

Article type: Advanced Review**Cognitive ecology – ecological factors, life-styles and cognition**

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Abstract

Cognitive ecology integrates cognition, ecology and neurobiology in one topic and has recently broadened into an exciting diversity of themes covering the entire range of cognition and ecological conditions. The review identifies three major environmental factors interacting with cognition: environmental variation (predictable and unpredictable), environmental complexity and predation. Generally, variable environments favour cognitive abilities such as exploration, learning, innovation, memory and also result in larger brains as compared to stable environments. Likewise, cognition is enhanced in complex versus simple environments, whereas the relationship between predation and cognitive abilities can be positive or negative. However, organisms have often evolved entire life-styles (e.g. residency vs migration, food-caching vs non-caching, generalism vs specialism) to deal with these environmental factors. Considering cognition within this framework provides a much more diverse picture of how cognitive abilities evolved in conjunction with other adaptations to environmental challenges. This integrated approach identifies gaps of knowledge and allows the formulation of hypotheses for future testing. Several recently emerged approaches study cognitive abilities at a new and in part highly integrated level. For example, the effect that environment has on the development of cognitive abilities during ontogeny will improve our understanding about cause and effect and gene x environment interactions. Together with two recently emerged highly integrative approaches that link personality and pace-of-life syndromes with cognitive ecology these new directions will improve insight how cognition is interlinked with other major organisational processes.

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Cognitive ecology is a relatively young field that studies cognitive adaptations to a species' or individual's environment. The term cognition encompasses a broad range of neural processes which are used to interpret the environment and include perception, learning, memory and decision making¹ which regulate behavioural responses. Like morphological traits it is assumed that cognitive traits are shaped by natural selection via the underlying neural substrates². The idea that behaviour and cognition are shaped by the environment is not a new one as the 'Umwelt' concept proposed already in 1909 by Uexküll states that individuals' behaviours have to be seen in relation to their environment and what they perceive and sense may differ even within the same environment³. In the 1970s several ecological approaches to human cognition emerged (e.g. Gibson's ecological approach to visual perception, Rosch's natural and prototypical categorisation and concept formation⁴ and Soviet's cultural-historical activity theory⁵) emphasising that cognition has evolved in specific environments to extract information efficiently. Activity theory proposes that cognition has to be studied in the context of the environment and that the mind, brain and body act together⁵. Recently, Keller⁶ applied this approach to great apes. However, it took until the 1980s that cognitive ecology emerged as a field in animal research. Based on the finding that the hippocampus is important for processing spatial information it was hypothesised that extreme environmental demands on spatial abilities select for adaptations in behaviour and respective brain regions². Initial support for the hypothesis came primarily from studies comparing spatial memory of closely related food-caching and non-caching species or species that depended to different degrees on caching. Birds and other taxa cache food (mainly seeds and nuts) in autumn when there is an overabundance of these resources and retrieve caches later in the season when resources are scarce. Species more dependent on cached food often have a better spatial memory and a relatively larger hippocampus in relation to the rest of the brain than species less dependent on cached food⁷. A few studies tested the hypothesis in other systems such as brood parasitic birds where females but not males have to remember the locations of many host nests and found a relatively larger hippocampus in females⁸. Likewise, migratory birds were found to have a longer lasting spatial memory and relatively larger hippocampi than resident birds coinciding with the demand in migrants to remember their natal or breeding area until next spring^{9, 10}. But only recently has cognitive ecology become much broader by studying processing information, learning, problem-solving and memory in a broad range of ecological factors such as environmental complexity, resource distribution and variability, and predation pressure. The review aims to include as many of these different directions to show the breadth of this exciting field. Moreover, I attempt to present the different cognitive adaptations in a larger framework of general adaptations (life-styles) to environmental factors. Before doing so, I will first describe how cognitive adaptations to the environment are measured and then introduce the main environmental factors shaping cognition.

THE BIGGER PICTURE – WHICH ENVIRONMENTAL FACTORS SHAPE COGNITIVE ABILITIES?

Cognition is beneficial under specific environmental conditions (see below) as it allows adaptation to local or new conditions¹¹ or dealing with complex environments¹². Cognition has been linked to individual foraging efficiency¹³, survival¹⁴, population development¹⁵ and invasion success¹⁶ indicating selective advantages for individuals with better cognitive abilities.

Measuring cognitive adaptations

At the heart of cognitive ecology lays the comparative approach either between a) closely related species or populations within the same species with different ecologies to demonstrate cognitive divergence or b) distantly related species of similar ecology to demonstrate cognitive convergence¹⁷. Ideally, both approaches are combined. Cognitive ecology consists of three-way associations¹⁸ between cognitive performance, associated brain structures and ecological conditions. However, such data are relatively rare and it is more likely to find studies linking cognition with ecology or brain structures with ecology but not all three aspects. Moreover, many studies only compare two species. While most studies are correlational, in a few, more recent studies environmental conditions have been manipulated during early development to get a better understanding of cause and effect and gene x environment interactions^{11, 19}.

The substrate for selection acting on cognition is the brain which can adapt in different ways to environmental conditions over evolutionary times. On the one hand, the brain can increase in size which allows for more capacity to process, integrate and store information¹⁶. Increases in brain size have been related to more flexible behaviour such as innovation²⁰ and learning¹⁶. On the other hand, individual brain structures (e.g. hippocampus, prefrontal white matter, song nuclei) can increase or decrease independent of brain size in relation to their ecological requirement (mosaic brain;^{21, 22}). Unaware of but possibly reflecting these two pathways two contrasting hypotheses regarding brain evolution have been proposed; the General Purpose Problem Solving Brain hypothesis and the Adaptive Specialisation hypothesis²³. The former assumes that an organism improves in all cognitive abilities due to having a larger brain, whereas the latter predicts that cognitive abilities only improve in the required domain, e.g. spatial cognition with an accompanying increase in the hippocampus (modularity²³). Only recently have these two opinions somehow been linked by proposing functional specificity (modularity) for some cognitive abilities and more integration for other cognitive abilities²⁴. For example, the hippocampus has repeatedly been shown to change size independent of other brain areas and is particularly involved in processing spatial information²¹, whereas the forebrain/ neocortex is more involved in higher order and multimodal integration²⁵. The latter is particularly involved in flexible behaviour such as sampling unfamiliar resources, learning and problem-solving (innovation)¹¹ and its size often correlates with overall brain size²⁶. Smaers & Soligo²¹ have shown that both brain size increases and size independent structural (mosaic) changes differentiate Great apes (including humans) from other primates with mosaic changes explaining more of the variance.

Having a larger brain not only bears advantages but also incurs costs and can be seen as a factor limiting brain evolution²⁷. Visual receptors in resting insects consume 10% of the total energy used, whereas human brains use up to 20%²⁸. Larger brains are assumed to have more parallel processing (e.g. from different modalities) and more storage capacity resulting in a higher quantity of information processing (higher accuracy, more detail, more redundant information²⁹) but also higher metabolism²⁷. Memory accuracy, a widely used measure in spatial memory tasks, for example has been suggested to have high costs due to maintenance of redundant pathways (which increase accuracy) and repair³⁰. A way to counteract higher costs is to trade-off a) different brain areas by only enlarging areas that are necessary and down-regulate less important ones³¹ or trade-off b) costs of brains against other body parts (e.g. increased brains correlate with decreased flight muscle mass in birds²⁷). Additionally to neuronal costs, sampling the environment and learning take time¹¹ not available for other tasks such as foraging or vigilance and may also expose the organism to predation. As a consequence there is strong selection on cognitive abilities which will only evolve

when the benefits outweigh the costs³². But under which environmental conditions are cognitive abilities beneficial?

Environmental factors and life-style strategies

One of the main environmental factors shaping cognition is **variation** in resources; organisms not only adapt cognitively to such variation but often also physiologically and morphologically. In the following paragraph I will briefly describe the life-styles animals adopt under different environmental conditions.

Under spatiotemporal stable environmental conditions residents are favoured³³ (Fig. 1) as well as specialists³⁴ which are more efficient at exploiting resources than generalists³⁵. The picture becomes more diverse under variable conditions (Fig. 1). Here, two types of variation have to be considered; predictable and unpredictable variation in resources. One of the best known examples of predictable variation is seasonality of conditions and resources; and organisms have evolved a variety of life-styles to it. Two main life-styles have evolved in response to seasonal variation in the environment; residency and migration. For the latter predominantly endogenously controlled migration programmes have evolved in response to seasonality accompanied by morphological and physiological adaptations³⁶. Migration repeatedly confronts organisms with unfamiliar habitats in which they stay for relatively short periods of time. However, most migrants return to their breeding ground or even territory year after year³⁷. Residents, in contrast, remain in the same area throughout their life and have to deal with seasonal variation in climate and resources. Residents can further be divided into subgroups with special adaptations to their environment. For example, some species deal with seasonality by caching food during overabundance of cacheable resources which can be used during periods of food scarcity⁷. This adaptation is obviously restricted to species feeding on nuts and seeds (but see Smith & Erb 2013³⁸) but often includes generalists (see below). Furthermore, tool-use can evolve as an adaptation to seasonality and may serve different functions. Tools may be used to a) overcome energetic bottlenecks (necessity hypothesis), b) provide an opportunity to supplement diet (opportunity hypothesis), or c) access more profitable food (relative profitability hypothesis)³⁹. Organisms can also use tools to reach food rather than directly grabbing it in presumed risky situations⁴⁰. Another adaptation of residents to counteract periods of extreme food shortage is hibernation. Finally, independent of being resident or migratory further distinct life-styles can be identified depending on the diet, habitat and harshness of environmental conditions. Species can be specialists or generalists regarding diet or habitat use with specialists usually using a few resources very efficiently and generalists utilising several resources but less efficient⁴¹.

Which one of these life-styles is favoured depends in part on a species' diet and habitat (migration – often open habitats, frugivory and insectivory⁴², food cacher – seeds and nuts, tool-user – invertebrates and nuts) and possibly the harshness of the environment. Under increasingly harsh conditions, migration, food caching, tool use and hibernation may be favoured over generalism (Fig. 1) due to extended periods of time with no food (snow cover, temperature, draught etc.). Interestingly, Brodin⁴³ found in a model that food caching is the optimal strategy over putting on fat reserves (as a non-caching individual would do) due to mass-dependent costs of the latter.

Most of the above mentioned life-styles do not work when environmental variation is unpredictable (Fig. 1). Life-styles adapted to unpredictable resources are nomadism where organisms follow patchily distributed, superabundant food sources³³ and generalism where organisms utilise a variety

of resources. However, under extreme conditions (extended draught) specialists dominate over generalists⁴⁴.

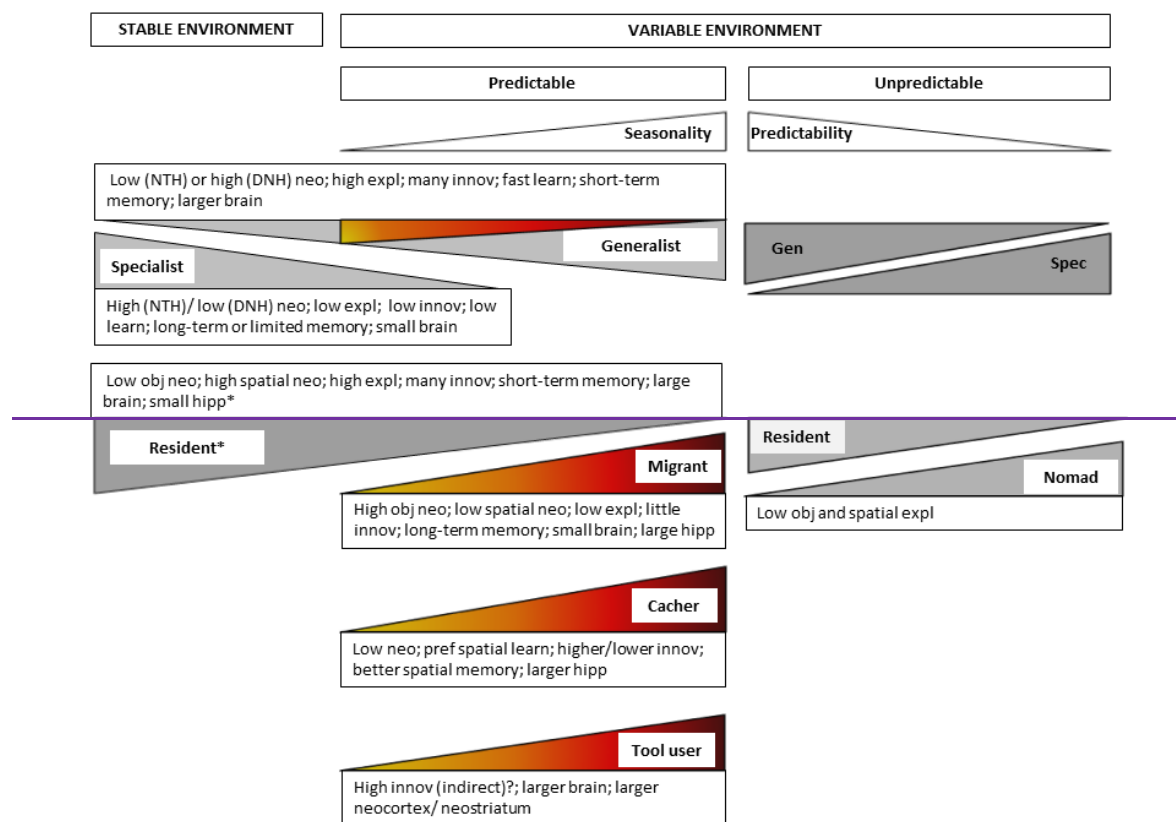


Figure 1: Cognitive adaptations to variable environmental factors under consideration of specific life-styles. The occurrence of particular life-styles across different environmental factors is shown for increasing seasonality within predictable conditions and decreasing predictability within unpredictable conditions. Furthermore, effects of increasing harshness on life-styles are indicated along a yellow-red gradient (yellow: mild; red: harsh) Cognitive adaptations are linked to particular life-styles.

* Occurrence of residents and accompanying cognitive adaptations are depicted for residents without specific adaptations (caching, tool use) and in relation to occurrence of migrants and their cognitive adaptations.

Neo: neophobia; NTH: Neophobia Threshold hypothesis; DNH: Dangerous Niche hypothesis; expl: exploration; innov: innovation; learn: learning; obj: object; hipp: hippocampus; Gen: Generalist; Spec: Specialist

Complexity is another environmental factor that can shape cognitive abilities. Independent of whether resources are variable or stable, environments can be simple or complex. To my knowledge the only life-style that can be associated with complexity is generalism. Following Godfrey-Smith⁴⁵ complexity emerges due to different stimuli having different variability which introduces heterogeneity in environmental variability. Particularly social complexity has been linked to the evolution of large brains and higher cognitive abilities in primates (Social Brain hypothesis⁴⁶). However, due to the extent of this field we will only discuss examples of cognition in relation to non-social environmental complexity. Finally, **predation** is an environmental factor shaping cognition and can favour or hinder cognition^{47, 48}). Examples will be discussed.

COGNITIVE ADAPTATIONS TO ENVIRONMENTAL CONDITIONS

Each of the life-styles and special adaptations mentioned above favour specific cognitive adaptations based on costs and benefits. This section will compare cognitive abilities between organisms of contrasting life-styles such as residents and migrants or caching and non-caching species as most studies follow this approach. Whenever possible the following cognitive abilities will be reviewed; attention, neophobia as an important trait hindering learning⁴⁹, neophilia (attraction to novelty; exploration; see Sidebar for a comparison of neophobia and neophilia), innovation (problem-solving), learning, flexibility, tool-use, memory and brain structures and size. Regarding the latter it should be mentioned that brains increase allometrically with body size and therefore, relative brain size in relation to body size or other brain structures is reported where appropriate (e.g. for birds, whereas absolute brain size works better for primates²⁶). Brain size is often used as a proxy for underlying changes in the brain for example a larger hippocampus links to larger neuron size, higher neuron density etc.⁵⁰. Likewise, overall brain size is sometimes used as a proxy for forebrain size in mammals⁴⁶ and mesopallium and nidopallium in birds²⁶ as they correlate and are more readily available than volumes of particular brain structures.

Cognitive adaptations to stable environments

Generally, models predict little information gathering⁵⁵, innate behaviours rather than learning⁵⁶ and reduced usefulness of memory⁵⁷ in stable environments though Sheenaja & Thomas⁵⁸ predicted an advantage for long-term memory in stable environments.

For example, spatiotemporal variation in food (fruits, buds) as compared to more stable food sources seems to favour exploration in birds^{51, 59}. Similarly, spatial exploration in ants (*Lasius*) was higher after periods of food shortage⁶⁰. Darwin's finches foraging on concealed food (year-round available=stable) were slower at relearning a colour discrimination task than finches foraging on more accessible but seasonal (variable) food indicating more flexibility in the latter⁶¹. Furthermore, several studies found differences in learning between fish from ponds (stable) and rivers (variable) with river fish learning a spatial route overall faster than pond fish⁵⁸. They also used different learning strategies; river fish preferred route learning (turns, as landmarks are unreliable in rivers), whereas pond fish used both landmarks and route learning⁶². Snell-Rood & Papaj⁶³ suggested that in stable environments innate preferences can reduce costs of learning and demonstrated innate biases for a particular host plant in butterflies but also the ability to learn when environments change. Other studies found that innovation rates in birds and primates are positively associated with seasonality¹¹. Regarding brain size, larger brained parrots were found to be more tolerant of climatic variability (i.e. inhabited areas strongly differing in temperature and precipitation), particularly in open and climatically unstable habitats⁶⁴. This may be linked to a greater plasticity in behavioural and cognitive reactions. However, seasonal variation in diet can also have negative consequences for cognition. In Strepsirrhine and Catarrhine monkeys, brain size decreased with increasing seasonality due to energetic constraints imposed on brain size (Constraint hypothesis^{65, 66}). Nonetheless, Catarrhine with larger brains were better able to buffer negative effects of seasonality (Cognitive Buffer hypothesis⁶⁵).

In summary, the studies mentioned above support the predictions from models and indicate lower cognitive abilities in species living in more stable environments (Fig. 1). Interestingly, the contradictory predictions for memory have not been tested so far.

SIDEBAR

Neophobia and neophilia are two independent motivations

Novelty elicits two opposite tendencies – avoidance (neophobia) but also approach to explore the novel (neophilia). Approach-avoidance behaviour is often seen as a continuum. However, they are governed by independent motivations⁵¹ and are modulated by different gene expressions^{52, 53}. A single-factor model moves along one dimension resulting in parallel changes in neophobia and neophilia (i.e. when neophobia decreases does neophilia increase possibly resulting in approach and exploration). In contrast, a two-factor model has two dimensions (one for the motivation to approach and one for the motivation to avoid something novel) resulting in four states⁵⁴; an individual can be a) attracted to novelty (neophilia) and be little neophobic resulting in approach, b) little attracted to novelty but neophobic resulting in avoidance, c) little attracted to novelty but also not be neophobic resulting in no approach, and d) attracted by novelty but also neophobic resulting in an ambivalent reaction of approach and avoidance. The first two reactions are consistent with the one-factor model but the latter two are not. The combination of neophobia and neophilia depends on the costs and benefits of approaching or avoiding novelty. Greenberg & Mettke-Hofmann⁵⁴ used costs and benefits to predict under which environmental conditions a) – d) are likely to occur (Fig. 2).

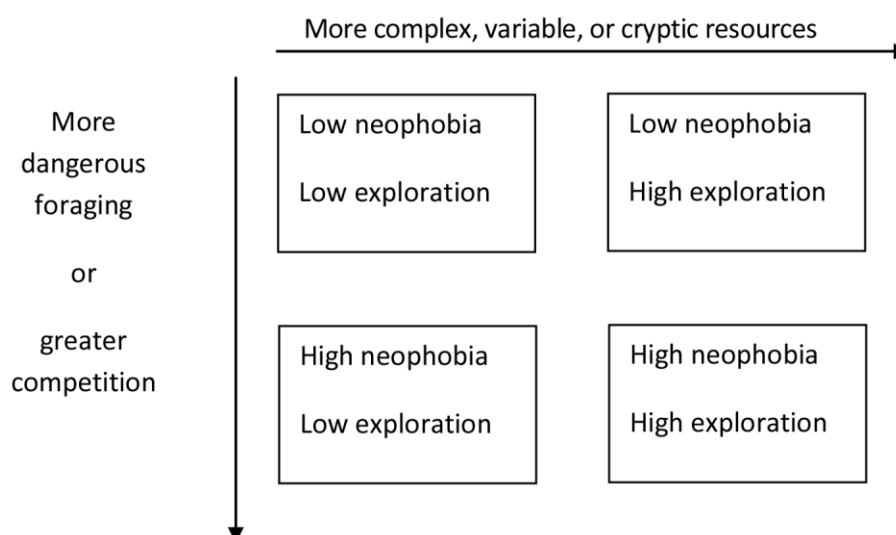


Figure 2 (Sidebar): Two-factor model for the occurrence of neophilia (exploration) and neophobia in response to general environmental variables. Adopted from Greenberg & Mettke-Hofmann 2001⁵⁴, Fig. 1. With kind permission from Springer Science+Business Media B.V.

Cognitive adaptations to predictable variable environments

In general, predictable variation in the environment favours information gathering⁵⁵ to reduce uncertainty as well as learning⁵⁶ and memory⁵⁷ under medium variability to reduce resampling of recurring situations. However, although each of the life-styles depicted below follows this general pattern, they differ profoundly in the degree to which these cognitive abilities are expressed.

Residency versus migration

Residents stay in the same area for their entire life and have to cope with temporal (seasonal) and in part spatial variation in the environment. Particularly in birds it has been shown that residents explore more than closely related migrants⁶⁷. Similarly, residents are less neophobic to feed beside a novel object than migrants⁶⁸. Both, high neophilia and low neophobia help residents to find and exploit new resources over the year. Furthermore, resident birds are also more likely to innovate than migrants, particularly in winter⁶⁹, which may further help them to stay resident. The relative size of the overall brain is also larger in residents than migrants consistent with their higher flexibility (exploration, innovation) to deal with environmental change⁶⁹. However, residents have a relatively smaller hippocampus⁷⁰ or a less densely packed hippocampus⁷¹ than migrants and also have a shorter-lasting spatial memory^{9, 71}. Residents may not need a long-term memory as they can update their knowledge whenever necessary⁹.

Migrants, in contrast, are repeatedly confronted with novel environments in which they stay for only relatively short periods of time. While migrants have to explore their environment they do this more superficially as their short-term stay of a few days to months does not allow use of this information in the long-term⁶⁷. Furthermore, they have an exploration strategy favouring speed over accuracy by moving fast through a novel environment which allows them to locate areas with food quickly⁷². Their reduced exploration may also be linked to their smaller brains, particularly forebrains⁷³ which may restrict processing information to what is absolutely essential. Nonetheless, their larger hippocampal formation and better spatial memory persistence⁹ and accuracy¹⁰ allow dealing with their spatial demands such as remembering high-quality stop-over sites for the next migration season⁹.

Interestingly, partial migrants (individuals in a population can switch between being resident or migratory over time) show some opposing cognitive patterns to migrants; partially migratory species in New Zealand were found to be the most successful invaders, whereas the same study found migrants to be the least successful ones⁷⁴. Along this line, migratory individuals in a partially migratory population of Blue tits (*Cyanistes caeruleus*) were more explorative than resident individuals⁷⁵. Partial migrants are more influenced by environmental cues rather than endogenous migration programmes and may continuously explore their environment for suitability of settlement⁷⁵.

Taken together residents and migrants show very clear cognitive adaptations to their ecological conditions. However, most of these findings are based on a few species-pairs comparisons with the exception of innovations. More research is required into the other cognitive abilities to allow for more generalisations. Overall, residents are more flexible in their behaviour (exploration of novel objects, innovation rate) than migrants in concordance with a larger forebrain, whereas migrants have a better spatial memory associated with an enlarged hippocampal formation (Fig. 1).

Surprisingly, no literature was found about learning in residents and migrants. Do migrants learn spatial information faster than residents due to their larger hippocampus and do residents outperform migrants in non-spatial learning?

Caching versus non-caching species and other systems that rely on spatial information

Cognitive adaptations to caching have been studied in a variety of species ranging from birds to mammals. The main body of research has been done on spatial memory and related brain areas. Generally, species more dependent on cached food show a higher accuracy (e.g.^{76, 77}) and sometimes a longer persistence of spatial memory than species less dependent on cached food^{78, 79}), while no memory differences were found in non-spatial tasks⁸⁰. These findings have been supported by relatively larger hippocampi⁸¹ and/or more neurogenesis, more neurons⁸² and a seasonal increase in size⁸³ in this region. However, several studies have failed to find a relationship between dependence on cached food and changes in the brain (e.g.⁸⁴). This may in part be due to other cognitive adaptations processed in the hippocampus such as episodic memory² but the reasons in other studies are less clear. This has led Macphail & Bolhuis²³ to question the 'neuroecological approach' that a species' ecology (e.g. food caching) specifically shapes particular brain areas. Further differences between cachers and non-cachers are that cachers preferentially learn spatial over non-spatial cues, whereas no such preference was found in non-cachers⁸⁵. Conflicting results are found for innovation; in chickadees (*Parus*), populations from harsh environments (more dependent on caches) solved problems faster than populations from milder environments⁸⁰, whereas innovation rate in North American corvids and European parids was lowest in species that cached the most¹¹. The innovative chickadees were also less neophobic to approach the unfamiliar apparatus which may have benefitted faster problem-solving⁸⁰. I am not aware of any study investigating exploratory behaviour in relation to caching.

Another system relying on spatial information is brood parasitism. Brood-parasitic cowbirds (*Molothrus*) have to remember nest sites of their hosts to lay their egg at the right time in each of the nests and have a relatively larger hippocampus than closely related non-brood parasitic cowbird species supporting the idea that more demanding spatial abilities require a larger hippocampus⁸⁶. Recently, it has been shown that in Brown-headed cowbirds (*Molothrus ater*) where only females but not males search for host nest, the former have better spatial memory accuracy than the latter in concordance with findings that females have a relatively larger hippocampus than males in this species⁸⁷.

In summary, spatial memory and associated hippocampal structures have been well studied in food caching species and some other species that depend heavily on spatial information (Fig. 1), whereas little is known about learning in these systems. One may expect faster spatial learning in species more dependent on spatial information but possibly no differences in non-spatial learning.

Tool-users

Tool-use has been primarily studied in primates, but several bird species are also known as tool-users. Primate species frequently using tools have a larger neocortex and striatum (brain areas associated with innovation and social learning) than species using tools less frequently⁸⁸. In birds, true tool users (using a tool to manipulate another object) have a relatively larger brain size than pre-tool users (e.g. dropping a shell from a height on the street), possibly pointing to more

sophisticated skills required for true tool-use²⁰. This latter relationship was tested in two species-pairs which were taxonomically distant by comparing learning and problem-solving abilities (innovation) between a tool-user and closely-related non tool-user, each^{17, 89}. Surprisingly, tool-using bird species were not better in innovating solutions to a task whether tool-use related or not (opening a box) and were also not better in reversal learning than bird species that do not use tools speaking against the assumption that tool-use requires higher cognitive abilities. This is in contrast to other studies though they usually link innovation and tool-use indirectly via correlation with brain size⁹⁰. It is possible that selection on other abilities resulted in larger brains which then allowed the evolution of tool-use⁹⁰. More direct testing on a wider range of species is required in this area.

Hibernation

Few studies have been conducted investigating cognitive abilities in relation to hibernation. In European ground squirrels (*Spermophilus citellus*), hibernating squirrels showed a lower retention of a spatial and an operant task than squirrels prevented from hibernation but no differences existed in remembering familiar individuals⁹¹. In contrast, other studies on squirrels and bats (Chiroptera) did not find a reduction in spatial memory after hibernation but hibernation times may have been too short to find an effect^{91, 92}. Magarinos et al.⁹³ found that in hibernating hamsters (*Cricetus cricetus*) hippocampal dendrites were shorter and less branched than in active hamsters but that this difference disappeared within three hours after the end of hibernation. The changes in the hippocampus may cause memory loss⁹¹. Therefore, hibernation may have negative effects on memory. To my knowledge no other cognitive abilities in relation to hibernation have been studied.

Other cognitive adaptations to variable environments

There are an increasing number of studies that do not follow the large scale distinctions above but study cognitive adaptations to environmental variability in a variety of systems. Several cognitive adaptations to variation in food have been investigated. Darwin's finches (*Camarhynchus*), foraging on concealed food (more predictable as also available during the dry season) were less neophobic than finches feeding on more accessible (seasonal) food⁶¹. This finding is surprising but birds feeding to a high degree on easily accessible food may have more direct encounters with possibly dangerous invertebrates, whereas birds feeding more on concealed food use tools to extract prey. Higher neophobia has also been found in parrots feeding on possibly dangerous insects⁵¹. Furthermore, lizards with an active foraging style performed better in a reversal learning task than lizards with a sit-and-wait strategy as active foraging may require more flexibility to adapt to new situations (Pliancy hypothesis⁹⁴). However, no differences in spatial memory were found contradicting the expectation that active search requires more spatial memory⁹⁴. Sulikowski & Burke⁹⁵ investigated spatial working memory in birds with baited (either nectar or insects) and unbaited feeders. Spatial memory was better for nectar trials than insect trials resulting in fewer revisits. Spatial memory improves foraging efficiency on nectar, whereas invertebrates are often continuously distributed⁹⁵.

Cognitive adaptations to unpredictable variable environments

Under unpredictable conditions models predict random search⁹⁶, little learning⁵⁶ as situations may change rapidly and reduced usefulness of memory⁹⁷ as the situation may not exist any longer.

Nomadism

Nomadic species follow superabundant but spatiotemporal unpredictable food sources and, like migrants, repeatedly encounter new environments in which they stay for only limited periods of time³³. Similar to migrants nomads explore new environments or changes in the familiar environment less than residents^{33, 98} as they stay in a particular environment for only limited periods of time which makes information only useful in the short-term. Unfortunately, nothing else is known about cognitive abilities in nomads.

For the future areas of interest could be the following. Other than migrants nomads may not need an enlarged hippocampus for long-term memory but short-term spatial knowledge about prospective foraging sites may be important. This would fit to models that simulated nomadism by use of good short-term memory (to avoid recently depleted areas) and poor long-term memory (as unpredictability makes long-term information unreliable⁹⁷). Furthermore, nomads may not be very innovative given their strategy to follow food rather than finding new resources at a given location.

Generalists are also able to cope with unpredictable variable environments due to their flexibility (Fig.1, see below). They will be covered in the next section.

Adaptations to variable and complex environments

Specialists – generalists

A specialist or generalist life-style can evolve in response to both, environmental variability and environmental complexity (see above). For example, models have shown that generalists have an advantage over specialists in variable environments³⁵ as they may be able to exploit more resources, use a variety of habitats and/or are more flexible in their behaviour⁹⁹. However, flexibility in behaviours such as learning and innovation is also often linked to complex environments¹².

With regards to complexity, specialised insects pay attention to fewer cues than generalists which reduces heterogeneity in their environment⁴⁵ and speeds up decision-making (Neural Constraint hypothesis¹⁰⁰). Neophobia, in contrast, varies with stimulus complexity and the degree of deviation from what the organism has experienced before¹⁰¹ (variation) and the same may apply for exploration, innovation and learning⁵¹. Several studies ranging from birds to mammals have shown that diet or habitat generalists are less neophobic than diet and habitat specialists^{54, 102, 103} supporting the Neophobia Threshold hypothesis stating that experiences made early in life (e.g. number of food types/habitats) are protected by neophobia later in life¹⁰⁴. As generalists encounter more habitats/ food types early in life than specialists, they have a more diverse background against which novelty is rated, i.e., they are less neophobic. However, other studies in birds have found the opposite with generalists being more neophobic than specialists giving support for the Dangerous Niche hypothesis^{68, 101}. Here, organisms exposed to a variety of habitats/diets (i.e. generalists) may encounter more dangerous situations and neophobia protects them from this¹⁰¹. Moreover, all studies reviewed covering primates, insects and birds have found habitat and diet generalists to be more explorative than specialists (e. g.^{12, 59, 105}). Likewise, innovations occur more often in generalists and are correlated with low neophobia and high exploration²⁵. While innovations are mainly assumed to be associated with diet generalism, a study particularly testing this found that actually habitat but not diet generalism was linked to a higher innovation rate suggesting that the ability to invent new techniques that may allow eating similar food in novel environments may be the driving factor¹⁰⁶. Generalists are also better learners (insects, crabs, mammals^{102, 107, 108}) and show more

flexible behaviour¹⁰⁹. However, spatial working memory for nectar locations in a nectar specialist bat and spatial memory to home in a fish were better in the specialist as compared to the generalist due to their stronger reliance on a particular resource^{107, 110}. Finally, generalists often have a larger brain²⁵ and/or more connectivity in the brain²⁹.

Taken together, all findings equip a generalist with cognitive abilities to respond more flexibly to environmental change (Fig. 1) or complexity. Regarding the breadth of the investigated cognitive abilities this seems to be the best studied system.

Invasion and urbanisation

The ability to successfully invade new areas (including urban environments) has often been linked with flexibility to respond to novel situations¹¹¹ and likely includes the ability to respond to complexity (sensu Godfrey-Smith⁴⁵) and variation in the environment in the long-term. In support of higher flexibility, individuals from sparrow (*Passer*) populations with recent invasion history showed less food neophobia than birds from historic invasive populations but surprisingly did not differ in object neophobia¹¹². Also, successful invaders in birds and primates are characterised by a higher innovation rate than non-successful invaders¹¹ and invasive crabs (*Carcinus*) had a higher learning speed than non-invasive ones¹¹³. Successful invaders also have larger brains (birds, amphibian, reptiles^{16, 114}). However, in fish brain size was not related to invasion success but the latter correlated with lower fecundity¹¹⁵. Wright et al.¹¹⁶ proposed that flexibility may change along an invasion gradient with invading individuals having a high propensity of innovation, whereas later stages may be less flexible but possibly learn more socially. Urbanisation studies generally find similar results with birds from urban environments being less neophobic but more innovative than birds from rural areas¹¹⁷.

The above findings all support higher flexibility in invasive individuals. Surprisingly, although innovation and exploration are often positively correlated²⁵ suggesting that invasive species are also more explorative this has not been directly investigated so far.

Adaptations to complex environments

Several studies have directly investigated cognitive adaptations to complexity. For example, complex environments challenge neural processing and impose trade-offs in attention (limited attention) such that searching for cryptic prey slows down reaction to objects in the periphery (e.g. predators) as compared to searching for conspicuous prey¹¹⁸. Likewise, speed-accuracy trade-offs have been found between simple and complex habitats with fast but inaccurate exploration in simple habitats and slow and accurate exploration in complex habitats in insects¹¹⁹. Furthermore, studies on birds and rats showed that species from complex habitats were more explorative (object and spatial) than species from simpler habitats^{51, 120}. However, no differences in spatial exploration were found between fish from complex (benthic) and simple (limnetic) habitats but the former learned navigating a maze faster than the latter¹²¹. Likewise, bats from simple and complex habitats did not differ in their spatial exploration but the latter learned a complex rule faster than the former¹²². Also, fish from complex habitats had a better spatial memory than fish from simple habitats¹²³ and several studies from different types of complex and simple habitats show that fish from complex habitats have larger brains^{22, 123} as have bats¹²⁴. Finally, larger brains have been found in frugivorous langurs (*Strepsirrhini*) as compared to folivorous ones but this result was also influenced by

phylogeny¹²⁵. It was assumed that frugivory represents more spatiotemporal complexity as compared to folivory but this was strongly disputed by Sayers¹²⁶.

Overall, cognitive adaptations to complexity have been well studied and often show enhanced cognitive abilities with increasing complexity but not all areas are covered. Although complexity of objects is known to elicit stronger neophobia than simpler objects there seem to be no studies directly addressing neophobic responses in relation to complex environments. Also, innovation has not been studied in relation to complexity.

Predation

Predation is an environmental factor that possibly more often than not hinders cognition. For example, Trinidadian guppies (*Poecilia reticulata*) were highly neophobic to unknown predator cues when from high as compared to low predation rivers¹²⁷ indicating that neophobia has a protective function. However, neophobia can also have costs as shown in predators when avoiding unfamiliar prey which has often been linked to the evolution of aposematism¹²⁸. Furthermore, related to predation is the dangerousness of the prey itself. Parrots foraging on insects which may be harmful were more neophobic to approach food beside novel objects than parrots foraging on less dangerous food like seeds⁵¹. The higher innovation rate in urban environments and the higher object explorativeness of many island species has also been linked to lower predation in these environments^{51, 117}. Interestingly, a study comparing fish from low and high predation environment found the opposite with fish from high predation streams being more spatially explorative⁴⁸. They interpreted the result with the need to collect more information about the environment (e.g. refuges) to avoid predation. The same study also found high predation fish being slower in learning a spatial food location as a consequence of collecting more environmental information⁴⁸. However, other studies found that learning a location with a predator was faster under high predation⁴⁷.

The interaction between predation and cognition is still a new field and highlights the importance of considering other environmental factors than variability and complexity. The cognitive differences reported above may have evolved over evolutionary times as an adaptation to different predator regimes or may be the consequence of phenotypic plasticity in response to current predation. Examples for the latter are given in the next section.

Environmental effects on cognition during development

Most of the reported studies compare populations or species that have evolved under different environmental conditions or have evolved different responses to the same environmental challenge (e.g. migration and residency). However, environmental conditions also act on the developing organism; a field that is just emerging. For example, juvenile fish (cichlids) and wood frog tadpoles (*Rana sylvatica*) kept under high predation regimes for a week showed strong neophobia towards a novel predator, whereas individuals kept under low predation regime were not neophobic suggesting phenotypic plasticity in relation to environmental threats¹²⁷. Predator experience during development also affects brain size with smaller brains under high predation and low group density in common frog (*Rana temporalis*) tadpoles as compared to all other combinations of predation and density¹⁹. The quality of the habitat an organism grows up in also affects cognition. Individuals from high quality habitats explored their surrounding less than those from low quality habitats (squirrel, deer, caterpillars^{129, 130, 131}). Furthermore, variation in food (low-high ratio) as compared to stable

food ratios during ontogeny in fish led to faster learning of a food location later in life¹³². Also, low nutrition during development reduced associative learning in adult birds as compensatory growth was traded-off against learning¹³³. Other studies report about trade-offs between different cognitive abilities as summarised in Buchanan et al¹ with trade-offs between abilities to learn and memorise song versus spatial information and also associated trade-offs in the size of associated brain areas.

This again is a very young field which receives increasing attention. One of the exiting aspects of this field is that environmental conditions can be manipulated to gain more insight into cause and effect and gene x environment interactions.

How do personality and pace-of-life fit into the picture?

Recent research has shown that individuals respond to environmental challenges with entire suits of behavioural and physiological adaptations (termed personality, behavioural syndrome¹³⁴). Likewise, the pace-of-life syndrome predicts similar correlated adaptations in response to metabolism (high vs low metabolic rate) differentiating individuals of the same species but also species from each other¹³⁵. These are interesting approaches as most of the studies mentioned so far have only dealt with one or two cognitive adaptations to environmental conditions at a time. Only few studies have considered personality in relation to cognitive ecology. In sparrows, a personality syndrome was found between neophobia, risk-taking (feeding near predator) and activity in urban and rural populations, while only in rural populations food neophobia was also part of the syndrome¹³⁴ indicating that certain aspects of personality can differ along an urbanisation gradient. A study on fish showed that species with high behavioural heterogeneity are more likely to show behavioural correlations (syndromes) than species with lower behavioural flexibility¹³⁶. This is interesting as it suggests the need for more channelled behavioural combinations in flexible species such as generalists. Sih & Del Giudice¹³⁷ suggested that speed-accuracy trade-offs in cognition are linked to a fast-slow personality. Fast individuals explore a novel environment fast but superficial and are often more aggressive, take greater risk in dangerous situations and are generally more active, whereas the opposite is the case for slow explorers. They suggested that fast and slow explorers may differ in the way how they pay attention to novelty (high vs low attention), how much information they collect and also store which finally affects decision-making (fast-slow). Few studies have tested this so far but fish that made rapid, inaccurate decisions in a spatial memory task had a smaller telencephalon than their slow but accurate counterparts¹³⁸.

The pace-of-life syndrome suggests that organisms can be aligned along a slow-fast life history with a slow pace characterised by slow metabolism, late first reproduction and long life¹³⁹. This continuum may also shape specific cognitive abilities. For example, in muroids the lower the basic metabolic rate (BMR) was, the later species reproduced and the more thoroughly they explored¹³⁹ consistent with the idea that low BMR results in slow but thorough exploration (slow pace-of-life). In contrast, a study in lizards found best survival of individuals that combined low exploration with high BMR or high exploration with low BMR suggesting a trade-off between energy allocations¹⁴⁰. Finally, fast-lived shrews (*Sorex*) used a simpler learning strategy to find a food location than slow-lived bats (*Myotis*) and the latter also had a longer retention memory¹⁴¹, both in accordance with the pace-of-life syndrome. Snell-Rood¹⁴² suggested that behavioural plasticity which is advantageous in variable environments can be developmental (ability of a genotype to adopt different developmental trajectories) or activational (differential activation of underlying networks) with different costs and

benefits; developmental plasticity is slow but integrative, whereas activational plasticity is fast but may have high costs through maintaining different circuits. The former is therefore, expected to occur together with slow life-history traits, whereas the latter with fast life-history traits.

Conclusion

Over the last years, cognitive ecology has become an excitingly broad field ranging from comparisons between particular life-styles to directly testing the effect of specific environmental conditions on cognition. In many systems a broad range of cognitive abilities have been studied. However, the review also identified gaps of knowledge and in part formulated hypotheses how specific cognitive abilities may differ between species or life-styles. More recent studies address the effect environment has on cognitive abilities during development by manipulating environmental variables. This and the final part about personality and pace-of-life is possibly the one future research may focus on. Most of the studies have investigated a single cognitive ability at a time though in some cases an overall picture of a species' cognitive abilities could finally be built across several studies. However, investigating several cognitive abilities together will provide a deeper understanding how selection acts in concert across cognitive abilities; for example that particular combinations of cognitive abilities are favoured over others as has been suggested by Sih & Del Giudice¹³⁷ regarding speed-accuracy trade-offs and personality. Likewise, the idea that metabolism leads to particular pace-of-life trajectories, that may also shape cognitive abilities is intriguing. The review mentioned some examples of energetic constraints on brain size and trade-offs between different brain areas. However, that the way how information is gathered, learned and memorised may also be governed by pace-of-life favouring particular combinations over others has only recently received attention but will again provide a deeper insight how cognitive abilities are integrated with other systems in the body.

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Boesch C. What makes us human (*Homo sapiens*)? The challenge of cognitive cross-species comparison *J Comp Psychol* 2007, 121:227-240.

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