1.346	0.468, 2.371	0.178
	Polygynous	0.257	0.538	0.478	-0.324, 0.856	0.632
	Promiscuous	-0.071	0.548	-0.130	-0.689, 0.592	0.896
	Group size	0.417	0.219	1.896	0.024, 0.843	0.057
	(log10, scaled)					
	Mean body	-0.049	0.302	-0.163	-0.440, 0.379	0.870
	size (log10, scaled)					

Mean human population (log10, scaled)	0.310	0.167	1.859	-0.026, 0.644	0.063
Longevity (log10, scaled)	0.150	0.306	0.492	-0.347, 0.596	0.622
Litter size	-0.294	0.251	-0.171	-0.864, 0.075	0.241
Diet Breadth (scaled)	0.007	0.150	0.048	-0.289, 0.319	0.961

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585 **Table 3.** Variance inflation factors (VIF) values, suggesting that there is no meaningful
586 collinearity between the predictor variables in the full model (N = 151 species).

Social Structure - linear	Social Structure - quadratic	Biparental care	Alloparental care	Polygynous system	Promiscuous system
1.454	1.350	1.093	1.030	3.756	3.409

					Human
Group size	Body size	Diet breadth	Litter size	Longevity	population density
1.426	1.900	1.175	1.455	2.292	1.072

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588 **DISCUSSION**

589 Here we have explored the effect of behavioral, ecological and life-history traits on
590 extinction risk in mammals. These traits seem to be important to deal with environmental
591 challenges, like that caused by higher human population density which we confirm the
592 connection with higher extinction risk. We found that increased parental care reduces the
593 risk of extinction, as mammal species with biparental care of offspring have a lower
594 extinction risk than species with maternal care only (single and full models, Figure 1a).
595 Biparental care is advantageous for litter survival (Gubernick and Teferi 2000, Wright
596 2006, Lukas and Clutton-Brock 2013) due to the paternal, and sometimes alloparental
597 care, in addition to the maternal investment, thus increasing provisioning and/or
598 protection of offspring. This relationship is expected if we consider that the effort required
599 by coordinated biparental care could be selecting higher cognition (discussed in Whiten,
600 Waal's 2017 review) which could favor these species to deal with environmental
601 challenges.

602 Furthermore, we found that promiscuous species have a lower extinction risk than
603 monogamous species (Figure 1b). This result is compatible with the idea that cognition
604 is being, probably indirectly, selected by human impacts, via selection of certain sexual
605 systems (as promiscuity could require more coordinative capabilities). However,
606 considering that an alternative hypothesis poses that bond maintenance between

607 monogamous (in contrast to promiscuous) species is more cognitively demanding
608 (Schillaci 2006, Shultz and Dunbar 2007), it is important to recognize other, not mutually
609 exclusive explanations, such as the Allee effect, i.e. the positive relationship between
610 population size and fitness. One of the main reasons behind the Allee effect is mate
611 limitation (reviewed by Kramer et al. 2009), and since monogamy can limit mating
612 opportunities through, for example, reduction of encounter rates (Bessa-Gomes et al.
613 2003), monogamous species could be disfavored. Anyway, our results contrast with the
614 lack of relation between the mating system and conservation status in birds (Morrow and
615 Pitcher 2003) possibly because other factors, such as variation in reproductive success
616 and mate choice, can also influence this relationship (Bessa-Gomes et al. 2003).

617 Contrary to our expectations, however, species with social bonds and dominance
618 relationships had a higher extinction risk than solitary species (single model, Figure 1c)
619 and species with larger group sizes exhibit higher extinction risk (single model, Figure
620 1d). Social learning does not bring solely adaptive responses to challenging and changing
621 environments and can also, in some circumstances, restrict these responses (Barrett et al.
622 2019). Thus, although social learning can be advantageous because it accelerates the
623 access by several group members to public information (Duboscq et al. 2016, Canteloup
624 et al. 2021), social learning can also result in individuals relying on outdated information,
625 for example, if the information is transmitted before the environmental change (Barrett et
626 al. 2019, Donelan et al. 2020), leading to conservatism and functional fixedness (Gruber
627 2016). Thus, if sociality variation between species implies substantial social, in
628 comparison to the more costly individual learning, and if environmental changes outpace
629 social transmission, outdated information could increase extinction risks. Thus, it is
630 possible that the ever-increasing velocity of human changes impinged upon the natural
631 environment has outpaced the capacity of most non-human social learning systems. This

632 possibility could also help to explain the unexpected and significant positive association
633 between maximum longevity and extinction risks. If conservatism is associated with
634 extinction risks, one would predict that short-lived species would show lower extinction
635 risks, as information would be more likely to be updated across many successive short
636 generations. Notwithstanding this rationale, it should also be noted that human impact
637 could more directly hamper social learning by disrupting information transmission
638 (Barret et al. 2019), so that species more prone to social learning through communication
639 would suffer the impact of human disturbances more strongly.

640 Social structures based on social bonds and dominance relationships could also be more
641 vulnerable to extinction in comparison to solitary species because their persistence relies
642 on the maintenance of the whole group, not only of individual organisms (Purvis et al.
643 2000). Indeed, besides higher cognition at the individual level in more social species,
644 there is also the possibility of emergent collective cognition at the social group level
645 (Feinerman and Korman 2017). Collective cognition, or even the very coordination of
646 activities observed in social living, implies higher interdependence within the group, and
647 these coordinated group responses emerging from inter-individual interactions could be
648 more difficult to adjust or to adapt (to disturbed habitats) than individual behaviors.

649 Moreover, we assumed that individuals from more social species exhibit higher cognitive
650 abilities that would help deal with rapid environmental change (Marino 2005, Ducatez et
651 al. 2020). But the intelligence required to deal with social life demands could be different
652 from the intelligence needed to deal with other ecological variables. There is no consensus
653 (Burkart et al. 2017) about the prevalence of a general, in contrast to modular cognition
654 in which cognitive specializations could evolve more or less independently from one
655 another. Also, although several studies have found evidence for general intelligence in
656 mammals, it is difficult to confirm that it actually results in higher fitness and behavioral

657 flexibility (see an extensive review by Burkart et al. 2017, Boogert et al. 2018, Rochais
658 et al. 2022). If the challenges posed by human impacts require skills that differ from those
659 acquired to deal with social life demands, and if cognition relies largely on specialized
660 brain modules, human impacts would require new brain modules that could eventually
661 impose trade-offs between various specialized cognitive abilities, including social
662 capabilities.

663 Additionally, we found that mean human population density is connected to higher
664 extinction risks (single model), which is consistent with previous findings. For instance,
665 changes in human footprint values were associated with extinction risk in mammals (Di
666 Marco et al. 2018) and primates (Lootvoet et al. 2015), while there is a positive
667 association between human population density and the extent of agricultural activities
668 (Davies et al. 2006).

669 We also found that larger body sizes are associated with higher extinction risks (single
670 model), a result that agrees with past findings for mammals (Cardillo et al. 2005, Fritz et
671 al. 2009), and is probably a consequence of larger animals being preferential targets of
672 human exploitation, added to the higher energetic demands of big bodies (Cardillo and
673 Bromham 2001). According to our expectations, litter size was inversely related to
674 extinction risk, a pattern that makes sense especially in challenging environments that
675 reduce survival rates, an outcome that can be potentially compensated by bigger offspring
676 production (Purvis et al. 2000).

677 Finally, we found an unexpected positive relationship between diet breadth and extinction
678 risk. Although we expected that the exploration of more types of resources could help
679 animals deal with environmental challenges (Ducatez et al. 2020), narrow diets were not
680 associated with extinction risk in bat species (Safi and Kerth 2004). The quality of the

681 diet (in terms of energy and nutrition benefits) could be more relevant to survival and
682 reproduction than the number of dietary items for each species.

683 Our results highlight that distinct sociality components are particularly relevant for the
684 conservation of species facing human impacts. Biparental care seems to be an especially
685 relevant characteristic to reduce vulnerability. Furthermore, social components, such as
686 solitary living, promiscuous mating system, and small group sizes, along with life-history
687 traits such as smaller bodies, smaller diet breadth, larger litter sizes and lower longevity,
688 have here emerged as traits potentially enhancing resilience to human environmental
689 disturbances. This is critical to conservational purposes, since more socially structured
690 species within larger groups, as well as monogamous species and species relying
691 exclusively on maternal care, should receive more attention and protection, so as to reduce
692 their increasing extinction risks. Furthermore, the investigation of the actual mechanisms
693 fostering the connection between sociality components and extinction risks could lead to
694 precise management procedures for the conservation of some of our most cherished,
695 socially distinct species.

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Capítulo II

931

Artigo a ser submetido ao periódico *Animal Cognition***Longevity correlates with cognitive abilities in primates**Juliana Lucatelli¹, Alex Thornton², Neeltje Boogert², Hilton F. Japyassú^{1,3}

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932 **Abstract**

933 The social intelligence hypothesis suggests that managing social relationships can be
934 challenging and sociality could be a determining factor for the evolution of cognition.

935 Evidence for this hypothesis is controversial, largely because studies often rely on
936 contentious proxies of cognitive abilities and social complexity such as brain and group

937 size. The meaning of neuroanatomical measures can be difficult to unveil, and social
938 group size does not capture some intricacies of social relationships. Thus, taking into

939 account individual-based cognitive tests and sociality metrics, such as social structure
940 may provide new insights when testing the social intelligence hypothesis. Life history and

941 ecological traits are also potentially linked to cognitive abilities because longevity was
942 found to covary with brain size and behavioural plasticity, and diet breadth can be a

943 metabolic facilitator of brain growth. We test here these hypotheses by correlating social
944 structure, care system, longevity and diet breadth to cognitive performance data across a

945 range of tasks. Through comparative phylogenetic analyses of non-human primate

946 species collected in a systematic literature review, we found support only for our
947 hypothesis that greater longevity correlates with higher cognitive abilities across species.
948 This link may be explained by a correlated evolution between life history and cognitive
949 abilities, in which higher plasticity can help animals to overcome environmental
950 challenges, benefiting survival. Our study also highlights gaps in the cognitive, social and
951 ecological data available in the research literature, which inhibits progress in testing the
952 social intelligence hypothesis. We, therefore, suggest that future data collection efforts
953 will be concerted and coordinated to generate a database that is standardised and
954 taxonomically representative.

955 **Keywords:** cognition, general intelligence, life history, sociality, diet

956 **Introduction**

957 The social intelligence hypothesis, also known as the social complexity, social brain or
958 Machiavellian intelligence hypothesis, suggests that the information-processing demands
959 associated with living in groups is the main selective pressure for the evolution of larger
960 brains and advanced cognitive abilities, and was originally proposed for primate species
961 (Humphrey 1976, Byrne and Whiten 1988, Dunbar 1992, Dunbar 1998). The acquisition,
962 retention and use of information are considered cognitive processes (Shettleworth 2009).
963 Advanced cognitive abilities are thought to be necessary for maintaining social
964 relationships (Shultz and Dunbar 2022). For instance, recognising group members,
965 predicting their behaviour and remembering social interactions should be cognitively
966 challenging (Aureli and Schino 2019).

967 Evidence for the social intelligence hypothesis is mainly based on comparative studies of
968 neuroanatomy. However, these studies find controversial relationships between brain
969 structure or brain size measures and sociality. For instance, telencephalon volume fraction

970 correlates positively with social structure categories considered to be more complex
971 across 154 avian species (Burish et al. 2004). Social ungulates have larger relative brain
972 and neocortex sizes (i.e., corrected for body size) than solitary ungulates (Shultz and
973 Dunbar 2006). Relative neocortex size is correlated with the size of grooming cliques and
974 with group size in 30 primate species (Kudo and Dunbar 2001). Moreover, Pérez-Barbería
975 et al. (2007) results suggest coevolution between relative brain size and degree of sociality
976 (based on indices considering group size and categories of sociality) in 206 species of
977 ungulate, carnivore, and primate mammals. In contrast, however, group size did not
978 correlate with brain volume or frontal cortex volume in 36 Carnivora species (Holekamp
979 et al. 2015). Similarly, for 289 Carnivora species, social, in comparison with solitary
980 species, did not exhibit larger relative brain sizes (Finarelli and Flynn 2009), and relative
981 brain size was not correlated with group size for more than 140 primate species (DeCasiel
982 et al. 2017). There are several issues concerning the use of brain measures as a proxy for
983 cognitive performance. For instance, the heterogeneity of interspecific measures and of
984 the evolutionary histories; the actual meaning of these measures, since different parts of
985 the brain can contribute to a particular behaviour as well as distinct behaviours can
986 influence a single brain structure; and the potential influence of confounding ecological
987 and life history factors when they are not taken into account (Healy and Rowe 2007,
988 Logan et al. 2018, Powell et al. 2017, Wartel et al. 2019). Thus, it remains important to
989 assess whether sociality correlates directly with cognitive abilities across several species
990 beyond correlations with relative brain size.

991 Most studies using behavioural data of cognitive performance compared just a couple or
992 a few species. For example, species considered more social performed better on socio-
993 cognitive tasks in comparisons between two (Bond et al. 2003) and four species of corvids
994 (Bond et al. 2010). Two social Carnivora species performed better on a novel problem-

995 solving task than two non-social Carnivora species (Borrego and Gaines 2016).
996 Furthermore, two more social primate species outperformed two less social species on a
997 gaze-following task (that measures the ability to look in the same direction that other
998 individuals and possibly of gathering environmental information), but their performance
999 did not differ in self-control tasks (Chen et al. 2017). Nevertheless, larger-scale
1000 comparative studies are needed, which are limited to date. Group size of several Carnivora
1001 species did not predict success in a problem-solving task, which measures the ability to
1002 perform a novel task (Benson-Amram et al. 2016), but this type of performance (e.g.,
1003 puzzle-box tasks) lack clarity regarding the cognitive process measured and may be more
1004 susceptible to contextual and individual variability (Boogert et al. 2018, Thornton et al.
1005 2014). Primate species group size didn't correlate with self-control (or inhibitory-control)
1006 tests (MacLean et al. 2014), which intend to measure the animal's ability to inhibit an
1007 impulsive behaviour that could be unfavourable. Self-control is crucial for decision-
1008 making and is potentially worthwhile in social situations (Hare et al. 2009). But even
1009 group size constituting an important aspect of sociality, it has been identified as an
1010 insufficient measure to represent the extent to which different social systems generate
1011 cognitive challenges (Bergman and Beehner 2015, Kappeler 2019).

1012 Therefore, group size does not necessarily capture other relevant aspects of sociality, such
1013 as social structure. For instance, both within and between primate species, when group
1014 sizes are too large, group cohesion, i.e. the intensity of the link between individuals in a
1015 social group, is expected to decrease because of spatial and temporal constraints on social
1016 interactions (Lehmann et al. 2007). Thus, the social structure, which comprises the
1017 patterning, quality and content of social interactions (Kappeler 2019) should also be taken
1018 into account, because it has more information regarding social relationships, the

1019 fundamental phenomenon demanding higher cognitive abilities (Rudolph and Fitchel
1020 2017).

1021 Despite the difficulties in characterising sociality through commonly used measures,
1022 some social categorical traits can be used in comparative studies (Kapeller 2019) and are
1023 potentially relevant in the evolution of cognition. Species with social bonds (mainly
1024 affiliative behaviours in the social group with no clearly structured hierarchies) could
1025 differ in cognitive abilities from species with dominance relationships, which modulate
1026 access to breeding and resources in several species (Kappeler 2019). Dominance
1027 relationships promote more differentiated relationships and more conflict of interest, and
1028 hence could be more cognitively demanding (Bergman and Beehner 2015, Kappeler
1029 2019), including the needed memory of previous interactions. However, once established,
1030 dominance relationships are often based on relatively simple rules that do not demand
1031 substantial cognition, such as the uniform aggression of lower-ranked group members
1032 (Hobson et al. 2021). In addition, dominance relationships could reduce uncertainty
1033 regarding social relations once established, and could therefore be cognitively less
1034 demanding than social interactions in more egalitarian societies. Furthermore, the type of
1035 offspring care exhibited might correlate with cognitive performance across species. For
1036 example, biparental and alloparental care requires management and coordination of
1037 offspring provisioning and care activities and could be more cognitively (although less
1038 energetically) demanding than maternal care alone (Burkart and van Schaik 2010; but see
1039 Thornton and McAuliffe 2015).

1040 Along with the social intelligence hypothesis, there are competing hypotheses singling
1041 out other factors as the main drivers of cognitive evolution, such as life history or
1042 ecological factors. Longer longevity enables the evolution of greater plasticity in variable
1043 environments, while plasticity in turn favours survival, selecting longer longevity

1044 (Ratikainen and Kokko 2019), suggesting a possible association of longevity with
1045 cognitive abilities. Indeed, mammals with longer lifetimes exhibited larger brains
1046 (González-Lagos et al. 2010) as well as primate relative and absolute brain volume was
1047 correlated with juvenile period and reproductive lifespan (Navarrete et al. 2016). The
1048 ecological intelligence hypothesis focuses on ecological challenges, such as acquiring
1049 food with spatially and temporally variable distributions, as selective pressures for higher
1050 cognitive abilities (Parker and Gibson 1977, Milton 1988, Clarin et al. 2013).
1051 Specifically, considering that fruits are relatively less predictable food items as compared
1052 to other forms of vegetation, and require extractive foraging information, frugivory
1053 should be more cognitively demanding than folivory (Rosati et al. 2014, DeCasien et al.
1054 2017). Diet breadth correlates to self-control in primates (MacLean et al. 2014), and could
1055 metabolically facilitate cognition.

1056 Despite the social and ecological intelligence hypotheses being sometimes treated as
1057 competing hypotheses (DeCasien et al. 2017), biological phenomena are rarely affected
1058 or caused by a single factor, and multiple aspects should be considered whenever possible.
1059 This idea that both hypotheses are not mutually exclusive contrasts with the possible
1060 domain-specific nature of cognition. According to this view, cognition evolved in
1061 response to specific conditions and would be modularised, thus social and ecological
1062 processes could mould different cognitive abilities, as discussed by Rosati (2017). Lack
1063 of correlations between distinct cognitive abilities, supporting cognitive modularity, were
1064 found between primate (Amici et al. 2012) and bird (Anderson et al. 2017) species. In
1065 contrast, the domain-general view defends the idea of consistent cognition differences
1066 across species, with cognitive abilities remaining similar in distinct conditions. Statistical
1067 grouping (i.e. principal components) or positive correlations between different cognitive
1068 abilities supports the domain-general view for primate, bird and carnivore species

1069 (Borrego and Gaines 2016, Damerius et al. 2019, Deaner et al. 2006, Fernandes et al.
1070 2014, Reader et al. 2011, Shaw et al. 2015).

1071
1072 Herein we evaluate the relation of social, ecological and life-history variables with
1073 measures of cognition across primate species. We gather data from published studies on
1074 cognitive performance and evaluate the support for domain-specific vs domain-general
1075 views of cognition by testing the correlation between the cognitive variables. We then use
1076 phylogenetic generalized least squares (PGLS) to evaluate the statistical support for social
1077 structure, care system (social intelligence hypothesis), diet breadth, percentage of fruit in
1078 the diet (ecological intelligence hypothesis) and longevity (life history hypothesis) as
1079 predictors of cognitive abilities. Our predictions are that i) social bonds structure
1080 associates with better cognitive performance than dominance relationship structure, ii)
1081 biparental and alloparental care are associated with better cognitive performance than
1082 maternal care only, iii) diet breadth, or a higher percentage of fruit in the diet, correlates
1083 positively with cognitive performance, and iv) longevity correlates positively with
1084 cognitive performance, across primate species.

1085 **Methods**

1086 *Data collection*

1087 We conducted a systematic review of studies assessing the relationship between sociality
1088 and cognition in order to access the state of the art of the field, and the availability of
1089 cognitive and social variables. We focused on Mammalia, since, relative to other
1090 taxonomic groups, mammals' social behaviour and cognitive abilities are extensively
1091 studied. Even so, due to limited data availability, our compiled dataset ended up being
1092 restricted to primates.

1093 In the first search, we selected published scientific articles, dissertations or theses in
1094 English using the search string “((((sociality or group-living) and (cognit* or learning
1095 abilities)) or social intelligence hypothesis or social complexity hypothesis or
1096 machiavellian intelligence hypothesis) and mammal*)”. These searches resulted in 3941
1097 titles (480 titles were found in Google Scholar and 3461 titles were found in Scopus). The
1098 selection procedure comprised three steps: inspection of 1) titles and study type,
1099 excluding studies that did not explicitly address the topic relevant to this study or were
1100 not articles or theses (specifically, we excluded books or book chapters, non-scientific
1101 texts, and studies focusing on taxa other than non-human mammals) – this reduced the
1102 database to 1049 titles, after also removing duplicates); 2) abstracts and, if necessary,
1103 methods, excluding studies that were not directly relevant (i.e., studies on topics not
1104 related to the focus of this work, studies on taxa other than mammals, reviews or studies
1105 not measuring the potential variables of interest for this study) – this resulted in 125
1106 remaining titles); and 3) full text, recording the types of cognitive measures used, if the
1107 data were available and in what format (i.e. processed data, such as a mean value per
1108 species, or raw data) – resulting in 53 titles. We repeated the three selection steps in the
1109 studies that cited the selected studies (“forward snowball sampling”). The studies
1110 compiled in this first search informed us about the most used social and cognitive
1111 measures and the availability of data for comparison across species. This information then
1112 allowed us to choose the terms of the next searches and our study variables.

1113 Thus, after this scanning, we performed more refined and directed new searches of
1114 cognitive data, including in the keywords each type of cognitive domain/task, along with
1115 “mammals” and excluding “human” or “children” data. For instance, the specific search
1116 “(inhibition or inhibitory control or self-control) and mammal* and animal* - human or -
1117 children”, (where “-” means minus). We selected the most frequent cognitive

1118 domains/tasks, as well as variables with clear biological and ecological relevance (such
1119 as memory, self-control and innovation).

1120 The operationalisation of cognitive variables raises many debates, including concerns
1121 about the standardisation of measures for species with very different characteristics,
1122 rearing and test conditions (Thornton and Lukas, 2012) and sensory systems, which may
1123 lead to unfair comparisons, as well as the influence of personality, attention, motivation,
1124 hormonal levels, or test subjects' previous experiences (see reviews by Shaw and
1125 Schmelz 2017 and Boogert et al. 2018). Although the scale of our study did not allow us
1126 to consider all these issues, we included commonly studied cognitive domains or
1127 behaviours that are likely to capture evolutionarily relevant, and specific, cognitive traits:
1128 (1) inhibition or inhibitory control or self-control (MacLean et al. 2014, Miller et al.
1129 2019), (2) memory (Cowan 2008, Jonides et al. 2008), (3) innovation (Lefebvre 2000,
1130 Reader and Laland 2002, Reader and Laland 2003, Reader 2003), (4) social learning
1131 (Reader and Laland 2002, Reader and Laland 2003), (5) general cognition score or
1132 performance, psychometric g, global cognition estimate, general intelligence (G), or
1133 general factor, which is a synthetic measure extracted from the correlation between
1134 multiple cognitive tests that evaluate different cognitive domains (Reader et al. 2011,
1135 Shaw and Schmelz 2017).

1136 For the searches within each specific cognitive domain, we selected the articles based on
1137 the same three steps aforementioned, used in the first search (inclusion/exclusion based
1138 on inspection of the titles and study types of the total of 1395 titles found; abstract and
1139 methods; and full text, resulting in 19 studies, in which we also excluded studies when
1140 data of interest were not available). Additionally, we excluded studies testing domestic
1141 animals because we were interested in the cognitive traits resulting from the process of
1142 natural selection. We also excluded studies testing the effect of experimental restrictions,

1143 such as the impact of specific diets, administered substances or particular conditions (e.g.,
1144 specific mutations). We performed forward snowball sampling of the selected articles to
1145 complete the search. We were especially interested in studies that compared cognitive
1146 performance across species, since they tend to be more homogenous in their
1147 methodology, in addition to the independent studies that followed the same protocols as
1148 the selected comparative studies, of which the data could then be added to the interspecific
1149 dataset. After the collection of the response variables, i.e., the cognitive performance data,
1150 from 6 studies that met our criteria, we then searched the literature for the data of the
1151 predictor variables for those species in our cognition database.

1152 *Response and predictor variables included in the study*

1153 The response variables included in the analyses were (1) Deaneer's global cognition (G)
1154 (based on the tasks in captivity of the cognitive tasks detour, patterned string, invisible
1155 displacement, tool use, object discrimination learning, reversal learning, oddity, sorting,
1156 and delayed response – Deaneer et al. 2006 and Deaneer et al. 2007, but with species-level
1157 data collected from van Schaik et al. 2021, N = 23); (2) Reader's general intelligence
1158 factor (g) (comprising data mainly on captivity but also on field behavioural contexts of
1159 the cognitive domains of behavioural innovation, social learning, tool use, extractive
1160 foraging and tactical deception - Reader et al. 2011, N = 27 species); (3) the innovation
1161 rate (i.e. the number of behavioural innovations mainly in captivity but also in field
1162 observations found in literature surveys, including cases qualified as tool use, extractive
1163 foraging or tactical deception, but excluding species with zero records - Reader et al.
1164 2011, N = 38); (4) social learning (i.e. the number of occurrences of social learning mainly
1165 in captive but also in field observations found in literature surveys, excluding species with
1166 zero records - Reader et al. 2011 - N = 29); (5) mean memory (average percentage value
1167 based on success on performance in delayed response task in short (0 s), medium (15 s)

1168 and long (30 s) conditions in captivity - Many Primates et al. (2022) , N = 39; we used
1169 the mean value because the memory tasks were correlated); and (6) mean self-control or
1170 inhibitory control domain (average percentage value based on success on performance in
1171 the cylinder and A not B tasks in captivity - MacLean et al. 2014, Chen et al. 2017, King
1172 2021, N = 18; we used the mean value because the self-control tasks were intercorrelated).

1173 The social, ecological and life history variables were selected based on scientific rationale
1174 but were also restricted by the sample size of our cognitive variables since, to test our
1175 hypothesis in a statistically robust manner, the sample size of the response variable should
1176 be much larger than the number of predictors in the models (Mundry 2014). We included
1177 species-specific mean values of diet breadth (Jones et al., 2009, MacLean et al., 2014)
1178 and percentage of fruit in the diet (when the data was available, DeCasien et al. 2017) as
1179 an ecological measure, and maximum longevity as a life history measure (González-
1180 Lagos et al. 2010).

1181 On account of the difficulties associated with the definition and operationalisation of
1182 social complexity measures, especially across studies and species, Kappeler (2019) has
1183 distinguished complementary components of sociality that are viable for use in
1184 interspecific studies, which we used as social variables to test the social intelligence
1185 hypothesis. Specifically, we included the social structure and care system (Kappeler,
1186 2019). We collected data on social structure and care system of each species in the online
1187 database Quaarvark Animal Diversity Web (Myers et al. 2021) or in the primary
1188 literature (Fedigan and Baxter 1984, Porter and Garber 2009, Volampeno et al. 2011).

1189 For the variable “social structure”, we categorised primate species into those with social
1190 bonds or those with dominance relationships. The “social bonds” category included
1191 species characterised by relatively high affiliation and low agonism (Kappeler 2019), and

1192 no clearly structured hierarchies. The “dominance relationships” category included
1193 species commonly exhibiting repeated agonistic interactions, leading to differentiations
1194 between access to resources and mating (Kappeler 2019). It is worth noting, however,
1195 that these social structures are not strictly mutually exclusive, since species exhibiting
1196 dominance relationships can also develop social bonds through, for example, post-
1197 conflict interactions and reconciliation. Therefore, we distinguished social bonds and
1198 dominance relationships categories based on the description of the behaviour of the
1199 species. A social species was considered to have dominance relationships only if it clearly
1200 exhibits some dominance hierarchy structure between individuals. The care system
1201 categories were “maternal” (offspring care performed only or almost only by the mother
1202 – when general care, such as protection of the group, is performed by the father, we still
1203 considered it maternal), “biparental” (both parents care for their offspring) or
1204 “alloparental” (care can also be performed by other conspecifics of the group).

1205 The predictor life-history and ecological data were collected in the databases Pantheria
1206 (Jones et al., 2009), Quaarvark Animal Diversity Web (Myers et al. 2021), IUCN Red
1207 List website, AnAge: The Animal Ageing and Longevity Database at the Human Ageing
1208 Genomic Resources (Tacutu et al., 2018). Additionally, data were extracted from specific
1209 references when not found in previous searches (Abee et al., 2012, Easton et al. 2011,
1210 Lahann, 2007, Thierry et al., 1994, Thomas et al., 2018). Longevity is herein represented
1211 by the maximum longevity (expected maximum age reached by adults either in captivity
1212 or in the field) registered for the species, in months. Diet breadth is quantified as the
1213 number of elements in the diet, considering 8 (sets of) dietary elements: 1) vertebrates, 2)
1214 invertebrates, 3) fruits, 4) flowers, pollen, nectar, gum, 5) seeds, 6) grass, 7) leaves,
1215 branches, bark, and 8) roots, tubers.

1216 Our final dataset, including 81 non-human primate species belonging to 12 families, is
1217 available in Supplementary material 1 (SM1). The species considered belong to the
1218 families Cercopithecidae (N = 31 species), Callitrichidae (10), Atelidae (7), Lemuridae
1219 (7), Hylobatidae (7), Hominidae (5), Cebidae (5), Lorisidae (3), Cheirogaleidae (2),
1220 Indriidae (2), Aotidae (1) and Pitheciidae (1).

1221 *Statistical analyses*

1222 We performed phylogenetic generalised least squares (PGLS) analyses to account for the
1223 potential phylogenetic dependence, through maximum likelihood (ML) estimations, in
1224 which lambda values varies from 0 to 1, comprising a gradient from none to a strong
1225 phylogenetic signal (Symonds and Blomberg 2014). The phylogenetic information was
1226 based on the supplementary information of Fritz et al. (2009).

1227 We conducted multiple PGLS models, including social structure, care system, longevity
1228 and diet breadth as predictor variables, and each cognitive measure as response variable
1229 (i.e. Deaner's G, Reader's g, social learning, innovation, memory, self-control) in turn.
1230 The selection criteria of the variables were the scientific rationale and the data availability
1231 for interspecific comparison. We excluded species information when our dataset had less
1232 than five cases for some key feature of social structure or care system, since rare cases
1233 could be too influential while having lower informational power (Mundry 2014). In some
1234 analyses, this resulted in the exclusion of the care system as one of the predictor variables,
1235 because data were missing for too many species. To test for cognitive modularity vs. a
1236 general cognitive ability, we also explored whether species-specific cognitive abilities
1237 including general cognitive values were correlated through PGLS analyses.

1238 We evaluated potential impacts of highly influential datapoints in the fitted models
1239 through Cook's distance measure (based on the linear models since we cannot evaluate it

1240 directly in the PGLS models and we did not find an indication of phylogenetic signal).
1241 Specifically, an observation was considered influential if it was more than four times the
1242 mean Cook's Distance (Cook 1979). We furthermore checked for collinearity between
1243 predictors through variance inflation factors (VIF).

1244 All analyses were performed in the software R (R Core Team 2021, version 4.0.5). We
1245 used the packages "tidyverse" (Wickham et al. 2019) for data manipulation, "ape"
1246 (Paradis and Schliep 2019) and "phytools" (Revell 2012) to manipulate the phylogenetic
1247 data and plot the phylogenetic trees, "caper" (Orme et al. 2018) and "geiger" (Pennell et
1248 al. 2014) to perform the analyses, "base" (R Core Team 2021) to calculate Cook's
1249 Distance, "ggplot2" (Wickham 2016), "magrittr" (Bache and Wickham 2020) and
1250 "patchwork" (Pedersen 2020) to plot and manipulate the graphs, and "rms" (Harrell Jr
1251 2021) to calculate VIF values.

1252 **Results**

1253 The majority of cognitive ability measures were correlated with each other, after taking
1254 into account the phylogeny (Supplementary material 2 – SM2). The exception was mean
1255 memory, which did not correlate with social learning (Figure 1 and Supplementary
1256 material 3 – SM3). Furthermore, all lambda values indicate a lack of phylogenetic signal
1257 in the relationships (Table 1).

1258	Reader's g	0.36 **			
1259					
1260	Innovation	0.19 *			
1261	Social Learning	0.44 *		0.74 ****	
1262	Mean Memory	0.67 ****	0.28 *	0.26 *	0.11
1263	Mean Self Control	0.54 *	0.56 *	0.46 **	0.35 *
1264		Deaner's G	Reader's g	Innovation	Social Learning
1265					Mean Memory

1266 **Figure 1.** Phylogenetic Generalized Least Squares (PGLS) results and adjusted R²
 1267 between response variables. The presence of asterisks and shades of blue indicate that the
 1268 relationship was significant, with stronger correlations indicated with darker hues. Since
 1269 innovation and social learning values were already part of Reader's g index, their
 1270 correlations were not included.

1271 We consistently found that maximum longevity was positively correlated with cognitive
 1272 performance (Table 1) including Deaner's G (Estimate = 0.720 ± 0.187 , $P = 0.001$, $N =$
 1273 23), Reader's g (Estimate = 0.720 ± 0.243 , $P = 0.033$, $N = 27$), innovation (Estimate =
 1274 0.669 ± 0.159 , $P < 0.001$, $N = 38$), social learning (Estimate = 0.469 ± 0.211 , $P = 0.036$,
 1275 $N = 29$), mean memory (for the model including diet breadth as the diet predictor:
 1276 Estimate = 0.464 ± 0.209 , $P = 0.035$, $N = 39$, and for the model including the percentage
 1277 of fruit as the diet predictor: Estimate = 0.531 ± 0.192 , $P = 0.010$, $N = 39$) and mean self-

1278 control (Estimate = 0.565 ± 0.178 , $P = 0.009$, $N = 18$) as cognitive response variables
 1279 (Figure 2).

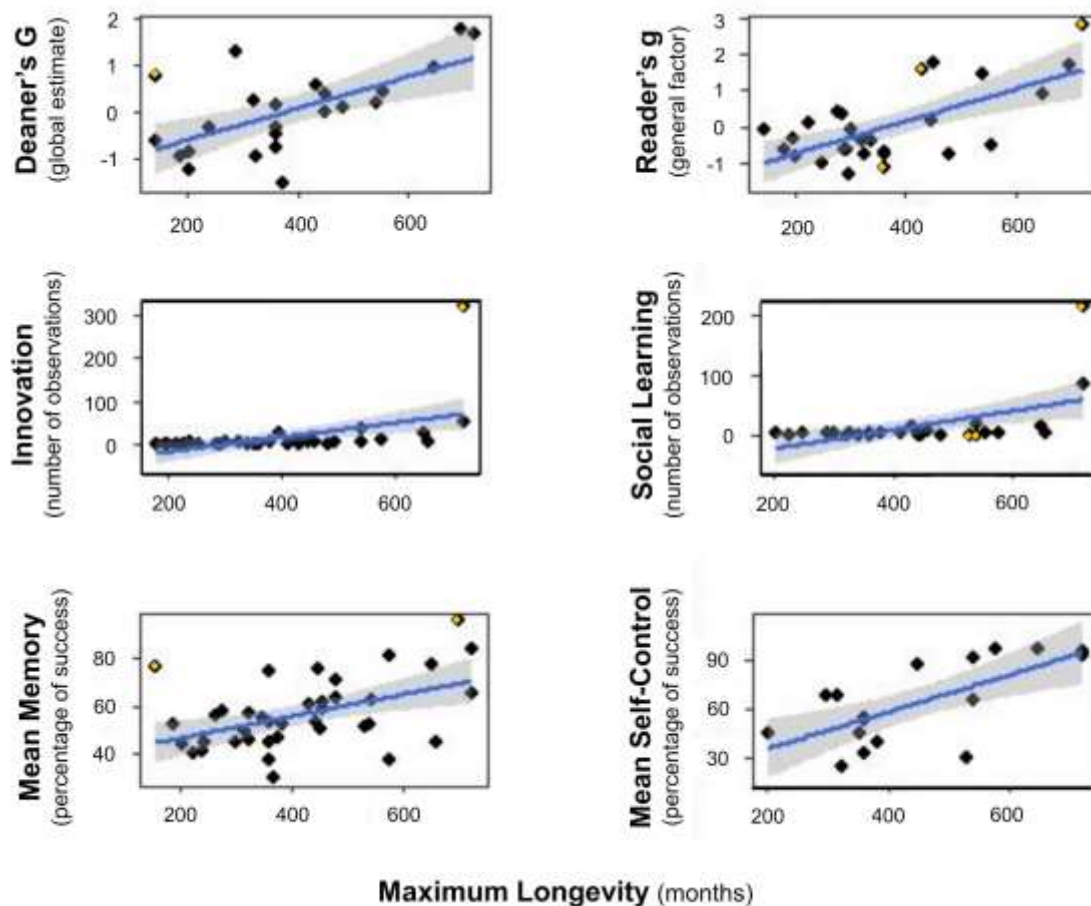
1280 However, contrary to predictions, none of the other factors included in the models showed
 1281 significant correlations with any of the cognitive response variables (Table 1). The results
 1282 of the analyses excluding influential cases according to Cook's distance criteria
 1283 (Supplementary material 4 – SM4) were qualitatively similar to the results including
 1284 influential observations (Table 1), except for the Reader's g result. In this case, we
 1285 excluded influential data from three species (*Aotus azarae*, *Macaca mulatta* and *Pan*
 1286 *trogodytes*) and excluded the care system variable (due to the reduced number of cases
 1287 of key characteristics, preventing comparison). This model excluding influential
 1288 datapoints showed a significant positive correlation between diet breadth and Reader's g
 1289 (Estimate = 0.453 , $P = 0.009$, $N = 24$, SM4), which was not found in the model including
 1290 the influential datapoints.

1291 **Table 1.** Summary of the PGLS models' statistical results correlating social, ecological
 1292 and life history traits with cognitive abilities in primate species. For each model we show
 1293 the sample size (N), the variables included as predictors (social structure – SS, care
 1294 system – CS, longevity – LG and diet breadth – DB or percentage of fruit in the diet -
 1295 PF), the phylogenetic signal parameter (Lambda), the coefficient estimate (Estimate), the
 1296 standard error (s.e.), the t-statistics (t-value), Wald-type P-value (with significant
 1297 associations indicated with asterisks) and the variance inflation factors (VIF) for each
 1298 predictor included.

Response	Predictors, model statistics	Key feature or variable levels	Estimate	s.e.	t-value	P - value	VI F
----------	------------------------------------	-----------------------------------	----------	------	---------	-----------	---------

Deaner's G							
SS + LG + DB		Intercept	0.242	0.314	0.768	0.453	
N = 23							
Lambda = 0							
R ² = 0.383	Dominance vs social bonds	-0.495	0.375	-1.318	0.205	1.167	
F – statistic:							
4.937	Longevity	0.720	0.187	3.837	0.001	1.229	
P-value:							
0.022	Diet Breadth	-0.138	0.148	-0.931	0.365	1.066	
Reader's g							
SS + LG + DB		Intercept	-0.275	0.327	-0.841	0.409	
N = 27							
Lambda = 0							
R ² = 0.291	Dominance vs social bonds	0.337	0.243	0.774	0.447	1.285	
F – statistic:							
4.297							
P-value:							
0.016	Longevity	0.554	0.243	2.272	0.033	1.303	
	Diet Breadth	0.193	0.178	1.087	0.289	1.070	
Innovation							
SS + CS + LG + DB		Intercept	-0.199	0.238	-0.835	0.409	
N = 38							
Lambda = 0							
R ² = 0.491	Dominance vs social bonds	0.153	0.312	0.4903	0.627	1.688	
F – statistic:							
	Alloparental vs maternal	0.639	0.359	1.780	0.084.		

Mean Memory N = 39	SS + CS + LG + PF	Intercept	-0.195	0.363	-0.536			
	Lambda = 0 R ² = 0.213	Dominance vs social bonds	0.182	0.389	0.469		1.0 18	
		Alloparental vs maternal	0.091	0.376	0.244	0.808	1.4 06	
	F – statistic: 3.107	Longevity	0.531	0.192	2.762	0.010	1.4 06	
	P – value: 0.031	Percentage of fruit in the diet	0.126	0.148	0.853	0.401	1.3 02	
	Mean Self Control N = 18	SS + LG + DB	Intercept	-0.025	0.339	-0.075	0.941	
		Lambda = 0 R ² = 0.541	Dominance vs social bonds	0.197	0.411	0.480	0.640	1.2 50
Longevity			0.565	0.178	3.157	0.009	1.2 49	
F – statistic: 6.511	P-value: 0.008	Diet Breadth	0.249	0.165	1.502	0.161	1.1 10	



1300 **Figure 2.** The relation between maximum longevity and Deaner's G, Reader's g,
 1301 innovation, social learning, mean memory and mean self-control. The values that are
 1302 outliers according to Cook's distance are shown with a yellow dot in the graphs.

1303 Discussion

1304 Our analyses based on cognitive, social, ecological and life history data of 81 primate
 1305 species indicated life history as essential to the evolution of general cognition since the
 1306 majority of cognitive abilities we considered in the study are correlated. The general
 1307 cognitive measures, Deaner's G and Reader's, and the measures of innovation, social
 1308 learning, self-control and memory are correlated, except for social learning and memory.
 1309 This indicates that primates tend to perform similarly in distinct cognitive tasks, thus
 1310 supporting the idea of a general-domain cognition, in contrast to a modular or domain-
 1311 specific intelligence. Our results concur with recent findings in primate brain evolution,

1312 which seems to be driven by multiple, instead of specific, cognitive challenges (Shultz
1313 and Dunbar 2022). Deaner's G and Reader's g correlations to all the cognitive abilities
1314 measures, added to the multiple correlations found between cognitive variables, including
1315 group-level (i.e., social learning; some observations of innovation that include tactical
1316 deception; social learning and tactical deception tasks included in Reader's g) and
1317 individual-level (i.e., Deaner's G, most tasks included in Reader's g, several observations
1318 of innovation, memory and self-control) data, provides empirical support for the general
1319 cognition concept. The only exception, i.e., the lack of a correlation between social
1320 learning and memory measures, may indicate that the overall short-term memory
1321 evaluated in the tasks (maximum of 30 seconds of retention), or the type of task, may not
1322 be associated with the cognitive processes involved in conspecifics learning from each
1323 other. There is also the possibility that group-level advantages of (social) learning
1324 compete with the individual (memory) level advantages of learning, thus precluding a
1325 correlation. However, the quantification of memory in the wild, as well as the use of
1326 medium and long term-memory tasks, would be ideal to test whether this result is robust.

1327 Longevity was consistently correlated with the cognitive abilities considered in this study.
1328 Our results align with the cognitive buffer hypothesis (Deaner et al. 2003, Sol 2009),
1329 which posits that cultural learning and large brains, favoured by greater longevity, benefit
1330 survival and thus greater longevity itself. Behavioural plasticity and longevity seem to
1331 have indeed a correlated evolution (Ratikainen and Kokko 2019). Novel behavioural
1332 responses would increase survival in challenging and variable environments. The number
1333 of experiences and changes in the ecological and social environments that one individual
1334 can have and deal with is likely to increase with a longer lifetime. At the organism level,
1335 the idea that time is crucial for individual or social learning, for refinement of memory,
1336 self-control or general cognitive abilities through the experience of distinct and new

1337 conditions is reasonable, as is the idea of increased opportunity of transmission of
1338 acquired skills to offspring and conspecifics. Furthermore, our results concur with
1339 findings of interspecific studies evaluating the correlation of brain measures with
1340 longevity in mammals (González-Lagos et al. 2010) and primates (Barton and Capellini
1341 2011 – although not when the duration of maternal investment is taken into account), and
1342 with life history composite measure in primates (Navarrete et al. 2016); also, social
1343 learning was correlated to longevity 117 primate species (Street et al. 2017).

1344 Social structure did not correlate with cognitive abilities. We recognised alternative
1345 predictions for the expected difference between these social structures. Specifically, the
1346 differentiated relationships demanding recognition of conspecifics and their roles in the
1347 group, added to the higher probabilities of conflict of interest in dominance hierarchy
1348 species could demand higher cognitive abilities when compared to social bonding species
1349 (Bergman and Beehner 2015, Kappeler 2019). Alternatively, it's possible that simple
1350 rules mediate the hierarchical relationships (Hobson et al. 2021), reducing the uncertainty
1351 about conflicts in species with dominance relationships, which would experience less
1352 cognitive demands than the more unpredictable relationships in social bonds species.
1353 Therefore, it is possible that the absence of cognitive differences between these two
1354 categories of social structure is because both types of relationships are similarly
1355 demanding in their specific cognitive challenges.

1356 Additionally, distinct social structures could emerge from simple rules driving foraging
1357 decisions, without the demand for distinct cognitive skills (Boyer and Ramos-Fernandez
1358 2018). However, the measure we considered is a simple one that could not capture all the
1359 intricacies of group structures, such as variations in cohesiveness and diversity of social
1360 relationships. This can be one reason why our results do not support the social intelligence
1361 hypothesis. The fact that several studies founding support for the social intelligence

1362 hypothesis use brain measures (Kudo and Dunbar 2001, Burish et al. 2004, Shultz and
1363 Dunbar 2006, Pérez-Barbería et al. 2007) and that the brain is not the only responsible for
1364 cognitive performances (which we evaluate) is an alternative explanation for the differing
1365 results from our predictions.

1366 Another aspect that can influence the investigation of the relationship between cognitive
1367 ability and social structure is the interlacing between the scale of the variables and the
1368 availability of measures. Our social measure is at the group level while the cognitive
1369 measures are mainly at the individual level. Our hypotheses consider the point of view of
1370 the individuals within the group, but while we can only presume the nature of their
1371 perceptions of socioenvironmental complexities (Aureli and Schino 2019, Hobson et al.
1372 2019), group-level metrics can fail to reflect the information-processing challenges faced
1373 by individuals within their groups. Probably due to the greater difficulty in collecting
1374 behavioural data in the field, studies generally collect cognitive data from captive
1375 individuals that are kept in groups of various sizes. Considering that individuals'
1376 development within a particular group size and structure may influence their cognitive
1377 performance (Ashton et al. 2018, Testard et al. 2022), ontogenetic factors may also
1378 confound attempts to test the social intelligence hypothesis (Boogert et al. 2018).

1379 Similar to our social structure results, variation in the care systems was not associated
1380 with any cognitive ability we considered. This imply that maternal, biparental or
1381 alloparental care in primates may be equally cognitively demanding within their distinct
1382 contexts. Several issues with the prediction that variation in the care system would lead
1383 to variation in cognitive abilities are raised by Thornton and McAuliffe (2015). Through
1384 a detailed review, they argue that there is no empirical evidence, nor are there theoretical
1385 reasons, for expecting this relationship, since the cognitive traits proposed as important
1386 for the relationship (i.e., prosociality, coordination, social learning and teaching) are not

1387 especially found or increased in cooperative breeders. Consistent with ours results,
1388 reproductive cooperation (which consider allomothering, cooperative breeding, paternal
1389 care and collective action) was not correlated to brain measures in primates (Shultz and
1390 Dunbar 2022).

1391 The diet accessed by primate species should influence their cognitive abilities and brain
1392 measures, due to extractive foraging demands of certain food types, such as fruits and
1393 seeds, the memory needed to deal with food spatial and temporal information, and energy
1394 necessary for brain growth (MacLean et al. 2014, DeCasien et al. 2017, Shultz and
1395 Dunbar 2022). However, we did not find evidence for the relationship between the
1396 cognitive measures considered here and diet breadth or percentage of fruit in the diet. Our
1397 result agrees with the lack of relationship between cognitive abilities and the percentage
1398 of fruit in the diet, but contrasted with the self-control association with diet breadth found
1399 by MacLean et al. (2014). One possibility to explain this difference in results is that we
1400 added some primate species to the dataset of self-control and we considered distinct
1401 variables in our models. It is possible that the inclusion of longevity in the model, which
1402 here was correlated to all cognitive measures, has some influence that was not taken into
1403 account in the diet breadth-self-control relationship found in MacLean et al. (2014).

1404 Within our results, only one diverged from the main trend of the lack of association with
1405 diet breadth: the Reader's g measure was correlated with diet breadth when we excluded
1406 three highly influential points (i.e., species) from the data. But given the majority of our
1407 results to the contrary, the main response seems to be more robust than this contrasting
1408 one. We do not believe that our results imply discarding diet features as relevant to the
1409 evolution of cognition. However, recognising other aspects of the diet, such as measures
1410 that consider the metabolic quality over the quantity of the dietary items, could be a more
1411 fruitful focus of future investigations. Also, it seems advisable to investigate if the

1412 response we found is maintained for more representative samples of primates and
1413 cognitive abilities or for the frugivory since these data were limited in our dataset.

1414 *Some things to crave, some things to chase in our field*

1415 Anyone aiming to test the social or ecological intelligence hypotheses must consider a
1416 myriad of potentially important variables. Our process of searching and categorising the
1417 primary research literature brought into light some gaps in the cognitive, social and
1418 ecological data available. Beyond restriction in the variables' data availability, we also
1419 faced taxonomic data constraints. Although the social intelligence hypothesis has been
1420 originally put forward to explain primates' relatively large brain size, it can arguably
1421 apply to other taxa, as long as there is interspecific variation in social behavioural
1422 complexity and in the cognitive demands to deal with the challenges imposed by sociality.
1423 We intended to focus our comparative study on mammal species in general, so we could
1424 test the social intelligence hypothesis on a greater breadth of taxa, and compare primates
1425 and other mammals in terms of their cognitive abilities. We were able to include only
1426 primates instead because there was not enough data available for other mammal species.

1427 Therefore, sharing the compilations we made during the development of this study can
1428 guide future research efforts to the missing information. We identified several cognitive
1429 measures belonging to different general categories or domains of cognition, such as
1430 associative learning, discrimination learning, spatial learning, procedural learning and
1431 abstract learning (Supplementary material 5 comprises our compilation of the cognitive
1432 information from the studies found in our first search, including the general categories of
1433 cognition, their tasks and respective meanings and references). However, from our
1434 searches, we were able to include (yet with relatively small samples) in the present study
1435 only cognitive measures of innovation, social learning, inhibition and memory as well as

1436 two general-domain measures (SM1). Besides independent research efforts comprising
1437 the understudied aforementioned cognitive measures, we would like to encourage further
1438 joint efforts of researchers interested in evolutionary questions regarding similar
1439 cognitive processes. One good example is the “Many Primates” initiative
1440 (<https://manyprimates.github.io>), which involves independent researchers'
1441 collaborations, including the collection and sharing of cognitive performance data from
1442 primate species. Resources and access to collect animal behavioural data are often
1443 limited, but if researchers of different institutions are able to measure cognition (and other
1444 behaviours) in a coordinated and standardised way, our knowledge about species patterns
1445 and about similarities and differences between species can be substantially amplified.

1446 We further identified distinct social, ecological and life history variables we intended to
1447 add in the analyses as interspecific predictors of cognitive abilities and could not due to
1448 data not being available. These potential predictors are compiled in Table 2, which
1449 exhibits the predictions of the relationship with cognition, their associated rationale and
1450 references. Beyond the predictors included in our study, Table 2 also include social
1451 structure and organisation variables, such as intragroup kinship, relational complexity,
1452 the existence of fission-fusion dynamics and group size. It also included other factors,
1453 such as diet diversity and body size. From the 12 predictors compiled in Table 2, our
1454 analyses included only 3 to 4, due to the lack of available data or because we chose
1455 variables considered more important since our sample size of cognitive variables was also
1456 limited thus restricting the inclusion of predictors in the analyses.

1457 **Table 2.** Compilation of possible social, ecological and life-history predictors of
1458 cognitive abilities, including the expected relationships, respective rationale and
1459 reference.

PREDICTORS (measures)	PREDICTION	RATIONALE and REFERENCE
Average kinship (mean by species)	Negative relationship	High intragroup kinship associated with more stability and should be less cognitively demanding than low kinship - Lukas and Clutton-Brock (2018)
Relational complexity (rate by species based on the presence or absence of the three traits dominance hierarchy, coalition formation and rate of aggression above mammalian average)	Positive relationship	Higher relational complexity associated with less stability and should be more cognitively demanding than low relational complexity - Lukas and Clutton-Brock (2018)
Fission-fusion (presence or absence)	Presence of fission-fusion associated with higher cognitive abilities	Fission-fusion dynamics tend to be associated with less stability/cohesion and this should be more cognitively demanding - Aureli et al. (2008)
Group size (mean by species)	Positive relationship	Larger group sizes increase the probability of more differentiated relationships and less stability/cohesion and should be more cognitively demanding. Also, increases in number of relationships should increase information-processing demands. Furthermore, larger group sizes are associated with lower intra-group kinship. - Bergman and Beehner (2015), Dunbar (1998), Dyble and Clutton-Brock (2020).
Social structure (categorical: social bonds, dominance hierarchy)	Dominance hierarchy and social bonding species differ in cognitive abilities	Dominance relationships would promote more differentiated relationships and more conflict of interest in comparison with social bonding species and should be more cognitively demanding - Bergman and Beehner (2015), Kappeler (2019), MacLean et al. (2008). Alternatively, dominance relationships could

		reduce uncertainty about conflicts and could be less cognitively demanding.
Care system (categorical: maternal, biparental, alloparental)	Biparental and alloparental care associated with higher cognitive abilities than maternal care	Biparental and alloparental care require management of intimate coordination and synchrony and should be more cognitively demanding than maternal care (Burkart and van Schaik 2010; but see Thornton and McAuliffe 2015)
Mating system (categorical: monogamous, polygynous, polyandrous, promiscuous)	Promiscuous associated with higher cognitive abilities, or monogamous associated with higher cognitive abilities	Promiscuous species have more interactions and relationships between more individuals and could be more cognitively demanding, or monogamous species require bond maintenance and could be more cognitively demanding - Shultz and Dunbar (2007), Schillaci (2006).
Body size (mean by species)	Positive relationship	Possible confounding variable, since there is evidence of positive association between body size and brain size (and brain size can be associated with cognitive abilities) - Wartel et al. (2019).
Longevity (maximum value by species)	Positive relationship	Positive association with brain size (which can be associated with cognitive abilities) - González-Lagos et al. (2010), Bergman and Beehner (2015). Longer life history can favour and be favoured by cognitive abilities and they possibly co-evolve – Deaner et al. 2003, Sol 2009.
Percentage fruit in diet (mean by species)	Positive relationship	Fruits are less temporally and spatially predictable than leaves and should be more cognitively demanding to acquire - DeCasien et al. (2017).

Diet breadth (number of types of dietary items)	Positive relationship	Diet breadth could be a metabolic facilitator of the evolution of cognition - MacLean et al. (2014).
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Diet diversity (categories: folivore, folivore/frugivore, frugivore, gummivore, insectivore/frugivore, omnivore)	Folivore species associated with lower cognitive abilities than other categories	Leaves are more predictable temporally and spatially than other resources and should be less cognitively demanding to acquire - DeCasien et al. (2017).
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1460 Thus, our data collection revealed missing information, which we consider fruitful
 1461 avenues to focus on gathering data in future studies. We presented the content we
 1462 accessed and compiled through our study highlighting the missing content we identified,
 1463 but we are far from deeper theoretical and methodological insights, such as those found
 1464 in reviews approaching challenges concerning the studies focused on the evolution of
 1465 cognition (Thornton and Lukas 2012, Morand-Ferron et al. 2016, Logan et al. 2018) and
 1466 social cognition (Thornton and Clutton-Brock 2011). Nonetheless, based on our
 1467 compilations (SM5 and Table 2), we suggest that our field will benefit from more
 1468 representative datasets, including a higher diversity of species and taxonomic groups, and
 1469 collecting currently lacking data on social, ecological, life history predictors and
 1470 potentially confounding variables, and behavioural cognitive response variables. We
 1471 should also focus on the systematic and standardised collection of laboratory and field
 1472 data through the coordinated collection in distinct research groups, supporting existing
 1473 initiatives like Many Primates, and creating similar ones for other taxa. This would reduce
 1474 heterogeneity and increase the representativeness, reliability and elucidative potential of
 1475 interspecific studies.

1476 Future cognitive studies should also focus on the repeatability of cognitive tests, have
 1477 clarity about the cognitive processes of interest and their ecological importance and

1478 heritability, and consider the contextual and ontogenetic factors potentially influencing
1479 the abilities (Thornton et al. 2014, Boogert et al. 2018). Furthermore, our study highlights
1480 a general cognition tendency in primates and its connection with longevity. But it is
1481 noteworthy that our analyses do not allow inference of causality or direction of the
1482 relationship. It is likely that longevity and cognitive abilities influence each other and co-
1483 evolve. This is one more question that interdisciplinary efforts from behavioural ecology,
1484 evolutionary ecology and cognition fields can tackle.

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1771 **Supplementary Material (SM 1, 2, 3, 4 and 5)**

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1773 SM1. Study dataset.

Cognitive measure	Species	Identified homotypic synonym	Family	Cognition value	Social Structure (SS)	Care System (CS)	Longevity (LG)	Diet Breadth (DB)
Deaner G	<i>Aotus azarae</i>	na	Aotidae	-0.34	social bonds	biparental	360	7
Deaner G	<i>Ateles fusciceps</i>	na	Atelidae	1.28	social bonds	maternal	288	2
Deaner G	<i>Callithrix jacchus</i>	na	Callitrichidae	-1.22	social bonds	alloparental	201.6	5
Deaner G	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	0.19	dominance relationships	alloparental	541.2	7
Deaner G	<i>Cercocebus atys</i>	na	Cercopithecidae	0.25	dominance relationships	maternal	321.6	5
Deaner G	<i>Cercopithecus diana</i>	na	Cercopithecidae	0.39	dominance relationships	maternal	447.6	3
Deaner G	<i>Eulemur macaco</i>	na	Lemuridae	-0.47	dominance relationships	maternal	360	4
Deaner G	<i>Galago senegalensis</i>	na	Lorisidae	-0.86	dominance relationships	maternal	204	3
Deaner G	<i>Gorilla gorilla</i>	na	Hominidae	0.96	dominance relationships	maternal	648	3
Deaner G	<i>Hylobates lar</i>	na	Hylobatidae	0.11	social bonds	maternal	480	4
Deaner G	<i>Lagothrix lagotricha</i>	na	Atelidae	0.12	dominance relationships	maternal	360	4
Deaner G	<i>Lemur catta</i>	na	Lemuridae	-0.75	dominance relationships	maternal	360	4
Deaner G	<i>Macaca mulatta</i>	na	Cercopithecidae	0.55	dominance relationships	maternal	432	1
Deaner G	<i>Mandrillus sphinx</i>	na	Cercopithecidae	0.43	dominance relationships	maternal	555.96	4
Deaner G	<i>Microcebus murinus</i>	na	Cheirogaleidae	-0.96	dominance relationships	maternal	186	5
Deaner G	<i>Miopithecus talapoin</i>	na	Cercopithecidae	-1.53	dominance relationships	maternal	370.8	3
Deaner G	<i>Pan troglodytes</i>	na	Hominidae	1.66	dominance relationships	maternal	720	6
Deaner G	<i>Papio anubis</i>	na	Cercopithecidae	0	dominance relationships	alloparental	450	6

Deaner G	<i>Phaner furcifer</i>	na	Cheirogaleidae	-0.62	social bonds	maternal	144	3
Deaner G	<i>Pongo abelii</i>	na	Hominidae	1.75	social bonds	maternal	696	5
Deaner G	<i>Presbytis comata</i>	na	Cercopithecidae	0.76	social bonds	maternal	144	4
Deaner G	<i>Saimiri sciureus</i>	na	Cebidae	-0.94	dominance relationships	maternal	324	3
Deaner G	<i>Varecia rubra</i>	na	Lemuridae	-0.35	social bonds	maternal	240	3
Reader G	<i>Alouatta seniculus</i>	na	Atelidae	-0.07	dominance relationships	maternal	300	6
Reader G	<i>Aotus azarae</i>	na	Aotidae	-1.17	social bonds	biparental	360	7
Reader G	<i>Ateles fusciceps</i>	na	Atelidae	-0.63	social bonds	maternal	288	2
Reader G	<i>Callithrix jacchus</i>	na	Callitrichidae	-0.85	social bonds	alloparental	201.6	5
Reader G	<i>Callithrix pygmaea</i>	<i>Cebuella pygmaea</i>	Callitrichidae	-0.65	social bonds	alloparental	181.2	4
Reader G	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	1.45	dominance relationships	alloparental	541.2	7
Reader G	<i>Cercocebus atys</i>	na	Cercopithecidae	-0.38	dominance relationships	maternal	321.6	5
Reader G	<i>Cercopithecus diana</i>	na	Cercopithecidae	0.13	dominance relationships	maternal	447.6	3
Reader G	<i>Colobus guereza</i>	na	Cercopithecidae	-0.65	dominance relationships	maternal	294	2
Reader G	<i>Erythrocebus patas</i>	na	Cercopithecidae	0.37	social bonds	maternal	286.8	4
Reader G	<i>Eulemur macaco</i>	na	Lemuridae	-0.68	dominance relationships	maternal	360	4
Reader G	<i>Gorilla gorilla</i>	na	Hominidae	0.9	dominance relationships	maternal	648	3
Reader G	<i>Hylobates lar</i>	na	Hylobatidae	-0.75	social bonds	maternal	480	4
Reader G	<i>Lemur catta</i>	na	Lemuridae	-0.77	dominance relationships	maternal	360	4
Reader G	<i>Leontopithecus rosalia</i>	na	Callitrichidae	-1.33	social bonds	alloparental	297.6	3
Reader G	<i>Loris tardigradus</i>	na	Lorisidae	-0.32	social bonds	maternal	196.8	4
Reader G	<i>Macaca mulatta</i>	na	Cercopithecidae	1.6	dominance relationships	maternal	432	1
Reader G	<i>Mandrillus sphinx</i>	na	Cercopithecidae	-0.53	dominance relationships	maternal	555.96	4

Reader G	<i>Otolemur crassicaudatus</i>	na	Lorisidae	0.08	social bonds	maternal	225.6	5
Reader G	<i>Pan troglodytes</i>	na	Hominidae	2.83	dominance relationships	maternal	720	6
Reader G	<i>Papio anubis</i>	na	Cercopithecidae	1.8	dominance relationships	alloparental	450	6
Reader G	<i>Pongo abelii</i>	na	Hominidae	1.73	social bonds	maternal	696	5
Reader G	<i>Presbytis comata</i>	na	Cercopithecidae	-0.07	social bonds	maternal	144	4
Reader G	<i>Propithecus verreauxi</i>	na	Indriidae	-1	dominance relationships	biparental	247.2	3
Reader G	<i>Saguinus oedipus</i>	na	Callitrichidae	0.4	dominance relationships	alloparental	277.2	4
Reader G	<i>Saimiri sciureus</i>	na	Cebidae	-0.78	dominance relationships	maternal	324	3
Reader G	<i>Theropithecus gelada</i>	na	Cercopithecidae	-0.4	dominance relationships	maternal	336	2
Innovation	<i>Alouatta caraya</i>	na	Atelidae	1	social bonds	maternal	243.6	3
Innovation	<i>Alouatta seniculus</i>	na	Atelidae	4	dominance relationships	maternal	300	6
Innovation	<i>Callimico goeldii</i>	na	Callitrichidae	1	social bonds	alloparental	214.8	2
Innovation	<i>Callithrix jacchus</i>	na	Callitrichidae	1	social bonds	alloparental	201.6	5
Innovation	<i>Callithrix pygmaea</i>	<i>Cebuella pygmaea</i>	Callitrichidae	1	social bonds	alloparental	181.2	4
Innovation	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	39	dominance relationships	alloparental	541.2	7
Innovation	<i>Cebus capucinus</i>	na	Cebidae	4	dominance relationships	maternal	657.6	4
Innovation	<i>Cebus olivaceus</i>	na	Cebidae	4	dominance relationships	maternal	492	4
Innovation	<i>Cercopithecus ascanius</i>	na	Cercopithecidae	1	dominance relationships	maternal	339.6	4
Innovation	<i>Cercopithecus mitis</i>	na	Cercopithecidae	4	dominance relationships	maternal	325.2	4
Innovation	<i>Chiropotes satanas</i>	na	Pitheciidae	2	social bonds	maternal	216	3
Innovation	<i>Chlorocebus aethiops</i>	na	Cercopithecidae	4	dominance relationships	maternal	379.2	2
Innovation	<i>Colobus guereza</i>	na	Cercopithecidae	1	dominance relationships	maternal	294	2

Innovation	<i>Erythrocebus patas</i>	na	Cercopithecidae	1	social bonds	maternal	286.8	4
Innovation	<i>Eulemur fulvus</i>	na	Lemuridae	3	dominance relationships	maternal	444	3
Innovation	<i>Eulemur macaco</i>	na	Lemuridae	1	dominance relationships	maternal	360	4
Innovation	<i>Eulemur mongoz</i>	na	Lemuridae	1	dominance relationships	maternal	360	4
Innovation	<i>Gorilla gorilla</i>	na	Hominidae	25	dominance relationships	maternal	648	3
Innovation	<i>Hylobates pileatus</i>	na	Hylobatidae	1	social bonds	maternal	432	5
Innovation	<i>Lemur catta</i>	na	Lemuridae	2	dominance relationships	maternal	360	4
Innovation	<i>Leontopithecus chrysomelas</i>	na	Callitrichidae	1	social bonds	maternal	255.6	3
Innovation	<i>Loris tardigradus</i>	na	Lorisidae	1	social bonds	maternal	196.8	4
Innovation	<i>Macaca arctoides</i>	na	Cercopithecidae	1	dominance relationships	maternal	360	1
Innovation	<i>Macaca fascicularis</i>	na	Cercopithecidae	7	dominance relationships	maternal	456	3
Innovation	<i>Macaca fuscata</i>	na	Cercopithecidae	26	dominance relationships	biparental	396	5
Innovation	<i>Macaca mulatta</i>	na	Cercopithecidae	5	dominance relationships	maternal	432	1
Innovation	<i>Macaca nemestrina</i>	na	Cercopithecidae	1	dominance relationships	maternal	411.6	4
Innovation	<i>Macaca radiata</i>	na	Cercopithecidae	2	social bonds	maternal	360	6
Innovation	<i>Macaca silenus</i>	na	Cercopithecidae	1	dominance relationships	maternal	480	4
Innovation	<i>Otolemur crassicaudatus</i>	na	Lorisidae	2	social bonds	maternal	225.6	5
Innovation	<i>Pan paniscus</i>	na	Hominidae	10	dominance relationships	maternal	576	6
Innovation	<i>Pan troglodytes</i>	na	Hominidae	321	dominance relationships	maternal	720	6
Innovation	<i>Papio anubis</i>	na	Cercopithecidae	12	dominance relationships	alloparental	450	6

Innovation	<i>Papio hamadryas</i>	na	Cercopithecidae	6	social bonds	maternal	540	2
Innovation	<i>Papio ursinus</i>	na	Cercopithecidae	4	dominance relationships	biparental	540	6
Innovation	<i>Pongo pygmaeus</i>	na	Hominidae	53	dominance relationships	maternal	720	5
Innovation	<i>Rhinopithecus roxellana</i>	<i>Pygathrix roxellana</i>	Cercopithecidae	1	social bonds	maternal	354	4
Innovation	<i>Saguinus mystax</i>	na	Callitrichidae	4	social bonds	alloparental	240	5
Innovation	<i>Saimiri sciureus</i>	na	Cebidae	3	dominance relationships	maternal	324	3
Innovation	<i>Semnopithecus entellus</i>	na	Cercopithecidae	7	dominance relationships	maternal	300	2
Social Learning	<i>Alouatta palliata</i>	na	Atelidae	3	dominance relationships	maternal	300	2
Social Learning	<i>Ateles geoffroyi</i>	na	Atelidae	2	social bonds	maternal	327.6	2
Social Learning	<i>Callithrix jacchus</i>	na	Callitrichidae	2	social bonds	alloparental	201.6	5
Social Learning	<i>Cebus albifrons</i>	na	Cebidae	1	dominance relationships	alloparental	528	5
Social Learning	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	17	dominance relationships	alloparental	541.2	7
Social Learning	<i>Cebus capucinus</i>	na	Cebidae	5	dominance relationships	maternal	657.6	4
Social Learning	<i>Cercocebus torquatus</i>	na	Cercopithecidae	1	social bonds	maternal	360	1
Social Learning	<i>Cercopithecus ascanius</i>	na	Cercopithecidae	1	dominance relationships	maternal	339.6	4
Social Learning	<i>Cercopithecus diana</i>	na	Cercopithecidae	1	dominance relationships	maternal	447.6	3
Social Learning	<i>Chlorocebus aethiops</i>	na	Cercopithecidae	5	dominance relationships	maternal	379.2	2
Social Learning	<i>Erythrocebus patas</i>	na	Cercopithecidae	2	social bonds	maternal	286.8	4
Social Learning	<i>Eulemur fulvus</i>	na	Lemuridae	1	dominance relationships	maternal	444	3
Social Learning	<i>Gorilla gorilla</i>	na	Hominidae	13	dominance relationships	maternal	648	3
Social Learning	<i>Lemur catta</i>	na	Lemuridae	4	dominance relationships	maternal	360	4

Social Learning	<i>Macaca arctoides</i>	na	Cercopithecidae	1	dominance relationships	maternal	360	1
Social Learning	<i>Macaca fascicularis</i>	na	Cercopithecidae	7	dominance relationships	maternal	456	3
Social Learning	<i>Macaca mulatta</i>	na	Cercopithecidae	15	dominance relationships	maternal	432	1
Social Learning	<i>Macaca nemestrina</i>	na	Cercopithecidae	3	dominance relationships	maternal	411.6	4
Social Learning	<i>Macaca silenus</i>	na	Cercopithecidae	1	dominance relationships	maternal	480	4
Social Learning	<i>Mandrillus sphinx</i>	na	Cercopithecidae	3	dominance relationships	maternal	555.96	4
Social Learning	<i>Otolemur crassicaudatus</i>	na	Lorisidae	1	social bonds	maternal	225.6	5
Social Learning	<i>Pan paniscus</i>	na	Hominidae	5	dominance relationships	maternal	576	6
Social Learning	<i>Pan troglodytes</i>	na	Hominidae	214	dominance relationships	maternal	720	6
Social Learning	<i>Papio anubis</i>	na	Cercopithecidae	4	dominance relationships	alloparental	450	6
Social Learning	<i>Papio hamadryas</i>	na	Cercopithecidae	1	social bonds	maternal	540	2
Social Learning	<i>Pongo pygmaeus</i>	na	Hominidae	86	dominance relationships	maternal	720	5
Social Learning	<i>Saguinus labiatus</i>	na	Callitrichidae	2	social bonds	alloparental	246	3
Social Learning	<i>Saimiri sciureus</i>	na	Cebidae	1	dominance relationships	maternal	324	3
Social Learning	<i>Semnopithecus entellus</i>	na	Cercopithecidae	2	dominance relationships	maternal	300	2
Mean Memory	<i>Allenopithecus nigroviridis</i>	na	Cercopithecidae	58.3	social bonds	maternal	276	3
Mean Memory	<i>Ateles chamek</i>	na	Atelidae	37	dominance relationships	maternal	576	4
Mean Memory	<i>Callithrix jacchus</i>	na	Callitrichidae	43.77	social bonds	alloparental	201.6	5
Mean Memory	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	62.97	dominance relationships	alloparental	541.2	7
Mean Memory	<i>Cebus capucinus</i>	na	Cebidae	45.1	dominance relationships	maternal	657.6	4

Mean Memory	<i>Cercopithecus diana</i>	na	Cercopithecidae	76.07	dominance relationships	maternal	447.6	3
Mean Memory	<i>Cercopithecus hamlyni</i>	na	Cercopithecidae	57.4	dominance relationships	maternal	324	2
Mean Memory	<i>Chlorocebus sabaesus</i>	na	Cercopithecidae	76.37	dominance relationships	maternal	156	4
Mean Memory	<i>Colobus polykomos</i>	na	Cercopithecidae	29.6	dominance relationships	maternal	366	2
Mean Memory	<i>Eulemur coronatus</i>	na	Lemuridae	40.43	dominance relationships	maternal	220.8	4
Mean Memory	<i>Eulemur fulvus</i>	na	Lemuridae	53.22	dominance relationships	maternal	444	3
Mean Memory	<i>Eulemur macaco</i>	na	Lemuridae	74.97	dominance relationships	maternal	360	4
Mean Memory	<i>Eulemur mongoz</i>	na	Lemuridae	36.9	dominance relationships	maternal	360	4
Mean Memory	<i>Gorilla gorilla</i>	na	Hominidae	77.63	dominance relationships	maternal	648	3
Mean Memory	<i>Hylobates lar</i>	na	Hylobatidae	63.87	social bonds	maternal	480	4
Mean Memory	<i>Hylobates moloch</i>	na	Hylobatidae	51.83	social bonds	maternal	540	4
Mean Memory	<i>Hylobates muelleri</i>	na	Hylobatidae	55.5	social bonds	maternal	348	4
Mean Memory	<i>Lagothrix lagotricha</i>	na	Atelidae	53.67	dominance relationships	maternal	360	4
Mean Memory	<i>Lemur catta</i>	na	Lemuridae	44.7	dominance relationships	maternal	360	4
Mean Memory	<i>Leontopithecus rosalia</i>	na	Callitrichidae	44.4	social bonds	alloparental	297.6	3
Mean Memory	<i>Macaca fascicularis</i>	na	Cercopithecidae	58.67	dominance relationships	maternal	456	3
Mean Memory	<i>Macaca mulatta</i>	na	Cercopithecidae	61.03	dominance relationships	maternal	432	1
Mean Memory	<i>Macaca silenus</i>	na	Cercopithecidae	70.8	dominance relationships	maternal	480	4
Mean Memory	<i>Macaca sylvanus</i>	na	Cercopithecidae	55.74	dominance relationships	alloparental	264	6
Mean Memory	<i>Nomascus leucogenys</i>	<i>Hylobates leucogenys</i>	Hylobatidae	51.8	dominance relationships	maternal	529.2	4

Mean Memory	<i>Pan paniscus</i>	na	Hominidae	81.46	dominance relationships	maternal	576	6
Mean Memory	<i>Pan troglodytes</i>	na	Hominidae	84.1	dominance relationships	maternal	720	6
Mean Memory	<i>Papio anubis</i>	na	Cercopithecidae	50.43	dominance relationships	alloparental	450	6
Mean Memory	<i>Pongo abelii</i>	na	Hominidae	96	social bonds	maternal	696	5
Mean Memory	<i>Pongo pygmaeus</i>	na	Hominidae	65.5	dominance relationships	maternal	720	5
Mean Memory	<i>Propithecus coquereli</i>	na	Indriidae	45.17	dominance relationships	maternal	360	4
Mean Memory	<i>Saguinus imperator</i>	na	Callitrichidae	44.4	dominance relationships	alloparental	242.4	2
Mean Memory	<i>Saguinus midas</i>	na	Callitrichidae	52.73	dominance relationships	alloparental	184.8	4
Mean Memory	<i>Saimiri sciureus</i>	na	Cebidae	46.17	dominance relationships	maternal	324	3
Mean Memory	<i>Symphalangus syndactylus</i>	<i>Hylobates syndactylus</i>	Hylobatidae	62	dominance relationships	maternal	456	4
Mean Memory	<i>Trachypitecus auratus</i>	na	Cercopithecidae	46.93	dominance relationships	alloparental	373.2	5
Mean Memory	<i>Trachypitecus francoisi</i>	na	Cercopithecidae	49.6	dominance relationships	alloparental	315.6	3
Mean Memory	<i>Varecia rubra</i>	na	Lemuridae	41.13	social bonds	maternal	240	3
Mean Memory	<i>Varecia variegata</i>	na	Lemuridae	52	social bonds	maternal	384	4
Mean Self Control	<i>Callithrix jacchus</i>	na	Callitrichidae	46	social bonds	alloparental	201.6	5
Mean Self Control	<i>Cebus apella</i>	<i>Sapajus apella</i>	Cebidae	91.1	dominance relationships	alloparental	541.2	7
Mean Self Control	<i>Eulemur macaco</i>	na	Lemuridae	55.5	dominance relationships	maternal	360	4
Mean Self Control	<i>Eulemur mongoz</i>	na	Lemuridae	54.5	dominance relationships	maternal	360	4
Mean Self Control	<i>Gorilla gorilla</i>	na	Hominidae	97.2	dominance relationships	maternal	648	3
Mean Self Control	<i>Bunopithecus hoolock</i>	<i>Hylobates hoolock/Hoolock leuconedys</i>	Hylobatidae	69	social bonds	alloparental	300	4

Mean Self Control	<i>Lemur catta</i>	na	Lemuridae	54	dominance relationships	maternal	360	4
Mean Self Control	<i>Nomascus leucogenys</i>	<i>Hylobates leucogenys</i>	Hylobatidae	31	dominance relationships	maternal	529.2	4
Mean Self Control	<i>Pan paniscus</i>	na	Hominidae	97.5	dominance relationships	maternal	576	6
Mean Self Control	<i>Pan troglodytes</i>	na	Hominidae	93.3	dominance relationships	maternal	720	6
Mean Self Control	<i>Papio anubis</i>	na	Cercopithecidae	88.1	dominance relationships	alloparental	450	6
Mean Self Control	<i>Papio hamadryas</i>	na	Cercopithecidae	65.7	social bonds	maternal	540	2
Mean Self Control	<i>Pongo pygmaeus</i>	na	Hominidae	95.4	dominance relationships	maternal	720	5
Mean Self Control	<i>Propithecus coquereli</i>	na	Indriidae	33.2	dominance relationships	maternal	360	4
Mean Self Control	<i>Rhinopithecus roxellana</i>	<i>Pygathrix roxellana</i>	Cercopithecidae	45.3	social bonds	maternal	354	4
Mean Self Control	<i>Saimiri sciureus</i>	na	Cebidae	24.7	dominance relationships	maternal	324	3
Mean Self Control	<i>Trachypithecus francoisi</i>	na	Cercopithecidae	68.4	dominance relationships	alloparental	315.6	3
Mean Self Control	<i>Varecia variegata</i>	na	Lemuridae	39.8	social bonds	maternal	384	4

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1776 **SM2.** Phylogenies of species included in the tested models predicting cognitive abilities.

1777 Deaneer's G (a), Reader's g (b), Innovation (c), Social learning (d), Mean memory (e) and

1778 Mean self-control (f) phylogenies and value of cognition for each species.

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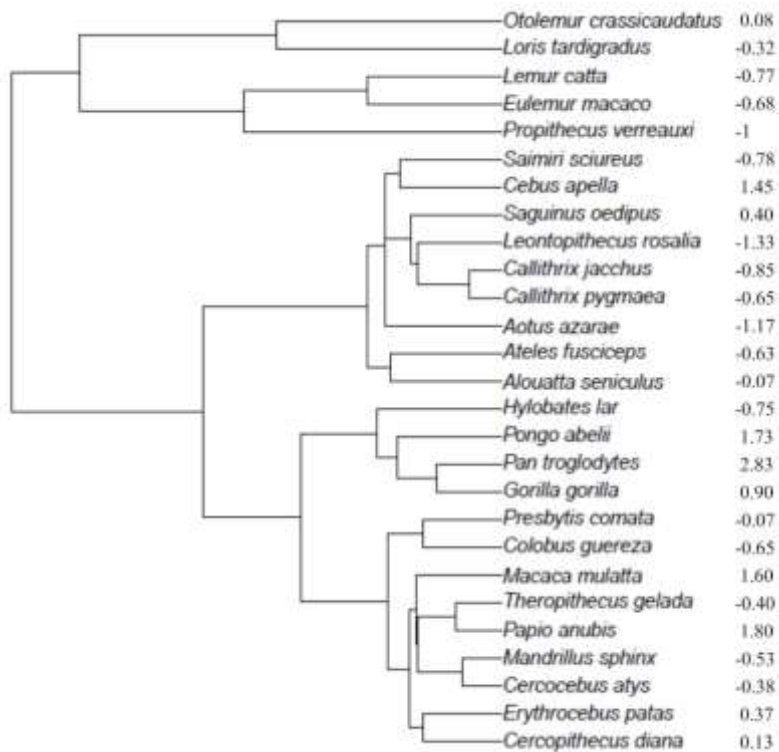
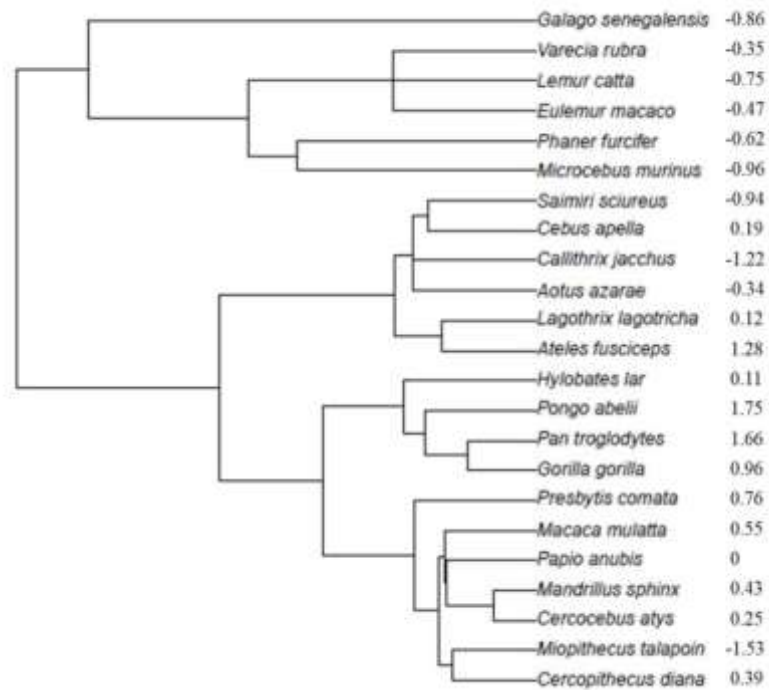
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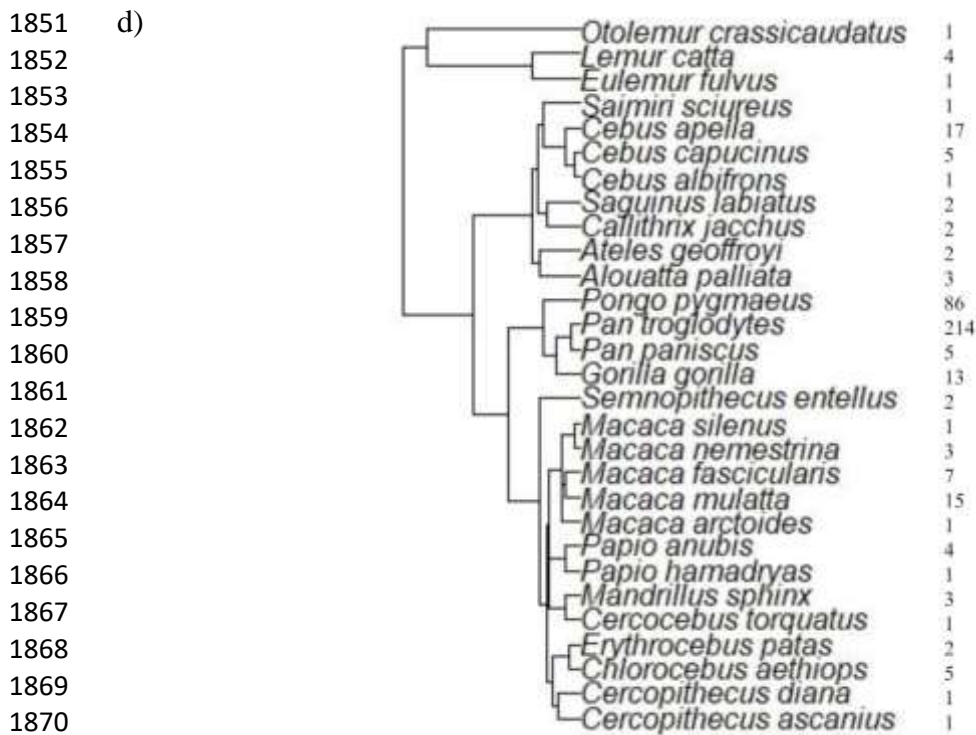
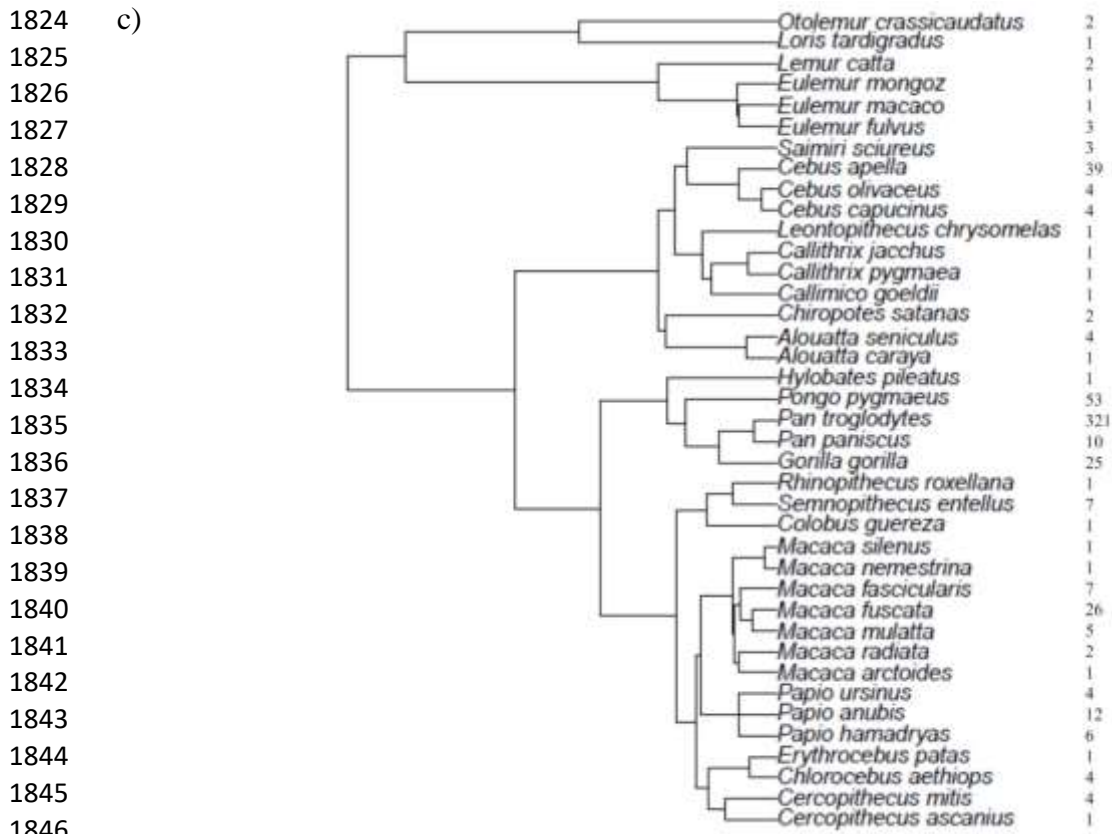
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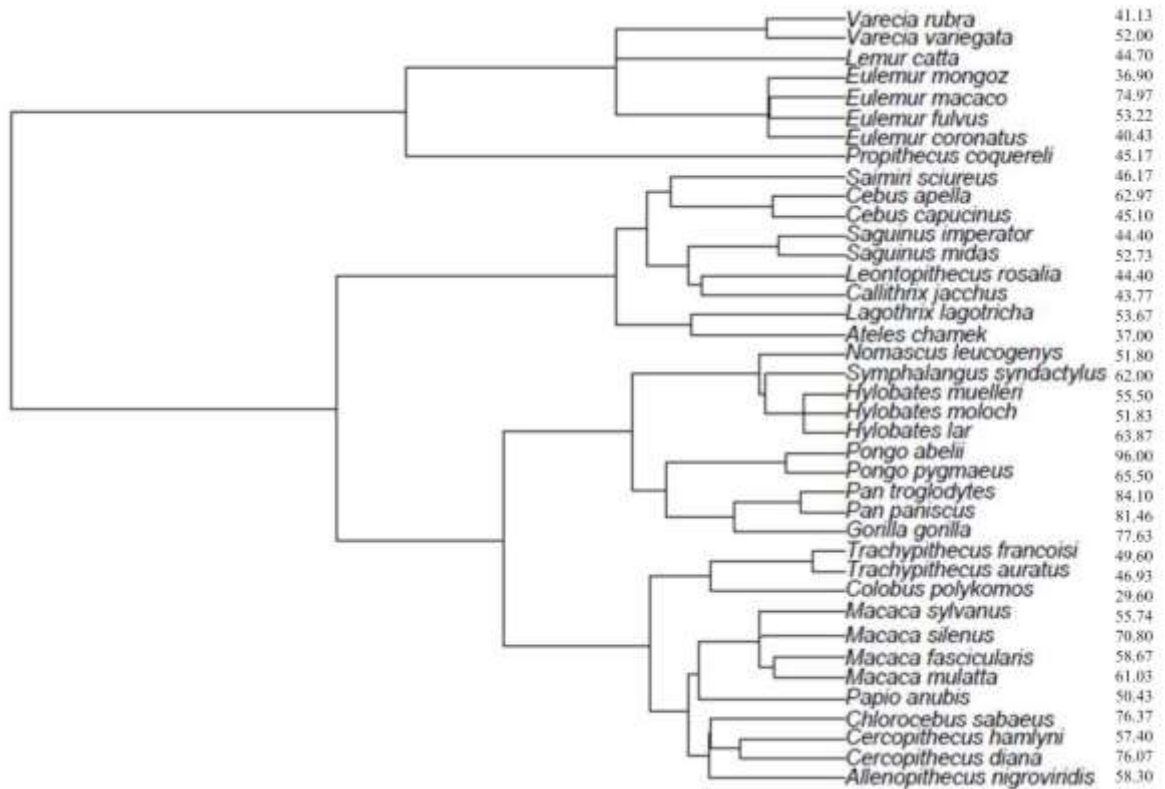


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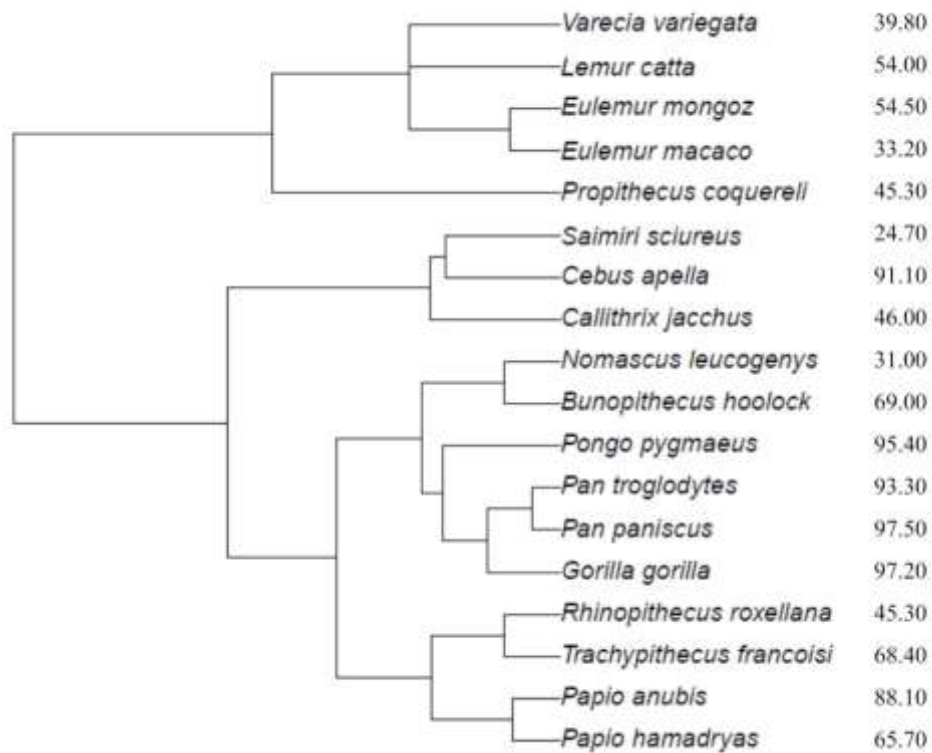
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1900 **SM3.** Summary of the PGLS models' statistical results of the relationships between
 1901 cognitive variables (log10-transformed and scaled) comprising the primate species
 1902 considered in the present study. We exhibit the sample sizes of each model (N), the
 1903 phylogenetic signal parameter (Lambda), the coefficient estimate (Estimate), the standard
 1904 error (s.e.), the t-statistics (t-value) and Wald-type P-value (with significant associations
 1905 bold highlighted).

1906

Response	Predictor (N)	Lambda	Estimate	s.e.	t-value	P-value
	Reader's g (17)	0.000	0.439	0.140	3.134	0.006
	Innovation (9)	0.052	0.125	0.052	2.392	0.027
Deaner's G	Social Learning (10)	0.853	0.422	0.137	3.071	0.015
	Memory (14)	0.000	0.695	0.134	5.178	0.0002
	Self-Control (8)	0.000	0.669	0.220	3.035	0.022
	Innovation (16)	1.000	0.826	0.101	8.130	1.135⁻⁰⁶
	Social Learning (13)	0.000	0.822	0.174	4.708	0.0006
Reader's g	Memory (13)	0.000	0.749	0.313	2.389	0.035
	Self-Control (8)	0.000	0.998	0.313	3.181	0.019

	Social Learning (24)	0.000	0.864	0.106	8.146	4.366⁻⁰⁸
Innovation	Memory (15)	0.000	0.773	0.318	2.430	0.030
	Self-Control (12)	0.321	0.999	0.308	3.238	0.008
	Memory (15)	0.577	0.348	0.055	1.659	0.120
Social Learning	Self-Control (10)	0.000	0.832	0.341	2.437	0.040
	Self-Control (15)	0.000	0.574	0.195	2.940	0.011
	Mean Memory					

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1909 **SM4.** Models' results excluding species considered influential cases according to Cook's

1910 distance values, specifically, species with more than three times the cook value with

1911 significant associations bold highlighted.

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Respon	Predictors	Key feature	Estimate	s.e.	t-	P –	VI
e	and model's				value	value	F
	statistics						
Deaner's G	SS + LG + DB	Intercept	0.242	0.314	0.768	0.453	
N = 22							

	$R^2 = 0.475$	Dominance	0.166	0.321	0.517	0.608	1.7
	F – statistic:	x social					05
	8.945	bonds					
	P-value:	Alloparental					
	<0.001	x maternal	0.679	0.396	1.715	0.096	1.2
							98
		Longevity	0.672	0.162	4.140	<0.001	1.8
							93
		Diet Breadth	0.122	0.140	0.871	0.390	1.1
							75
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Social							
Learning	SS + CS + LG +	Intercept	-0.009	0.384	-0.025	0.980	
g	DB						
N = 26							
	Lambda = 0	Dominance	-0.058	0.433	-0.134	0.894	1.8
	$R^2 = 0.310$	x social					04
	F – statistic:	bonds					
	3.706	Alloparental					
	P-value:	xmaternal	0.625	0.468	1.334	0.196	1.5
	0.020						74
		Longevity	0.581	0.198	2.926	0.008	2.0
							0
		Diet Breadth	-0.046	0.183	-0.256	0.800	1.5
							54
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Mean							
Memory	SS + CS + LG	Intercept	-0.093	0.355	-0.263	0.794	
	N = 37	+ DB					
		Dominance	0.136	0.377	0.362	0.719	1.0
	Lambda = 0	x social					95
	R ² = 0.224	bonds					
	F – statistic:	Alloparental	-0.158	0.422	-0.374	0.710	1.6
	3.245	x maternal					12
	P – value:	Longevity	0.464	0.209	2.216	0.035	1.6
	0.026						79
		Diet Breadth	0.169	0.160	1.057	0.299	1.3
							89

1913

1914 **SM5.** Cognitive information compiled from the studies selected in the first data search
1915 and organised by general domains or categories of cognition. The reference list is below
1916 the table.

General categories or domains of cognition - and the different terms used	Tasks or tests	Meaning of the task or test	References
Inhibition domain (1) - or inhibitory control (7,18) or self-control (8,35)	A not B task or IN1 (1,7,35)	Inhibition tasks - e.g., suppressing prepotent responses; A not B task - "refraining from choosing the now empty opaque cup under which they previously retrieved a reward" (1)	(1) Amici et al. 2012/ (7) Chen et al. 2017/ (8) Chiappa et al. 2018/ (18) Forss et al. 2016/ (35) MacLean et al. 2014
Inhibition domain	Middle cup task or IN2 (1,42)	"Refraining from choosing an empty opaque cup close to an opaque cup from which they previously retrieved a reward" (1)	(1) Amici et al. 2012/ (42) Rudolph and Fichtel 2017
Inhibition domain	Plexiglas hole task or IN3 (1)	"Refraining from reaching toward a reward directly through a plexiglas panel and	(1) Amici et al. 2012

		instead taking a detour movement through one hole" (1)	
Inhibition domain	Swing door task or IN4 (1)	"Refraining from reaching toward a reward directly through a transparent door and instead taking a detour movement through another transparent door to grab the reward from behind" (1)	(1) Amici et al. 2012
Inhibition domain	Delay of gratification task or IN5 (1)	"Refraining from reaching for a smaller immediate reward to obtain a larger delayed one" (1)	(1) Amici et al. 2012
Inhibition domain	Detour-reaching tests (10,11,18,48)	Inhibition of a default response that is not effective under the conditions of the task. (10)	(10) Damerius et al. 2019/ (11) Damerius et al. 2017/ (18) Forss et al. 2016/ (48) Vlamings et al. 2010
Inhibition domain	Cylinder task (7,8,26,35,42)	"Inhibition of the impulse to reach for the food directly (bumping into the cylinder) in favor of the detour response" (35); it is a scaled-down detour-reaching test (26)	(7) Chen et al. 2017/ (8) Chiappa et al. 2018/ (26) Johnson-Ulrich and Holekamp 2019/ (35) MacLean et al. 2014/ (42) Rudolph and Fichtel 2017
Memory	30 ss - Short-term memory (ME1), 30 min - Long-term memory (ME2) (2,52)	Short- or long-term memory performances e.g., retrieving hidden food after delay (1); touchscreen discrimination (52)	(1) Amici et al. 2012/(52) Wallis 2016 (Thesis)
Memory	Spatial memory task (29,33,40,41)	Memory for spatial location of rewards including 3 experiments in (40): long delay, multiple locations and motivational control and also in (41): recall after a long-delay, learning mechanisms supporting memory and recall of multiple locations in a complex environment	(29) Kittler 2017 (Thesis) (31) Kittler et al. 2015/ (33) Lacreuse et al. 2014/ (40) Rosati 2019/ (41) Rosati et al. 2014
Memory	Delayed response - DR (14)	Investigates a subject's memory or ability to maintain a representation of an item when it is no longer available to immediate perception (14)	(14) Deaner et al. 2007
Object discrimination learning set paradigm (14) or associative learning (10)	Colour discrimination task (14)	Involves the tracking ability of dyadic relationship. "The learning set phenomenon refers to the observation that if the subject is given another discrimination problem, with two novel stimuli, it will tend to learn this second discrimination problem more quickly than it did the first one" (14)	(10) Damerius et al. 2019/ (14) Deaner et al. 2007

Discrimination learning	Pairwise task (43)	"Ability to respond to items in the correct order - likened to the ability to judge and represent the relative rank of other monkeys in their social group" (43)	(43) Scarf and Colombo 2008
Discrimination learning	Auditory discrimination learning (45)	Ability to use the auditory cues presented (45)	(45) Stuermer and Wetzel 2006
Discrimination learning	Shuttle box go/ No-go (45)	Discrimination between two frequency-modulated tones - "ability to learn the conditioned responses tested in the shuttle box experiments" (45)	(45) Stuermer and Wetzel 2006
Discrimination learning	Discrimination task - touch screen (49,50, 51,52)	Numerical abilities (49)/ A series of natural concept discrimination tasks on a touchscreen computer, in which the discriminations vary in degree of abstraction (50,51)	(49) Vonk and Beran 2012 Animal Behaviour/ (50) Vonk and Galvan 2014 Animal Behavior and Cognition/ (51) Vonk et al. 2012 Animal Behaviour/ (52) Wallis 2016 (Thesis)
Discrimination learning	Associative learning tests (10,11)	Ability to form a mental connection between two or more stimuli (Shettleworth 2010)/ Association learning - learn the association between food and location, which can be enhanced by the different shapes and colors (10)	(10) Damerius et al. 2019/ (11) Damerius et al. 2017
Discrimination learning	Reversal learning tests (10,11,14,18,41)	Aprehend behavioural flexibility. The reversal learning or intra-dimensional shift paradigm investigates the ability to reverse a previously learned discrimination. (14)	(10) Damerius et al. 2019 Intelligence/ (11) Damerius et al. 2017 Animal Behaviour/ (14) Deaner et al. 2007/ (18) Forss et al. 2016/ (41) Rosati et al. 2014
Spatial learning	Transposition (TR1; TR2; TR3; TR4) (1, 29,33)	Keeping track of invisible displacements (1)	(1) Amici et al. 2012/ (29) Kittler 2017 (Thesis)/ (31) Kittler et al. 2015/ (33) Lacreuse et al. 2014
Spatial learning/ spatial memory (17)	Detour problems or tasks (17); Patterned-string problems: Invisible displacement (14) and Parallel strings	Detour problems investigate the ability to form and act on spatial representations (14)/ Reveal that spatial memory of individuals for hidden objects in a detour task was guided by flexibility in processing spatial information (17)/ Patterned-string problems investigate the ability to represent spatial representations among objects (14). Invisible displacement (1, 14) indicates if the individual	(1) Amici et al. 2012/ (14) Deaner et al. 2007/ (17) Fiset et al. 2007

		can represent the existence and spatial movements of unperceived objects (14)	
Spatial learning	Rotation (29,33)	Scale space examines the ability to track objects in space in four tasks: rotation, also spatial memory, object permanence, and transposition (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Procedural knowledge innovation (11,16)/novel-technical problem (6,7)	Support (1)	Understanding of mean-end connections, by selecting the tool to which food is attached (1)	(1) Amici et al. 2012/ (6) Brunon et al. 2014/ (7) Chen et al. 2017/ (16) Fernandes et al. 2014
Procedural learning	Novel foraging task (21)	"Knowing how" or "knowing what to do" (Shettleworth 2010)/ Artificial foraging task - a liquid-retrieval task comparable to that used by Lehner, Burkart & Van Schaik (2011) (21)	(21) Harrison and Whiten 2018
Procedural learning	Motor (foraging) tasks (33)	Novel motor skills in a motor task	(33) Lacreuse et al. 2014
Procedural learning	Puzzle box task (2,3,11,22,23,25)	Problem-solving ability - success opening the puzzle box (2,3,4)/ Problem-solving ability, problem-solving speed, and latency to approach a novel apparatus (25)	(2) Benson-Amram et al. 2016/ (3) Benson-Amram et al. 2014/ (4) Borrego and Gaines 2016/ (11) Damerius et al. 2017/ (22) Holekamp et al. 2017/ (23) Holekamp et al. 2015/ (25) Howard 2018 (Thesis)
Procedural learning	Complex two-step foraging task (5)	Ability to solve complex manipulation tasks (5, 13)/ Food box cognitive challenge - two-step (5)	(5) Briefer et al. 2014
Procedural learning	Texture (6), Shape (6,29,33) and Color tests (6)	Ability to solve complex manipulation tasks (6)/ "The scale causality consists of four tasks: noise, shape, tool use and tool properties to examine the ability to understand spatial-causal relationships" (29)	(6) Brunon et al. 2014/ (29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Procedural learning	Box task (10,11,12,32)	Open box - tests flexibility after learning phase (10)	(10) Damerius et al. 2019/ (11) Damerius et al. 2017/ (12) Day et al. 2003/ (32) Kulahci et al. 2018
Procedural learning	Tube trap task (10,11,18)	Causal reasoning and learning ability (10,11)	(10) Damerius et al. 2019/ (11) Damerius et al. 2017/ (18) Forss et al. 2016
Procedural learning	Honey tool task (10,11,18)	Ability of tool use and causal reasoning (10,11)	(10) Damerius et al. 2019/ (11) Damerius et al. 2017/ (18) Forss et al. 2016

Procedural learning	Natural tasks (12,16)	Extractive processing of an unfamiliar food (12)	(12) Day et al. 2003/ (16) Fernandes et al. 2014
Procedural learning	Tool use tests (14,29)	"Tool use addresses abilities to understand and manipulate how one's actions affect an intermediate object (the tool), and how the intermediate object affects another object or substrate. It thus involves aspects of causal reasoning, spatial representation, and motor coordination" (14)	(14) Deaner et al. 2007/ (16) Fernandes et al. 2014/ (29) Kittler 2017 (Thesis)
Procedural learning	Novel extractive foraging tasks (15,16)	Extractive foraging refers to the capacity to extract food items that are concealed in some way. "This capacity relates to general intelligence and brain size both theoretically and empirically" (16)	(15) Drea 2006/ (16) Fernandes et al. 2014
Procedural learning	Tube task - Aesop's Fable paradigm (19)	Novel tool mediated problem- Aesop's Fable paradigm - "wherein subjects drop stones into a cylinder half-filled with water to acquire floating out-of-reach food items" (19)	(19) Gormley 2015 (Thesis)
Procedural learning	Honey-trap experiment (20)	How wild animals categorise their tools as meaningful objects in their environment (20)	20) Gruber 2016
Procedural learning	Functional fixedness: raking and honey-dipping task (20)	"Disinclination to use familiar objects in novel ways" (Brosnan and Hopper 2014, p. 2) (20)	(20) Gruber 2016
Procedural learning	Multi-access box (MAB) (26)	Measures repeated innovation, the number of unique innovations learned across trials - included persistence, motor diversity, motivation, activity, efficiency, inhibitory control, and neophobia (26)	(26) Johnson-Ulrich et al. 2018
Procedural learning	Stick task (30)	"Ability to reason about the relation between the stick and the reward, as well as the ability to manipulate the stick" (30)	(30) Kittler et al. 2018
Procedural learning	Tool properties task (29,33)	"The scale causality consists of four tasks: noise, shape, tool use and tool properties to examine the ability to understand spatial-causal relationships" (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014

Procedural learning	Noise task (29,33)	"The scale causality consists of four tasks: noise, shape, tool use and tool properties to examine the ability to understand spatial-causal relationships" (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Procedural learning	Relative numbers task (29,33)	"The scale causality consists of four tasks: noise, shape, tool use and tool properties to examine the ability to understand spatial-causal relationships" (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Procedural learning	Addition numbers (29); Quantity judgement task (quantity discrimination) (53)	"The scale quantity tests the numerical understanding of individuals and consists of two tasks: relative numbers and addition numbers - quantities of rewards" (29)/ "Quantity judgement or preference - opportunity to choose between two different amounts of the same food reward type" (53)	(29) Kittler 2017 (Thesis)/ (53) Ward 2007 (Thesis)
Procedural learning	Means-end reasoning (30)	Choice task: subjects chose between a food item on a continuous or on a discontinuous support (30)	(30) Kittler et al. 2018
Procedural learning	Tube and tool task (34)	"Inspired by the challenge of acquiring water from a deep tree hole in the wild" (34)	(34) Lehner et al. 2011
Procedural learning	Anvil-choice task (37)	Means-end comprehension - transfer test involving novel anvil objects (37)	(37) Müller 2010
General cognition score/performance, psychometric g (10)/global cognition estimate (14)/ G: general intelligence (16)	Distinct task performances to be correlated or grouped in principal components	Cognitive abilities being similar in distinct conditions. Commonly measured by principal component analysis results; or global cognition estimate; or performances correlation; or generated by the 'reduced model' (i.e., estimates of general cognitive ability (14))	(10) Damerius et al. 2019/ (14) Deaner et al. 2007/ (16) Fernandes et al. 2014
Social learning (16)	Transitive inference (28,36)	Evidence and/or accuracy of transitive inference in species, "e.g., if A dominates B and B dominates C, then A dominates C" (36)/ There are social and nonsocial versions of a transitive inference task (28)	(28) Kaiser 2014 (Thesis)/ (36) MacLean et al. 2008
Social learning	Gaze-following (7,29,33,52)	Gaze-following refers to the "ability to look in the direction that others are looking" - and "might aid animals in gathering information about their physical and social world" (7)/ in the scale Theory of	(7) Chen et al. 2017/ (29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014/ (52) Wallis 2016 (Thesis)

		Mind, individuals were confronted with two tasks: gaze following and intentions (29)	
Social learning	Cache or caching task - cooperative context (24)	If individuals flexibly adapt their caching behaviors to a cooperative context	(24) Hopewell 2008 (Thesis)
Social learning	Naturalistic social foraging task (15)	Modeled after traditional visual discrimination paradigms, individuals identify food signs through color discrimination learning in a group context (15)	(15) Drea 2006
Social learning	Cooperative problem solving (15)	Requires that two animals perform similar or complementary actions (15)	(15) Drea 2006
Social learning	Tactical deception (16)	Tactical deception refers to "behaviors deployed in certain situations that are intended to deceive others" (Byrne & Whiten, 1985) (16)	(16) Fernandes et al. 2014
Social learning	Object-choice task (38,39)	Ability to use different human cues (pointing and/or gazing) in an object-choice task	(38) Oliva et al. 2019/ (39) Plotnik et al. 2013
Social learning	Social information (29)	"Scale social learning examines in one task whether individuals use social information provided by a human demonstrator to solve a problem." (29)	(29) Kittler 2017 (Thesis)
Social learning	Comprehension task (29,33)	"The scale communication examines whether individuals are able to understand communicative cues given by humans in three tasks: comprehension, pointing cups and attentional state" (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Social learning	Pointing cups task (29)	"The scale communication examines whether individuals are able to understand communicative cues given by humans in three tasks: comprehension, pointing cups and attentional state" (29)	(29) Kittler 2017 (Thesis)
Social learning	Attentional state task (29,33)	"The scale communication examines whether individuals are able to understand communicative cues given by humans in three tasks: comprehension, pointing cups and attentional state" (29)	(29) Kittler 2017 (Thesis)/ (33) Lacreuse et al. 2014
Social learning	Intentions task (29)	"In the scale Theory of Mind, individuals were confronted with two tasks: gaze following and	(29) Kittler 2017 (Thesis)

		intentions" (29) Focus on individuals attention to human clue	
Social learning	Production task (33)	Into communication paradigm, "ability to produce communicative signals to indicate a hidden food item" (33)	(33) Lacreuse et al. 2014
Social learning	Social tool use task (44)	Tests spontaneous and repeated social tool use (44)	(44) Schweinfurth et al. 2018
Social learning	Matching-to-sample task (46) and List learning task (46)	Discrimination test and a list learning task employing conspecific faces as stimuli. Tests "ability to discriminate the faces, sexual identities and dominance relationships of conspecifics" (46)	(46) Talbot 2016 (Dissertation)
Social learning	Informed forager test (47)	Aspects of spatial learning and foraging strategies in a competitive context (47)	(47) van Nieuwamerongen et al. 2017
Social learning	Sustained attention test (52)	"Selective attention tests depends on an individual's level of executive attentional control, and crucially involves active inhibition (Cepeda et al., 2001); Sustained attention - attention to two stimuli, as indicated by time spent with the head (used as a proxy for gaze direction) directed toward the stimuli" (52)	(52) Wallis 2016 (Thesis)
Abstract learning or simple- and complex-rule learning performance (9)	Maze tasks with foraging reward (9)	"Species-fair crawling maze to test simple- and complex-rule learning, flexibility and re-learning performance" (9)	(9) Clarin et al. 2013
Abstract learning	Traveling salesperson problem (TSP) - Maze with reward (13)	"Requires minimizing the total distance traveled - maze with reward" (13)	(13) De Jong et al. 2011
Abstract learning	Serial-order task (43)	"Serial-order task - subjects are trained to respond to five stimuli in a specific order, (e.g., A→B→C→D→E) to obtain a reward" (43)	(43) Scarf and Colombo 2008
Abstract learning	Oddity learning ability test (14)	"Ability to use a relational or abstract concept. e.g., a subject is simultaneously provided with three visual stimuli, two of which are identical, and one that differs; the subject is rewarded for choosing the differing or odd stimulus" (14)	(14) Deaneer et al. 2007

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Conclusões gerais

As características comportamentais podem ser relevantes para o favorecimento de determinadas espécies diante de ambientes desafiadores, como aqueles sob a influência de atividades humanas. Neste trabalho, avaliamos o possível papel de variáveis sociais, ecológicas e de história de vida no risco de extinção de espécies de mamíferos no primeiro capítulo, e investigamos os fatores que estão associados às habilidades cognitivas de primatas, potencialmente decisivas para a capacidade de ajuste das espécies, no segundo capítulo.

Nosso estudo indica que um maior risco de extinção de espécies de mamíferos está associado a maiores densidades populacionais humanas, conforme esperado (Davies et al. 2016). Ademais, distintos fatores socioecológicos se associam ao risco de extinção. As espécies que desempenham cuidado biparental possuem menor risco de extinção que espécies com cuidado apenas materno da prole. Espécies solitárias e espécies que formam grupos sociais menores têm menor risco que espécies sociais e que formam grupos maiores. Mamíferos cujo sistema de acasalamento é promíscuo possuem menor risco de extinção que os monogâmicos. Espécies de menor tamanho do corpo são menos susceptíveis à extinção, bem como as que acessam menos itens na dieta. As espécies que possuem menor longevidade e maior tamanho da ninhada também tendem a possuir menor risco de extinção.

Também encontramos que a espécies mais longevas de primatas possuem melhor desempenho em tarefas cognitivas. O nosso estudo considerou diversas medidas comportamentais de habilidades cognitivas que se correlacionaram entre si. E esse resultado relacionando cognição geral com a longevidade coaduna com outros resultados

baseados em neuroanatomia (González-Lagos et al. 2010, Navarrete et al. 2016) e modelagem baseada no indivíduo (Ratikainen and Kokko 2019). Esse conjunto de resultados parece apontar para uma co-evolução entre longevidade e habilidades cognitivas.

Apesar de uma parte de nossos resultados corroborarem algumas de nossas previsões, também obtivemos resultados inesperados. Algumas previsões a respeito do risco de extinção colocavam as habilidades cognitivas como principais características que poderiam proporcionar um melhor ajuste de espécies consideradas mais inteligentes em ambientes submetidos às rápidas mudanças. Assim, alguns fatores comportamentais, ecológicos e de história de vida que podem estar associados à cognição seriam potencialmente relevantes para a persistência das espécies. No entanto, os nossos resultados relacionando risco de extinção à estrutura social, tamanho do grupo, longevidade e dieta foram contrários às nossas expectativas que estavam de acordo com o que sugeria a literatura sobre a relação dessas variáveis com a cognição ou diretamente com o risco de extinção.

Uma possível explicação para essas respostas é uma falha em nossas premissas, ou seja, as habilidades cognitivas dos mamíferos não estarem associadas às variáveis estrutura social e tamanho do grupo. Encontramos essa falta de relação entre as estruturas de laços sociais e relação de dominância e habilidades cognitivas para primatas, mas não possuímos evidências da ocorrência dessa relação considerando espécies de mamíferos, bem como comparando com espécies solitárias e com estrutura social colonial. Nosso processo de estudo indica que também faltam dados que permitam comparações considerando múltiplas espécies e táxons. A mesma falta de evidência e dados ocorre para outras medidas de estrutura social, a exemplo da comparação entre espécies que possuem ou não dinâmica de fissão-fusão dos grupos. Dessa forma, parece profícuo que novos

estudos supram a carência dessas informações, bem como investiguem a existência da relação entre habilidades cognitivas e estruturas sociais diversas, considerando mais espécies e táxons.

Outra possibilidade de justificativa para os resultados inesperados, na qual as nossas premissas de relação entre habilidades cognitivas e estruturas/organização social estão corretas, é que melhores habilidades cognitivas não necessariamente ajudam no ajuste das espécies aos desafios ambientais. Uma das possíveis vantagens da vida social é a aprendizagem entre co-específicos para lidar com desafios, mas se o ambiente muda muito rapidamente, informações transmitidas que poderiam ser vantajosas podem ficar desatualizadas e tender a aumentar o risco de extinção. Ou ainda, independente da relação com a cognição, o maior risco de extinção pode vir diretamente da vida social. Nesse caso, os indivíduos em seus grupos podem ficar mais vulneráveis à percepção de predadores ou caçadores humanos, ou mesmo ter mais dificuldade de manter e coordenar indivíduos em coletividade quando comparado à vida solitária. Também é pertinente que estudos futuros investiguem exatamente como as distintas características sociais afetam a persistência das espécies.

Um maior risco de extinção também se associou, de forma inesperada, com maior longevidade de mamíferos. Imaginávamos que a possível relação entre longevidade e habilidades cognitivas favoreceria a persistência das espécies. De fato encontramos uma relação entre distintas habilidades cognitivas e a longevidade de primatas. Portanto, nossos resultados sugerem que é possível que as habilidades cognitivas não se relacionem com o risco de extinção das espécies mais longevas, ou mesmo as desfavoreçam. As espécies de mamíferos com maior amplitude da dieta, que seria metabolicamente um facilitador da cognição, em nossos resultados, afinal, possuem maior risco de extinção. E as espécies de primatas com dietas mais amplas não diferem das menos amplas em relação

às habilidades cognitivas. É possível, e válido investigar, se outros aspectos da alimentação, relativos à qualidade da dieta, por exemplo, são mais relevantes tanto para as habilidades cognitivas, quanto para sobrevivência e reprodução das espécies.

Num cenário de impactos humanos que mudam o ambiente de forma relativamente rápida (Sih et al. 2011) afetando a biodiversidade (Davies et al. 2006), nosso estudo traz respostas que podem lançar luz sobre quais características são relevantes em esforços conservacionistas. Especificamente, as espécies de mamíferos socialmente estruturadas e que possuem grupos relativamente maiores, as espécies de sistema de acasalamento monogâmico, e as com cuidado parental apenas materno tendem a ser mais vulneráveis. Nosso estudo também revela focos frutíferos para estudos futuros, uma vez que nos deparamos com lacunas de informações durante as nossas coletas de dados. Além da necessidade de ampliar taxonomicamente a coleta de dados comportamentais, para que possamos responder perguntas socioecológicas em escalas amplas e em escopo evolutivo, sugerimos fortemente que esses dados sejam pensados e coletados coletivamente, coordenados e sistematizados. Esse esforço coletivo permitirá o aumento da representatividade e da robustez dos estudos a nível interespecífico, uma vez que serão metodologicamente homogêneos. Estudos de natureza coletiva teriam o poder de potencializar os esforços de pesquisadores que muitas vezes enfrentam limitação de recursos. Ademais, favorecem a possibilidade de pesquisas envolvendo múltiplas espécies, e aspectos comportamentais de forma mais profunda, com medidas que capturem melhor a complexidade das variáveis estudadas.

No presente trabalho, integramos conhecimentos dos campos da ecologia comportamental, ecologia evolutiva e da cognição animal. A associação entre essas áreas se mostrou frutífera, mas além das lacunas de dados a serem coletados, ainda possuímos muitas perguntas que devem ser exploradas, integrando o conhecimento em vários níveis.

A exemplo de quais os mecanismos envolvidos na relação entre aspectos sociais e riscos de extinção, se medidas que capturam melhor a complexidade das variáveis ecológicas e comportamentais se associam à cognição, e se a cognição está associada à aptidão animal. Uma produção de conhecimento integrando os trabalhos de diversos pesquisadores e de diferentes áreas nos parece a maneira mais promissora de desvendarmos as complexidades intrínsecas à natureza e suas relações.

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