## Vertebrate neuron counts

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Summary table (with uncertainties)

Why count vertebrate neurons?

**Reptiles** 

**Amphibians** 

<u>Fish</u>

**Mammals** 

**Birds** 

Farmed animals and pets

Neuron count timeline

**References** 

| Vertebrate<br>class | Average Weight (g) | Average weight<br>uncertainty | Average<br>Neurons<br>(millions) | Neuron count<br>uncertainty | Overall<br>uncertainty |
|---------------------|--------------------|-------------------------------|----------------------------------|-----------------------------|------------------------|
| Fish                | 5.7                | Very low                      | 19.9                             | Medium                      | Low                    |
| Amphibians          | 7                  | Medium                        | 9.8                              | High                        | Medium-high            |
| Reptiles            | 18.7               | Medium-high                   | 4.4                              | Low                         | Medium                 |
| Wild mammals        | 850                | Medium                        | 874.5                            | Very low                    | Low                    |
| Wild birds          | 80                 | Medium                        | 574.8                            | Low                         | Medium-low             |

### Summary table (with uncertainties)

### Why count vertebrate neurons?

Since at least some animals merit moral consideration, evaluating whether the world is, on net, good or bad requires one to consider the wellbeing of animals other than humans. But perhaps not all animals merit equal consideration. Although this issue is controversial to say the least, many people would feel worse about harming an elephant than they would a tadpole.

Although we don't know how to measure 'degree of moral concern merited' directly, intelligence may be a reasonable proxy. Experts consider neuron count the best

available proxy for intelligence (e.g. Herculano-Houzel, 2017; Roth & Dicke, 2012). In this essay, I use scientific data to estimate total neuron counts for various kinds of vertebrates. These estimates in part shaped the discussion of animal welfare issues in *What We Owe the Future*. However, because this work is so uncertain and my research is ongoing, the numbers in this document may differ from those that appear in print copies of the book.

Experts have proposed a number of characteristics that confer moral status<sup>1</sup> to animals. These include cognitive capacity, practical reasoning ability, moral capacity, and sentience (Jaworska & Tannenbaum, 2021; Shepherd, 2018; Korsgaard, 2018; McMahan, 2005; Warren, 2000). Of these, cognitive capacity is perhaps the most highly cited.<sup>2</sup> Cognitive capacity is difficult to measure directly and compare across species, but given it is often used as a synonym of intelligence, it is, likewise, plausibly correlated with neuron count. That makes neuron count a plausible, quantifiable proxy of moral status–albeit an imperfect one.<sup>3</sup>

Here I consider only major vertebrate groups: reptiles, amphibians, fish, mammals, and birds. Vertebrates have relatively large brains among animals, and a wider survey was infeasible. This means that some plausible, high-intelligence animals, such as octopuses, are neglected by this analysis. Nevertheless, vertebrates may be a cut-off point for the evolution of both high intelligence and sentience (Allen & Trestman, 2020; Andrews & Monsó, 2021)

In general, data are lacking in this area. This means that, in most cases, I use one or a few species for which neuron-count data are available as representatives of large groups of species.

<sup>&</sup>lt;sup>1</sup> A short and precise definition of moral status is: "An entity has moral status if and only if it or its interests morally matter to some degree for the entity's own sake. For instance, an animal may be said to have moral status if its suffering is at least somewhat morally bad, on account of this animal itself and regardless of the consequences for other beings." (Jaworska & Tannenbaum, 2021).

<sup>&</sup>lt;sup>2</sup> Shepherd (2018, Part I) offers the most accessible yet thorough introduction to the subject that I am aware of. For a much shorter but less elegant overview than Shepherd's, see my own overview (Fabiano, 2021, pp. 2–4).

Shepherd (2018) defends the increasingly popular view that the basis for moral concern is possessing certain kinds of conscious experiences. Unlike cognitive capacity, sentience is not synonymous with intelligence. Consciousness' physical basis is notoriously hard to pinpoint, but high intelligence is a plausible proxy for sentience in naturally evolving life forms. As I will mention next, vertebrates are a reasonable cut-off point for the evolution of both high intelligence and sentience.

<sup>&</sup>lt;sup>3</sup> Two important caveats. Firstly, some philosophers disagree with the view that moral status can vary beyond a two-tier system between human and non-human animals; therefore, they would count all non-human animals equally. Others and I reject this view (DeGrazia, 2008; Douglas, 2013; Fabiano, 2021, pp. 4–5). Secondly, on a case-by-case comparison, we might often have better proxies for moral status based on behavioural analysis and neuroscientific data. However, conducting such analysis for every vertebrate would be unfeasible.

## Reptiles

A recent study by leading experts in the area counted the neurons of Nile crocodiles (Ngwenya et al., 2016). Given this species grows indefinitely, it offers a wide range of body weights and brain sizes. At 90 kg, it had a 20 g brain and 80.5 million neurons. At 92 g, it had a 1 g brain and 45 million neurons (Ngwenya et al., 2016). A 20-fold increase in brain weight implied only a 1.8-fold increase in neuron count. In a dataset covering 99% of reptile species, the mean body mass was 18.7 g (Feldman et al., 2016, Tab. 2). Reptiles at this weight have a brain of around 1 g (van Dongen, 1998, p. 2109), so the average number of neurons per reptile would be about 45 million. However, this is likely an overestimation given that it's based on the juvenile stage of a species with a much larger adult weight, and neuron count doesn't change that much as individuals age.

Luckly, two recent studies counted the neurons of the small lizards *Paroedura picta* (Kverková et al., 2020b), *Anolis cristatellus*, and *Anolis evermanni* (Storks et al., 2020). These studies gave the following numbers for average weight and neuron count:<sup>4</sup>

- Paroedura picta: 15.9 g, 4.4 million neurons (Kverková et al., 2020a, 2020b),
- Anolis cristatellus: 4.0 g, 4.27 million neurons (Storks et al., 2020)
- Anolis evermanni: 4.3 g, 4.92 million neurons (Storks et al., 2020)

Of these, *Paroedura picta* is closest to the mean weight for all reptiles. In fact, one specimen in that study weighed exactly 18.7 g and had **4.4 million neurons** (Kverková et al., 2020a, 2020b). Since this is also close to the average for all three of these species, I will use 4.4 million as the average neuron count for all reptiles.

<sup>&</sup>lt;sup>4</sup> The Feldman et al. (2016) survey measured these species at 15.3g, 9.8g and 9.8g respectively. So the individuals for *Anolis cristatellus* and *Anolis evermanni* in the neuron count study may have been smaller than average.



*Paroedura picta* (ocelot gecko), an average-sized reptile weighing 16g with 4.4 million neurons<sup>5</sup>

## Amphibians

I could only find one, very old, neuron count estimate for an amphibian: 9.8 million brain neurons counted for the common European frog *Rana esculenta* (Kemali & Braitenberg, 1969, p. 9). Frogs in that sample weighed between 11.6 g and 21.4 g, and a different study estimated the average weight for this species at 19.93 g (Santini et al., 2018, Suppl. 2). That makes *Rana esculenta* larger than the average amphibian, which weighs around 7g (Bar-On et al., 2018; Santini et al., 2018). However, 9.8 million neurons is somewhat larger, but broadly similar to, our neuron count for reptiles; therefore, lacking any other amphibian neuron count, I'll use **9.8 million** as the average neuron count for all amphibians.

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*Rana esculenta* (edible frog), a representative amphibian weighing about 20 g with 9.8 million neurons<sup>6</sup>

## Fish

Several studies have counted brain cells or neurons for different species of fish:

- Brown ghost knifefish weigh about 10 g and have about 100 million brain cells (Binohlan & Froese, 2022; Froese et al., 2014; Zupanc & Horschke, 1995, p. 230). In other species, about half of brain cells are neurons, so this suggests they have about 50 million neurons (Ridgway et al., 2019, Tab. S1).
- Bluestreak cleaner wrasses weigh 3.52 g on average and have about 40 million total brain cells, suggesting 20 million neurons (Triki et al., 2020).
- Rainbowfish weigh 0.366 g on average and have 4.3 million neurons (Marhounová et al., 2019).
- One study examined major brain areas of white seabream and counted about 5.5 million brain cells (Pereira et al., 2016, fig. 5). I judge that this accounts for about

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half of its total brain mass (Bshary et al., 2014, fig. 1; Porter & Mueller, 2020, fig. 8), which would imply a total of about 5.5 million neurons.

• Zebrafish weigh 0.88 g (Clark et al., 2018) and have 5 million neurons (Hinsch & Zupanc, 2007).

However, the overwhelming majority of fishes are <u>mesopelagic fish</u> (i.e. live at least 200m below the surface) with an average weight of 5.7g (Froese et al., 2014; Jarre-Teichmann & Ortañez, 2022; Nishimura et al., 1999; Porteiro et al., 2017).<sup>7</sup> This implies that the bluestreak cleaner wrasse is the most representative species. Therefore, I take **19.9 million neurons** to be the average fish neuron count.



*Labroides dimidiatus* (bluestreak cleaner wrasse), a representative fish weighing 3.52g with 19.8 million neurons<sup>8</sup>

<sup>&</sup>lt;sup>7</sup> Calculated using cited data here: **1** Mesopelagic Fish Weight

<sup>&</sup>lt;sup>8</sup> Image credit: Elias Levy, CC BY 2.0 <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons

#### Mammals

I use two estimates for mammals. First, an estimate of the average mammalian neuron count pre-humans. Second, an estimate of the *current* average number of neurons in *non-human wild* mammals.<sup>9</sup>

The pre-human average mammal body weight has been estimated at 850g (Trammer, 2011, fig. 7). Mammal neuron count seems to vary more between orders than it does for other groups of vertebrates. So, rather than trying to find a representative species, I will use the average neuron count of all species in a 2015 database (Herculano-Houzel et al., 2015, fig. 5) whose weight is within a factor of two of this average (i.e. between 425 g and 1,700 g). This encompasses six species from three major clades (rodents, primates and <u>Afrotheria</u>), including hyraxes, squirrels, bush babies, and monkeys. The geometric mean of their neuron count is **874.5 million** (arithmetic mean: 1,174.5). I'll use that figure as the average pre-human mammalian neuron count (Herculano-Houzel et al., 2015, fig. 5).<sup>10</sup>



<sup>&</sup>lt;sup>9</sup> The difference is due to the <u>extinction of many megafauna</u>.

<sup>&</sup>lt;sup>10</sup> Calculated using cited data: 🖬 Average-size mammals neuron count

Saimiri sciureus (common squirrel monkey) weighs 859 g and has 3.2 billion neurons<sup>11</sup>

For a rough estimate of the *current* wild mammal average neuron count, I will consider the Guinea pig's **233.6 million** neurons (Herculano-Houzel et al., 2015, fig. 5). At 311 g, Guinea pigs are close to the median current mammalian weight of 268 g (Maurer et al., 1992, p. 951).<sup>12</sup>

# Birds

One study, based on a British sample, found that the average weight of wild birds is 80 g (Bar-On et al., 2018, Suppl. p. 38). The most comprehensive study to date includes 11,009 species, with an average mass of 267 g (Tobias, 2021), but doesn't take into account the relative abundance of different species. Smaller birds are more numerous than large birds, so I will use 80 g as the average bird body mass. A neuron count study of birds includes four species with a body mass between 60 g and 100 g. Their average neuron count is **574.8 million**, which I'll use as the average for all wild birds (Olkowicz et al., 2016, Tab. S1).

<sup>&</sup>lt;sup>11</sup> Image credit: Ruben Undheim from Trondheim, Norway, CC BY-SA 2.0

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<sup>&</sup>lt;sup>12</sup> Feldman et al. (2016, p. 194) reports Meiri et al. (2011) found 261 g, but I could not locate that in the cited source.



Cyanopica cyanus (azure-winged magpie)weighs 84 g and has 700 million neurons<sup>13</sup>

### Farmed animals and pets

In addition to wild animals, many billions of animals in the world are found in farms (either on land or in water).

First, farmed fish. Using FAO statistics for the total weight of fish captured globally and the estimated mean weight of each species, one report has estimated a generic mean weight of 67.5 g for commercial, farmed fish (Mood & Brooke, 2019). I will use the neuron count of the brown ghost knifefish, which weighs 10 g, as an approximation. It has about 50 million neurons. Although this fish is smaller than the average farmed fish, neuron count increases very slowly with body weight. (Zupanc & Horschke, 1995, p. 230).

Luckly, we know how many neurons chickens have: 220.84 million (Herculano-Houzel et al., 2015, fig. 5). We also know pigs have 2.2 billion neurons (Olkowicz et al., 2016,

<sup>&</sup>lt;sup>13</sup> Image credit: DickDaniels (http://carolinabirds.org/), CC BY-SA 3.0

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Tab. S1). However, I could not find any neuron count data for cattle. The closest species available seems to be the Greater kudu, which is in the same bovine sub-family and has similar brain weight – 308 g vs 480 g (Ballarin et al., 2016; Kazu et al., 2014). Greater kudu have 6.1 billion neurons (Kazu et al., 2014).

As for other farmed animals, I found figures for (Herculano-Houzel et al., 2015, fig. 5; Kverková et al., 2022):

- Turkeys (492.9 million)
- Ducks (386.9 million)
- Geese (738.2 million)
- Rabbits (494.2 million)

The two main species missing are sheep and goats. They have brain weights of 115-120 g (Massen, 2021). This is similar to the Springbok, which weighs 102 g and is also in the bovid family. So I'll use the Springbok's neuron count of 3.1 million (Kazu et al., 2014).

Regarding the two most common pets, one study found that dogs have 2.2 billion neurons and cats have 1.2 billion (Jardim-Messeder et al., 2017, Tab. 1). However, another study – which used a larger sample of eight dog breeds weighing between 4 kg and 48 kg – found an average neuron count of 3.3 billion (Salajková, 2020, p. 22). I will use the latter figure.

## **Neuron count timeline**

Using my <u>vertebrate population through time estimations made elsewhere</u>, we can get a sense of how vertebrates' total neurons have varied throughout time by multiplying neurons by yearly population.

Because they are so numerous, wild fish and amphibians dominate the total neuron count. They comprise, respectively, 77.4% and 21% of all vertebrates' neuron-years. They are even more dominant currently. Today, 91.3% of all vertebrate neurons belong to fish (amphibians contribute 2.4% of the total). Wild reptiles, mammals and birds each correspond to less than 1.3% of all vertebrates' neuron-years and current neurons. Humans correspond to 4% of all current vertebrate neurons, farmed animals to 0.2% and pets to 0.02%. Plotting everything in a log-scale looks like this:



### References

Allen, C., & Trestman, M. (2020). Animal Consciousness. In E. N. Zalta (Ed.), Stanford Encyclopedia of Philosophy (Winter 2020). Metaphysics Research Lab, Stanford University.

https://plato.stanford.edu/archives/win2020/entries/consciousness-animal/

- Andrews, K., & Monsó, S. (2021). Animal Cognition. In E. N. Zalta (Ed.), Stanford Encyclopedia of Philosophy (Spring 2021). Metaphysics Research Lab, Stanford University. https://plato.stanford.edu/archives/spr2021/entries/cognition-animal/
- Ballarin, C., Povinelli, M., Granato, A., Panin, M., Corain, L., Peruffo, A., & Cozzi, B.(2016). The Brain of the Domestic Bos taurus: Weight, Encephalization and Cerebellar Quotients, and Comparison with Other Domestic and Wild

Cetartiodactyla. PLOS ONE, 11(4), e0154580.

https://doi.org/10.1371/journal.pone.0154580

- Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. Proceedings of the National Academy of Sciences, 115(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115
- Binohlan, C., & Froese, R. (2022). *Apteronotus leptorhynchus* [Web Page]. FishBase. https://www.fishbase.se/summary/Apteronotus-leptorhynchus.html
- Bshary, R., Gingins, S., & Vail, A. L. (2014). Social cognition in fishes. *Trends in Cognitive Sciences*, *18*(9), 465–471. https://doi.org/10.1016/j.tics.2014.04.005
- Clark, T. S., Pandolfo, L. M., Marshall, C. M., Mitra, A. K., & Schech, J. M. (2018). Body Condition Scoring for Adult Zebrafish (Danio rerio). *Journal of the American Association for Laboratory Animal Science*, 57(6), 698–702. https://doi.org/10.30802/AALAS-JAALAS-18-000045
- Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall Brain Size, and Not Encephalization Quotient, Best Predicts Cognitive Ability across Non-Human Primates. *Brain, Behavior and Evolution*, *70*(2), 115–124. https://doi.org/10.1159/000102973
- DeGrazia, D. (2008). Moral status as a matter of degree? *Southern Journal of Philosophy*, *46*(2), 181–198. https://doi.org/10.1111/j.2041-6962.2008.tb00075.x
- Douglas, T. (2013). Human enhancement and supra-personal moral status.

Philosophical Studies, 162(3), 473–497.

https://doi.org/10.1007/s11098-011-9778-2

Fabiano, J. (2021). Persons vs. Supra-persons and the undermining of individual

interests. The Journal of Value Inquiry.

https://doi.org/10.1007/s10790-021-09868-0

- Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I., & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara:
  Lepidosaur body sizes. *Global Ecology and Biogeography*, 25(2), 187–197.
  https://doi.org/10.1111/geb.12398
- Froese, R., Thorson, J. T., & Reyes, R. B. (2014). A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, *30*(1), 78–85. https://doi.org/10.1111/jai.12299
- Herculano-Houzel, S. (2017). Numbers of neurons as biological correlates of cognitive capability. *Current Opinion in Behavioral Sciences*, *16*, 1–7. https://doi.org/10.1016/j.cobeha.2017.02.004

Herculano-Houzel, S., Catania, K., Manger, P. R., & Kaas, J. H. (2015). Mammalian
Brains Are Made of These: A Dataset of the Numbers and Densities of Neuronal and Nonneuronal Cells in the Brain of Glires, Primates, Scandentia,
Eulipotyphlans, Afrotherians and Artiodactyls, and Their Relationship with Body
Mass. *Brain, Behavior and Evolution*, *86*(3–4), 145–163.
https://doi.org/10.1159/000437413

- Hinsch, K., & Zupanc, G. K. H. (2007). Generation and long-term persistence of new neurons in the adult zebrafish brain: A quantitative analysis. *Neuroscience*, *146*(2), 679–696. https://doi.org/10.1016/j.neuroscience.2007.01.071
- Jardim-Messeder, D., Lambert, K., Noctor, S., Pestana, F. M., de Castro Leal, M. E., Bertelsen, M. F., Alagaili, A. N., Mohammad, O. B., Manger, P. R., &

Herculano-Houzel, S. (2017). Dogs Have the Most Neurons, Though Not the Largest Brain: Trade-Off between Body Mass and Number of Neurons in the Cerebral Cortex of Large Carnivoran Species. *Frontiers in Neuroanatomy*, *11*, 118. https://doi.org/10.3389/fnana.2017.00118

- Jarre-Teichmann, A., & Ortañez, A. (2022). *Cyclothone pallida* [Web Page]. FishBase. https://www.fishbase.de/summary/6966
- Jaworska, A., & Tannenbaum, J. (2021). The Grounds of Moral Status. In E. N. Zalta (Ed.), *Stanford Encyclopedia of Philosophy* (Spring 2021). Metaphysics
   Research Lab, Stanford University.

https://plato.stanford.edu/archives/spr2021/entries/grounds-moral-status/

Kazu, R. S., Maldonado, J., Mota, B., Manger, P. R., & Herculano-Houzel, S. (2014).
Cellular scaling rules for the brain of Artiodactyla include a highly folded cortex with few neurons. *Frontiers in Neuroanatomy*, *8*.
https://doi.org/10.3389/fnana.2014.00128

Kemali, M., & Braitenberg, V. (1969). Atlas of the Frog's Brain. Springer-Verlag.

Korsgaard, C. M. (2018). Fellow Creatures: Our Obligations to the Other Animals. In Uehiro Series in Practical Ethics. Oxford University Press. https://doi.org/10.1093/oso/9780198753858.001.0001

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. https://doi.org/10.1073/pnas.2121624119 Kverková, K., Polonyiová, A., Kubička, L., & Němec, P. (2020a). Supplementary
 material from 'Individual and age-related variation of cellular brain composition in
 a squamate reptile'. *Biology Letters*, *16*(9).

https://doi.org/10.6084/M9.FIGSHARE.C.5120436

- Kverková, K., Polonyiová, A., Kubička, L., & Němec, P. (2020b). Individual and age-related variation of cellular brain composition in a squamate reptile. *Biology Letters*, 16(9), 20200280. https://doi.org/10.1098/rsbl.2020.0280
- 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. https://doi.org/10.1111/evo.13805
- Massen, J. (2021). SourceData of Yawn videos and published brain data [Dataset]. In *DataverseNL*. https://doi.org/10.34894/ROFNL1
- Maurer, B. A., Brown, J. H., & Rusler, R. D. (1992). The Micro and Macro in Body Size Evolution. *Evolution*, *46*(4), 939–953.

https://doi.org/10.1111/j.1558-5646.1992.tb00611.x

- McMahan, J. (2005). Our fellow creatures. *Journal of Ethics*, *9*(3–4), 353–380. https://doi.org/10.1007/s10892-005-3512-2
- Meiri, S., Raia, P., & Phillimore, A. B. (2011). Slaying dragons: Limited evidence for unusual body size evolution on islands: Island vertebrates and body size extremes. *Journal of Biogeography*, *38*(1), 89–100. https://doi.org/10.1111/j.1365-2699.2010.02390.x
- Mood, A., & Brooke, P. (2019). *Estimated numbers of individuals in global aquaculture production (FAO) of fish species (2017)* [Dataset]. FishCount.

http://fishcount.org.uk/studydatascreens2/2017/numbers-of-farmed-fish-A0-2017. php?sort2/full

- Ngwenya, A., Patzke, N., Manger, P. R., & Herculano-Houzel, S. (2016). Continued Growth of the Central Nervous System without Mandatory Addition of Neurons in the Nile Crocodile (Crocodylus niloticus). *Brain, Behavior and Evolution*, *87*(1), 19–38. https://doi.org/10.1159/000443201
- Nishimura, A., Nagasawa, K., Asanuma, T., Aoki, H., & Kubota, T. (1999). Age, Growth, and Feeding Habits of Lanternfish, Stenobrachius leucopsarus (Myctophidae), Collected from the Near-surface Layer in the Bering Sea. *Fisheries Science*, *65*(1), 11–15. https://doi.org/10.2331/fishsci.65.11
- Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, *113*(26), 7255–7260.
  https://doi.org/10.1073/pnas.1517131113
- Pereira, P., Puga, S., Cardoso, V., Pinto-Ribeiro, F., Raimundo, J., Barata, M.,
  Pousão-Ferreira, P., Pacheco, M., & Almeida, A. (2016). Inorganic mercury accumulation in brain following waterborne exposure elicits a deficit on the number of brain cells and impairs swimming behavior in fish (white seabream—Diplodus sargus). *Aquatic Toxicology*, *170*, 400–412. https://doi.org/10.1016/j.aquatox.2015.11.031
- Porteiro, F., Sutton, T., Byrkjedal, I., Orlov, A., Heini, M., Menezes, G., & Bergstad, O. (2017). Fishes of the Northern Mid-Atlantic Ridge Collected During the MAR-ECO Cruise. *Arquipelago Life and Marine Sciences, Supplement 10*.

http://www.okeanos.uac.pt/arquipelago\_journal/supplement-10/

- Porter, B. A., & Mueller, T. (2020). The Zebrafish Amygdaloid Complex Functional Ground Plan, Molecular Delineation, and Everted Topology. *Frontiers in Neuroscience*, *14*, 608. https://doi.org/10.3389/fnins.2020.00608
- Ridgway, S. H., Brownson, R. H., Van Alstyne, K. R., & Hauser, R. A. (2019). Higher neuron densities in the cerebral cortex and larger cerebellums may limit dive times of delphinids compared to deep-diving toothed whales. *PLOS ONE*, *14*(12), e0226206. https://doi.org/10.1371/journal.pone.0226206
- Roth, G., & Dicke, U. (2012). Evolution of the brain and intelligence in primates. In *Progress in Brain Research* (Vol. 195, pp. 413–430). Elsevier. https://doi.org/10.1016/B978-0-444-53860-4.00020-9
- Salajková, V. (2020). *Pravidla buněčného škálování mozku u psů: Efekt domestikace a miniaturizace psích plemen* [PhD Thesis, Department of Zoology, Charles University]. http://hdl.handle.net/20.500.11956/116599
- Santini, L., Benítez-López, A., Ficetola, G. F., & Huijbregts, M. A. J. (2018). Length–mass allometries in amphibians. *Integrative Zoology*, *13*(1), 36–45. https://doi.org/10.1111/1749-4877.12268
- Shepherd, J. (2018). *Consciousness and Moral Status*. Routledge. https://doi.org/10.4324/9781315396347
- Storks, L., Powell, B. J., & Leal, M. (2020). Peeking Inside the Lizard Brain: Neuron Numbers in Anolis and Its Implications for Cognitive Performance and Vertebrate Brain Evolution. *Integrative and Comparative Biology*, icaa129. https://doi.org/10.1093/icb/icaa129

- Tobias, J. (2021). AVONET: Morphological, ecological and geographical data for all birds (Tobias et al 2021 Ecology Letters) [Dataset]. In *Figshare* (p. 60385406 Bytes). https://doi.org/10.6084/M9.FIGSHARE.16586228.V1
- Trammer, J. (2011). Differences in global biomass and energy use between dinosaurs and mammals. *Acta Geologica Polonica*, *61*(2), 125–132. https://geojournals.pgi.gov.pl/agp/article/view/9800/8335
- Triki, Z., Emery, Y., Teles, M. C., Oliveira, R. F., & Bshary, R. (2020). Brain morphology predicts social intelligence in wild cleaner fish. *Nature Communications*, *11*(1), 6423. https://doi.org/10.1038/s41467-020-20130-2
- van Dongen, P. A. M. (1998). Brain Size in Vertebrates. In R. Nieuwenhuys, H. J. ten Donkelaar, & C. Nicholson, *The Central Nervous System of Vertebrates* (pp. 2099–2134). Springer Berlin Heidelberg.

https://doi.org/10.1007/978-3-642-18262-4\_23

Warren, M. A. (2000). 1. The Concept of Moral Status. In *Moral Status* (pp. 3–23). Oxford University Press.

https://doi.org/10.1093/acprof:oso/9780198250401.001.0001

Wilczynski, W. (2009). Evolution of the Brain in Amphibians. In M. D. Binder, N.
Hirokawa, & U. Windhorst (Eds.), *Encyclopedia of Neuroscience* (pp. 1301–1305). Springer Berlin Heidelberg.
https://doi.org/10.1007/978-3-540-29678-2 3148

Zupanc, G., & Horschke, I. (1995). Proliferation zones in the brain of adult gymnotiform fish: A quantitative mapping study. *The Journal of Comparative Neurology*, 353(2), 213–233. https://doi.org/10.1002/cne.903530205