

book an almost ‘coffee table book’ quality. This rare combination of accurate and visually appealing science lends the book the potential to make a real contribution to the public understanding of a challenging domain. *Bird Brain* is a delightful book that could genuinely change perceptions of animal intelligence.

**Bird Brain: An Exploration of Avian Intelligence** by Nathan Emery, Princeton University Press, 2016. US, \$29.95/£16.59, hbk (192 pp.), ISBN 1782403140

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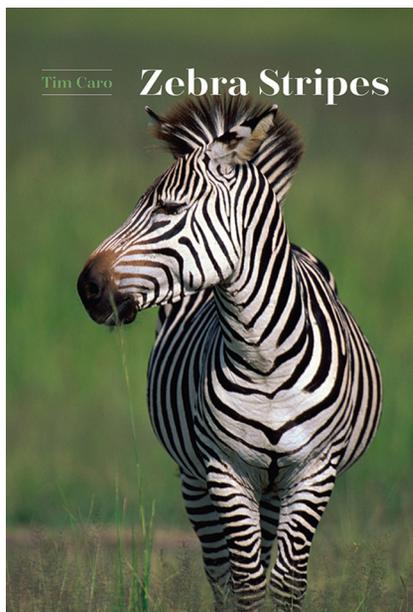
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## Book Review

# A Triumph of Multiple Hypothesis Testing

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In an era of big data, it might be considered quaint to spend over a decade studying a Victorian question, one that has been debated by Wallace [1], Darwin [2], and a cast of others: namely, the function of stripes on animals. And, indeed, why zebras, uniquely among equids (horses, zebras, and wild asses), have stripes. However, Tim Caro’s book, *Zebra Stripes*, is a testament to the power of comprehensive scholarship, logic, creativity, self-criticism, persistence, and passion, and shows that outstanding science can be done with limited support (he cites no sources of financial support).

Fittingly, the book begins with a Sherlock Holmes quote ‘... when you have eliminated the impossible, whatever remains, however improbable, must be the truth.’ [3]. And, it is in this spirit, that Caro attacks the puzzle over the function of zebra stripes.

After an introduction to the history of the problem of zebra stripes, and a sketch of equid diversity (Chapter 1), Caro dives into first sorting out hypotheses and then evaluating them systematically. Depending upon how you count, there are as many as 18 different functional hypotheses, including the anti-predator functions of crypsis (Chapter 2); warning coloration (Chapter 3); and predator confusion (Chapter 4); ectoparasite-repelling functions (Chapter 5); interspecific communication functions (Chapter 6); and temperature regulation (Chapter 7). Chapter 8 reports the results of multivariate analyses at the species and subspecies level and Chapter 9 systematically makes the case for his overall conclusion.

Caro’s scholarship is abundantly evident and he is widely read; from Kipling to Cott and much more. After clearly enumerating the diversity of ideas, he then sets out to use this scholarship to test them.

Following Wallace’s [4] advice to study questions of coloration as much as

possible in the field, he spent thousands of hours watching zebra and other ungulates in the wild, mostly at his Tanzanian study site and in zoos, and took detailed notes. He used paint and pelts and his social capital by waking colleagues up in the middle of the night to ask whether they could see or discriminate various objects at a distance. He evaluated the results of video games and hunting models, and watched Internet videos of predation and attempted predation. He set up patterned fly traps, drove around with pelts hanging off his truck, and, with a sartorial flair, had patterned suits custom-made in Dar es Salaam that he wore in the field and had an assistant count flies on them after walking through various habitats. He borrowed a thermal imaging camera and peered at zebras both during the day and night. Using data collected from museum specimens and data amassed in libraries and with the addition of satellite remote-sensing data, he used modern phylogenetic techniques to conduct comparative analyses.

Thus, by combining Victorian observational techniques, elegant field experiments, some technology, cutting-edge evolutionary analyses, and a smattering of 21st century media, Caro systematically and doggedly refuted hypothesis after hypothesis. He wrote that, for over a decade, he would return home to UC Davis after a summer of research and had nothing positive to report. Yet he persisted.

The book is inspiring. Caro describes break-through moments, such as the one that occurred in August 2014, when, after a decade of work, he finally conducted an experiment that used natural pelage and fly traps in zebra habitat to ask whether real pelts differentially attracted biting flies. And, as his book reveals, biting flies are his best current guess as to why zebras have stripes.

After over a decade of his study, in 2015, some drama was created when another group studying zebra coloration

[5]; full disclosure, they are my UCLA colleagues) drew a different conclusion from a bioclimatic analysis. Rather than dismissing the study, Caro politely and systematically shows how almost all of their results were congruent with the biting-fly hypothesis.

Science progresses when multiple hypotheses are pitted against each other. Yet, many studies report confirmatory analyses that support a pet hypothesis. Over time, many alternative hypotheses are created, but few are ever contrasted with other. Caro's genius has been to cut through the variety of confirmatory reports and hypotheses with logic and evidence, self-critically evaluating his own data as much as anyone else's and, in doing so, illustrating a powerful model for scholarship and discovery. The non-mutually exclusive nature of these functional hypotheses prevents formal strong inference, but I think that Platt [6], nevertheless, would be pleased.

My only criticism (and I really mean my only criticism) is that the tables had sparse legends and often lacked units. This forced me back into the text to better understand some of them. A minor cost for the benefits to be obtained from reading a stellar study that illustrates the power of excellent scholarship combined with multiple hypothesis testing.

**Zebra Stripes** by Tim Caro<sup>1</sup>, University of Chicago Press, 2016. US\$45.00/£31.50, cloth (xviii + 268 pp.) ISBN 978-0-226-41101-9

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## Spotlight

# New Allometric Scaling Laws Revealed for Microorganisms

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**Allometric scaling relationships based on microbial data sets are revealing novel biological principles; for example, the abundance and diversity of animal-associated microbes scale with individual animal mass. The global abundance of animal-associated microbes and biosphere species richness have also been estimated. The potential for further microbe-inclusive macroecological insights is high.**

### Macroecological Scaling Can Be Applied to Microorganisms

Macroecology has the power to reveal fundamental ecological and physiological principles shared among widely disparate species, but the tools of macroecology have seldom been applied to microorganisms [1]. A common approach is to test for consistent mathematical scaling relationships between biological parameters. An attribute, usually of animals, is quantified for many species and plotted against individual size, usually expressed as individual mass. Scaling can be either isometric (i.e. essentially linear) or allometric, usually represented as a power function. Plotting these data on a log-log scale has revealed scaling relationships with the general formula  $V \propto M^z$ , where  $V$  is the

measured variable,  $M$  is individual body mass, and  $z$  is the scaling exponent. Recently, this scaling approach has been extended to the tiniest organisms, including bacteria and Archaea [2–4]. The discovery that allometric scaling applies to the microbial world has been inspired by the surge in new information relating human and animal health to the mix of microbes present in the gut [5], and by the explosion in nucleic acid sequence data from the microbiomes of other natural environments [6]. By extending scaling studies to include prokaryotes, macroecologists are expanding the range of individual body masses to >12 orders of magnitude and bringing to light unifying concepts that take into account the most abundant and diverse forms of life on Earth.

### Microbial Abundance and Diversity Scale With Habitat Size, Including Animal Size

The first study featured here considered the abundance of animal-associated (primarily gut) microorganisms as a function of animal mass [2]. A human holobiome ( $M = \sim 7 \times 10^4$  g) comprises approximately  $3 \times 10^{13}$  *Homo sapiens* cells and approximately  $3.8 \times 10^{13}$  microbial cells [7]. Kieft and Simmons [2] questioned whether other animals and their microbiota follow a consistent pattern. Surveying animals from 1000-cell nematodes to whales (~12 orders of magnitude range in  $M$ ), they found a significant log-log scaling, with an exponent of 1.07 (Figure 1A). This relationship mimics the gut size-to-total animal mass pattern and also underscores the dependence of animals on microbes for energy. Combining this new microbial abundance-animal mass equation with the traditional animal abundance-animal mass equation [8] enabled a census of all animal-associated microbes on Earth. The total estimate reported by Kieft and Simmons of  $2 \times 10^{25}$  cells, mostly bacteria, is a small but important proportion of the approximately  $10^{30}$  prokaryotes on Earth [9]. Further calculations showed that most animal-associated microbes exist within