REVIEW

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

Johanna Henke-von der Malsburg [1,2,3] ⬥ Peter M. Kappeler [1,2] ⬥ Claudia Fichtel [1,3]

Abstract

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

Keywords Cognition · Ecological adaptation · Foraging style · Habitat complexity · *Ecological Intelligence Hypothesis* · Brain size

Introduction

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

✉ Johanna Henke-von der Malsburg
JMalsburg@dpz.eu

[1] Behavioral Ecology and Sociobiology Unit, German Primate Center, Leibniz Institute for Primatology, Göttingen, Germany

[2] Department of Sociobiology/Anthropology, Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany

[3] Leibniz ScienceCampus 'Primate Cognition', Göttingen, Germany

with brain size. Relative brain size varies considerably among species (e.g. Mace et al. 1981; Sol et al. 2008) and is indeed associated with variation in average species-typical cognitive performance (Deaner et al. 2006; Reader et al. 2011). Several hypotheses have been proposed to explain this link between interspecific variation in brain size and the associated cognitive abilities. The most prominent hypotheses are the *Social Intelligence Hypothesis* (SIH, Humphrey 1976) and the *Ecological Intelligence Hypothesis* (EIH, Parker and Gibson 1977; Milton 1988), which have been subsequently refined as the *Domain-General Hypothesis* (Deaner et al. 2006), *Domain-Specific Hypothesis* (Whiten and Byrne 1988), *Adaptive Intelligence Hypothesis* (Tooby and Cosmides 2003), *Machiavellian Intelligence Hypothesis* (Whiten and Byrne 1988), *Cultural Intelligence Hypothesis* (Herrmann et al. 2007; van Schaik and Burkart 2011), *Social Brain Hypothesis*

(Dunbar 1998; Dunbar and Shultz 2007) and *Cognitive Buffer Hypothesis* (CBH, Deaner et al. 2003)) (see Fig. 1).

The SIH suggests that bigger brains co-evolved with increasing social complexity, i.e. cognitive challenges to manage social relationships, which, in turn, have evolved as means of solving ecological problems (Jolly 1966; Humphrey 1976; Whiten and Byrne 1988; Barton 1996; Dunbar 1998; Kudo and Dunbar 2001; Dunbar and Shultz 2007; Byrne and Bates 2010). In contrast, the EIH posits that ecological challenges in food acquisition, including spatial or spatiotemporal processes to memorise seasonally available food or manipulative skills for extractive foraging, have ultimately selected for larger brains (e.g. Clutton-Brock and Harvey 1980; Heldstab et al. 2016; DeCasien et al. 2017; Powell et al. 2017). At the end of the day, the brains evolve within species, where environmentally induced changes in physiological traits, such as glucose concentrations and hormone levels, impact cognitive performance (Roth et al. 2010; Thornton and Lukas 2012; Maille and Schradin 2016).

Comparative studies investigating the link between measures of brain size and socioecological factors revealed inconsistent results, finding either a positive relationship between measures of brain size and sociality in primates and ungulates (Dunbar 1998; Pérez-Barbería et al. 2007; Dunbar and Bever 2010) or equivocal support in carnivores (Holekamp et al. 2007; Pérez-Barbería et al. 2007; Finarelli and Flynn 2009),

for instance. Among primates, the most recent comparative analyses indicated that brain size is better predicted by ecological than social factors (DeCasien et al. 2017; Powell et al. 2017). However, compared to social factors (Ashton et al. 2018b), less is known about the extent to which variation in specific ecological factors predicts cognitive performance (Fig. 1). Here, we therefore explore the question whether ecological adaptations can explain interspecific variation in cognitive abilities by first briefly summarising hypotheses about the evolution of cognitive abilities addressing potential links between cognition and brain size and sociality, as well as ecology, respectively. Second, we provide a summary of comparative studies relating interspecific variation in cognitive performance with ecology, specifically the degree of ecological specialisation. Using these studies, we also explore the relative impact of sociality and brain size on variation in cognitive performance. Finally, we discuss the effects of the degree of ecological specialisation, potentially confounding factors in experimental studies, and limitations of this review that may inform future research on this topic.

The link between cognition and brain size

Some comparative studies have suggested that measures of brain size covary positively with performance in cognitive tests (see Appendix 1 Table 3 for explanations of cognitive
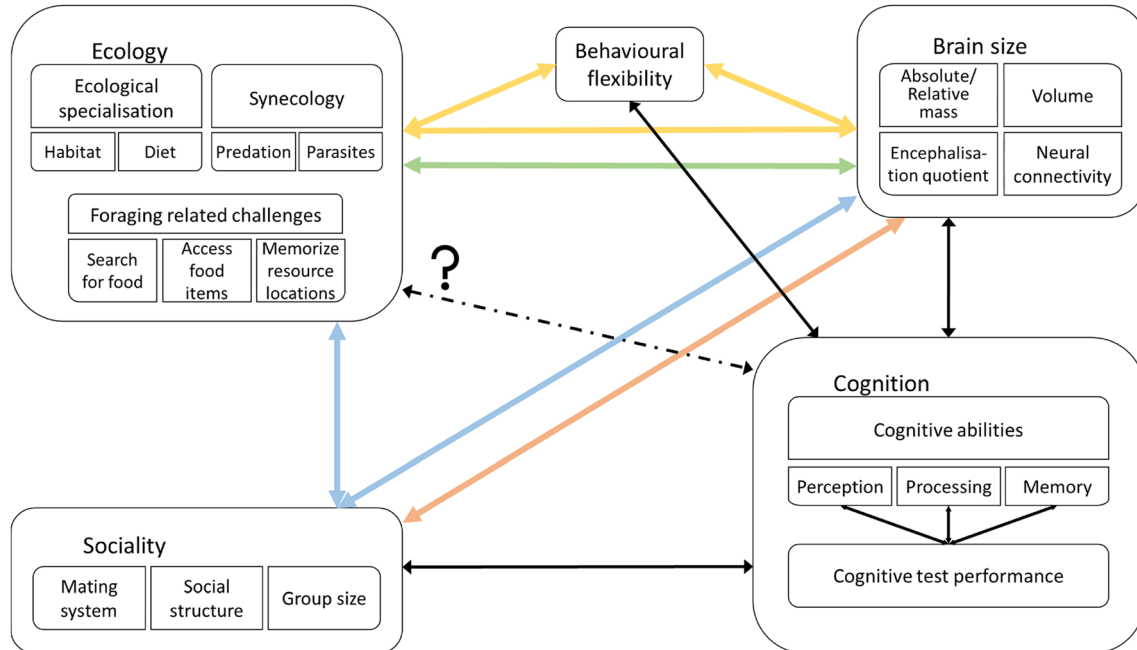
Fig. 1 Relationships between ecology, sociality, brain size measures and cognitive abilities. Main hypotheses related to particular links are represented with coloured thick lines: red for the *Social Intelligence Hypothesis* (challenges related to sociality drive brain development; Humphrey 1976), green for the *Ecological Intelligence Hypothesis* (challenges related to ecology drive brain evolution; Parker and Gibson 1977), blue for the *Social Brain Hypothesis* (ecological challenges predict sociality which drives brain size; Dunbar 1998; Dunbar and Shultz 2017) and yellow for the *Cognitive Buffer Hypothesis* (environmental variation drives brain size which favours adaptive behavioural flexibility; Deaner et al. 2003). Thinner black lines represent previously reported relationships between cognitive abilities and sociality, behavioural flexibility and brain size. The dashed line represents the relationship between cognitive abilities and ecology discussed in this article

terms), such as performance in inhibitory control across vertebrates (MacLean et al. 2012), a general intelligence (*g*)-*factor* extracted from performance in innovation, social learning, tool use, extractive foraging and tactical deception (Reader and Laland 2002; Reader et al. 2011), a *g-factor* extracted from performance in tests on spatial and causal understanding, reversal learning and delayed response (Deaner et al. 2006, 2007) or performance in problem-solving (Benson-Amram et al. 2016). In addition, guppies (*Poecilia reticulata*) selected for larger brains outperformed those with smaller brains in a numerical learning assay (Kotrschal et al. 2013), demonstrating this link also at the intraspecific level.

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

Alternatively, domain-specific cognition might support the notion of mosaic brain evolution (Barton and Harvey 2000). The vertebrate brain consists of several functionally different structures, of which many vary in size within and between clades (Striedter 2006). Differences in the relative size of different brain regions are thought to reflect both neurodevelopmental/functional size changes and selection for ecologically relevant cognitive and sensory specialisation (Barton 1996). For example, food-caching birds have relatively, but not absolutely, larger hippocampi (Krebs 1990), and brain regions associated with spatial processing are enlarged in species with better spatial abilities (Sherry et al. 1992; Clayton 1998). Moreover, group-living primates with high-quality diets have larger brain regions for olfactory or visual processing, whereas solitary species or those with low-quality diets have larger brain regions for processing spatial memory (DeCasien and Higham 2019). Finally, the number of neurons in the mammalian cerebral cortex, or in the bird pallium,

appears to be good predictors of inhibitory control (Herculano-Houzel 2017). Hence, specific neuroanatomical measures can be broadly associated with variation in cognitive performance.

The link between cognition and sociality

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

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

The link between cognition and ecology

Ecological challenges, such as variable schedules of resource availability, habitat complexity, predation risk or parasite exposure, may have contributed to cognitive evolution (Garamszegi et al. 2007; Lefebvre and Sol 2008; Shumway 2008; Soler et al. 2012; Morand-Ferron et al. 2016; Sayol et al. 2016). With respect to resource variation, the CBH posits that larger brains evolved to allow species to adjust their behaviour adaptively in response to variable environmental conditions (Deaner et al. 2003). For instance, frugivorous species, which have on average larger brains than folivorous species, rely more on resources that vary in their spatiotemporal distribution than folivorous species (Clutton-Brock and Harvey 1980; Mace et al. 2009). Moreover, birds and Old World primates

exposed to seasonal changes in food availability tend to have larger brains than species living in non-seasonal habitats (van Woerden et al. 2012; Sayol et al. 2016). Innovativeness, which is adaptive in variable environmental conditions, correlates positively with brain size in primates and birds (Reader and Laland 2002; Lefebvre et al. 2004; Overington et al. 2009), but it also correlates positively with parasitism and immunocompetence in birds (Møller et al. 2005; Garamszegi et al. 2007; Vas et al. 2011), though the link between innovation and the transmission mode of parasite types is not obvious (Ducatez et al. 2020a). Finally, in line with the EIH, brain size was best predicted by diet or home range size in primates (DeCasien et al. 2017; Powell et al. 2017).

Comparisons within species also revealed evidence that variation in cognitive abilities is associated with parasitism (Dunn et al. 2011; Bókony et al. 2014), predation (Brown and Braithwaite 2005; Park et al. 2008; Ferrari 2014), habitat complexity (Roth et al. 2010; Tebbich and Teschke 2014; Croston et al. 2017; Morand-Ferron et al. 2019) or foraging behaviour (Mazza et al. 2019; Sonnenberg et al. 2019). However, only a few comparative studies explicitly explored which cognitive skills might be associated with which species-specific ecological challenges. In birds, innovation was positively correlated with parasitism (Garamszegi et al. 2007; Vas et al. 2011; Soler et al. 2012) or habitat breadth (Overington et al. 2011), but not with predation (Overington et al. 2011). In primates, abundance of socially transmitted parasites was positively associated with rates of social learning, and environmentally transmitted parasites were positively associated with rates of exploration (McCabe et al. 2015). Habitat complexity was positively correlated with spatial cognition and brain size in rodents (Mackay and Pillay 2018) and fish (White and Brown 2015a, b). Hence, some results point towards an association between cognitive performance and ecological adaptations and a systematic summary of respective associations across species may contribute to a better understanding of potential causalities and their relative effect sizes.

The required assessment of a species' ecological adaptation can be based on a characterisation of its niche, which is a multidimensional space comprising all ecological factors that determine species viability (Hutchinson 1953; MacArthur 1957). Specialisation and generalisation represent the extremes of the continuous variation along each of the dimensions (Sargeant 2007). Utilising this niche concept, however, involves some difficulties. First, it is important to differentiate between intrinsic specialisations due to evolutionary adaptations (i.e. an individual's genetics describing its fundamental niche) and extrinsic specialisations due to interspecific competition over resources (i.e. the observed realised niche), for instance (Hutchinson 1957; Devictor et al. 2010). Second, niche breadth can be defined by the diversity of resources used by a species, or by its overlap, measured as the deviation from other species' resource values (Sargeant 2007). Considering

niche breadth, a specialist would then be a species consistently using a narrower niche than other species (Roughgarden 1972; Bolnick et al. 2003). Considering niche overlap, however, a specialist would use items/tactics that are rarely used within other species' niches (Bolnick et al. 2002). Moreover, classifications refer to only one niche axis (Futuyma and Moreno 1988), leading to species that can be highly specialised along one ecological gradient while being a generalist along another ecological gradient. It has therefore been proposed to use species co-occurrence as a measure of habitat breadth (Ducatez et al. 2014b). Finally, different studies use different terms for similar concepts without stating their definition, or they ignore differences between niche breadth and niche overlap, hampering broader comparisons (Colwell and Futuyma 1971; Devictor et al. 2010).

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

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

Merriam's

All selected studies (1) experimentally compared (2) cognitive abilities between (3) at least two species with the aim of investigating (4) different ecological adaptations with a focus on the degree of ecological specialisation. We controlled for potential phylogenetic effects by excluding studies comparing species across taxonomic classes. The remaining studies either compared species within the same genus (40%), family

(48%), or order (12%). Most of the studies compared wild-caught or semi-free ranging (72%) individuals in mammals (56%) or birds (24%) ($N = 2$ for each in reptiles and fish, $N = 1$ for invertebrates). The investigated ecological adaptations were mostly related to dietary challenges and variation in habitat complexity (Table 1). As studies of cognitive performance often differ in experimental conditions (animal housing, feeding regimes, environmental conditions, local and temporal conditions, experimental task and procedure, role of experimenter, etc.), measurement of cognitive performance and analysis in interspecific comparisons, we focused on explicitly comparative studies. Since only a few species were explicitly labelled as either generalist or specialist in the original studies, we assessed the relative degrees of habitat and/or dietary specialisation between the species investigated using additional literature. Similarly, if not mentioned in the original study, we gleaned information on group and brain size or proxies for brain size by consulting additional literature (Table 2).

Cognitive performance and ecological specialisation

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

Habitat exploration while searching and finding food

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

homogenous sandy shores (White and Brown 2015a). Also bank voles (*Myodes glareolus*), which occur in more complex habitats, exhibited better spatial search behaviour than root voles (*Microtus oeconomus*), which occur in more open habitats (Pleskacheva et al. 2000). Moreover, omnivorous bank voles and herbivorous common voles (*M. arvalis*) were similar in their efficiency of exploiting stable habitats, but the omnivorous bank voles were more efficient in exploiting habitats with temporally changing food locations (Haupt et al. 2010). However, striped mice (*Rhabdomys pumilio*, *R. bechuanae*, *R. dilectus*) occurring in habitats of different complexity did not differ in spatial learning abilities, possibly due to phylogenetic constraints (Mackay and Pillay 2018). Finally, adapting to and persisting in urban landscapes have been suggested to be associated with behavioural flexibility in several species (Sih 2013; Sol et al. 2013; Ducatez et al. 2020b). However, Eastern blue-tongued skinks (*Tiliqua scincoides scincoides*) originating from urbanised areas did not perform better in a reversal learning task than sleepy lizards (*T. rugosa asper*) originating from rural areas (Szabo and Whiting 2020). Hence, variation in habitat complexity seems to covary with learning abilities in most cases, in particular spatial learning abilities and decision-making.

Regarding the search for food, animals use specific ranging behaviour to track the spatiotemporal distribution of dietary items. By using specific navigational heuristics, i.e., decision rules applied to certain situations (Gigerenzer 2008), animals can improve their exploitation of the environment while reducing cognitive effort and energy expenditure. The use of such heuristics varies with the distribution of food items or the mobility of preferred food items. In primates, the more frugivorous Tonkean macaques (*Macaca tonkeana*) exhibited more goal-directed search strategies while foraging than the less frugivorous long-tailed macaques (*M. fascicularis*) or capuchin monkeys (*Sapajus apella*; Trapanese et al. 2019). The mobility of food items also influenced search strategies in three lemur species (Teichroeb and Vining 2019). Fat-tailed dwarf lemurs (*Cheirogaleus medius*), which are specialised on stationary fruits, performed best in a multi-destination array with several feeding platforms. Their superiority was explained by the efficient use of specific heuristics for exploration and feeder exploitation. In comparison, dietary generalist grey mouse lemurs (*Microcebus murinus*), which feed on stationary food items like flowers and gum but also on mobile food items such as insects, used fewer heuristics. Aye-ayes (*Daubentonia madagascariensis*), which are specialised on mobile and ephemeral insect larvae, used basically no heuristics at all, resulting in greater explorative effort and lower cognitive task performance. Similarly, Saussure's long-nosed bats (*Leptonycteris yerbabuenae*), which are specialised on nectar, foraged more efficiently in a feeder setup with artificial flowers by revisiting the feeders less often and depleting them more than long-tongued bats (*Glossophaga soricina*),

Table 1 Table of studies comparing cognitive abilities between at least two species within the same phylogenetic class expressing different ecological adaptations

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Habitat exploration while searching and finding food					
Clarin et al. (2013)	Long-fingered bat (*Myotis capaccinii*) Greater mouse-eared bat (*M. myotis*) Geoffroy's bat (*M. emarginatus*)	Same genus	Wild-caught	Spatial discrimination (plus maze)	No difference between *M. capaccinii* (open water forager), *M. myotis* (passive listening gleaner) and *M. emarginatus* (clutter specialist)
Clarin et al. (2013)	Long-fingered bat (*M. capaccinii*) Greater mouse-eared bat (*M. myotis*) Geoffroy's bat (*M. emarginatus*)	Same genus	Wild-caught	Spatial reversal learning (plus maze)	*M. myotis* (passive listening gleaner) and *M. emarginatus* (clutter specialist)
Clarin et al. (2013)	Long-fingered bat (*M. capaccinii*) Greater mouse-eared bat (*M. myotis*) Geoffroy's bat (*M. emarginatus*)	Same genus	Wild-caught	Complex spatial discrimination (extended plus maze)	*M. myotis* (passive listening gleaner) and *M. emarginatus* (clutter specialist)
Day et al. (1999a)	Nidua fringe-toed lizard (*Acanthodactylus scutellatus*) Bosc's fringe-toed lizard (*A. boskianus*)	Same genus	Wild-caught	Visual discrimination (colour/shape/pattern discrimination)	No difference between *A. scutellatus* (sit-and-wait predator) and *A. boskianus* (active forager)
Day et al. (1999a)	Nidua fringe-toed lizard (*A. scutellatus*) Bosc's fringe-toed lizard (*A. boskianus*)	Same genus	Wild-caught	Behavioural flexibility (colour/shape/pattern reversal learning)	*A. boskianus* (active forager)
Gingins and Bshary (2016)	Bluestreak cleaner wrasse (*Labroides dimidiatus*) Other labrids (*Pseudocheilinus hexataenia, Halichoeres melanurus, Thalassoma lunare, Hemigymnus melapterus, Labrichthys unilineatus*)	Same family	Wild-caught	Spatial discrimination (association of food source with location)	No difference between 6 labrid species due to ecological irrelevance of the task
Haupt et al. (2010)	Common vole (*Microtus arvalis*) Bank vole (*Myodes glareolus*)	Same family	Captivity	Spatial reference memory (operant home cage)	*M. glareolus* (more complex habitat, omnivorous)
Haupt et al. (2010)	Common vole (*M. arvalis*) Bank vole (*M. glareolus*)	Same family	Captivity	Spatial working memory (win-shift task)	*M. glareolus* (more complex habitat, omnivorous)
Henry and Stoner (2011)	Saussure's long-nosed bat (*Leptonycteris yerbabuenae*) Palla's long-tongued bat (*Glossophaga soricina*)	Same family	Wild-caught	Spatial working memory (foraging task)	*L. yerbabuenae* (dietary specialist)
Jones et al. (2017)	Sprague Dawley rat (*Rattus norvegicus*) D57BL/6J mouse (*Mus musculus*)	Same family	Laboratory	Learning (Go/NoGo judgement bias task)	Differential learning: *R. norvegicus* (opportunistically omnivorous, moving food) learns NoGo condition; *M. musculus* (largely herbivorous, active predators, static food) learns Go condition
Mackay and Pillay (2018)	Three striped mice (*Rhabdomys pumilio, R. bechuanae, R. dilectus*)	Same genus	Wild-caught	Spatial learning (Barnes maze)	No difference between *R. pumilio* (low scrubby bushes, open habitat), *R. bechuanae* (grassy cover, savanna) and *R. dilectus* (grassy cover, mosaic forest)
Pleskacheva et al. (2000)	Bank vole (*Myodes glareolus*) Root vole (*Microtus oeconomus*)	Same family	Wild-caught	Spatial search (Morris water test)	*M. glareolus* (more complex habitat, dispersed seeds)
Szabo and Whiting (2020)	Sleepy lizard (*Tiliqua rugosa asper*) Eastern blue-tongued skink (*T. scincoides scincoides*)	Same genus	Wild-caught	Visual discrimination (colour/pattern discrimination)	No difference between *T. r. asper* (rural habitat) and *T. s. scincoides* (urban habitat)
Szabo and Whiting (2020)	Sleepy lizard (*Tiliqua rugosa asper*) Eastern blue-tongued skink (*T. scincoides scincoides*)	Same genus	Wild-caught	Behavioural flexibility (colour/pattern reversal learning)	*T. r. asper* (rural habitat)

Table 1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Teichroeb and Vining (2019)	Grey mouse lemur (*M. murinus*) Fat-tailed dwarf lemur (*Cheirogaleus medius*) Aye-aye (*Daubentonia madagascariensis*)	Same order	Captivity	Spatial navigation (multi-destination array with 6 feeding platforms)	*C. medius* (stationary food) > *M. murinus* (stationary and mobile/ephemeral food)
Trapanese et al. (2019)	Tonkean macaque (*Macaca tonkeana*) Long-tailed macaque (*M. fascicularis*) Capuchin monkey (*Sapajus apella*)	Same order	Semi-free ranging	Foraging decision and goal-directed travel (feeding boxes)	*M. tonkeana* (most frugivory)
White & Brown (2015a)	Cocos frillgoby (*Bathygobius cocosensis*) Krefft's goby (*B. krefftii*) Eastern long-finned goby (*Favonigobius lentiginosus*) Hoese's Sandgoby (*Istigobius hoesei*)	Same family	Wild-caught	Spatial learning (T-maze)	*B. cocosensis* & *B. krefftii* (more complex habitat)

Accessing food sources

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Day et al. (2003)	Lion tamarin (*Leontopithecus* spp.) Tamarin (*Saguinus* spp.) Marmoset (*Callithrix* spp.)	Same family	Captivity	Innovative abilities (novel extractive foraging tasks)	*Leontopithecus* spp. (manipulative extractive foraging) > *Callithrix* spp. (extractive foraging)
Griffin and Diquelou (2015)	Indian myna (*Acridotheres tristis*) Noisy myner (*Manorina melanocephala*)	Same order	Wild-caught	Innovative abilities (novel foraging tasks)	*A. tristis* (opportunistic niche occupation, introduced species)
Henke-von der Malsburg and Fichtel (2018)	Grey mouse lemur (*Microcebus murinus*) Mme Berthe's mouse lemur (*M. berthae*)	Same genus	Wild-caught	Innovative abilities (novel food extraction task)	*M. berthae* (diet and habitat specialist)

Memorising (previous) resource locations

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
Barkley and Jacobs (2007)	Merriam's kangaroo rat (*Dipodomys merriami*) Great Basin kangaroo rat (*D. microps*)	Same genus	Wild-caught	Spatial memory accuracy (cache simulation task)	*D. merriami* (intensive scatter hoarder)
Bond et al. (2007)	Pinyon jays (*Gymnorhinus cyanocephalus*) Clark's nutcrackers (*Nucifraga columbiana*) Western scrub jays (*Aphelocoma californica*)	Same family	Wild-caught	Visual discrimination (colour discrimination)	No difference between *N. columbiana* (highly dependent on food-caching), *G. cyanocephalus* (less dependent on food-caching) and *A. californica* (not dependent on food-caching)
Bond et al. (2007)	Pinyon jays (*G. cyanocephalus*) Clark's nutcrackers (*N. columbiana*) Western scrub jays (*A. californica*)	Same family	Wild-caught	Spatial discrimination (two-choice task)	*N. columbiana* (highly dependent on food-caching)
Bond et al. (2007)	Pinyon jays (*G. cyanocephalus*) Clark's nutcrackers (*N. columbiana*) Western scrub jays (*A. californica*)	Same family	Wild-caught	Behavioural flexibility (colour/spatial reversal learning)	*G. cyanocephalus* (less dependent on food-caching)
Cristol et al. (2003)	Two dark-eyed juncos (*Junco hyemalis hyemalis*, *J. h. carolinensis*)	Different subspecies	Wild-caught	Spatial memory accuracy (one-trial associative memory test)	*J. h. hyemalis* (migratory)
Gibson and Kamil (2005)	Pinyon jays (*G. cyanocephalus*) Clark's nutcrackers (*N. columbiana*) Western scrub jays (*A. californica*)	Same family	Wild-caught	Spatial discrimination (landmark distance discrimination)	*A. californica* (not dependent on food caching; pilfer caches of conspecifics) and *G. cyanocephalus* (highly dependent on food caching; pilfer caches of conspecifics)
Healy and Suhonen (1996)	Willow tit (*Poecile montanus*) Marsh tit (*P. palustris*)	Same genus	Wild-caught	Food retrieval performance (retrieving stored food after delays)	No difference between *P. montanus* (store food for a several weeks) and *P. palustris* (store food for a few

Table 1 (continued)

Reference	Species	Phylogenetic distance	Test environment	Cognitive measure (experimental task)	Greater performance (ecological characteristic)
					hours/days)
Platt et al. (1996)	Wied's marmoset (*Callithrix kuhlii*) Golden lion tamarin (*Leontopithecus rosalia*)	Same family	Captivity	Spatial memory retention (radial maze, delayed matching-to-sample task; short retrieval intervals)	*C. kuhlii* (revisit food patches several times a day)
Platt et al. (1996)	Wied's marmoset (*C. kuhlii*) Golden lion tamarin (*L. rosalia*)	Same family	Captivity	Spatial memory retention (radial maze, delayed matching-to-sample task; long retrieval intervals)	*L. rosalia* (revisit food patches several times a week)
Rosati and Hare (2012)	Chimpanzee (*Pan troglodytes*) Bonobo (*P. paniscus*)	Same genus	Semi-free ranging	Spatial working memory (foraging task)	*P. troglodytes* (dependence on patchily distributed food)
Rosati et al. (2014)	Ruffed lemur (*Varecia* spp.) Ring-tailed lemur (*Lemur catta*) Mongoose lemur (*Eulemur mongoz*) Coquerel's sifaka (*Propithecus coquereli*)	Same family	Captivity	Spatial memory (food retrieval tasks)	*Varecia* spp. (most frugivorous diet)
Other challenges					
Bednekoff and Balda (1996)	Clark's nutcracker (*N. columbiana*) Mexican jay (*Aphelocoma ultramarina*)	Same family	Wild-caught	Observational spatial memory (pair cache/recovery tasks)	*A. ultramarina* (non-specialized cacher)
Day et al. (1999a)	Nidua fringe-toed lizard (*A. scutellatus*) Bosc's fringe-toed lizard (*A. boskianus*)	Same genus	Wild-caught	Spatial memory accuracy (Barnes maze, local cue version)	No difference between *A. scutellatus* (distributed mobile prey) and *A. boskianus* (clumped sedentary prey)
Hoedjes et al. (2012)	3 wasps (*Nasonia vitripennis*, *N. longicornis*, *N. giraulti*)	Same genus	Laboratory	Olfactory memory (T-maze olfactometer)	*N. vitripennis* (host generalist), *N. longicornis* (lesser host generalist)

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

which complement their nectar and pollen diet additionally with fruits and insects according to seasonal availability (Henry and Stoner 2011). Thus, the reliance on more mobile food items seems to increase exploration, which results in lower task performance in spatial cognition tests.

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

Accessing food items

Once an animal has solved the problem of locating a given food patch, it encounters the next challenge: the extraction of the actual food item. Depending on the item's characteristics, superior sensorimotor coordination or manipulative skills, including extractive foraging techniques or tool use, are beneficial but also energetically more costly and ultimately require a larger brain (Parker and Gibson 1977; Heldstab et al. 2016). Sensorimotor control and extractive foraging abilities seem to be especially helpful for solving innovative problems, and the majority of innovative behaviours has indeed been recorded in the foraging domain (Reader and Laland 2002); Indian mynas (*Acridotheres tristis*), which exhibited greater diversity in motor behaviours, were more innovative than noisy miners (*Manorina melanocephala*) (Griffin and Diquelou 2015). Madame Berthe's mouse lemurs (*Microcebus berthae*) that expressed better motor control than grey mouse lemurs subsequently learned a modified innovative problem faster

Table 2 Overview of studies comparing cognitive abilities under certain ecological relevance, indicating the degree of ecological specialisation (habitat/dietary) of the best performing species, as well as its group size as indicator for sociality and an indicator for brain size, each as relative measure to the species in comparison

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance Species	Ecological lifestyle	Social organization	Brain size
Habitat exploration							
Bond et al. (2007)	Pinyon jays (G. cyanocephalus) Clark's nutcrackers (N. columbiana) Western scrub jays (A. californica)	Spatial discrimination	Habitat exploration: locating food patch	N. columbiana	Habitat specialist Dietary specialist	Smaller (solitary/pair-living) (Clary and Kelly 2011)	Similar to G. cyanocephalus, smaller than A. californica (relative hippocampal volume to body mass) (Pravosudov and De Kort 2005)
				Sign	- -	-	0/-
Clarin et al. (2013)	Long-fingered bat (M. capaccinii) Greater mouse-eared bat (M. myotis) Geoffroy's bat (M. emarginatus)	Spatial discrimination	Habitat exploration: locating food patch	No difference	M. capaccinii: Habitat specialist Dietary generalist (Dietz and Kiefer 2016) M. myotis: Habitat generalist Dietary generalist (Dietz and Kiefer 2016) M. emarginatus: Habitat generalist Dietary specialist (Dietz and Kiefer 2016)	Similar (males roost singly or in small colonies)	Relative skull length: M. capaccinii < M. emarginatus < M. myotis
				Sign	Not assigned (no difference in cognitive performance)		
Clarin et al. (2013)	Long-fingered bat (M. capaccinii) Greater mouse-eared bat (M. myotis) Geoffroy's bat (M. emarginatus)	Spatial reversal learning	Habitat exploration: modified food patch location	M. myotis M. emarginatus	M. myotis: Habitat generalist Dietary generalist (Dietz and Kiefer 2016) M. emarginatus: Habitat generalist Dietary generalist (Dietz and Kiefer 2016)	Similar (males roost singly or in small colonies)	Potentially larger (relative skull length)
				Sign	+ +	0	+
Clarin et al. (2013)	Long-fingered bat (M. capaccinii) Greater mouse-eared bat (M. myotis) Geoffroy's bat (M. emarginatus)	Complex spatial discrimination	Habitat exploration: locating food patch	M. myotis M. emarginatus	M. myotis: Habitat generalist Dietary generalist (Dietz and Kiefer 2016) M. emarginatus: Habitat generalist	Similar (males roost singly or in small colonies)	Potentially larger (relative skull length)

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance (Species / Sign)	Ecological lifestyle	Social organization	Brain size
					Dietary generalist (Dietz and Kiefer 2016) — + +	0	
Cristol et al. (2003)	Two dark-eyed juncos (J. h. hyemalis, J. h. carolinensis)	Spatial memory accuracy	Habitat exploration: locating previous food items	J. h. hyemalis / Sign	Similar habitat/dietary specialisation — 0 0	Similar (group-living) — 0	Smaller (fixed brain mass, telencephalon volume) — +
Day et al. (1999a)	Nidua fringe-toed lizard (A. scutellatus) Bosc's fringe-toed lizard (A. boskianus)	Spatial memory accuracy	Habitat exploration: locating preferable sites	No difference (ecological irrelevance of the task) / Sign	Similar habitat/dietary specialisation (Aicha et al. 2017, Roobas and Feulner 2013) Not assigned (no difference in cognitive performance) — + +	Similar (solitary)	Difference in relative medial/dorsal cortex volume (Day et al. 1999b) — −
Gibson and Kamil (2005)	Pinyon jays (G. cyanocephalus) Clark's nutcrackers (N. columbiana) Western scrub jays (A. californica)	Spatial discrimination	Habitat exploration: locating preferable sites	G. cyanocephalus A. californica / Not assigned (no difference in cognitive performance) / Sign	G. cyanocephalus: Habitat generalist Dietary generalist A. californica: Habitat generalist Dietary generalist — + +	Larger (flocks) (Bond et al. 2007) — +	Similar for G. cyanocephalus, larger for A. californica (relative hippocampal volume to body mass) (Pravosudov and De Kort 2005) — 0/+
Gingins and Bshary (2016)	Bluestreak cleaner wrasse (L. dimidiatus) Other labrids (P. hexataenia, H. melanurus, T. lunare, H. melapterus, L. unilineatus)	Spatial discrimination	Habitat exploration: locating preferable sites	No difference (ecological irrelevance of the task) / Not assigned (no difference in cognitive performance) / Sign	L. dimidiatus: Dietary specialist Others: Dietary generalist — + +	NA	NA
Haupt et al. (2010)	Common vole (M. arvalis) Bank vole (M. glareolus)	Spatial memory	Habitat exploration: locating food patches	M. glareolus / Sign	Habitat generalist Dietary generalist — + +	Smaller (solitary) (Lundrigan and Mueller 2003, and Noble 2017) — −	NA
Haupt et al. (2010)	Common vole (M. arvalis) Bank vole (M. glareolus)	Spatial memory		M. glareolus	Habitat generalist Dietary generalist	Smaller (solitary) (Lundrigan and	NA

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance Species	Sign	Ecological lifestyle	Social organization	Brain size
			Habitat exploration: locating food patches	Sign		+ +	Mueller 2003, and Noble 2017)	
							-	NA
Jones et al. (2017)	Sprague Dawley rat (*R. norvegicus*) D57BL/6J mouse (*M. musculus*)	Go/NoGo learning	Habitat exploration: locating preferable sites	Go-learning: *M. musculus* D57BL/6J NoGo-learning: *Rattus norvegicus* Sign		NA NA	NA NA	NA NA
Mackay and Pillay (2018)	Three striped mice (*R. pumilio, R. bechuanae, R. dilectus*)	Spatial learning	Habitat exploration: locating food patches	No difference (phylogenetical-ly constrained cognitive ability) Not assigned (no difference in cognitive performance) Sign		Different ecological characteristics (Du Toit et al. 2016, Meynard et al. 2012, Ganem et al. 2020)	*R. pumilio*: group-living (Schradin and Pillay 2004) *R. bechuanae*: solitary *R. dilectus*: solitary (Ganem et al. 2012)	NA
Pleskacheva et al. (2000)	Bank vole (*M. glareolus*) Root vole (*M. oeconomus*)	Spatial search	Habitat exploration: locating preferable sites	*M. glareolus* Sign		Habitat generalist Dietary generalist + +	Similar (solitary) (Lundrigan and Mueller 2003, Bieberich 2007) 0	Larger (relative brain mass, mossy fibre projection) +
Teichroeb and Vining (2019)	Grey mouse lemur (*M. murinus*) Fat-tailed dwarf lemur (*C. medius*) Aye-aye (*D. madagascariensis*)	Spatial navigation	Habitat exploration: locating food patches	*C. medius* Sign		Habitat generalist Dietary specialist + -	Similar (solitary) 0	Smaller (relative brain mass to body mass) (MacLean et al. 2009) -
Trapanese et al. (2019)	Tonkean macaque (*Macaca tonkeana*) Long-tailed macaque (*M. fascicularis*) Capuchin monkey (*Sapajus apella*)	Decision-making	Habitat exploration: choosing food patches	*C. medius* Sign		Habitat generalist Dietary specialist + -	Similar (solitary) 0	Smaller (relative brain mass to body mass) (MacLean et al. 2009) -

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance		Ecological lifestyle	Social organization	Brain size
				Species	Sign			
White and Brown (2015a)	Cocos frillgoby (B. cocosensis) Krefft's goby (B. krefftii) Eastern long-finned goby (F. lentiginosus) Hoese's Sandgoby (I. hoesei)	Spatial learning	Habitat exploration: locating food patches	B. cocosensis B. krefftii		NA	NA	Larger (relative telencephalon volume) (White and Brown 2015b)
				Sign	+	NA	NA	+
Foraging								
Barkley and Jacobs (2007)	Merriam's kangaroo rat (D. merriami) Great Basin kangaroo rat (D. microps)	Spatial memory accuracy	Foraging: food-caching	D. merriami		Similar habitat specialisation Dietary specialist (Timm et al. 2016, Cassola 2016)	Similar (solitary) (Howard 1994)	Larger (encephalisation quotient) (Hafner and Hafner 1984)
				Sign		0	0	+
Bednekoff and Balda (1996)	Clark's nutcracker (N. columbiana) Mexican jay (A. ultramarina)	Observational spatial memory	Foraging: food-caching	A. ultramarina		Habitat generalist Dietary generalist (Bond et al. 2007, McCormack and Smith 2008)	Larger (flocks of several dozen)	NA
				Sign		+	+	NA
Bond et al. (2007)	Pinyon jays (G. cyanocephalus) Clark's nutcrackers (N. columbiana) Western scrub jays (A. californica)	Visual discrimination	Foraging: identifying food item	No difference		G. cyanocephalus: Habitat generalist Dietary generalist N. columbiana: Habitat specialist Dietary specialist A. californica: Habitat generalist Dietary generalist	G. cyanocephalus: large flocks N. columbiana: solitary/pair-living A. californica: large flocks (Clary and Kelly 2011)	G. cyanocephalus = N. columbiana < A. californica (relative hippocampal volume to body mass) (Pravosudov and De Kort 2005)
				Sign		Not assigned (no difference in cognitive performance)	+	
Bond et al. (2007)	Pinyon jays (G. cyanocephalus) Clark's nutcrackers (N. columbiana) Western scrub jays (A. californica)	Behavioural flexibility	Foraging: identifying food item	G. cyanocephalus		Similar habitat/dietary specialisation to A. californica Habitat generalist Dietary generalist to N. columbiana	Similar to A. californica, larger than N. columbiana (Clary and Kelly 2011)	Similar to N. columbiana, smaller than A. californica (relative hippocampal volume to body mass) (Pravosudov and De Kort 2005)
				Sign		0/+ 0/+	0/+	

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance — Species	Ecological lifestyle	Social organization	Brain size
							0/-
Day et al. (1999a)	Nidua fringe-toed lizard (*A. scutellatus*) Bosc's fringe-toed lizard (*A. boskianus*)	Visual discrimination	Foraging: identifying food item	No difference	Similar habitat/dietary specialisation (Aicha et al. 2017, Roobas and Feulner 2013)	Similar (solitary)	Difference in relative medial/dorsal cortex volume (Day et al. 1999b)
				Sign	Not assigned (no difference in cognitive performance)		
Day et al. (1999a)	Nidua fringe-toed lizard (*A. scutellatus*) Bosc's fringe-toed lizard (*A. boskianus*)	Behavioural flexibility	Foraging: identifying food item	*A. scutellatus*	Similar habitat/dietary specialisation (Aicha et al. 2017, Roobas and Feulner 2013)	Similar (solitary)	Larger (relative medial/dorsal cortex volume) (Day et al. 1999b)
				Sign	0 0	0	+
Day et al. (2003)	Lion tamarin (*Leontopithecus* spp.) Tamarin (*Saguinus* spp.) Marmoset (*Callithrix* spp.)	Innovative problem-solving	Foraging; food extraction	*Leontopithecus* spp.	Habitat specialist Dietary generalist	Intermediate (group-living)	Intermediate (encephalisation quotient) (Hartwig et al. 2011)
				Sign	- +	0	0
Griffin and Diquelou (2015)	Indian myna (*A. tristis*) Noisy myner (*M. melanocephala*)	Innovative problem-solving	Foraging; food extraction	*A. tristis*	Habitat generalist Dietary generalist	Smaller (pair-living)	Smaller (lower positive residuals of brain size)
				Sign	+ +	-	-
Healy and Suhonen (1996)	Willow tit (*P. montanus*) Marsh tit (*P. palustris*)	Food retrieval performance	Foraging: food-caching	No difference (unsuitable study design)	Similar habitat/dietary specialisation (BirdLife International 2017), BirdLife International 2019)	Similar (pair-living) (BirdLife International 2017, BirdLife International 2019)	Relative hippocampal formation volume larger in *P. palustris* than *P. montanus* (Lucas et al. 2004)
				Sign	Not assigned (no difference in cognitive performance)		
Henke-von der Malsburg and Fichtel (2018)	Grey mouse lemur (*M. murinus*) Mme Berthe's mouse lemur (*M. berthae*)	Innovative problem-solving	Foraging; food extraction	*M. berthae*	Habitat specialist Dietary specialist	Similar (solitary) (Dammhahn and Kappeler 2005)	NA
				Sign	- -	0	NA
	L. yerbabuenae						NA

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance: Species	Ecological lifestyle	Social organization	Brain size
Henry and Stoner (2011)	Saussure's long-nosed bat (*L. yerbabuenae*) Palla's long-tongued bat (*G. soricina*)	Spatial working memory	Foraging: exploiting food patches	Sign	Habitat generalist Dietary specialist (Cole and Wilson 2006, Alvarez et al. 1991) + -	Larger (colonies of up to tens of thousands) +	NA
Hoedjes et al. (2012)	3 wasps (*N. vitripennis*, *N. longicornis*, *N. giraulti*)	Olfactory memory	Foraging: memorising food patch (here: host)	*N. vitripennis* Sign	Host generalist NA +	NA	NA
Platt et al. (1996)	Wied's marmoset (*C. kahlii*) Golden lion tamarin (*L. rosalia*)	Spatial memory retention	Foraging: food retrieval after a relatively short period (5 or 30 min)	*C. kahlii* Sign	Habitat generalist Dietary specialist (Day et al. 2003) + -	Smaller (Day et al. 2003) -	Potentially smaller (encephalisation quotient) (Hartwig et al. 2011) -
Platt et al. (1996)	Wied's marmoset (*C. kahlii*) Golden lion tamarin (*L. rosalia*)	Spatial memory retention	Foraging: food retrieval after a relatively long period (24 or 48 h)	*L. rosalia* Sign	Habitat specialist Dietary generalist (Day et al. 2003) - +	Larger (Day et al. 2003) +	Potentially larger (encephalisation quotient) (Hartwig et al. 2011) +
Rosati and Hare (2012)	Chimpanzee (*P. troglodytes*) Bonobo (*P. paniscus*)	Spatial working memory	Foraging: food retrieval	*P. troglodytes* Sign	Similar habitat/dietary specialisation (Rosati 2017) 0 0	Similar (group-living) (Rosati 2017) 0	Larger hippocampus, greater connection with other brain regions (Rosati 2017) +
Rosati et al. (2014)	Ruffed lemur (*Varecia* spp.) Ring-tailed lemur (*L. catta*) Mongoose lemur (*E. mongoz*) Coquerel's sifaka (*P. coquereli*)	Spatial memory retention	Foraging: food retrieval	*Varecia* spp. Sign	Dietary specialist (note: another dietary specialist performed the worst, two dietary generalist species performed on an intermediate level) NA -	Medium 0	Smaller (relative brain mass to body mass) (MacLean et al. 2009) -
Szabo and Whiting (2020)	Sleepy lizard (*T. r. asper*)	Visual discrimination	Foraging: identifying food patch	No difference	*T. r. asper*: Habitat generalist Dietary generalist	*T. r. asper*: pair-living	NA

Table 2 (continued)

Reference	Species	Cognitive measure	Primary ecological relevance	Best performance		Ecological lifestyle	Social organization	Brain size
				Species	Sign			
	Eastern blue-tongued skink (*T. s. scincoides*)				Sign	*T. s. scincoides*: Habitat specialist Dietary specialist / Not assigned (no difference in cognitive performance)	*T. s. scincoides*: solitary	
Szabo and Whiting (2020)	Sleepy lizard (*T. r. asper*)	Behavioural flexibility	Foraging; identifying food patch	*T. r. asper*		Habitat generalist Dietary generalist	Larger (pair-living)	NA
	Eastern blue-tongued skink (*T. s. scincoides*)				Sign	+	+	NA

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

(Henke-von der Malsburg and Fichtel 2018). In seven species of callitrichid monkeys, the existence of extractive foraging techniques predicted innovative abilities, with lion tamarins (*Leontopithecus* spp.), which are manipulative extractive foragers with a higher innovative potential, exceeding the gum-specialised, extractive foraging marmosets (*Callithrix* spp.) and the non-extractive, but only visually, foraging tamarins (*Saguinus* spp.) (Day et al. 2003). These examples suggests that efficient access to food sources can vary with cognitive abilities such as innovative behaviours, which also seemed to be influenced by motor coordination.

Memorising previous resource locations

When animals are highly reliant on cached food or when they migrate to other habitats, usually due to seasonal food shortage (Wall and Stephen 1990; Dingle 2014), they require well-developed spatial cognitive abilities. In both cases, animals with good spatial processing abilities are better at memorising locations of food patches than animals with no or only basic spatial processing abilities (Shettleworth 1990; Sherry et al. 1992). For example, compared to non-migratory dark-eyed juncos (*Junco hyemalis carolinensis*), migratory dark-eyed juncos (*J. h. hyemalis*) showed greater accuracy in remembering feeder locations that have been visited only once before a certain retrieval interval (Cristol et al. 2003). Moreover, Merriam's kangaroo rat (*Dipodomys merriami*), an intensive scatter hoarder, showed better spatial memory accuracy in a cache simulation task than the Great Basin kangaroo rat (*D. microps*), a leaf-eating specialist that does not rely on scatter hoarding (Barkley and Jacobs 2007). Furthermore, food-caching Clark's nutcrackers (*Nucifraga columbiana*) performed better in an initial spatial discrimination task than less food-caching pinyon (*Gymnorhinus cyanocephalus*) and non-food-caching Western scrub jays (*Aphelocoma californica*). Pinyon jays, however, performed better than the other two corvid species in serial reversal learning tasks (Bond et al. 2007) and Western scrub jays performed better in a distance discrimination task (Gibson and Kamil 2005). Thus, the reliance on food-caching can covary with spatial memory, but not necessarily with other cognitive abilities.

Although primates do not rely on food-caching, spatial memory abilities can be beneficial for relocating a certain food patch. Indeed, chimpanzees (*Pan troglodytes*) that feed on more patchy distributed foods than bonobos (*P. paniscus*) exhibited better retrieval performance when food items were hidden by a human demonstrator (Rosati and Hare 2012). Similarly, lemurs varied in performance in spatial memory tasks according to their diet. The most frugivorous ruffed lemurs (*Varecia* spp.) showed better spatial memory than ring-tailed lemurs (*Lemur catta*), mongoose lemurs (*Eulemur mongoz*) and Coquerel's sifakas (*Propithecus coquereli*), the latter being the most folivorous species (Rosati et al. 2014).

Wied's marmosets (*Callithrix kuhlii*) performed better than golden lion tamarins (*Leontopithecus rosalia*) in spatial memory experiments with relatively short retention intervals (5 or 30 min). However, they performed poorly after longer retention intervals (24 or 48 h), while the tamarins could maintain their performance level (Platt et al. 1996). Again, the observed interspecific differences match the species' foraging strategies: while marmosets revisit single food patches several times per day (Rylands 1989), tamarins do so only every 3 days (Peres 1989). Hence, spatial memory abilities also vary in accordance with a species-typical foraging ecology.

Ecological generalism versus ecological specialisation

Empirical comparisons of cognitive performance between generalists and specialists have either investigated effective habitat exploration in, for instance, spatial memory tasks (Pleskacheva et al. 2000; Haupt et al. 2010), or specific foraging abilities like innovative propensities (Day et al. 2003; Overington et al. 2009; Overington et al. 2011; Griffin and Diquelou 2015; Henke-von der Malsburg and Fichtel 2018), associative learning (Hoedjes et al. 2012) or behavioural flexibility (Day et al. 1999a), using a variety of problem-solving experiments, including food extraction tasks, visual or olfactory discriminations or reversal learning tasks.

Habitat exploration and the degree of habitat specialisation

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

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

Foraging and the degree of dietary specialisation

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

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

Individuals with greater innovative abilities are also expected to deal more efficiently with changing environmental conditions, including diet (Sol et al. 2005). Since generalist species are by definition exposed to more variable conditions, they are suggested to express greater behavioural flexibility and greater innovative propensities than specialists (Ducatez et al. 2014a; Navarrete et al. 2016). Among birds, habitat generalist species have indeed higher innovation rates than habitat specialists (Overington et al. 2011). Moreover, the omnivorous Indian myna showed a higher innovative propensity than the noisy miner, which is specialised on honey (Griffin and Diquelou 2015). In contrast, the more dietary and habitat specialised Madame Berthe's mouse lemur outperformed the sympatric generalist grey mouse lemur in innovative extractive foraging tasks with variable difficulties (Henke-von der Malsburg and Fichtel 2018). The better performance of the specialist might have been a result of enhanced executive control enabling individuals to inhibit the use of a previously learned problem-solving technique and to develop an adjusted solution to a modified problem, indicating that other factors than ecological specialisation may explain variation in performance. Across

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

In general, cognitive performance can be related to the degree of ecological specialisation. Twenty-one of the interspecific comparisons reviewed here report cognitive differences between species expressing a different degree of habitat/dietary specialisation, while four do not (sign-test: $p < 0.001$). Habitat generalists ($N = 14$) were more likely to outperform habitat specialists ($N = 4$; sign-test: $p = 0.031$), but the degree of dietary specialisation could not explain interspecific variation in cognitive performance (sign-test: $N_{generalist} = 13$, $N_{specialist} = 8$, $p = 0.383$).

Variation in cognitive performance in relation to group size

Because performance in cognitive tests in these studies might be explained by consistent differences in sociality, we scored the species included in this review with respect to their group size to index their social complexity (Table 2). While half of the comparisons ($N = 13$) are controlled for group size effects, the other half ($N = 11$) compared species living in differently sized groups, which also exhibit interspecific cognitive variation. However, we do not find species living in larger groups to generally perform better than those living in smaller groups, which might also be due to our small sample size (sign-test: $N_{larger} = 6$, $N_{smaller} = 5$, $p = 1$).

Five studies supported a positive link between group size and cognitive performance: Mexican and pinyon, as well as Western scrub jays, which live in larger flocks, performed better in spatial learning paradigms than Clark's nutcrackers (Bednekoff and Balda 1996; Gibson and Kamil 2005); Saussure's long-nosed bat, which form larger colonies, performed better in a spatial working paradigm than Palla's long-tongued bat (Henry and Stoner 2011); pair-living sleepy lizards were more behaviourally flexible in a visual reversal learning task than solitary Eastern blue-tongued skinks (Szabo and Whiting 2020); and golden lion tamarins, which live in relatively larger groups, showed better memory retention for longer retention intervals than Wied's marmosets (Platt et al. 1996). However, Wied's marmosets outperformed golden lion tamarins in the same task using a shorter retrieval period (Platt et al. 1996). In lemurs, performance in a spatial memory task was not linearly related to group size across four species (Rosati et al. 2014). Moreover, in innovative problem-solving paradigms, primates living in intermediate-sized (Day et al. 2003) or birds living in smaller groups (Griffin and Diquelou 2015) outperformed the respective species living in relatively larger groups.

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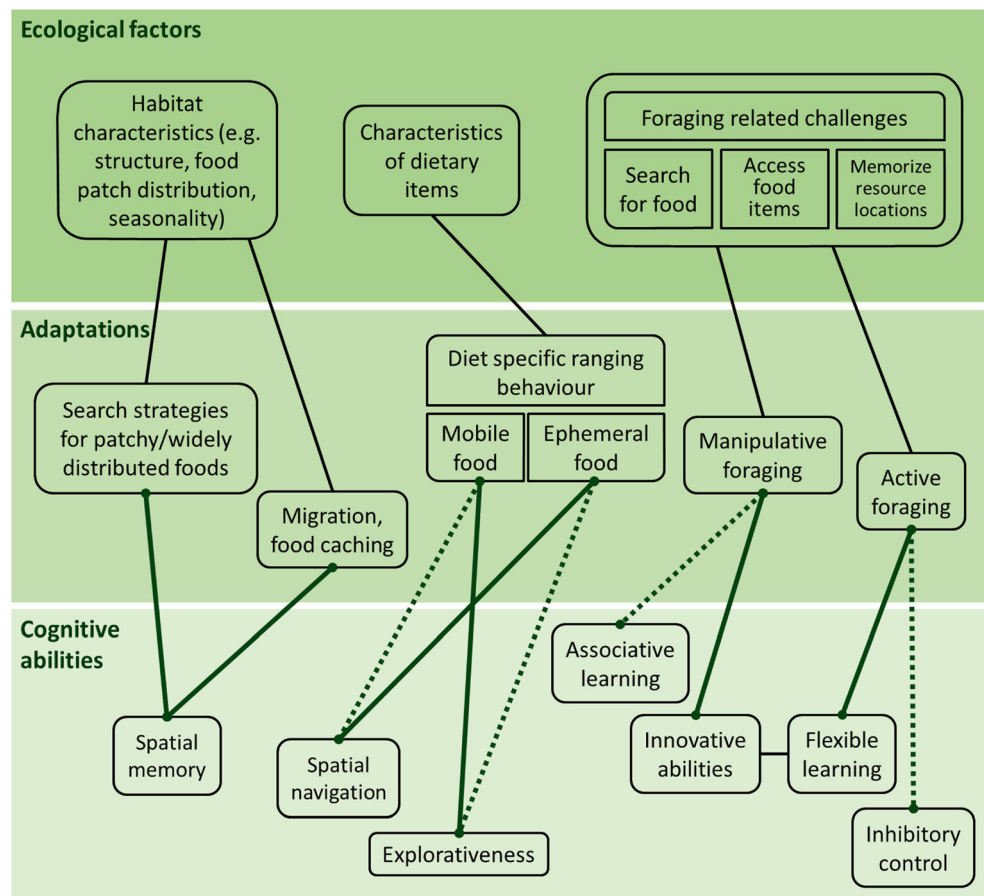
Variation in cognitive performance in relation to brain size

Brain size can be assessed via absolute or relative brain mass or volume, via an encephalisation quotient (Jerison 1973; Hartwig et al. 2011) or neural connectivity, for instance. Since the studies included in this review were not designed to compare potential effects of a certain brain size measure, we had to find comparable measures or proxies elsewhere (Table 2). With this information, we did not find evidence for a link between experimental cognitive performance and brain size in this sample (sign-test: $N_{bigger} = 9$, $N_{smaller} = 8$, $p = 1$). Since the available brain size measures differed between these relatively few studies, the observed lack of an effect of brain size on cognitive performance might reflect this methodological shortcoming.

Discussion

In this review, we summarised comparative research investigating variation in cognitive performance in relation to specific adaptations to ecological factors animals are exposed to in their daily life. Although these ecological factors can vary greatly among species in the same taxonomic group, studies systematically investigating the relationship between ecological factors and cognitive performance are still rare. Most studies reported a predicted relationship between the measured cognitive performance and an ecological factor differentiating the study species (Table 1), but we cannot know whether this pattern is affected by a publication bias against studies reporting no effect. Our rough control indicated that phylogeny as well as group and brain size did not have pervasive effects on the observed pattern. Nonetheless, some studies failed to find an effect of ecology, perhaps due to unsuitable study designs (Bednekoff and Balda 1996; Healy and Suhonen 1996) and/or ecological irrelevance of the respective

Fig. 2 Links between ecology and cognition. We identified several links (thick lines) between cognitive abilities and adaptations to ecological factors (thin lines) such as certain habitat characteristics, characteristics of dietary items or ecological challenges related to the foraging process (including the search for food, access to food items and memorising resource locations). Positive relationships between specific adaptations and cognitive abilities are represented with thick solid lines while negative relationships are represented with dashed lines

cognitive ability tested (Day et al. 1999a; Gingins and Bshary 2016). Below, we discuss the main correlates of interspecific variation in cognitive performance in terms of flexible foraging strategies, spatiotemporal habitat exploration and food patch exploitation, as well as the degree of ecological specialisation. Further, we highlight the importance of considering potentially confounding factors when designing a study appropriate for the investigation of species-specific ecological adaptations (Shaw and Schmelz 2017; Schubiger et al. 2020).

Adaptations to particular ecological factors correlate with cognitive performance

Flexible foraging strategies

Interspecific differences in cognitive performance have been reported as a function of variation in ranging behaviour and search strategies (Teichroeb and Vining 2019; Trapanese et al. 2019), foraging activity (Day et al. 1999a; Day et al. 2003; Jones et al. 2017), foraging techniques (Day et al. 2003), characteristics of preferred dietary items (Pleskacheva et al. 2000; Henry and Stoner 2011; Teichroeb and Vining 2019), adaptations to habitat complexity (Pleskacheva et al. 2000; Clarin et al. 2013; White and Brown 2015a) or adaptations to seasonality (Cristol et al. 2003; Barkley and Jacobs 2007; Henry and Stoner 2011) (Fig.

2). Active or manipulative extractive foragers have been reported to learn more flexibly (Day et al. 1999a) or to be more innovative (Day et al. 2003), respectively. Flexible learning and innovative abilities can be linked to innovators that possess the ability to invent a new behaviour or to modify an existing behaviour (Reader and Laland 2003) and to incorporate these into the behavioural repertoire via flexible learning mechanisms (Dukas and Ratcliffe 2009). In contrast to sit-and-wait predators, active foragers need to rapidly adjust the current foraging strategy to the behaviour of the prey of interest as well as to the environment while searching and hunting for prey. They would specifically benefit by learning the association of a certain stimulus with a reward (i.e. the prey) and to flexibly update such associations whenever the stimulus or other conditions change. This underlying behavioural flexibility is then an advantageous characteristic when environmental conditions change (Lee 2003; Lefebvre et al. 2004). Further, innovations appear predominantly in the foraging context (Reader and MacDonald 2003), favouring a link with a species' foraging ecology rather than with its sociality.

Spatiotemporal habitat exploration and food patch exploitation

When searching for food, animals always need to deal with the tradeoff between habitat exploration and food patch

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

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

Other ecological adaptations

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

How does cognitive performance correlate with the degree of ecological specialisation?

In several studies, we found the degree of ecological specialisation to be correlated with variation in certain cognitive abilities

(Platt et al. 1996; Pleskacheva et al. 2000; Day et al. 2003; Barkley and Jacobs 2007; Haupt et al. 2010; Henry and Stoner 2011; Hoedjes et al. 2012; Rosati et al. 2014; Griffin and Diquelou 2015; Henke-von der Malsburg and Fichtel 2018). We found that habitat generalists generally outperform habitat specialists, but the degree of dietary specialisation did not consistently vary with cognitive performance. Given that habitat generalists regularly face more challenges by exploring a broader, more variable habitat than specialists, they might specifically exhibit better spatial processing abilities and more behavioural flexibility (Overington et al. 2011), at least in the sense of 'behavioural flexibility' allowing for adaptations to variable environments (Lea et al. 2020). However, behavioural flexibility does not necessarily result in better cognitive performance per se because less behaviourally flexible species, as specialists, may instead possess other behavioural characteristics that promote better performance in certain cognitive skills (Henke-von der Malsburg and Fichtel 2018). In studies reporting the more specialised species to exhibit better performance than the generalist (e.g. Teichroeb and Vining 2019), better performance was linked to specific adaptations for habitat exploration or exploitation. In this context, efficiency can be of various nature: to not use certain paths multiple times while foraging, to deplete a certain food patch to a certain extent varying with search decision rules (Wilke et al. 2009) or to not use ineffective solutions but to inhibit the execution of related behaviours. Greater efficiency might be more likely to vary with specific adaptations to certain ecological challenges than to the degree of ecological generalism per se and would require a more detailed investigation than the currently available evidence allows.

Confounding factors and limitations of the review

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

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

reversal learning task than Clark's nutcracker and Mexican jays with a more generalist ecology (Bond et al. 2007).

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

Compliance with ethical standards

Conflict of interest   The authors declare no conflict of interest.

Ethics approval   Not applicable.

Consent to participate   Not applicable.

Consent for publication   Not applicable.

Table 3   Definitions and explanations of cognitive terms

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

Table 3 (continued)

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

Code availability   Not applicable.

Appendix 1

References

Aicha M, Hadjer A, Raounak K, Karima M (2017) Diet analysis of *Acanthodactylus scutellatus* (AUDOUIN, 1809) (Lacertidae) in the Algerian septentrional Sahara (Oued Souf). J Entomol Zool Stud 5:302–305

Alvarez J, Willig MR, Jones KJ, Webster DW (1991) *Glossophaga soricina*. Am Soc Mammal 379:1–7

Amici F, Aureli F, Call J, Street B (2008) Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol 18: 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Amici F, Call J, Watzek J, Brosnan S, Aureli F (2018) Social inhibition and behavioural flexibility when the context changes: a comparison across six primate species. Sci Rep 8:3067. https://doi.org/10.1038/s41598-018-21496-6

Ashton BJ, Ridley AR, Edwards EK, Thornton A (2018a) Cognitive performance is linked to group size and affects fitness in Australian magpies. Nature 554:364–367. https://doi.org/10.1038/nature25503

Ashton BJ, Thornton A, Ridley AR (2018b) An intraspecific appraisal of the social intelligence hypothesis. Phil Trans R Soc B 373: 20170288. https://doi.org/10.1098/rstb.2017.0288

Ashton BJ, Thornton A, Ridley AR (2019) Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. Anim Behav 158:1–7. https://doi.org/10.1016/j.anbehav.2019.10.004

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, Schaik CP (2008) Fission-fusion dynamics. Curr Anthropol 49:627–654. https://doi.org/10.1086/586708

Barkley CL, Jacobs LF (2007) Sex and species differences in spatial memory in food-storing kangaroo rats. Anim Behav 73:321–329. https://doi.org/10.1016/j.anbehav.2006.07.009

Barton RA (1996) Neocortex size and behavioural ecology in primates. Proc R Soc Lond B 263:173–177. https://doi.org/10.1098/rspb.1996.0028

Barton RA, Harvey PH (2000) Mosaic evolution of brain structure in mammals. Nature 405:1055–1058. https://doi.org/10.1038/35016580

Bednekoff PA, Balda RP (1996) Observational spatial memory in Clark's nutcrackers and Mexican jays. Anim Behav 52:833–839. https://doi.org/10.1006/anbe.1996.0228

Bednekoff PA, Balda RP, Kamil AC, Hile AG (1997) Long-term spatial memory in four seed-caching corvid species. Anim Behav 53:335–341. https://doi.org/10.1006/anbe.1996.0395

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE (2016) Brain size predicts problem-solving ability in mammalian carnivores. P Natl Acad Sci USA 113:2532–2537. https://doi.org/10.1073/pnas.1505913113

Bieberich C (2007) "*Microtus oeconomus*" (On-line). In: Anim Divers Web. https://animaldiversity.org/accounts/Microtus_oeconomus/. Accessed 12 Sep 2020

BirdLife International (2017) *Poecile palustris*. IUCN Red List Threatened Species 2017:eT22735995A118837418 8235

BirdLife International (2019) Threatened. IUCN Red List Threatened Species 2019:eT155139697A155139155 8235

Bókony V, Lendvai ÁZ, Vágási CI et al (2014) Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. Behav Ecol 25:124–135. https://doi.org/10.1093/beheco/art094

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28. https://doi.org/10.1086/343878

Bond AB, Kamil AC, Balda RP (2003) Social complexity and transitive inference in corvids. Anim Behav 65:479–487. https://doi.org/10.1006/anbe.2003.2101

Bond AB, Kamil AC, Balda RP (2007) Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica). J Comp Psychol 121:372–379. https://doi.org/10.1037/0735-7036.121.4.372

Bräuer J, Hanus D, Pika S, Gray R, Uomini N (2020) Old and new approaches to animal cognition: there is not "one cognition". J Intell 8:1–28. https://doi.org/10.3390/jintelligence8030028

Brown C, Braithwaite VA (2005) Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. Behav Ecol 16:482–487. https://doi.org/10.1093/beheco/ari016

Burkart JM, Schubiger MN, van Schaik CP (2017) The evolution of general intelligence. Behav Brain Sci 40:e195. https://doi.org/10.1017/S0140525X16000959

Byrne RW, Bates LA (2010) Primate social cognition: uniquely primate, uniquely social, or just unique? Neuron 65:815–830. https://doi.org/10.1016/j.neuron.2010.03.010

Cassola F (2016) *Dipodomys microps*. In: IUCN Red List Threatened Species 2016:eT42603A22227645. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T42603A22227645.en

Clarin TMA, Ruczyński I, Page RA, Siemers BM (2013) Foraging ecology predicts learning performance in insectivorous bats. PLoS ONE 8:e64823. https://doi.org/10.1371/journal.pone.0064823

Clary D, Kelly DM (2011) Cache protection strategies of a non-social food-caching corvid, Clark's nutcracker (*Nucifraga columbiana*). Anim Cogn 14:735–744. https://doi.org/10.1007/s10071-011-0408-3

Clayton NS (1998) Memory and the hippocampus in food-storing birds: a comparative approach. Neuropharmacology 37:441–452. https://doi.org/10.1016/S0028-3908(98)00037-9

Clayton NS, Krebs JR (1994a) One-trial associative memory: comparison of food-storing and nonstoring species of birds. Anim Learn Behav 22:366–372. https://doi.org/10.3758/BF03209155

Clayton NS, Krebs JR (1994b) Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 174:371–379. https://doi.org/10.1007/BF00240218

Clutton-Brock TH, Harvey PH (1980) Primates, brains and ecology. J Zool 190:309–323. https://doi.org/10.1111/j.1469-7998.1980.tb01430.x

Cole FR, Wilson DE (2006) *Leptonycteris yerbabuenae*. Mamm Species 797:1–7. https://doi.org/10.1644/797.1

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576. https://doi.org/10.2307/1934144

Cristol DA, Reynolds EB, Leclerc JE, Donner AH, Farabaugh CS, Ziegenfus CWS (2003) Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. Anim Behav 66:317–328. https://doi.org/10.1006/anbe.2003.2194

Croston R, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Parchman TL, Pravosudov VV (2017) Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. Anim Behav 123:139–149. https://doi.org/10.1016/j.anbehav.2016.10.004

Damerius LA, Burkart JM, van Noordwijk MA, Haun DBM, Kosonen ZK, Galdikas BMF, Saraswati Y, Kurniawan D, van Schaik CP (2019) General cognitive abilities in orangutans (*Pongo abelii* and *Pongo pygmaeus*). Intelligence 74:3–11. https://doi.org/10.1016/j.intell.2018.10.008

Dammhahn M, Kappeler PM (2005) Social system of Microcebus berthae, the world's smallest primate. Int J Primatol 26:407–435. https://doi.org/10.1007/s10764-005-2931-z

Day LB, Crews D, Wilczynski W (1999a) Spatial and reversal learning in congeneric lizards with different foraging strategies. Anim Behav 57:393–407. https://doi.org/10.1006/anbe.1998.1007

Day LB, Crews D, Wilczynski W (1999b) Relative medial and dorsal cortex volume in relation to foraging ecology in congeneric lizards. Brain Behav Evol 54:314–322. https://doi.org/10.1159/000006631

Day RL, Coe RL, Kendal JR, Laland KN (2003) Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. Anim Behav 65:559–571. https://doi.org/10.1006/anbe.2003.2074

Deaner RO, Barton RA, van Schaik CP (2003) Primate brains and life histories: renewing the connection. In: Kappeler PM, Pereira ME (eds) Primates life histories and socioecology. The University of Chicago Press, Chicago, pp 233–265

Deaner RO, van Schaik CP, Johnson V (2006) Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. Evol Psychol 4:147470490600400. https://doi.org/10.1177/147470490600400114

Deaner RO, Isler K, Burkart JM, van Schaik CP (2007) Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. Brain Behav Evol 70:115–124. https://doi.org/10.1159/000102973

DeCasien AR, Higham JP (2019) Primate mosaic brain evolution reflects selection on sensory and cognitive specialization. Nat Ecol Evol 3:1483–1493. https://doi.org/10.1038/s41559-019-0969-0

DeCasien AR, Williams SA, Higham JP (2017) Primate brain size is predicted by diet but not sociality. Nat Ecol Evol 1:112. https://doi.org/10.1038/s41559-017-0112

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N (2010) Defining and measuring ecological specialization. J Appl Ecol 47:15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x

Dietz C, Kiefer A (2016) Bats of Britain and Europe. Bloomsbury Publishing, London

Dingle H (2014) Migration. Oxford University Press, Oxford

Du Toit N, Pillay N, Ganem G, Rekton C (2016) A conservation assessment of *Rhabdomys* spp. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (eds) The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, pp 1–6

Ducatez S, Clavel J, Lefebvre L (2014a) Ecological generalism and behavioural innovation in birds: technical intelligence or the simple incorporation of new foods? J Anim Ecol 84:79–89. https://doi.org/10.1111/1365-2656.12255

Ducatez S, Tingley R, Shine R (2014b) Using species co-occurrence patterns to quantify relative habitat breadth in terrestrial vertebrates. Ecosphere 5:1–12. https://doi.org/10.1890/ES14-00332.1

Ducatez S, Lefebvre L, Sayol F, Audet J-N, Sol D (2020a) Host cognition and parasitism in birds: a review of the main mechanisms. Front Ecol Evol 8:1–102. https://doi.org/10.3389/fevo.2020.00102

Ducatez S, Sol D, Sayol F, Lefebvre L (2020b) Behavioural plasticity is associated with reduced extinction risk in birds. Nat Ecol Evol 4: 788–793. https://doi.org/10.1038/s41559-020-1168-8

Dukas R, Ratcliffe JM (2009) Cognitive ecology II. The University of Chicago Press, Chicago

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6:178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar RIM, Bever J (2010) Neocortex size predicts group size in carnivores and some insectivores. Ethology 104:695–708. https://doi.org/10.1111/j.1439-0310.1998.tb00103.x

Dunbar RIM, Shultz S (2007) Evolution in the social brain. Science 317: 1344–1347. https://doi.org/10.1126/science.1145463

Dunbar RIM, Shultz S (2017) Why are there so many explanations for primate brain evolution? Phil Trans R Soc B 372:20160244. https://doi.org/10.1098/rstb.2016.0244

Dunn JC, Cole EF, Quinn JL (2011) Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. Behav Ecol Sociobiol 65:1459–1471. https://doi.org/10.1007/s00265-011-1156-8

Fernandes HBFF, Woodley MA, te Nijenhuis J (2014) Differences in cognitive abilities among primates are concentrated on G: phenotypic and phylogenetic comparisons with two meta-analytical databases. Intelligence 46:311–322. https://doi.org/10.1016/j.intell.2014.07.007

Ferrari MCO (2014) Short-term environmental variation in predation risk leads to differential performance in predation-related cognitive function. Anim Behav 95:9–14. https://doi.org/10.1016/j.anbehav.2014.06.001

Fichtel C, Dinter K, Kappeler PM (2020) The lemur baseline: how lemurs compare to monkeys and apes in the Primate Cognition Test Battery. PeerJ 8:e10025. https://doi.org/10.7717/peerj.10025

Finarelli JA, Flynn JJ (2009) Brain-size evolution and sociality in Carnivora. P Natl Acad Sci USA 106:9345–9349. https://doi.org/10.1073/pnas.0901780106

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. Annu Rev Ecol Syst 19:207–233. https://doi.org/10.1146/annurev.es.19.110188.001231

Galsworthy MJ, Arden R, Chabris CF (2014) Animal models of general cognitive ability for genetic research into cognitive functioning. In: Finkel D, Reynolds CA (eds) Behavior Genetics of Cognition Across the Lifespan. Springer New York, New York, NY, pp 257–278

Ganem G, Meynard CN, Perigault M, Lancaster J, Edwards S, Caminade P, Watson J, Pillay N (2012) Environmental correlates and co-occurrence of three mitochondrial lineages of striped mice (*Rhabdomys*) in the Free State Province (South Africa). Acta Oecologica 42:30–40. https://doi.org/10.1016/j.actao.2012.01.003

Ganem G, Dufour CMS, Avenant NL, Caminade P, Eiseb SJ, Tougard C, Pillay N (2020) An update on the distribution and diversification of *Rhabdomys* sp. (Muridae, Rodentia). J Vertebr Biol 69:1. https://doi.org/10.25225/jvb.20013

Garamszegi LZ, Erritzøe J, Møller AP (2007) Feeding innovations and parasitism in birds. Biol J Linn Soc 90:441–455. https://doi.org/10.1111/j.1095-8312.2007.00733.x

Gibson BM, Kamil AC (2005) The fine-grained spatial abilities of three seed-caching corvids. Learn Behav 33:59–66. https://doi.org/10.3758/bf03196050

Gigerenzer G (2008) Why heuristics work. Perspect Psychol Sci 3:20–29. https://doi.org/10.1111/j.1745-6916.2008.00058.x

Gingins S, Bshary R (2016) The cleaner wrasse outperforms other labrids in ecologically relevant contexts, but not in spatial discrimination. Anim Behav 115:145–155. https://doi.org/10.1016/j.anbehav.2016.02.022

Griffin AS, Diquelou MC (2015) Innovative problem solving in birds: a cross-species comparison of two highly successful passerines. Anim Behav 100:84–94. https://doi.org/10.1016/j.anbehav.2014.11.012

Hafner MS, Hafner JC (1984) Brain size, adaptation and heterochrony in geomyoid rodents. Evolution 38:1088–1098. https://doi.org/10.1111/j.1558-5646.1984.tb00378.x

Hartwig W, Rosenberger AL, Norconk MA, Owl MY (2011) Relative brain size, gut size, and evolution in New World monkeys. Anat Rec 294:2207–2221. https://doi.org/10.1002/ar.21515

Haupt M, Eccard JA, Winter Y (2010) Does spatial learning ability of common voles (*Microtus arvalis*) and bank voles (*Myodes glareolus*) constrain foraging efficiency? Anim Cogn 13:783–791. https://doi.org/10.1007/s10071-010-0327-8

Healy SD, Rowe C (2007) A critique of comparative studies of brain size. Proc R Soc Lond B 274:453–464. https://doi.org/10.1098/rspb.2006.3748

Healy SD, Suhonen J (1996) Memory for locations of stored food in willow tits and marsh tits. Behaviour 133:71–80. https://doi.org/10.1163/156853996X00035

Heldstab SA, Kosonen ZK, Koski SE, Burkart JM, van Schaik CP, Isler K (2016) Manipulation complexity in primates coevolved with brain size and terrestriality. Sci Rep 6:24528. https://doi.org/10.1038/srep24528

Henke-von der Malsburg J, Fichtel C (2018) Are generalists more innovative than specialists? A comparison of innovative abilities in two wild sympatric mouse lemur species. R Soc Open Sci 5:180480. https://doi.org/10.1098/rsos.180480

Henry M, Stoner KE (2011) Relationship between spatial working memory performance and diet specialization in two sympatric nectar bats. PLoS ONE 6:e23773. https://doi.org/10.1371/journal.pone.0023773

Herculano-Houzel S (2017) Numbers of neurons as biological correlates of cognitive capability. Curr Opin Behav Sci 16:1–7. https://doi.org/10.1016/j.cobeha.2017.02.004

Herrmann E, Call J, Hernandez-Lloreda MV, Hare B, Tomasello M (2007) Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. Science 317:1360–1366. https://doi.org/10.1126/science.1146282

Hills TT, Todd PM, Lazer D, Redish AD, Couzin ID (2015) Exploration versus exploitation in space, mind, and society. Trends Cogn Sci 19: 46–54. https://doi.org/10.1016/j.tics.2014.10.004

Hoedjes KM, Steidle JLMM, Werren JH, Vet LEMM, Smid HM (2012) High-throughput olfactory conditioning and memory retention test show variation in Nasonia parasitic wasps. Genes, Brain Behav 11: 879–887. https://doi.org/10.1111/j.1601-183X.2012.00823.x

Holekamp KE, Sakai ST, Lundrigan BL (2007) Social intelligence in the spotted hyena (*Crocuta crocuta*). Phil Trans R Soc B 362:523–538. https://doi.org/10.1098/rstb.2006.1993

Howard VWJ (1994) Kangaroo rats. In: Hygnstrom SE, Timm RM, Larson GE (eds) The handbook: Prevention and control of wildlife damage, University of Nebraska-Lincoln, Lincoln, pp B–101–B–104

Hughes JB (2000) The scale of resource specialization and the distribution and abundance of lycaenid butterflies. Oecologia 123:375–383. https://doi.org/10.1007/s004420051024

Humphrey N (1976) The social function of intellect. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317

Hutchinson GE (1953) The concept of pattern in ecology. P Acad Nat Sci Phila 105:1–12

Hutchinson GE (1957) Concluding remarks. Cold Spring Harb Sym 22: 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Jensen AR (1985) The nature of the black–white difference on various psychometric tests: Spearman's hypothesis. Behav Brain Sci 8:193–219. https://doi.org/10.1017/S0140525X00020392

Jerison HJ (1973) Evolution of the brain and intelligence. Academic Press, New York

Jolly A (1966) Lemur social behavior and primate intelligence. Science 153:501–506. https://doi.org/10.1126/science.153.3735.501

Jones S, Paul ES, Dayan P, Robinson ESJ, Mendl M (2017) Pavlovian influences on learning differ between rats and mice in a counterbalanced Go/NoGo judgement bias task. Behav Brain Res 331:214–224. https://doi.org/10.1016/j.bbr.2017.05.044

Kappeler PM (2019) A framework for studying social complexity. Behav Ecol Sociobiol 73:1–14. https://doi.org/10.1007/s00265-018-2601-8

Kotrschal A, Rogell B, Bundsen A, Svensson B, Zajitschek S, Brännström I, Immler S, Maklakov AA, Kolm N (2013) Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. Curr Biol 23:168–171. https://doi.org/10.1016/j.cub.2012.11.058

Krebs JR (1990) Food-storing birds: adaptive specialization in brain and behaviour? Phil Trans R Soc B 329:153–160. https://doi.org/10.1098/rstb.1990.0160

Kudo H, Dunbar RIM (2001) Neocortex size and social network size in primates. Anim Behav 62:711–722. https://doi.org/10.1006/anbe.2001.1808

Lea SEG, Chow PKY, Leaver LA, McLaren IPL (2020) Behavioral flexibility: a review, a model, and some exploratory tests. Learn Behav 48:173–187. https://doi.org/10.3758/s13420-020-00421-w

Lee PC (2003) Innovation as a behavioural response to environmental challenges: a cost and benefit approach. In: Reader SM, Laland KN (eds) Animal Innovation. Oxford University Press, Oxford, pp 261–278

Lefebvre L, Sol D (2008) Brains, lifestyles and cognition: are there general trends? Brain Behav Evol 72:135–144. https://doi.org/10.1159/000151473

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233–246. https://doi.org/10.1159/000076784

Lucas JR, Brodin A, de Kort SR, Clayton NS (2004) Does hippocampal size correlate with the degree of caching specialization? Proc R Soc Lond B 271:2423–2429. https://doi.org/10.1098/rspb.2004.2912

Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. Science 341:526–530. https://doi.org/10.1126/science.1238677

Lundrigan B, Mueller M (2003) "Myodes glareolus" (On-line). In: Anim Divers Web. https://animaldiversity.org/accounts/Myodes_glareolus/. Accessed 12 Sep 2020

MacArthur RH (1957) On the relative abundance of the bird species. Zoology 43:293–295

Mace GM, Harvey PH, Clutton-Brock TH (2009) Brain size and ecology in small mammals. J Zool 193:333–354. https://doi.org/10.1111/j.1469-7998.1981.tb03449.x

Mackay MK, Pillay N (2018) Similarities in spatial cognition in sister species of the striped mouse Rhabdomys originating from different ecological contexts. Behaviour 154:1397–1420. https://doi.org/10.1163/1568539X-00003474

MacLean EL, Merritt DJ, Brannon EM, Tin DUS, Ritt JMER, Non EMB, Merritt DJ, Brannon EM (2008) Social complexity predicts

transitive reasoning in prosimian primates. Anim Behav 76:479–486. https://doi.org/10.1016/j.anbehav.2008.01.025

MacLean EL, Barrickman NL, Johnson EM, Wall CE (2009) Sociality, ecology, and relative brain size in lemurs. J Hum Evol 56:471–478. https://doi.org/10.1016/j.jhevol.2008.12.005

MacLean EL, Matthews LJ, Hare BA et al (2012) How does cognition evolve? Phylogenetic comparative psychology. Anim Cogn 15: 223–238. https://doi.org/10.1007/s10071-011-0448-8

MacLean EL, Hare B, Nunn CL et al (2014) The evolution of self-control. P Natl Acad Sci USA 111:E2140–E2148. https://doi.org/10.1073/pnas.1323533111

Maille A, Schradin C (2016) Ecophysiology of cognition: how do environmentally induced changes in physiology affect cognitive performance? Biol Rev 92:1101–1112. https://doi.org/10.1111/brv.12270

Martin AE, Fahrig L (2018) Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. Ecology 99:2058–2066. https://doi.org/10.1002/ecy.2428

Mazza V, Jacob J, Dammhahn M, Zaccaroni M, Eccard JA (2019) Individual variation in cognitive style reflects foraging and antipredator strategies in a small mammal. Sci Rep 9:10157. https://doi.org/10.1038/s41598-019-46582-1

McCabe CM, Reader SM, Nunn CL (2015) Infectious disease, behavioural flexibility and the evolution of culture in primates. Proc R Soc B 282:20140862. https://doi.org/10.1098/rspb.2014.0862

McCormack JE, Smith TB (2008) Niche expansion leads to small-scale adaptive divergence along an elevation gradient in a medium-sized passerine bird. Proc R Soc B 275:2155–2164. https://doi.org/10.1098/rspb.2008.0470

Mettke-Hofmann C (2014) Cognitive ecology: ecological factors, lifestyles, and cognition. WIRE Cogn Sci 5:345–360. https://doi.org/10.1002/wcs.1289

Meynard CN, Pillay N, Perrigault M, Caminade P, Ganem G (2012) Evidence of environmental niche differentiation in the striped mouse (Rhabdomys sp.): Inference from its current distribution in southern Africa. Ecol Evol 2:1008–1023. https://doi.org/10.1002/ece3.219

Milton K (1988) Foraging behaviour and the evolution of primate intelligence. In: Byrne RW, Whiten A (eds) Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford University Press, New York, NY, pp 285–305

Møller AP, Erritzøe J, Garamszegi LZ (2005) Covariation between brain size and immunity in birds: implications for brain size evolution. J Evol Biol 18:223–237. https://doi.org/10.1111/j.1420-9101.2004.00805.x

Morand-Ferron J, Cole EF, Quinn JL (2016) Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. Biol Rev 91:367–389. https://doi.org/10.1111/brv.12174

Morand-Ferron J, Hermer E, Jones TB, Thompson MJ (2019) Environmental variability, the value of information, and learning in winter residents. Anim Behav 147:137–145

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN (2016) The coevolution of innovation and technical intelligence in primates. Phil Trans R Soc B 371:20150186. https://doi.org/10.1098/rstb.2015.0186

Noble S (2017) "Microtus arvalis" (On-line). In: Anim Divers Web. https://animaldiversity.org/accounts/Microtus_arvalis/. Accessed 12 Sep 2020

Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L (2009) Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav 78:1001–1010. https://doi.org/10.1016/j.anbehav.2009.06.033

Overington SE, Griffin AS, Sol D, Lefebvre L (2011) Are innovative species ecological generalists? A test in North American birds. Behav Ecol 22:1286–1293. https://doi.org/10.1093/beheco/arr130

Park CR, Zoladz PR, Conrad CD, Fleshner M, Diamond DM (2008) Acute predator stress impairs the consolidation and retrieval of

hippocampus-dependent memory in male and female rats. Learn Mem 15:271–280. https://doi.org/10.1101/lm.721108

Parker ST, Gibson KR (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. J Hum Evol 6:623–641. https://doi.org/10.1016/S0047-2484(77)80135-8

Peckre L, Kappeler PM, Fichtel C (2019) Clarifying and expanding the social complexity hypothesis for communicative complexity. Behav Ecol Sociobiol 73:11. https://doi.org/10.1007/s00265-018-2605-4

Peres CA (1989) Exudate-eating by wild golden lion tamarins, *Leontopithecus rosalia*. Biotropica 21:287–288

Pérez-Barbería FJ, Shultz S, Dunbar RIM (2007) Evidence for coevolution of sociality and relative brain size in three orders of mammals. Evolution 61:2811–2821. https://doi.org/10.1111/j.1558-5646.2007.00229.x

Platt ML, Brannon EM, Briese TL, French JA (1996) Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhlii*) on spatial and visual memory tasks. Anim Learn Behav 24:384–393. https://doi.org/10.3758/BF03199010

Pleskacheva MG, Wolfer DP, Kupriyanova IF, Nikolenko DL, Scheffrahn H, Dell'Omo G, Lipp H-P (2000) Hippocampal mossy fibers and swimming navigation learning in two vole species occupying different habitats. Hippocampus 10:17–30. https://doi.org/10.1002/(SICI)1098-1063(2000)10:1<17::AID-HIPO2>3.0.CO;2-O

Powell LE, Isler K, Barton RA (2017) Re-evaluating the link between brain size and behavioural ecology in primates. Proc R Soc B 284: 20171765. https://doi.org/10.1098/rspb.2017.1765

Pravosudov VV, De Kort SR (2005) Is the western scrub-jay (*Aphelocoma californica*) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? Brain Behav Evol 67:1–9. https://doi.org/10.1159/000088855

Reader SM (2003) Innovation and social learning: individual variation and brain evolution. Anim Biol 53:147–158. https://doi.org/10.1163/157075603769700340

Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. P Natl Acad Sci USA 99:4436–4441. https://doi.org/10.1073/pnas.062041299

Reader SM, Laland KN (2003) Animal innovation. Oxford University Press, Oxford

Reader SM, MacDonald K (2003) Environmental variability and primate behavioural flexibility. In: Reader SM, Laland KN (eds) Animal Innovation. Oxford University Press, Oxford, pp 83–116

Reader SM, Hager Y, Laland KN (2011) The evolution of primate general and cultural intelligence. Phil Trans R Soc B 366:1017–1027. https://doi.org/10.1098/rstb.2010.0342

Roobas B, Feulner GR (2013) A population of Bosk's fringe-toed lizard *Acanthodactylus boskianus* (Daudin, 1802) in the Hajar Mountain foothills of the UAE. Tribulus. Emirates Natural History Group, In, pp 24–37

Rosati AG (2017) Foraging cognition: reviving the ecological intelligence hypothesis. Trends Cogn Sci 21:691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rosati AG, Hare B (2012) Chimpanzees and bonobos exhibit divergent spatial memory development. Dev Sci 6:840–853. https://doi.org/10.1111/j.1467-7687.2012.01182.x

Rosati AG, Rodriguez K, Hare B (2014) The ecology of spatial memory in four lemur species. Anim Cogn 17:947–961. https://doi.org/10.1007/s10071-014-0727-2

Roth TC, Pravosudov VV (2009) Hippocampal volumes and neuron numbers increase along a gradient of environmental harshness: a large-scale comparison. Proc R Soc Lond B 276:401–405. https://doi.org/10.1098/rspb.2008.1184

Roth TC, LaDage LD, Pravosudov VV (2010) Learning capabilities enhanced in harsh environments: a common garden approach. Proc R Soc B 277:3187–3193. https://doi.org/10.1098/rspb.2010.0630

Roughgarden J (1972) Evolution of niche width. Am Nat 106:683–718

Rylands AB (1989) Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhlii*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. J Hum Evol 18:679–695. https://doi.org/10.1016/0047-2484(89)90100-0

Sargeant BL (2007) Individual foraging specialization: niche width versus niche overlap. Oikos 116:1431–1437. https://doi.org/10.1111/j.2007.0030-1299.15833.x

Sayol F, Maspons J, Lapiedra O, Iwaniuk AN, Székely T, Sol D (2016) Environmental variation and the evolution of large brains in birds. Nat Commun 7:13971. https://doi.org/10.1038/ncomms13971

Schnitzler HU, Moss CF, Denzinger A (2003) From spatial orientation to food acquisition in echolocating bats. Trends Ecol Evol 18:386–394. https://doi.org/10.1016/S0169-5347(03)00185-X

Schradin C, Pillay N (2004) The striped mouse (*Rhabdomys pumilio*) from the succulent Karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. J Comp Psychol 118:37–47. https://doi.org/10.1037/0735-7036.118.1.37

Schubiger MN, Fichtel C, Burkart JM (2020) Validity of cognitive tests for non-human animals: pitfalls and prospects. Front Psychol 11: 1835. https://doi.org/10.3389/fpsyg.2020.01835

Shaw RC, Schmelz M (2017) Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. Anim Cogn 20:1003–1018. https://doi.org/10.1007/s10071-017-1135-1

Sherry DF, Jacobs LF, Gaulin SJC (1992) Spatial memory and adaptive specialization of the hippocampus. Trends Neurosci 15:298–303. https://doi.org/10.1016/0166-2236(92)90080-R

Shettleworth SJ (1990) Spatial memory in food-storing birds. Phil Trans R Soc Ser B 329:143–151. https://doi.org/10.1098/rstb.1990.0159

Shettleworth SJ (2009) Cognition, evolution, and behavior, 2nd edn. Oxford University Press, Oxford

Shumway CA (2008) Habitat complexity, brain, and behavior. Brain Behav Evol 72:123–134. https://doi.org/10.1159/000151472

Sih A (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim Behav 85:1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. P Natl Acad Sci USA 102:5460–5465. https://doi.org/10.1073/pnas.0408145102

Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of mammal species introduced into novel environments. Am Nat 172:S63–S71. https://doi.org/10.1086/588304

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Soler JJ, Peralta-Sánchez JM, Martín-Vivaldi M, Martín-Platero AM, Flensted-Jensen E, Møller AP (2012) Cognitive skills and bacterial load: comparative evidence of costs of cognitive proficiency in birds. Naturwissenschaften 99:111–122. https://doi.org/10.1007/s00114-011-0875-z

Sonnenberg BR, Branch CL, Pitera AM, Bridge E, Pravosudov VV (2019) Natural selection and spatial cognition in wild food-caching mountain chickadees. Curr Biol 29:670-676.e3. https://doi.org/10.1016/j.cub.2019.01.006

Spearman C (1904) "General intelligence" objectively determined and measured. Am J Psychol 15:201–292

Striedter GF (2006) Précis of principles of brain evolution. Behav Brain Sci 29:1–12. https://doi.org/10.1017/S0140525X06009010

Szabo B, Whiting MJ (2020) Do lizards have enhanced inhibition? A test in two species differing in ecology and sociobiology. Behav Process 172:104043. https://doi.org/10.1016/j.beproc.2020.104043

Tebbich S, Teschke I (2014) Coping with uncertainty: woodpecker finches (*Cactospiza pallida*) from an unpredictable habitat are more flexible than birds from a stable habitat. PLoS ONE 9:e91718. https://doi.org/10.1371/journal.pone.0091718

Teichroeb JA, Vining AQ (2019) Navigation strategies in three nocturnal lemur species: diet predicts heuristic use and degree of exploratory behavior. Anim Cogn 22:343–354. https://doi.org/10.1007/s10071-019-01247-4

Thornton A, Lukas D (2012) Individual variation in cognitive performance: developmental and evolutionary perspectives. Phil Trans R Soc B 367:2773–2783. https://doi.org/10.1098/rstb.2012.0214

Timm R, Álvarez-Castaeda ST, Lacher T (2016) *Dipodomys merriami*. In: IUCN Red List Threatened Species 2016, p eT92465716A115515430

Tooby J, Cosmides L (2003) The psychological foundations of culture. In: Barkow J, Cosmides L, Tooby J (eds) The Adapted Mind: Evolutionary Psychology and the Generation of Culture. Psychology Press, New York, NY, pp 19–136

Trapanese C, Robira B, Tonachella G, di Gristina S, Meunier H, Masi S (2019) Where and what? Frugivory is associated with more efficient foraging in three semi-free ranging primate species. R Soc Open Sci 6:181722. https://doi.org/10.1098/rsos.181722

van Schaik CP, Burkart JM (2011) Social learning and evolution: the cultural intelligence hypothesis. Phil Trans R Soc B 366:1008–1016. https://doi.org/10.1098/rstb.2010.0304

van Woerden JT, Willems EP, van Schaik CP, Isler K (2012) Large brains buffer energetic effects of seasonal habitats in catarrhine primates. Evolution 66:191–199. https://doi.org/10.1111/j.1558-5646.2011.01434.x

Vas Z, Lefebvre L, Johnson KP, Reiczigel J, Rózsa L (2011) Clever birds are lousy: co-variation between avian innovation and the taxonomic richness of their amblyceran lice. Int J Parasitol 41:1295–1300. https://doi.org/10.1016/j.ijpara.2011.07.011

Völter CJ, Tinklenberg B, Call J, Seed AM (2018) Comparative psychometrics: establishing what differs is central to understanding what evolves. Phil Trans R Soc B 373:20170283. https://doi.org/10.1098/rstb.2017.0283

Wall V, Stephen B (1990) Food hoarding in animals. University of Chicago Press, Chicago

White GE, Brown C (2015a) Cue choice and spatial learning ability are affected by habitat complexity in intertidal gobies. Behav Ecol 26:178–184. https://doi.org/10.1093/beheco/aru178

White GE, Brown C (2015b) Microhabitat use affects brain size and structure in intertidal gobies. Brain Behav Evol 85:107–116. https://doi.org/10.1159/000380875

Whiten A, Byrne RW (1988) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford University Press, New York

Wilke A, Hutchinson JMCC, Todd PM, Czienskowski U (2009) Fishing for the right words: decision rules for human foraging behavior in internal search tasks. Cogn Sci 33:497–529. https://doi.org/10.1111/j.1551-6709.2009.01020.x