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Evolution of brain complexity and processing and cognitive capacity in selected vertebrates

Evoluce komplexity a procesní a kognitivní kapacity mozku u vybraných obratlovců

Autoreferát disertační práce

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Abstract

Brain processing capacity has traditionally been inferred from data on brain size. However, recent studies have shown that similarly sized brains of distantly related species can differ markedly in the number and distribution of neurons, their basic computational units. Therefore, a finer-grained approach is needed to reveal the evolutionary paths to increased cognitive capacity. This quantitative approach to the evolution of brain processing capacity at the cellular level is relatively new, since quick and reliable estimation of the number of neurons in whole brains or large brain regions has only become possible in the past 15 years or so with the introduction of the isotropic fractionator. This method of determining brain cellular composition is applicable to a wide range of questions. We can assess intraspecific variation, both at the individual and population level, examine the effect of sex and age, and the study selection at the intraspecific level. At the other side of the spectrum, we can study large macroevolutionary trends or try to isolate the effect of specific selective pressures by comparing more closely related and ecologically similar species. In this thesis, I explored variation in brain size and brain cellular composition across vertebrates at both intraspecies and interspecies level.

In Chapter 1, we showed that different populations of the Madagascar ground gecko can vary substantially in the number of brain neurons. There were no sex differences in brain size, number of neurons, or neuron density, even though the species is moderately sexually dimorphic. We also provided evidence that postnatal neurogenesis in geckos does not only replace lost neurons but adds new ones and that this is especially pronounced in the adult telencephalon.

In Chapter 2, we assessed the effect of artificial selection for large relative brain size in guppies on the numbers of neurons. We discovered that it leads to a corresponding increase in the number of neurons. Female guppies in the small-brained and large-brained groups did not differ in neuron density, so the larger brains translated linearly to an increase in neurons. This might explain a host of enhanced cognitive abilities previously described in the large-brained guppies.

In Chapter 3, we tested the social brain hypothesis by directly looking at neuron numbers for the first time. Using Bayesian phylogenetic generalized linear mixed models, we found no association between sociality and any measure of brain size or proxy of brain capacity, showing that sociality in and of itself does not necessarily lead to larger brains and intelligence. It seems that metabolic constraints and possibly increased hypoxia tolerance outweigh any potential benefits of higher brain processing capacity in this specific case and that the nature of social complexity (organisational vs. relational) might be an important factor.

Finally, in Chapter 4, we reconstructed the evolution of brain neuron numbers in amniotes. We analysed a dataset comprising brain sizes of almost 4000 species of amniotes and neuron numbers in three major brain parts of 251 species. We found that non-avian

reptiles have rather low absolute numbers of neurons. Besides their low encephalization (brain size relative to body size), they also feature lower neuron densities, resulting in substantially fewer neurons per body mass compared to endotherms. This holds despite the fact that, across amniotes, neuron densities go down with increasing brain size. Using reversible jump MCMC, we were able to identify significant changes in neuron-brain scaling along amniote phylogeny, without any *a priori* hypotheses. We found that birds and mammals have independently increased not only brain size, but also neuron density, converging on a similar scaling relationship, while there were no significant shifts within non-avian reptiles over the span of 325 million years. This again highlights the importance of energetic constraints in brain evolution. Moreover, this difference between endotherms and ectotherms is most pronounced in the cerebellum, not in the telencephalon. Other two major increases in relative brain size and neuron density occurred in anthropoid primates and core landbirds (Telluraves), again resulting in similar scaling.

Abstrakt

Procesní kapacita mozku bývá tradičně odhadována na základě velikosti mozku. Z nedávných studií však vyplývá, že u vzdáleně příbuzných druhů s podobnou velikostí mozku se může podstatně lišit počet neuronů, tedy základních výpočetních jednotek, i jejich distribuce do různých částí mozku. Abychom tedy dokázali odhalit, jakým způsobem se v evoluci kognitivní kapacita mění, potřebujeme pracovat s daty na jemnější škále. Takový kvantitativní přístup k evoluci procesní kapacity mozku na buněčné úrovni je relativně nový. Možnost rychle získat spolehlivé odhady počty neuronů v celém mozku nebo jeho větších částech je totiž k dispozici až v posledních zhruba 15 letech díky rozšíření metody izotropní frakcionace. Ta otevírá dveře k řešení celé řady otázek. S její pomocí můžeme zjišťovat vnitrodruhovou variabilitu na úrovni jedinců i populací, podívat se na efekt pohlaví a věku, nebo studovat selekci na vnitrodruhové úrovni. Z druhé strany spektra pak můžeme sledovat velké makroevoluční trendy nebo se zaměřit na porovnání blízce příbuzných a ekologicky podobných druhů a pokusit se tak studovat vliv jednotlivých selekčních tlaků.

Ve své disertaci se zabývám variabilitou velikosti mozku a jeho buněčného složení mozku napříč obratlovci, a to jak na vnitrodruhové, tak na mezidruhové úrovni. V kapitole 1 jsme ukázali, že různé populace gekona madagaskarského se mohou významně lišit počtem neuronů v mozku. Zároveň jsme nenašli žádné rozdíly mezi pohlavími ve velikosti mozku, počtu neuronů ani hustotě neuronů, přestože se jedná o druh s mírným pohlavním dimorfismem. Prokázali jsme také, že postnatální neurogeneze u gekononů neslouží jen k nahrazení ztracených neuronů, ale že neuronů v průběhu života přibývá, což je obzvláště patrné v koncovém mozku dospělců.

V kapitole 2 jsme zkoumali, jak se umělá selekce na větší relativní velikost mozku u živorodek *Poecilia reticulata* odrazí v počtech neuronů. Zjistili jsme, že tato selekce má za následek odpovídající narůst v počtu neuronů. Samice živorodek ze skupiny s malými a velkými mozky se mezi sebou nelišily v neuronální hustotě, takže zvětšení mozku se přímo lineárně promítlo do vyššího počtu neuronů. Vysvětluje to lepší výkon v celé řadě kognitivních úloh, který byl u těchto živorodek selektovaných na relativně větší mozky popsán.

V kapitole 3 jsme provedli první test hypotézy sociálního mozku s přímým porovnáním počtu neuronů. Bayesiánské lineární smíšené modely s fylogenetickou korekcí neprokázaly žádné spojení mezi socialitou a velikostí nebo procesní kapacitou mozku. Ukázali jsme tak, že socialita sama o sobě k evoluci velkých mozků a inteligence nestačí. Metabolická omezení a potenciálně vyšší tolerance k hypoxii mohou v tomto konkrétním případě jít proti potenciálním přínosům větší kapacity mozku. Dalším důležitým faktorem může být samotná povaha sociální komplexity u ryposů (organizační, nikoli relační).

V kapitole 4 jsme rekonstruovali evoluci počtu neuronů u amniot. Analyzovali jsme rozsáhlý dataset velikostí mozku, který čítal téměř 4000 druhů amniot, a počty neuronů ve třech velkých částech mozku u 251 druhů. Ukázalo se, že neptačí plazi mají poměrně malé

absolutní počty neuronů. Kromě nízké encefalizace (velikosti mozku relativně k velikosti těla) mají také nižší hustoty neuronů, takže v porovnání s endotermními skupinami mají ve výsledku podstatně méně neuronů na stejnou hmotnost těla, a to přesto, že u amniot obecně hustoty neuronů s rostoucí velikostí mozku klesají. Pomocí MCMC s reverzibilními skoky jsme detekovali významné změny ve škálování počtu neronů s velikostí mozku a těla ve fylogenezi amniot, aniž bychom museli specifikovat *a priori* hypotézy ohledně toho, ve kterých skupinách k nim došlo. Zjistili jsme, že ptáci i savci nezávisle zvětšili nejen mozky, ale také hustoty neuronů, přičemž obě skupiny konvergentně dospěly k podobnému škálování. Naproti tomu uvnitř neptačích plazů žádné výrazné změny během 325 milionů let evoluce neproběhly. Znovu to poukazuje na důležitou roli, kterou v evoluci mozku hrají energetická omezení. Tento rozdíl mezi endotermními a ektotermními amnioty je navíc nejvýraznější v mozečku, nikoli v koncovém mozku. K dalším dvěma zvětšením relativní velikosti mozku a hustoty neuronů došlo u antropoidních primátů a ptačí skupiny Telluraves, přičemž výsledné škálování u těchto dvou skupin je opět podobné.

Introduction

The variation in brain sizes and cognitive abilities in vertebrates, their interrelationship and correlates have long been a central theme in comparative neuroscience, evolutionary biology and comparative psychology. Despite remarkable progress accomplished during the past decade, some key concepts remain controversial. First, there is still no clear consensus on the relationship between "brain size" and cognitive abilities.

Traditionally, relative brain size was taken to be the most relevant factor, whether expressed as the encephalization quotient (Jerison, 1973), or as residuals from regression of brain size on body size (e.g. Clutton-Brock and Harvey, 1980). It is supposed to control for the parts of the brain that are involved in managing somatic tissue and represent the "excess" brain capacity that is involved in higher cognition. Perhaps the ubiquity of this assumption is based on an intuitive understanding that the relative size of an organ gives us some clue about its relative importance, coupled with the fact that humans have much larger brains than expected for their body size. Recently, this view has been challenged by the idea that absolute brain size better corresponds to actual brain processing capacity and the body has little do to with it (e.g. Deaner et al., 2007; MacLean et al., 2014).

However, it is neurons and their connections that provide the substrate for cognition. More specifically, the number of neurons, neuron packing density, interneuronal distance and axonal conduction velocity have been suggested as factors that determine information processing capacity, which is thought to govern general intelligence (Dicke and Roth, 2016; Herculano-Houzel, 2017). This has been mostly ignored in practice, probably because it is laborious to count neurons in whole brains, while it is easy to weigh them.

With the introduction of the isotropic fractionator method, it has become technically feasible to relatively quickly determine numbers and densities of neurons and non-neuronal cells in whole brains and their parts (Herculano-Houzel and Lent, 2005). The method has been independently shown to produce reliable results, comparable to the much lengthier and less effective stereological techniques (Bahney and Bartheld, 2014; Miller et al., 2014).

By using this approach, it transpired that brains of mammals and birds belonging to distantly related clades differ starkly in neuronal densities, neuronal numbers and allocation of neurons into brain compartments (reviewed in (Herculano-Houzel et al., 2015a; Olkowicz et al., 2016). This means that knowledge of neuronal scaling rules is indispensable for comparing the information processing capacities of brains on larger phylogenetic scales. However, neuron counts were available only for a limited number of species of mammals and birds.

To understand the evolution of brain size and complexity in tetrapods, it is imperative to include data on non-avian reptiles and amphibians, yet such data are sorely lacking. Brains of reptiles are generally understudied and comprehensive data on comparative quantitative neuroanatomy are virtually non-existent. Reptiles show the lowest encephalization among amniotes, with absolute brain sizes generally lower than those of mammals or birds (Jerison, 1973). The only larger dataset of whole brain and brain region sizes in reptiles was compiled by Platel more than 40 years ago (Platel, 1980, 1976, 1975) and it comprises data on about 50 species of squamates (Squamata) and turtles (Chelonia). Since then, there has not been much development except for smaller-scale studies (e.g. Font et al., 2019; Ngwenya et al., 2013; Northcutt, 2013).

To get out of the rut caused by reliance on old datasets, we increased phylogenetic coverage, including data on ectotherms, and we adopted a more fine-grained approach by counting neurons and glial cells in whole brains and major brain parts. At this neuronal level, we assessed individual variation, effect of sex and age, response to selection pressures, as well as large patterns of evolutionary changes in brain composition and scaling. By addressing these questions, we can get to the heart of a much larger mystery: what underlies the apparent differences in cognition across species, what evolutionary forces shape them and what is the underlying neural substrate.

Aims

1. To establish the extent of individual variation in ectothermic vertebrates with extended neurogenesis.

2. To explore the effect of artificial selection for relative brain size on the cellular composition of the brain.

3. To test the social brain hypothesis at the neuronal level in an ecologically uniform clade.

4. To reconstruct the evolution of brain size, neuron numbers and densities in amniotes.

Summary of the included publications

Chapter 1

To establish the extent of individual variation in neuron numbers in a species with extensive adult neurogenesis and assess the effect of sex and age, we used the Madagascar ground gecko (*Paroedura picta*). We examined brain size, neuron and glial cell numbers and densities in the telencephalon and the rest of brain in 14 hatchlings, 10 young adults and 10 fully grown adults from one population and 10 fully grown adults from another population to assess interpopulation differences. Surprisingly, the variation in brain size and neuron numbers across both populations was similar to that of laboratory mice of the same age and sex from one population (Herculano-Houzel et al., 2015b). There were no differences between the sexes in any of the parameters, but the two populations differed significantly in everything but neuron density, most notably in the number of non-neuronal cells. The hatchlings had significantly smaller brains and fewer neurons than either of the adult groups and the fully-grown adults had larger brains but not more neurons overall than the young adults. In the telencephalon, however, fully-grown adults had significantly more neurons, suggesting that substantial neurogenesis leads to the addition of new telencephalic neurons throughout life. Including adult but not fully grown animals in comparative studies thus may not significantly affect the results in terms of absolute numbers of brain cells, but might slightly skew the results in terms of neuron densities. Neuronal density seems to be the most conserved feature in this species, in contrast to rodents (Herculano-Houzel et al., 2015; Kverková et al., 2018).

Chapter 2

It has previously been shown that guppies *Poecilia reticulata* selected for large or small relative brain size differ in performance in a number of cognitive tasks (Buechel et al., 2018; Kotrschal et al., 2015, 2013), with the larger-brained group generally outperforming the smaller-brained one. To get to the bottom of this effect, we looked at the cellular composition of brains of 53 adult female guppies that had been selected for either small or large relative brain size over 5 generations. The large-brained guppies had substantially more neurons in both the whole brain and the telencephalon, but they did not differ in neuron densities (i.e. followed the same neuron-brain scaling). At the same time, there were some pronounced individual differences in neuronal density within both groups. Unlike mice (Herculano-Houzel et al., 2015b), larger-brained guppies thus exhibit a matching increase in the number of neurons, potentially explaining their enhanced cognitive abilities. In terms of neuron number variation, guppies are similar to geckos and mice. Interestingly, absolute neuron densities in the guppy brain are the highest reported to date, suggesting that the previously established pattern of decreasing neuron densities with increasing brain size holds for all vertebrates (Herculano-Houzel et al., 2015a). This high neuron-packing density might be part of the reason why small-bodied animals with tiny brains are able to solve surprisingly complex problems.

Chapter 3

The social brain hypothesis (SBH) posits that animals with complex social lives require complex brains to deal with the associated cognitive demands. It has been very influential, especially when it comes to theories about primate and specifically human brain evolution. However, the empirical evidence for this hypothesis is equivocal, with numerous studies finding support and more than a fair share finding none (e.g. DeCasien et al., 2017; Dunbar, 1992; Powell et al., 2017; Shultz and Dunbar, 2007; Vidal-Cordasco et al., 2020). These studies are usually heavily confounded by differences in ecology but also by differences in the type of social complexity. To avoid these pitfalls, we tested the hypothesis in an ecologically uniform clade – the African mole-rats (Bathyergidae). These subterranean rodents are all well adapted to life under ground, with reduced eyes, powerful incisors for digging their tunnels, and multiple physiological adaptations, including lowered metabolic rates and high hypoxia tolerance (Begall et al., 2007; Ivy et al., 2020; Yap et al., 2022). They feed mostly on underground plant parts. Despite being very similar in all other aspects, they exhibit a wide array of social systems. Some are strictly solitary and territorial, the male and female meeting only for a short time to mate and the young leaving upon weaning. Others are cooperative breeders with colonies consisting of the breeding pair and their offspring who act as helpers. Some have been classified as eusocial with life-long philopatry, even though these definitions are somewhat blurry. The social species show complex vocalizations, division of labour and dominance hierarchies (Begall et al., 2007).

African mole-rats thus represent a good model group to test the effect of sociality on brain evolution without the confounding effects of differences in a host of other factors. We measured absolute and relative brain size, neocortex ratio (the ratio of neocortical volume to the rest of brain volume, a proxy for ‘“intelligence” previously used in testing the social brain hypothesis), numbers of neurons in 5 brain parts and volumes of 8 brain parts in 11 species of African mole-rats. We then used phylogenetic Bayesian generalized linear mixed models to look for associations between these brain measures and sociality, either as a categorical variable or as mean and maximum group size. We found no support for the social brain hypothesis; there was either no effect of sociality or the effect found was in the opposite direction, i.e. solitary species having more forebrain neurons and the neocortex ratio and neuron numbers going down with increasing group size. The demands of social interactions clearly do not promote the evolution of larger brains in these rodents, weakening the general support for the SBH. There might be two reasons behind this, even if the SBH generally holds. First, competition rather than cooperation might be the driving factor behind the previously reported increased brain size in social species. Competitive ‘“Machiavellian” interactions are not likely to be selected for in species with extreme reproductive skew and cooperative breeding, because they would decrease inclusive fitness. Second, metabolic constraints might be too strong for any potential benefits of increased cognitive capacity to outweigh the considerable cost of neural tissue. Sociality in mole-rats might have evolved to deal with unfavourable environmental conditions and patchily distributed food resources (Faulkes and Bennett, 2013), and, whether or not that is the case, social species tend to occupy harsher environments (Burda et al., 2000), which would exert more pressure to conserve energy at the expense of costly brains. In any case, this highlights the point that energetic constraints play a crucial role in brain evolution and should always be taken into account.

Chapter 4

To uncover macroevolutionary patterns in brain cellular composition across amniotes, we compiled a large dataset of brain sizes for almost 4000 amniote species and estimated numbers of neurons in three main brain parts in 144 species of birds and non-avian reptiles, more than doubling the number of vertebrate species with known neuron numbers. We then combined these with previously published data and analysed the resulting dataset of 251 species of amniotes. Using reversible-jump Markov chain Monte Carlo analysis, we were able to detect significant shifts in neuron-brain and neuron-body scaling along the amniote phylogeny with no prior assumptions about the location of these shifts. It turns out that birds and mammals independently increased the number of neurons for brain mass, arriving at similar levels, with two other subsequent increases in core landbirds and anthropoid primates. We suggest these convergent increases in neuron numbers coincide with the advent of endothermy, an energetically expensive mode of life. Neurons are metabolically costly and require a steady supply of energy; having large numbers of neurons thus might not be advantageous for animals with low energy intake and expenditure, such as non-avian reptiles. Accordingly, we observed no major increase in neuron-brain scaling within squamate reptiles and turtles in over 300 million years of evolution. The scaling of neurons with brain and body mass is rather conserved, with a handful of dramatic shifts, whereas mosaic changes in specific brain regions are more frequent. There was an additional decrease in cerebellar neurons in snakes, likely connected to the loss of limbs, as a similar pattern is evident in all legless lizards. We also detected a secondary decrease in telencephalic neurons in Accipitriformes, a clade within the core landbirds. However, our sample included only four species, so this finding still needs to be confirmed.

The distribution of neurons to the three major brain parts, telencephalon, cerebellum, and ''rest of brain", shows distinct patterns in different amniote groups. Mammals and birds outside of Telluraves are characterized by the preponderance of cerebellar neurons that make up ~60 to over 90% of all brain neurons. In Telluraves, the telencephalon is the dominant fraction, containing ~40 to 80 % of brain neurons. In non-avian reptiles, the cerebellum is much less developed, and holds typically only about 20-30% of all brain neurons in squamates, with some turtles having a larger cerebellar fraction of about 40 % and the cerebellum becomes dominant in the Nile crocodile (and, presumably, all crocodilians), where it houses 49% of brain neurons. The rest of brain (comprising the brain stem, mesencephalon, and diencephalon) contains only a minor proportion of brain neurons in mammals and birds (often less than 10%) but is much more important in non-avian reptiles, where it can be the dominant fraction, with over 50% of brain neurons. The distributions of brain neurons are much more variable than the neuron-brain or neuron-body scaling, especially in non-avian reptiles. It seems the overall ''neuronal energy budget" can be flexibly allocated to brain structures depending on species-specific needs, with different regions or circuits having different per-neuron utility. A modest volumetric increase in a neuron-dense structure such as the cerebellum translates into a substantial number of added neurons. In fact, the cerebellum is the region that truly sets apart ectothermic and endothermic amniotes, with the latter having on average almost 60-fold more cerebellar neurons for equivalent body mass but only about 7-fold larger brains.

We additionally calculated the strength of allometric integration between the number of neurons in different brain parts and body size. It was similar in all the identified grades except for primates, who exhibit a weaker allometric integration, that is they have much higher rates of evolution and changes in neuron-body scaling happen quickly.

Primates also stand out in another aspect. Across amniotes, there is a clear positive relationship between relative brain size (brain mass for a given body mass) and relative neuron number (number of neurons for a given brain mass). This is despite the fact that absolute neuron density goes down with absolute brain mass. When we break the relationship down to look at reptiles, birds, and mammals separately, it turns out that the trend is very strong in birds, somewhat less pronounced in non-avian reptiles and non-existent in mammals. However, primates are an exception among mammals and they show a clear significant relationship. Cases where increases in relative brain size are coupled with increases in relative brain neuron numbers might represent evolutionary ‘‘signatures” of selection for higher brain processing capacity. When the brain is larger than expected for a given body size while neuron density is simultaneously higher than expected for a given brain size, it seems likely that selection favoured increased neuron numbers and therefore information processing capacity.

Conclusions

We found out that the inter-individual and interpopulation variation in the number of neurons and neuron densities in a reptile is comparable to that in mammals, despite the reptile brain growing through adulthood. Ectothermic vertebrates might have a tighter relationship between brain size and neuron number at the intraspecific level than endotherms, but robust data on individual variation and ontogenetic changes in birds are still missing.

Using the guppy model, we showed that selection can very quickly lead to increases in neuron numbers that apparently translate into improved cognitive abilities. This attests to a high evolvability in this trait, as these fish came from the same genetic background and have only been selected for 5 generations. However, more dramatic changes seem to be rather rare, as the ‘‘neuronal scaling rules” are quite conserved within smaller clades and truly dramatic shifts happened only a handful of times within amniotes.

Differences between reptiles and endotherms are more profound than we previously realized. At the same time, birds and mammals converged on a similar scaling despite having different brain organization. Convergent brain processing capacity increases in endotherms, coupled with no substantial changes within non-avian reptiles imply an important role of energetic constraints. This ties in well with the fact the African mole-rats show a pattern opposite to the social brain hypothesis and their overall neuron numbers seem to be constrained by the demands of underground life.

We found pronounced differences in brain neuron distributions between reptiles, birds, and mammals. Moreover, mammals show uncoupling of the evolution of relative brain size and relative neuron numbers, unlike the other groups. This could have important implications for the use of brain size as a proxy for information processing capacity.

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Yap, K.N., **Wong, H.S.**, **Ramanathan, C.**, **Rodriguez-Wagner, C.A.**, **Roberts, M.D.**, **Freeman, D.A.**, **Buffenstein, R.**, **Zhang, Y.**, 2022. Naked mole-rat and Damaraland mole-rat exhibit lower respiration in mitochondria, cellular and organismal levels. *Biochim. Biophys. Acta BBA - Bioenerg.* 1863, 148582. https://doi.org/10.1016/j.bbabio.2022.148582

CURRICULUM VITAE

Mgr. Kristina Kverková

EDUCATION

2016–present **Ph.D. degree in Zoology**
Charles University, Faculty of Science, Department of Zoology
Thesis: *Evolution of brain complexity and processing and cognitive capacity in selected vertebrates*

2014–2016 **Master's degree in Zoology**
Charles University, Faculty of Science, Department of Zoology
Thesis: *Brains of African mole-rats in numbers: Data for testing the social brain hypothesis*

2011–2014 **Bachelor's degree in Biology**
Charles University, Faculty of Science
Thesis: *Social Brain Hypothesis: A Survey of Evidence*

EMPLOYMENT

2018–present **Researcher** Department of Zoology, Faculty of Science, Charles University

TEACHING AT THE CHARLES UNIVERSITY

2016-present **Animal morphology**
2018-present **Vertebrate zoology**

THESIS SUPERVISION

Bachelor's thesis: Polonyiová A., Cognitive abilities in reptiles and relevant research methodology, defended 2018 (consultant)
Diploma thesis: Polonyiová A., The effect of incubation temperature on cognition and brain cellular composition in geckos *Paroedura picta*, defended 2020 (consultant)

PUBLICATIONS

5 publications in ISI-indexed peer-reviewed journals
(Scite: 103 citations, h-index = 5; accessed on 25th November 2022).

1. **Kverková, K.**, Bělíková, T., Olkowicz, S., Pavelková, Z., O'Riain, M. J., Šumbera, R., Burda, H., Bennett, N. C. & Němec, P. (2018). Sociality does not drive the evolution of large brains in eusocial African mole-rats. *Scientific Reports,* 8(1), 1-14. (38 citations)
2. Marhounová, L., Kotrschal, A., **Kverková, K.**, Kolm, N., & Němec, P. (2019). Artificial selection on brain size leads to matching changes in overall number of neurons. *Evolution*, 73(9), 2003-2012. RG: 37, (37 citations)
3. **Kverková, K.**, Polonyiová, A., Kubička, L., & Němec, P. (2020). Individual and age-related variation of cellular brain composition in a squamate reptile. *Biology letters*, 16(9), 20200280. (7 citations)
4. Frýdlová, P., Mrzílková, J., Šeremeta, M., Křemen, J., Dudák, J., Žemlička, J., Minnich B., **Kverková K.**, Němec, P., Zach, P. & Frynta, D. (2020). Determinate growth is predominant and likely ancestral in squamate reptiles. *Proceedings of the Royal Society B*, 287(1941), 20202737 (9 citations)
5. **Kverková, K.**, Marhounová, L., Polonyiová, A., Kocourek, M., Zhang, Y., Olkowicz, S., Straková B, Pavelková, Z., Vodička, R. Frynta, D. & Němec, P. (2022). The evolution of brain neuron numbers in amniotes. *Proceedings of the National Academy of Sciences*, 119(11), e2121624119. (12 citations)

CONFERENCE CONTRIBUTIONS

2016

8th European Conference on Comparative Neurobiology, Munich (poster)
Zoologické dny, České Budějovice (talk)

2017

44. Konference České a slovenské etologické společnosti, Jihlava (talk)

2018

Zoologické dny, Praha (talk)
9th European Conference on Behavioural Biology, Liverpool (talk)
45. Konference České a slovenské etologické společnosti, Ostrava (poster)

2019

9th European Conference on Comparative Neurobiology, Murcia (poster)
46. Konference České a slovenské etologické společnosti, Bratislava (talk)

2020

Zoologické dny, Olomouc (talk)

2022

10th European Conference on Comparative Neurobiology, Prague (talk, organizer)
International Congress Neuroethology, Lisbon (talk)
Congress of the European Society for Evolutionary Biology, Prague (talk)

INVITED TALKS

2021 Charles University, Biological Thursdays
2022 South Bohemian University, Department of Zoology seminar

AWARDS

2016
- Zoologické dny Best student talk – 2nd place

2017
- ČSEtS Jihlava Best student talk – 1st place

2018
- "Vakovlk Junior" Best student publication at the Department of Zoology
- ČSEtS Ostrava Best student poster– 1st place

2019
- ČSEtS Bratislava Best student talk – 2nd place