

Notes and references for:

In the Beat of a Heart: Life, Energy, and the Unity of Nature

by John Whitfield

Joseph Henry Press, 2006.

Where an author is mentioned in the text, the citation is given in the reference list. Notes indicate references that are unclear from the text, and footnotes to the text. A full reference list, incorporating that from the book, follows the notes.

1 Prologue: "I have taken to mathematics"

OG&F: D'Arcy Wentworth Thompson (1961). Unless otherwise stated, quotations are from this abridged edition.

RDT: Ruth D'Arcy Thompson (1958). This is by far the most comprehensive single biographical source on Thompson.

Page

- 2 "a fact discovered yesterday..." Thompson (1940) p. 3.
- 3 "all preface" Dobell (1949)
"a great theme" OG&F, footnote to p. 14
"Morphology..." OG&F p. 14
- 4 "dreary, weary boyhood" RDT p. 3
- 6 "The new-fangled idea..." RDT, p. 60.
"a queer fellow..." RDT, p. 127.
"you know you haven't got many friends" RDT, p. 127.
"...a pukka Sahib..." RDT, p. 125.
- 7 "I came to Trinity..." Dobell (1949).
"An east-windy..." RDT, p. 68.
- 9 "The seals..."; "The men employed..."; "We may hope..." Thompson (1897).
- 10 "You must show..." RDT, p. 126.
- 11 "I should be [equally] at a loss..." letter to Agnes Arber, 5 October 1921.
- 12 "You might think these things..." RDT, p. 127.
"He did not hide his impatience..." Berg (1969).
There is a short report on Thompson's talk in *Nature* 50:435; 1894.
"I have taken to mathematics..." RDT, p. 89.
- 13 "I became aware..." RDT, p. 89
"I confess..." RDT, p. 90. D'Arcy's papers shows that he thought Foster had thwarted his job applications. From Foster's side of the correspondence, it looks more likely that he did not actively oppose D'Arcy's ambitions, but nor did he work to support them.
- 14 "everyone will say..." RDT, p. 161.
"No man has ever..." and following. Thompson (1911).
- 15 "little one-shilling..." RDT, p. 161
- 16 "profoundly interesting" RDT, p. 160

- "a cold grey city..."; "A town of scholars...". Thompson (1940) p. 231; p. 228.
- 19 Thompson's ideas on bone development are discussed in Medawar (1958).
"The chromosome people..." Letter to Frederic Lewis at Harvard Medical School, 13/10/1923
- 20 "The perfection of mathematical beauty..." OG&F, p. 327
"These forms..." OG&F, 1942 edition pp. 848–849
- 21 "I for one..." OG&F, 1942 edition p. 873
"substantial and stately"; "a ripe philosopher...". RDT, p. 163.
"That the form of animals..." Letter from J. Gray, Cambridge Museum of Zoology, 20 October 1922.
- 22 "I wish to goodness..." Letter to Prof. Greenstreet, 14 March 1919.
"[We] will be glad..." Letter from Cambridge University Press, 8 May 1923.
"For the past few years..." Letter from CUP, October 1929.
"I must warn you..." Letter from CUP, 26 February 1941.
- 23 "I long for release." Dobell (1949).
- 25 "The little gift..." Dobell (1949).
- 26 "bespangled with dew..." OG&F p. 65
"not only the movements..." OG&F p. 327

2 The Slow Fire

Page

- 29–35 Bender (2002) and Garrow et al. (1999) and provide general introductions to respiration, nutrition and calorimetry.
- 37 "You should have won the Nobel prize..." Lusk (1932).
- 40 "A dog could probably carry..." quoted in Gunther (1975).
"Bobbed-haired girl scientists..." This cutting, dated 28 August 1926, is in D'Arcy Thompson's papers. The newspaper's name is not on the cutting.
- 41 ...food needs of employees at the state tobacco factory... Heusner (1985).
- 41–43 Bergmann's rule. Papers on this still appear regularly. Meiri and Dayan (2003) is a good place to start; McNab (1971) is the most trenchant criticism of the rule, and is still relevant. The study on woodrats mentioned on page 42 is Smith et al. (1995), and the one on museum bird specimens mentioned on the same page is Yom-Tov (2001). Key passages from Bergmann's original paper are translated into English in James (1970).
- 46 "a 36-year-old cretin" DuBois & DuBois (1916).
- 50 "There still remains some doubt..." DuBois (1936) p. 140.

3 Moving the Line

Page

- 52 "This experiment..." Kleiber (1967)
- 53 "I seem to have..." Kleiber (1967)
- 54 "Like much of Rubner's work..." quoted in Robert Joy's introduction to Rubner (1982) (see references to chapter 2).
- 57 "The gadgeteers..." Kleiber (1961) p. 201.
Thompson also discusses scaling in *Gulliver's Travels*

- 59 For power laws in sleep, see Lo et al. (2002), for power laws in waiting lists, see Smethurst & Williams (2001).
- 60 ...a seminal paper on fiddler crabs... Huxley (1924).
- 61 "I never thought it necessary..." letter to Julian Huxley 6/3/25.
"I do not know where..." quoted in Brody (1945), p. 352.
- 61–62 Gibson and Numa (2003) discuss the use of, problems with, and alternatives to surface area measurements in medicine.
- 63 "It is obvious..." Benedict (1938) p. 171; "It seems illogical..." *ibid* p. 173; "[A]ll attempts...[N]o unifying principle..." *ibid* p. 178.

4 Searching for Similarity

Page

- 69 Using a calculation based on the relative metabolic rate... Schmidt-Nielsen (1972) discusses different options for calculating the appropriate dose of LSD for an elephant.
- 71 Experiments on tissue metabolism are discussed in Schmidt-Nielsen (1984), pp. 90–94. and Kleiber (1961), pp. 196–200.
In the 1920s, separate French and German teams... References in Schmidt-Nielsen (1984), discussed on p. 92.
In 1941, Max Kleiber... Kleiber (1941).
Probably the best experiments... Krebs (1950).
In 1955, Arthur Martin and Frederick Fuhrman... Martin & Fuhrman (1955).
- 72 ...if you take some cells from an animal and culture them in a Petri dish... West et al. (2002)
- 73 Kleiber (1961) pp. 193–196 discusses body composition and metabolic rate. Schmidt-Nielsen (1984) discusses the scaling of brain size (p. 27) and heart size (p. 126).
Obesity researchers... Steven Heymsfield's group has been particularly active in this area. See e.g. Wang et al. (2001), Heymsfield et al. (2002).
Fudge factors. See Schmidt-Nielsen (1984) pp. 83–84.
- 74 Effect of gravity on metabolic rate: Economos (1979) finds that hypergravity increases energy expenditure, Plaut et al. (2003) find the reverse.
Kleiber thought that some average... A. A. Hesuner, pers. comm.
- 75 The metabolic ark. See Schmidt-Nielsen (1984) pp. 63–74. for a discussion of metabolic scaling in different animal groups.
- 77 The graph on this page is taken from Brown et al. (2000). They adapted it from Hemmingsen (1960).
- 78 Peters (1983) contains a large dataset on scaling of different biological parameters.
- 79 The Scottish town of Troon... Blaxter (1965).
- 80 ...*Tyrannosaurus* was too big to run... Hutchinson & Garcia (2002).
For biographical and professional details of Thomas McMahon see Farley (1999).
Elastic similarity is described in McMahon (1973) and McMahon & Bonner (1983).
- 81 ...an alternative life for Gordon McKay... McMahon (2003).
- 82 A leading skeptic... Heusner (1982, 1985, 1991).

83 ...biologists rode to defend Kleiber's rule... Feldman and McMahon (1982),
Bartels (1982).

85 ...about 200 quarter power scaling... G. West, pers. comm., quoted in Whitfield
(2001). See also Savage et al. (2004). For recent arguments against universal scaling, see
Dodds et al. (2001) and Bokma (2004).

5 Networking

Page

90 The mathematics of fractals opened up new ways of thinking about biological
scaling... West & Goldberger (1987) is a good introduction to this area. Sernetz et al.
(1985) also argue that metabolism is a fractal process, but in a different sense from West
et al.'s later model.

93 ...a weasel burns energy... Brown & Lasiewski (1972).

Jim Brown gives his manifesto for ecology in Brown (1981).

94 "A conservation biologist..." Calder (2000).

95 ...human hunters' lust for large prey... Whether people were the principal cause
of the Pleistocene extinctions is still controversial. See for example, Johnson (2002) for a
argument that they were not, and that body size was not a good predictor of extinction
risk.

96 See Kingsland (1995) for biographical details of Alfred Lotka. In later editions,
Lotka's *Elements of Physical Biology* was re-titled ...*Mathematical Biology*.

"...the habits of an elephant by means of a microscope..."; "What is needed..."
Lotka (1956) pp. 39–40.

"law of maximum energy flux" Lotka (1922a).

99 ...many large-scale trends in nature... see Brown (1995).

101 ...as near to 3/4 as makes no difference... But see Reich et al. (2006), who argue
that plant metabolic rate scales linearly with body mass, not to the 3/4 power.

104 ...the maximum capacity of each part of the respiratory system... see Taylor &
Weibel (1981), and subsequent papers in the same series.

105 "Panglossian paradigm" Gould & Lewontin (1979).

106 A moose chooses... Belovsky (1978).

"That this mechanism is the best possible..." OG&F pp. 127–128.

106–112. See West et al. (1997, 1999, 2000) for the fractal network theory of metabolic
rate. For criticisms of these papers, see Beuchat et al. (1997) and Kurz et al. (1998).
Dodds et al. (2001), Kozlowski & Konarzewski (2004) and Makarieva et al. (2005a) are
also critical of the theory. White & Seymour (2003) claim that metabolic rate scales to
body mass raised to the power of 2/3.

112 Networks in plants. West et al. (1999b) extends the network theory to plants.

114 Alternative routes. Jayanth Banavar and colleagues' model is described in
Banavar et al. (1999, 2002).

115 ...membranes are softer and leakier... Hulbert (2003).

...the amount of DNA in a cell... Kozlowski et al. (2003).

...ability to obtain food... Kooijman (2001).

..."allometric cascade"... Darveau (2002).

And there are others... Ones that I am aware of: Demetrius (2003), Bejan (2005), Makarieva et al. (2005b), He (2006).

116 Single Cells, Virtual Networks. West et al. (1999a) extends the network theory to unicellular organisms,

118 The metabolic rate of an isolated mitochondrion... And even in these isolated molecules... West et al. (2002) extends the network theory to organelles and enzymes.

119 The results were dramatic... Gillooly (2001) adds temperature to the metabolic model.

6 The pace of life

Page

123 "For the main features..." OG&F, 1917 edition, p. 152.

"Today biology is in its pre-Copernican period..." ; ""Only if the multiplicity..." Bertalanffy (1933).

124 "Living forms are not *in being*..." Bertalanffy (1952).

In 1934, Bertalanffy... Bertalanffy (1957) sums up his work in this area.

126 The network theory offers a new perspective on growth... West et al. (2001).

127 "as potentially important to the biological sciences..." Niklas (2001). See also Niklas (2004) for a review of the possibility of general laws in plant allometry.

...all plants' growth is proportional to the 3/4 power... Niklas & Enquist (2001).

...animals and plants show similar growth patterns... see Damuth (2001).

128 ...tumour growth also follows the growth law... Guiot et al. (2003).

Changes of life. See Peters (1983), chapter 8, for a general guide to the scaling of growth, development and reproduction.

The duration of all these phases... Gillooly et al. (2001).

Chemistry, then, is a third factor... Sterner & Elser (2002) is a good place to start reading about the role of chemistry in ecology, including Redfield ratios.

131 The 30-Tonne Gorilla. See Moses & Brown (2003).

134 955,787,040... Speakman et al. (2002).

Neil Armstrong... quoted in Van Voorhies (2004).

Austad (1997) discusses Max Rubner's work on aging.

135 For details of Raymond Pearl's life and work, see Kingsland (1984).

"The matters with which biostatistics..." Pearl (1928) p. 3.

138 Mice genetically engineered... Trifunovic (2004).

"It's the free radicals, stupid!" Nemoto & Finkel (2004).

139 ...many animals live far longer... Austad (1997)

...mice with faster metabolisms live *longer*... Speakman et al. (2004).

140 ...the indigenous people of cold climates... see, for example, Ruiz-Pesini et al. (2004).

142 In a lab dish, mitochondria from pigeons' cells... See, for example, Ku & Sohal (1993).

Flies bred to live longer... See, for example, Zwaan et al. 1995.

...the British aristocracy... Westendorp & Kirkwood (1998).

...birds of paradise... McNab (2003a).

143 ...and a group of bats... McNab (2003b).

"Animals have a lot of ways to bend the rules..." Whitfield (2004).

A group of physicists... Jennings et al. (2004).

144 The laws of metabolism are like gamelan music... I should also have said here that gamelan builds up complexity in a fractal fashion, by elaborating on simple foundations (Pickvance, 2005, p. 27).

7 Seeing the forest for the trees

Page

Brown et al. (2004) reviews the links between ecology and metabolism. It is part of a symposium, and is followed by many short commentaries on metabolic ecology, both pro and anti.

145 Looking at his data... See, for example, Gentry (1988).

146 Centinela Ridge... Dodson & Gentry (1991) gives a review of the issue.

151 ...bottom of the sea... Alanis Morissette.

154 ...self-thinning... the original paper is Yoda et al. (1963).

"the only generalization worthy of the name of a law..." Hutchings (1983).

155 ...self thinning did not stand the tests... See, for example, Weller (1987), Lonsdale (1990) and Niklas (1994).

...a paper showing that... Enquist et al. (1998).

156 ...the range of tree sizes in a forest... G.B. West, pers. comm..

157 ...data on body size and population density... Damuth (1981).

...a later study... Damuth (1987).

...the population density of parasites... George-Nascimento et al. (2004).

158 ...bring carnivores back into the metabolic fold... Carbone & Gittleman (2002).

...two styles of hunting...

159 The match between metabolic rate and population density... Silva et al. (1997).

161 ...Carbone, working with a team of other ecologists... Jetz et al. (2004).

162 ...the maximum rate of population growth... Savage et al. (2004).

...all forests are essentially the same... Enquist & Niklas (2001).

163 ...an upper limit on tree height... West et al. (1999b).

165 For details of FLUXNET see Baldocchi et al. (2001).

...measure ecosystem metabolism... Enquist et al. (2003) discusses how forests do and do not meet the predictions of metabolic theory.

167 ...a unity underpins the biology of different tree species... Enquist et al. (1999).

See the recent papers by Muller-Landau et al. (2006a, b) for a more negative view of the ability of metabolic theory to explain forest ecology.

168 What applies to wood also applies to leaves. See Wright et al. (2004) for more on global patterns in leaf investment and trade-offs.

What's the best way for a plant to divide up its resources?... Enquist & Niklas (2002).

8 The Cult of Santa Rosalia

Page

- 171 "Homage to Santa Rosalia" Hutchinson (1959).
- 173 ...he spilled the contents... L. Slobodkin, pers. comm..
- 175 "If the community is an organism..." quoted in Bocking (1997, p. 72).
- 176 The longest food chain... Rosenzweig (1995) p. 79. Rosenzweig also discusses the length of food chains, and the limitations of thermodynamic explanations, on pp. 320–322.
- 177 Plankton puzzled Hutchinson most... Hutchinson (1961).
...a way of thinking about species' place in nature... Hutchinson (1957).
- 178 ...the barnacle *Chthamalus*... Connell (1961). This is a classic study of niche differentiation.
- 179 "...a tedious set of case histories" MacArthur (1972, p. 169).
...the number of bird species in an area... See Rosenzweig (1995) p. 34.
- 180 MacArthur's influence on ecology... See, for example, Fretwell (1975).
...the best way to divide a cake... Cody & Diamond (1975).
- 182 ...packing using fractal geometry... Morse et al. (1985).
...in consorts of viols and recorders... Horn & May (1977).
- 183 ...Diamond studied the distribution... Diamond (1975). Gotelli & McCabe (2002) re-examine evidence for Diamond's assembly rules and find that they stand up in many cases.
- 184 ...a random spread, not a matching set... Simberloff & Boecklen (1981). See Simberloff (2004) for Simberloff's current views.
"as acerbic and as acrimonious..." Lewin (1983). See also Harvey & Silvertown (1983) for a journalistic discussion of this controversy.
- 185 "[had] caused a generation of ecologists..."; "silly"; "lacking in commons sense" Lewin (1983).
- 186 "in crisis"; "repugnantly complicated"; "in a quagmire". Quoted from Weiher & Keddy (1999). Rosenzweig (1995) describes limiting similarity as "quicksand that trapped the energies of community ecologists for more than ten years and nearly killed the sub-discipline".
Since then, Tilman and his colleagues... See, for example Tilman (2004) for a view of Tilman's current thinking on niches.
- 187 ...devised by Mark Ritchie and Han Olff... Ritchie & Olff (2000).
- 189 ...think that nature is not in balance... Michael Huston is a leading proponent of this view (Huston, 1994).
- 190 If starfish are taken off a beach... Paine (1966); this is another classic study.
...tropical trees do indeed find it harder to germinate... Silvertown (2005, pp. 62–66) has an excellent discussion of this idea, which is called the Janzen-Connell hypothesis.
- 191 One survey of alien species... Ruiz & Fotonoff (1999).
- 192 ...the patchwork of tree species... Hubbell (1979).
- 193 ...an idea to explain the number of species on an island... Described in Rosenzweig (199, p. 128–135).
- 196 Hubbell called his theoretical framework neutral ecology... Hubbell's book (2001) is a good place to start reading about neutral ecology. Whitfield (2002) is aimed at non-specialists.

197 There have also been challenges to the theory's science... Papers on this appear regularly — for example Dornelas et al. 2006. Gaston & Chown (2005) is a good place to get to grips with the debate.

A team led by Graham Bell... See Bell (2001), Bell et al. (2002).

198 ...other models of commonness and rarity... McGill (2003).

200 \$33 trillion... Costanza et al. (1997). How to put a monetary value on ecosystem services is still controversial.

...because otters eat sea urchins... Chapin et al. (2000)

201 ...less prone to booms and busts... McCann (2000)

9 Humboldt's gifts

Page

206 ...the oldest problem in ecology... Hawkins (2001).

"The Florae of different parts..." Willdenow (1805).

207 ...Baron Friedrich Heinrich Alexander von Humboldt... See Gendron (1961) and the introductions to Humboldt (1995) for biographies of Humboldt.

209 "I shall collect plants..." quoted in Malcolm Nicolson's historical introduction to Humboldt (1995), p. ix.

211 "The greatest..." Letter to J. D. Hooker, 6 August 1881.

"I shall never forget..." Letter to J. D. Hooker, 10 February 1845.

"combined meteorology, geography, geology..." Gendron (1961).

"The verdant carpet..." Humboldt (1849).

Discoveries made since Humboldt... See Gaston (2000) for a review. Pianka (1966), Rohde (1992) and Willig (2003) are among the many reviews discussing the merits and shortcomings of various theories to explain the diversity gradient.

Most human diseases... Guernier (2004).

212 ...also contain the most linguistic groups. Moore et al. (2002).

"So does my wife..." This exchange is reported in Gendron (1961). The empress Josephine was indeed devoted to gardening, and she employed Bonpland to tend her plant collection, for which he acquired roses from around the world and hybridized them into new varieties. But both Bonpland's and Napoleon's fortunes took a turn for the worse. By 1817, the emperor had lost the battle of Waterloo and been exiled to St Helena. That year, Bonpland, having quit his royal post when Josephine died in 1814, returned to South America, taking a job as professor of natural history in Buenos Aires. But while exploring the disputed border territory between Argentina and Paraguay, he was captured and thrown into a Paraguayan jail, where he spent the next nine years. He stayed in Argentina after his release, still sending plants back to Paris, and living off a pension that Humboldt had secured by donating his own plant collection to the French state. Bonpland died in 1858, in his home by the Uruguay River, aged 84.

213 "The extraordinary height..." Humboldt (1849). From the essay *Ideas for a Physiognomy of Plants*.

"Nature undergoes..." *ibid.*

"The nearer we approach..." *ibid.*

215 ...the same goes for North American Birds and butterflies... Currie (2004). See also Evans et al. (2004) for a review of this topic.

- 216 ...diversity can beget diversity. Emerson & Kolm (1996).
- 217 ...comparing the world to a pencil case... Colwell et al. (2004).
- 218 The first was in Madagascar... Colwell & Lees (2000). Kerr et al. (2006), however, claim that the data do not support this interpretation.
- 219 an evolutionary play acted out... Hutchinson (1965).
Alfred Russel Wallace... See, for example, Raby's (2001) biography.
- 221 "Instead of endless repetitions..." Wallace (1969), p. 241...267.
- 222 "Then it suddenly flashed..." Wallace (1908) p. 190.
"in a nice balance..." Wallace (1969) p. 268.
"Every place in Nature..." *ibid*, p. 268.
- 223 "destroying most of the larger..." *ibid*, p. 310.
...the eruption of Krakatoa... See, for example, Bush & Whitaker (1991).
...the most recent ice age... See, for example, Hawkins & Porter (2003).
North America has more tree species... This idea is quoted, for example, without a citation for its origin, in Begon et al. (1986) p. 799.
- 224 ...correlated more closely to its present climate... Hawkins & Porter (2003).
- 226 ...four of the 30 bird species... S. Pimm, pers. comm.
John Terborgh and Michael Rosenzweig... Rosenzweig (1995, pp. 284–286) is a good place to start.
But other ecologists have raised objections... See, for example, Rohde (1992).
- 227 Jim Brown's team has found... Gillooly et al. (2005).
- 228 Brown's team used temperature and metabolic rate... Allen et al. (2002).
David Jablonski has shown... Jablonski (1993).
...a back-of-the-envelope calculation... Allen, pers. comm. This work is now published: see Allen & Gillooly (2006), and Allen et al. (2006), which gives 10^{23} J as the energy needed to make a new species of foram.
- 229 ...yet to be ground down by the mill of academic scrutiny. See Bromham & Cardillo (2003), and Evans & Gaston (2005) for critical appraisals of the ability of evolutionary rates to explain the diversity gradient. Wright et al. (2006) give a more positive view.
- 230 Some ecologists are already employing... See, for example, Jetz & Rahbek (2002).

10 A Newton of the Grass Blade?

Page

There is a steady trickle of papers discussing whether ecology has general laws. Lawton (1999) is a good place to start.

- 231 [I]n terms of merely mechanical... Kant (1987) p. xxx.
- 233 "The ecologist and physicist..." MacArthur (1972) p. 239.
Andy Purvis and his colleagues... Gittleman & Purvis (1998).
- 234 "the ultimate aim..." From Crick's 1966 book *Of Molecules and Men*. Quoted in Mayr (1996).
...biology has concepts that physics cannot explain... Mayr (1996).
Lawrence Slobodkin... See, for example, Slobodkin (2001).

- 235 The physicist Freeman Dyson... quoted in Murray (2001).
236 ...similar to Newton's first law... Ginzburg & Colyvan (2004).
238 Chris Thomas and his colleagues... Thomas (2004).
241 "While the spirit of system..." Lavoiser (1777).
245 ...the highland mangabey... Jones et al. (2005). Since then, the mangabey has been assigned to a new genus, the first new genus of African primate for more than 80 years.
246 ...4 million in a tonne of soil... Curtis et al. (2002).
The biggest estimate for global bacterial diversity... Dykhuizen (1998).
The overwhelming diversity of microbes... Nee (2004).
Worldwide, it's been estimated... Whitman et al. (1998).
247 ...the population density of marine plankton...
...the patterns in microbial biodiversity... Whitfield (2005) describes the current debate.

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