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Annual plants, pigeons and flies: first signs of quantitative ecological thinking in Linnaeus's works

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ABSTRACT: Thinking about the dynamics of populations of plants and animals goes back to Linnaeus. He used at least three examples to show what happens when the population of a species grows without limitations and to illustrate the potential reproductive capacity of organisms. We examined the mathematical precision of calculations Linnaeus used in presenting these examples and reviewed the assumptions under which Linnaeus's conclusions are valid. In the case of a slowly reproducing annual plant, additionally cited by Darwin, the final result was incorrect, although little different from the true value. In the example of a pair of pigeons, the calculations were accurate, although the well-known fact that pigeons breed several times throughout their lifetime was ignored. Though the input parameters must have been unknown to Linnaeus, a short statement in *Systema naturae* regarding the population increase and feeding capacity of bluebottle flies was found fairly correct and robust enough to withstand minor changes in input parameters.

KEYWORDS: *Amoenitates academicae* – bluebottle fly – *Calliphora vomitoria* – domestic pigeon – *Columba livia domestica* – *Oeconomia naturae* – population growth – reproduction.

INTRODUCTION

One of the oldest links between exact mathematical thinking and population biology in the Western world goes back to the early thirteenth century. In "Liber Abaci"[1], completed in 1202, Fibonacci (Leonardo of Pisa, or Leonardo Bonacci, *c*.1175–*c*.1250) presented an example for the growth of a rabbit population.[2] He asked how many pairs of rabbits would constitute the population at the end of a year with the following assumptions: first, there is a single newborn pair in January; second, rabbits reach maturity after one month and keep mating every month thereafter; and third, each pair produces both female and male offspring.[3] Outside mathematics, Thomas Malthus (1766–1834) has been generally credited as the first scientist to develop the idea of population growth in detail, with special reference to human society. In several editions of his famous study he expressed his concerns about the contrast between the potentially unlimited, exponential growth of the human population and the merely arithmetic increase of food production achievable by mankind (Malthus 1798). It is also widely acknowledged that Charles Darwin (1809–1882) was greatly influenced by Malthus's views when elaborating his theory on natural selection (Ariew 2007), thus generating even wider publicity and reputation for those views. It is perhaps less generally known, however, that in "The struggle for existence", the third chapter of *On the origin of species* (Darwin 1859), the first numerical example of unlimited population growth was taken from the works of Carl Linnaeus (1707–1778). It was the great Swedish naturalist, together with his students, who played first with this idea, about half a century earlier than Malthus. According to the general belief of Linnaeus's time, the Earth was around 6,000 years old.[4] Through this relatively short period of time, it had to become populated starting from a single initial pair of each sexual species, or a single individual of every asexual organism. To answer the intriguing question of how this could happen made Linnaeus develop the first mathematical explanation of population growth by a naturalist. His hypothetical case, mentioned by Darwin (1859), was an annual plant producing only two seeds per year (Linnaeus 1744, 1751). If reproduction continues unregulated, the species will reach a population size of around a million in 20 years. Another vivid example presented by Linnaeus, and his student, Isaac Isaacson Biberg (1726–1804), illuminates the reproductive potential of birds: if a pair of pigeons breeds nine times a year then, as suggested, 14,762 offspring will be produced in four years (Biberg 1749, 1951).[5] There is a third relevant, although non-numerical, example presented briefly in Linnaeus's works emphasizing the ability of dipteran larvae to grow rapidly and feed voraciously on animal carcasses (Linnaeus 1767). These examples can be considered to be the earliest instances of quantitative biogeographical and ecological thinking in the history of life sciences (regarding the first two, see Egerton 2012). Nevertheless, as our literature overview suggests, there are still some uncertainties regarding Linnaeus's calculations and assumptions, as well as the manner in which they are cited, reproduced and interpreted. Thus, an objective of this paper is to clarify these issues in a historical account.

THE SOURCES

Amoenitates academicae contained 186 dissertations of students supervised by Linnaeus and many lectures of his own (Kiger *et al.* 1999).[6] The dissertations were edited by Linnaeus, and in many cases he added comments, so the version published in *Amoenitates academicae* differs from the original, separate dissertations. In the past, Linnaeus was generally considered the sole author while the students were credited only as translators who organized the text into Latin and defended the theses in public lectures. As Stafleu (1971: 144) noted "the contents of the thesis were actually almost irrelevant, as long as one could talk about them". Nevertheless, we cannot exclude the possibility that students had actively contributed to the text by their own suggestions as well. According to Heller (1983: 245), it is advisable to consider "all of the Linnaean dissertations as being at least in part the work of Linnaeus". There is no authority problem with the lectures delivered by Linnaeus himself, whose written versions are appended to the second volume of *Amoenitates* (Pulteney 1805). This second volume is of particular interest: one dissertation by a student and a lecture by Linnaeus include demographic examples. We shall begin with the latter, concerning the reproduction of a hypothetical plant – thus maintaining the temporal sequence of their presentation.

Systema naturae is one of the most significant and best known works by Linnaeus in the different editions of which the author elaborated his views on the classification of the natural world into the plant, animal and mineral kingdoms. Whereas the first edition (Linnaeus 1735) contained only the classification schemes in tabular form, plus some observations on a few additional pages, the twelfth edition, the last one prepared by the author himself provided a full account of about ten thousand species known at that time. We shall be concerned with the second part of the first volume (Linnaeus 1767) which is devoted to the classes of insects and worms, and shall take a short statement from there on the reproductive and feeding ability of flies.

DEMOGRAPHY OF AN ANNUAL PLANT

On 12 April 1743, Linnaeus presented a lecture on the occasion of conferring a degree on Johan Westman (1714–1785), which was published the following year (Linnaeus 1744) and later still in *Amoenitates* (Linnaeus 1751: 430–459).[7] Placed into a general geological context, Linnaeus attempted to explain how the habitable Earth was repopulated starting from the Biblical situation, with a single pair or one individual of every species. By listing several examples of plants with high productivity (several thousand seeds per plant, for example, *Nicotiana*), Linnaeus explained how easily plants could have solved this problem. To make his point even more convincing, he then referred to an annual plant with a single flower, producing only two seeds, as an opposite example with extremely low productivity. He argued that even this hypothetical species with a low reproductive rate can reach a large number of progeny in 20 years, after having only four descendants in the second year, eight in the third, and so on (Figure 1). It is obvious from this passage that Linnaeus started with a geometric progression in which population size doubles every year. He gave the final result in the Latin text, rather than by numerical characters: "*millia nonaginta* & *unum millia*, *ducenta* & *nonaginta sex* individua" which can be translated literally as "thousand ninety & one thousand, two hundred & ninety six individuals". This ambiguous expression may be interpreted numerically in different ways, the most reasonable being (1,000 + 91) ×1,000 + 296 = 1,091,296, but it can easily be misrepresented as 91,296 (that is 90,000 +1,000 + 296).

Oratio de telluris habitabilis incremento was translated into English by the Reverend F. J. Brand (1781) (Figure 2). The result was expressed in numerals and is quite different, namely 1,048,600. There is no explanation by Brand, and we conclude that this figure was derived by the translator himself. Darwin knew Linnaeus's work from this translation and referred to it in *On the origin of species* by rounding the number down to the next million when he wrote: "Linnæus has calculated that if an annual plant produced only two seeds – and there is no plant so unproductive as this – and their seedlings next year produced two, and so on, then in twenty years there would be a million plants" (Darwin 1859: 64).[8] The relatively few authors who mention Linnaeus's suggestions, including Haeckel (1914: 277)[9] and Thompson (1942: **1**: 144), probably took the result directly from Darwin's book without consulting the original publication or bothering with arithmetic accuracy.

None of those calculations are right, because the correct value of 2^{20} is 1,048,576. Less well-known publications do mention this precise result as early as the first half of the nineteenth century (Smithurst 1832; Anonymous 1841). Thus, Linnaeus over-estimated the value considerably[10], by 4%, while Brand apparently rounded it up to the next hundred. We made an experiment to simulate errors potentially introduced in the multiplication of 2 by 2 twenty times (taking all possible one-digit errors into account during the twenty consecutive multiplications) and found that there is no single mistake that would explain the incorrect number calculated by Linnaeus. Cole (1954) has an interesting comment: in most sources he found only 91,296 based on an obvious misunderstanding of Linnaeus's method for writing large numbers in Latin. Nevertheless, the correct value is also reproduced by Howerth (1918) and, quite naturally, by modern references to Linnaeus's suggestion (for example, Kirkham

60. Ponamus plantam aliquam annuam, unico flore & binis tantum ſeminibus inſtructam. Hæc primo anno binos daret fœtus, ſecundo quatuor, tertio octo; poſt viginti tamen annos exiſterent hujus plantæ *millia nonaginta* & *unum millia*, *ducenta* & *nonaginta ſex* individua. Quid ergo dicendum eſt fieri potuiſſe ſex millenniis? ſed perpaucula adeo planta non reperitur; ſunt enim ſingulæ pluribus ſeminibus inſtructæ, ut in ſuperioribus dictum eſt.

Figure 1. Extract from Linnaeus's *Oratio de telluris habitabilis incremento* (1751: 449) describing exponential population growth of an annual plant. Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh.

It appears from this view of the ſubject, that even a ſingle plant, if it were preſerved from animals and every other accident, might have cloathed and covered the ſurface of the globe.----Let us ſuppoſe that plant to have been a ſingle annual, with one flower, and two ſeeds only; in the firſt year it would produce two, the ſecond four, the third eight, and on the twentieth year there would be 1,048,600 individuals of that ſpecies.--- What myriads would 6000 years have produced? but a plant whoſe increaſe is ſo ſlow is not to be found in nature, for as we have obſerved above they all produce ſeeds in great numbers.

Figure 2. Extract from F. J. Brand's translation of *Oratio de telluris habitabilis incremento* (Linnaeus (1751: 449) describing exponential population growth of an annual plant (Brand 1781: 94–95).

2005). For a present-day student, the calculation should not be a problem, so that Roberts *et al.* (2000: 691) leave the derivation of the result to the reader.

THE DESCENDANTS OF A SINGLE PAIR OF PIGEONS

On 4 March 1749, Biberg defended his thesis *Oeconomia naturae* (Biberg 1749, 1751). This work, generally attributed to Linnaeus as with all other theses in *Amoenitates*, represents a landmark in the history of ecology (Egerton 2012). In it, Biberg discussed the problem of the reproductive ability of plants and animals, and introduced a new zoological example, the domesticated pigeon. As suggested in *Amoenitates* (Figure 3), a pair, hatching two eggs nine times a year, will have 14,762 descendants in four years. However, in contrast to the annual plant, the initial conditions are unclear (regarding life-span and sex ratio, for example) and there are no hints relating to the calculation either.

As in the previous case, the English translation (Stillingfleet 1759: 75) added new conditions to the subject. According to notes added by the translator, Benjamin Stillingfleet

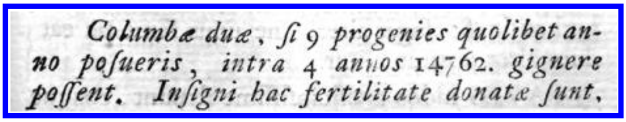
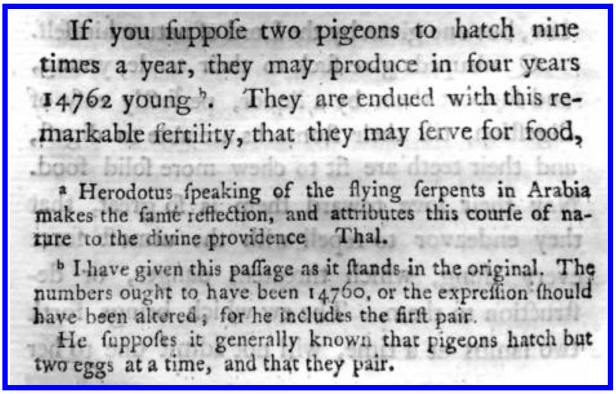

Columbæ duæ, ſi 9 progenies quolibet anno poſueris, intra 4 annos 14762. gignere poſſent. Inſigni hac fertilitate donatæ ſunt.

Figure 3. The pigeon example from *Oeconomia naturae* defended by I. I. Biberg (1751: 35). Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh.


If you ſuppoſe two pigeons to hatch nine times a year, they may produce in four years 14762 young [b]. They are endued with this remarkable fertility, that they may ſerve for food,

[a] Herodotus ſpeaking of the flying ſerpents in Arabia makes the ſame reflection, and attributes this courſe of nature to the divine providence. Thal.

[b] I have given this paſſage as it ſtands in the original. The numbers ought to have been 14760, or the expreſſion ſhould have been altered; for he includes the firſt pair.

He ſuppoſes it generally known that pigeons hatch but two eggs at a time, and that they pair.

Figure 4. Extract from B. Stillingfleet's translation of *Oeconomia naturae* (Biberg 1751: 35) with comments on the reproductive ability of pigeons (Stillingfleet 1759: 75). Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh.

(1702–1771), it was implied by the original proponent that pigeons lay but two eggs at a time, and that from these different sexes always hatch (Figure 4). He corrected the number to 14,760 in a footnote since the first pair has to be excluded from the total. Details of calculation do not appear even here, however.

This number has an interesting afterlife. Several authors in the early nineteenth century (for example, Daniel 1801: 345; Clinton 1815: 114; Johnson 1831: 675) attributed the value of 14,760 to Pliny and even claimed that Linnaeus raised the number beyond 18,000 – an obvious mistake which may be traced back to Pennant (1768: 90) who appears to refer there to Pliny as the original proponent of this number while later he correctly referred to *Oeconomia* in Stillingfleet's tracts (Pennant 1768: 220). In the fourth edition, Pennant (1776: 295) only retained the latter citation – a correction that obviously escaped the attention of Daniel, Clinton and Johnson. Other popular books and encyclopaedias from the same period and later (for example, Anonymous 1837: entry *Columba*; Knight 1866: entry *Columbidae*) give proper credit to Biberg. There are many books that mention 14,760 without citing the source but nevertheless taking this number as granted for pigeons (for example, Anonymous 1831: 150). It is particularly demonstrative to cite a passage from Bedfield (1858: 372) who, by paraphrasing Anonymous (1837: 372), reflected quite well the general view prevailing in the nineteenth century: "The astonishing fecundity of the domesticated pigeon is shown by the fact, that hatching as they do, nine or ten times a year, a single pair may produce, in four years, 14,760 young!"

The next century witnessed less enthusiasm about this problem. In the sole book we found, Kligerman (1978: 36) mistakenly referred to Darwin suggesting that he had the "authority of the French Naturalist, Georges Buffon, for this figure".[5] Then, it is Egerton (2012) who, in his monograph on the early history of ecology, called attention again to Linnaeus who "calculated that two pigeons breeding nine times a year could produce 14,672 [*sic*][11] offspring [with the first pair included] in four years" in reference to *Oeconomia naturae* defended by Biberg.

The number of progeny nor the circumstances that lead to exactly 14,760 are never explained. Is it indeed true that two pigeons breeding nine times a year can produce that many offspring, perhaps less or even more? The answer is that the above score is correct only if we assume that every generation is productive only in one year. Thus, in the first year there are nine new pairs, these produce 9 × 9 = 81 newly hatched pairs in the second year, the resulting 81 pairs have 81 × 9 = 729 descendant pairs in the third year, and these latter give rise to 729 × 9 = 6,561 pairs in the fourth year. Then, the total number of such pairs will be 7,380 (9 + 81 + 729 + 6,561) which, multiplied by 2, produces the stated result. This logic of derivation is not realistic, however. All available evidence suggests that pigeons keep on reproducing throughout their life (Marchesan 2002), which was well known before Linnaeus's time.[12] Domestic pigeons may live up to 15 years, wild relatives have a life span of four or five years and therefore it is more plausible to assume that each pair of pigeons produces nine pairs of offspring every year during their lifetime. Thus, in the first year one parent pair produces nine descendant pairs, these pairs together will produce 90 pairs of offspring in the second year, the surviving 100 will give rise to 900 pairs in year three and, finally, these 1,000 pairs will have 9,000 descendants in year four. The sum of descendant pairs is thus 9,999 (9 + 90 + 900 + 9,000), so that we can conclude that a single pair of pigeons, breeding nine times a year and producing a male and a female in each case, such that the offspring has the same productivity as the parents, will have a total of 19,998 descending individuals in four years – provided that the process is entirely unregulated.

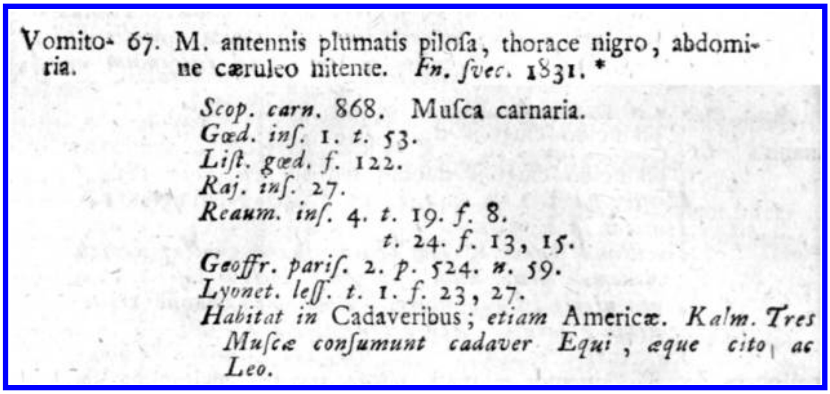
Some remarks are in order here. If we consider a pigeon or dove species living in the wild, the production of nine clutches annually is an over-estimation of their breeding capacity. Nevertheless, nine clutches are often produced annually by domestic pigeons in captivity, although this is not typical for their feral counterparts.

THREE BLUEBOTTLE FLIES, A DEAD HORSE AND A LION

The description of *Musca vomitoria* (*Calliphora vomitoria* (Linnaeus, 1758), a blowfly commonly known as the bluebottle fly) in *Systema naturae* (Linnaeus 1767: 989–990) (Figure 5) ends with a famous statement: "*Tres Muscæ consumunt cadaver Equi, æque cito ac Leo* [three flies consume the carcass of a horse as quickly as a lion]". In a historical review of necrophagous flies, Papavero *et al.* (2010) quoted this sentence as an epigraph, while Dayananda and Kiran (2013) took it as an early recognition of the importance of insects in the decomposition of human bodies – referring to the recent application of this species in forensic analysis.[13]

Some references to this example state that "Linnaeus calculated that three flesh Flies and their immediate progeny would eat up the carcass of a horse sooner than a lion would do it" (Hooker 1883). However, Linnaeus neither referred to the source of this information, nor presented any detail of the calculation. This sentence is more like an aphorism rather than a strict scientific statement supported by direct evidence, leaving almost all concrete details to the imagination of the reader.

The short statement should not be taken literally. Linnaeus did not mean that three adult flies, the imagoes, eat up the carcass. He implied that the three individuals produce a large quantity of progeny very fast so that the feeding capacity of the larval population (the maggots) compares to that of large carnivorous mammals. "The progeny of" is therefore added by some authors to the translation to clarify the issue (for example, Sachs 2001).[14] Malewski *et al.*



Vomito- 67. M. antennis plumatis piloſa, thorace nigro, abdomi-
ria. ne cæruleo nitente. *Fn. ſvec.* 1831. *

Scop. carn. 868. Muſca carnaria.
Gœd. inſ. 1. *t.* 53.
Liſt. gœd. f. 122.
Raj. inſ. 27.
Reaum. inſ. 4. *t.* 19. *f.* 8.
t. 24. *f.* 13, 15.
Geoffr. pariſ. 2. *p.* 524. *n.* 59.
Lyonet. leſſ. t. 1. *f.* 23, 27.
Habitat in Cadaveribus; *etiam* Americæ. *Kalm. Tres Muſcæ conſumunt cadaver Equi, æque cito, ac Leo.*

Figure 5. Linnaeus's (1767: 989–990) comment in the twelfth edition of *Systema naturae* about the feeding capacity of *Musca vomitoria*.

(2010) also pointed out that large masses of maggots produced by the imagoes are meant here. Moreover, maggots do not directly feed on the dead cadaver tissues, rather they mostly feed on the emerging fluids. To a certain degree, this fluid is produced by the maggots themselves, their piercing mouthparts are capable of degrading cadaver tissues and they excrete digestive enzymes to dissolve necrotic tissues. However, they most probably also depend on the bacteria that significantly contribute to cadaver fluidization.

Nevertheless, it is worth scrutinizing Linnaeus's suggestion step-by-step, in order to see how close his proposal is to reality. First, we ask how long does it take for a lion to eat a horse. Then, we examine how many offspring three bluebottle flies could produce within the same time and calculate the quantity of carcass that would be consumed by the population of larvae (see Appendices A and B).

We found that the time needed by a hypothetical lion to consume a horse carcass versus the three bluebottle flies (and their offspring) depends on several factors that were not specified by Linnaeus nor by authors citing him. In spite of that, we can safely conclude that Linnaeus was quite right in estimating the magnitudes of these time periods. Thanks to the extensive research carried out by forensic entomologists, we can confirm his statement, and even add a few details to make it a bit more precise: three *Calliphora vomitoria* female flies and their offspring can consume the carcass of a horse as quickly as, or perhaps even more quickly than a lion. Even with minor perturbations of the parameters used here, Linnaeus's statement remains reasonably good (see Appendix B). It is also easy to see, however, that for extremely hungry and greedy male lions (which would finish the horse before day 52) and for smaller horses (whose body would be eaten by the average lion before day 52) the statement becomes false and only about 15 kg of meat would be consumed by maggots. Of course, the actual amount for all partners in this system depends on many other factors that we did not consider such as temperature, survival rate of maggots, unequal sex ratio, larval density, natural enemies, and so on.

DISCUSSION

Historical studies in the past decades have made clear that Linnaeus was interested in many more disciplines than generally thought and is not only the father of modern taxonomy.

Linnaeus developed and published new ideas collected in *Amoenitates academicae* which may now be considered as early contributions to biogeography and ecology (Egerton 2007). In several cases, Linnaeus presented numerical data to illustrate the subject although he was not always precise in his mathematical calculations. As has been shown in an analysis of *Philosophia botanica* (Podani and Szilágyi 2016), his calculation of the possible number of genera was burdened by trivial errors at several places, often remaining unchanged in later translations and references to his work. In his early suggestions regarding population growth, Linnaeus also used concrete figures to support his arguments – with more or less accuracy.

In the hypothetical annual plant example, the basic assumptions were clearly formulated and the arithmetic operations were properly initiated, yet the final result was erroneous, although only 4% higher than the correct value. In the pigeon example, perhaps derived in collaboration with his student, Isaac Biberg, the figure was almost correct but the underlying assumptions were unclear. We have shown the conditions that lead to the number they, or more precisely the English translator suggested, and argued that there is a more plausible calculation – giving a much higher estimate for offspring population size. For the third example, on the growing and feeding capacity of the flesh-eating bluebottle flies, no calculation was presented by Linnaeus. In this case, therefore, the question was to reveal how far from reality his short statement was, as estimated from data regarding horse body mass, lion feeding capacity, and fly life cycle and feeding parameters.

As noted, the annual plant example was merely hypothetical and unrealistic, and Darwin (1859) was absolutely correct to note that no such species exists in nature. Annual plants complete their life cycle in one year (or less) and then die, so they must produce sufficient number of seeds to guarantee survival of the species in the next season. Two seeds per plant are thus the minimum for population increase, one seed per year would at best maintain the population – provided that the population is unregulated. Linnaeus was probably aware of this fact and he deliberately chose the two-seed case to demonstrate that even a poorly reproducing plant could have colonized the bare Earth after enough time.

The next two examples refer to actual living species. In demonstrating the reproductive ability of animals, the pigeon was used. Given that this species has been well known from ancient times, the starting parameters appear reasonable, but Linnaeus and his student apparently disregarded the fact that a pair can keep on breeding through several years. Therefore, the numbers describing unlimited population growth were underestimated, although arithmetically correct.

Interestingly, Linnaeus devoted only a single and short sentence to a problem which is much more complex than that of the annual plant or the pigeons. Three species are involved and in order to state that three flies and their offspring can eat as much flesh as a lion, and that this amounts to the body of a dead horse we must know the following: the life cycle parameters of the fly, the efficiency by which the fly converts food into its own tissues, the weight of the edible parts of a horse and how long it takes for a lion to eat a horse. We relied upon estimated and experimentally determined population parameters and reached the – perhaps unexpected – conclusion that Linnaeus was fairly close to the truth: during the period in which a male lion would consume a horse, the offspring of three female bluebottle flies could also consume approximately the same amount of food. After minor changes to the values of the various parameters, Linnaeus's conclusion remains reasonably good.

In addition to arithmetic precision and logical issues, we call attention to incorrect and mistaken references, as well as instances when authors considered Linnaeus's figures uncritically. Such carelessness may be responsible for distortion of information in scientific communication, which may not be as rare as it should be. This is especially dangerous when well-known authorities, such as Linnaeus are wrongly cited and, thus, interpreted mistakenly.

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NOTES

[1] In this manuscript, Leonardo of Pisa described for first time the Hindu-Arabic numeral system. The Fibonacci series was in fact noted earlier by Indian mathematicians (Singh 1985).

[2] While the term "population" was not understood in the same sense as today, scientific views on population growth are nevertheless comparable.

[3] The number of pairs of rabbits at the end of the *i*th month is the number of mature pairs (that is, the number of rabbits at the end of the *i*-2th month, n_{i-2}) plus the number of non-breading pairs last month (n_{i-1}). Thus the answer is obtained by using the recursive formula $n_i = n_{i-2} + n_{i-1}$., where $n_0 = 0$, $n_1=1$. The resulting sequence n_1, n_2, n_3, n_4, n_5, n_6 (0, 1, 1, 2, 3, 5 …) is the Fibonacci sequence, n_i is the *i*th Fibonacci number.

[4] Linnaeus agreed initially with the view that the Earth was created about 6,000 years before his time (Eriksson 1994: 89) but later assumed that this figure might have been five to ten times higher (Frängsmyr 1994: 154).

[5] Although Darwin himself was greatly interested in pigeons, whose reproduction and variability also served a central role in the development of his ideas, this case escaped his attention. More precisely, we did not find any evidence in Darwin's work that he had ever mentioned this example in his writings and notebooks. He did mention, however, the unlimited reproduction of elephants as another example of his own, inventing implicitly and unintentionally the tribonacci sequence ($n_i = n_{i-3} + n_{i-2} + n_{i-1}$) decades before mathematicians developed it (Podani *et al.* 2018).

[6] Seven volumes were published in Linnaeus's lifetime in Leiden and Stockholm (1749–1769), and three volumes later in Erlangen (1785–1790, edited by Schreber), although the last one contains no dissertations. See full list in Kiger *et al.* (1999: 232–263).

[7] It was not a defence of a thesis by Johan Westman, as sometimes mentioned in the literature of the history of biology. His name appears in a letter written on 19 February 1745, in which Linnaeus informed A. Bäck (Leipzig, Germany) that his student, Johan Westman is deputy provincial medical officer in Västerås, Sweden (Linnaean correspondence, Uppsala, https://www.alvin-portal.org/alvin/view.jsf?dswid=6016&searchType=EXTENDED&query=westman++B%C3%A4ck&aq=%5B%5B%7B%22A_FQ%22%3A%22westman++B%C3%A4ck%22%7D%5D%5D&aqe=%5B%5D&af=%5B%5D&pid=alvin-record%3A223550&c=1#alvin-record%3A223550) (accessed 18 February 2021).

[8] None of the printed editions of *Origin* specifies the source of this information. The long manuscript from which *Origin* was derived (Stauffer 1975), however, clarifies the situation: "Linnaeus in the Amoenitates Acad. says that an annual plant producing a single flower with only two seeds (& no plant nearly so barren exists) in twenty years would yield one million plants" and then Darwin cited "On the increase of the habitable Earth" (Brand 1781: 94–95).

[9] Haeckel's translator wrote "Even Linnaeus calculated", reflecting that this was a sort of achievement not expected to occur that early in the Swedish naturalist's work.

[10] It is therefore misleading to say that Linnaeus "correctly" calculated the number (for example, Egerton 2007, but then cancelled in Egerton 2012).

[11] Egerton (2012) pointed out an obvious typographic error in the body text (the numerals 6 and 7 were transposed giving 14,672). This error appeared first in the second edition (Stillingfleet 1762: 90) and remained there in two reprints in 1775 and 1791.

[12] For example, Bradley (1736: 9) refers to Ulisse Aldrovandi: "Aldrovandus tells us of a pigeon, which continued alive two and twenty years, and bred all that time except the last six months".

[13] In addition, the flies may carry several pathogens, causing anthrax and tuberculosis, for example, so that this species is of central importance in public health as well.

[14] See also A. J. Patzak, 2011, "Successional patterns of necrophilous beetles on domestic pig carcasses in urban and sylvan areas during Spring and Summer – a comparative study between four study sites in and around Vienna". Unpublished Master of Science thesis, University of Vienna. Available at: http://othes.univie.ac.at/13490/ (accessed 16 February 2021).

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APPENDICES

Appendix A. Assumptions and simple calculations in the fly example.

As it is often the case with domesticated animals, different breeds of domestic horses (*Equus ferus caballus* Linnaeus, 1758) vary extremely in size. The body mass of an average adult animal is estimated to range from 380 kg to 450 kg (Vaughan *et al*. 2011: tables 2 and 3) or to 550 kg (Bongianni 1987); an eighteenth-century stallion named Mammoth had the largest body weight, approximately 1,524 kg, ever recorded for domestic horses (Whitaker and Whitelaw 2007), whereas some dwarf horses can have a body mass of as little as 26 kg (Martin 2006). Let us choose a relatively large horse carcass with 450 kg soft tissue plus the skeleton that is mostly not consumable. We also need to presume that meat spoilage due to decomposing bacteria would not make the cadaver inedible to a lion. A male lion eats about 7 kg a day – occasionally, a large hungry male can eat as much as 30 kg in a single sitting (Guggisberg 1961) but then this animal may not eat anything for several days – while a female consumes about 5 kg food daily (Schaller 1972). Thus, assuming that their diet includes all the soft tissues, they would consume a horse cadaver within 64 and 90 days, respectively. Also, we can safely suppose that Linnaeus had an adult male lion in mind, because the male sex had represented almost exclusively the lions in fictions, tales and artworks (sculptures, paintings, mosaics) since ancient times. Therefore, we shall use the 64-days' time period as a reference basis.

The next issue to be examined is the productivity of flies. Waldbauer (2003) provides some calculations to check whether Linnaeus' statement is a gross exaggeration of the reproductive potential of bluebottle flies. Without specifying the source of data, Waldbauer claims that each female lays 300 eggs. Thus, the three females produce 900 eggs at a time – thereby assuming that Linnaeus also had three female flies in mind. Then, Waldbauer immediately gives expected population size: "if the weather is warm and all of their offspring survive, after about 22 days, they will have well over 20 million grandchildren in the form of fully-grown maggots". This figure is not supported by additional information, however. In order to estimate the number of maggots in the third generation (the "grandchildren") we should know at least the sex ratio in the progeny of the flies. The next question is whether the three females lay egg batches again and again within the 22 days mentioned, and if so, how often? Finally, we should know the time period required by different developmental stages of flies, and also the amount of food consumed by the maggots. However, a large body of literature is now available on the life cycle of bluebottle fly and its close relatives. One reason for increased interest is that forensic science requires a precise knowledge of the duration and the course of larval stages. Linnaeus mentioned three flies that we presume to be fertilized females arriving to the carcass and starting oviposition immediately after the death of the animal – assumptions implicit in forensic science as well. We calculate the unlimited population growth of their progeny under ideally favourable conditions up to the sixty-fourth day.

Adult bluebottle flies lay a batch of about 200–300 eggs on a cadaver at one time, and this is the number of offspring that many authors, like Waldbauer (2003), used to claim that each female can produce between 200 and 300 offspring. This is erroneous, however, because the adult stage of these flies lasts about 26 days (Kamal 1958) during which they lay about ten egg batches, producing as many as around 3,000 eggs in their lifetime (Erzinçlioglu 2013; Shah *et al*. 2015). Presuming an offspring sex-ratio of 50:50 (for a closely related species, *Calliphora vicina* Robineau-Desvoidy 1830, see Tate 1948), this means that a single female can produce 1,000–1,500 females for the next generation. We shall use mean values here, namely 10 × 250 eggs for each female, totalling 2,500 offspring – half of which are females.

We suppose that all the three females (the first generation) are of the same age and are in a status of maximum productivity, so they produce 750 eggs at a time. They do it ten times within 26 days, thus producing a total of 7,500 eggs. We assume further that no mortality occurs through the egg, larva, and pupa stages. Linnaeus's aphorism does not only concern population growth, but it also implies that the maggots can consume voraciously a large mass of carcass. Therefore, the next question to examine is how much flesh can a single maggot eat during the three larval stages of the life cycle? Waldbauer (2003) assumes that a fully-grown maggot weighs 100 mg and that this corresponds to 50% of its full diet consumed during development – so that a larva would consume a total of 0.2 g meat before pupation. Greenberg and Kunich (2002) provided more precise data for a related species, *Calliphora vicina*, which we can use here safely: the newly hatched maggot is only 0.1 mg, and five days later it weighs about 0.84 g – implying a weight increase of about 8,000 times (the authors erroneously wrote "800 times"). Assuming 50% efficiency as above, this would mean a consumption of 1.7 g meat. More recently, Shah *et al.* (2015) have determined food consumption of blowfly (Calliphoridae) maggots experimentally without giving species details, and concluded that in general the average amount of meat consumed by one larva is 1.93 g.

According to Kamal (1958), the eggs take about 26 hours to hatch and the maggots feed intensively through the next five and a half days. This is followed by non-feeding pre-pupa and pupa stages that last 15 and 14 days (Figure A1). We also neglect the carcass fluids consumed by adult flies. Thus, the offspring from the last egg batches of the second generation cease feeding on the thirty sixth day (= 1.1 + 5.5 + 15 + 14). An adult *C. vomitoria* female starts laying eggs only around twelve and a half days after hatching from the pupa (Kamal 1958), so that the fly requires about 48 days to reach sexual maturity after which it lives for further 26 days.

As a quick evaluation of Linnaeus's prediction, let us examine how much meat the maggots eat until day 55. The second generation, containing 10 batches, feeds from around day 1 to day ~33. Since each batch contains 3 × 250 = 750 individuals, the total number of maggots of the

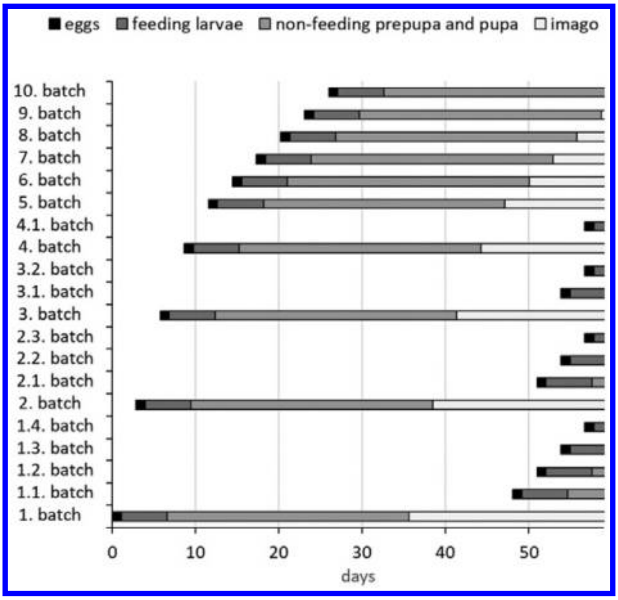

Figure A1. Timing of bluebottle fly second and third generation cohorts based on Kamal (1958). This scenario starts with fertilized females which lay a first batch of eggs on day 0 and produce a total of 10 cohorts (batches 1–10) through the following 26 days of imago life. The larvae hatch after 26 hours then feed through 5.5 days. This is followed by an inactive prepupa and pupa period for 29 days, then a new generation of imagoes hatch. They need further 12.5 days to start oviposition. The emergence of subsequent cohorts (1.1–4.1 batches) is shown here until day 59, when they exhaust their food resource.

second generation is 7,500. If a single maggot eats 1.93 g meat, then the total consumption of the second generation is 1.93 × 7,500 g ≈ 14.5 kg. Since the number of females in the second generation is 750/2 = 375 per batch, each of the third-generation batches will have 375 × 250 = 93,750 maggots. They consume a total of 180.9 kg of meat during the five and a half days of their larval stage – which corresponds to a mean daily consumption of 32.9 kg if we assume, for simplicity, a constant feeding activity over time. The first batch of the third generation (day ~1) will eat from day ~50 to day ~55; batches (1.2) and (2.1) eat between days ~52 and ~57; whereas batches (1.3), (2.2) and (3.1) eat between days ~54 and ~60. By day 55, batch (1.1) will complete the larval stage, which requires 180.9 kg meat. Batches (1.2) and (2.1) will have ~55-51.7 = ~3.3 days for eating a total of 3.3 × 32.9 = 217 kg. The remaining three batches will have less than a day for eating (55–54.3 = ~0.7), so their total consumption is 0.7 × 3 × 32.9 = 69 kg. Thus, the total meat consumption of all maggots until day 55 is 14.5 + 180.9 + 217 + 69 = 481.4 kg. However, our calculations underestimate the true value, because the growth and meat consumption of larvae are not linear in time: smaller maggots eat less than larger ones. Calculations are more correct if we consider logistic growth of larvae. These calculations (see Appendix B) show that 500 kg meat is gone approximately by day 56.

It must be noted that the above data on timing are not at all precise for several other reasons as well. First, the development of *C. vomitoria* is considerably slower than that of comparable other species the data of which were used here as estimates. Second, Kamal (1958) also gave ranges to indicate a huge variability of timing that we have neglected. Third, other authors (Marchenko 2001; Ames and Turner 2003; Ireland and Turner 2006; Niederegger *et al.* 2010) tend to provide shorter developmental periods for *C. vomitoria.* Overall, these points suggest that we have overestimated the time need of the three flies to consume a horse carcass. Contrarily, we did not involve the mortality of larval developmental stages into the calculations, which can reach even 15–80% in the laboratory, depending on details of environmental conditions (Kamal 1958; Ireland and Turner 2006).

Appendix B. Mathematical models of blowfly population increase

Let $\mathbf{p}[t]$ denote the population vector of the female blowfly population at the end of time period t. To be consistent with the parameters used in the text, time is measured in 0.1–day units. In the following calculations, we use data from Kamal (1958). Square brackets emphasize that we use discrete time representation. Each element of the population vector is the number of females in the respective age class. Different elements of this vector correspond to different developmental stages: $p_1[t]$ denotes the number of newly laid eggs at the end of their 0.1 day, $p_2[t]$ denotes the number of 0.2 day old eggs, etc., while $p_{11}[t]$ is the number of 1.1–day old eggs (at the end of this developmental stage). As the lifetime of a maggot is about 5.5 days, $p_{12}[t],\ldots, p_{66}[t]$ denote the number of maggots. Similarly, $p_{67}[t],\ldots, p_{356}[t]$ and $p_{357}[t],\ldots, p_{481}[t]$ denote the number of pupae and sexually immature adults at different times in the given developmental stage. The last 260 elements of the population vector ($p_{482}[t]\ldots p_{741}[t]$) correspond to the imago stage.

The discrete dynamics of the female population can be described by the following equation:

$$\mathbf{p}[t+1] = \mathbf{L}\mathbf{p}[t],$$

where $\mathbf{L}$ is the Leslie matrix of the system. According to the life-history of the individuals, the Leslie matrix has the following form: all sub-diagonal elements are 1, $L_{i,i+1} = 1$ ($i = 1,\ldots, 740$) since there is no mortality during the whole life-history. As we assumed, an adult female, during its lifetime, lays about 10 egg batches for 29 days, each of them consisting of 250 eggs on the average. Thus, the elements of the Leslie matrix corresponding to fecundity are the following: $L_{1,482} = 125$, $L_{1,511} = 125$, $L_{1,540} = 125,\ldots, L_{1,712} = 125$, $L_{1,741} = 125$, as these values represent the female offspring of adult individuals. All other elements of the matrix are zero. We assume 1:1 sex ratio, as mentioned in the main text, so the total number of individuals in a respective age-class is the double of the corresponding elements of the population vector.

The total number of eggs and maggots at time t can be calculated as

$$2\sum_{i=1}^{11} p_i[t] \text{ and } 2\sum_{i=12}^{66} p_i[t]$$

respectively. The corresponding values for pupa, immature and adult phases can be calculated similarly. The time course of the number of individuals of different developmental stages (irrespective of the age-classes) is seen in Figure B1.

To analyze the resource consumption of maggots in detail, we assume that the cumulative food consumption (the total amount of food consumed by a maggot until its lifetime t, measured in mg) follows a logistic function:

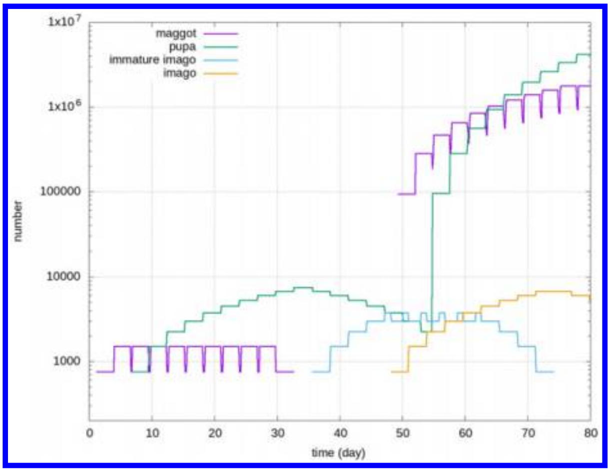

Figure B1. The number of individuals of different developmental stages. Purple curve denotes the total number of maggots irrespective of their age classes as the function of time ($\sum_{i=12}^{66} p_i(t)$). Similarly, green, blue and yellow curves denote the total number of pupae, immature imagoes and imagoes, respectively.

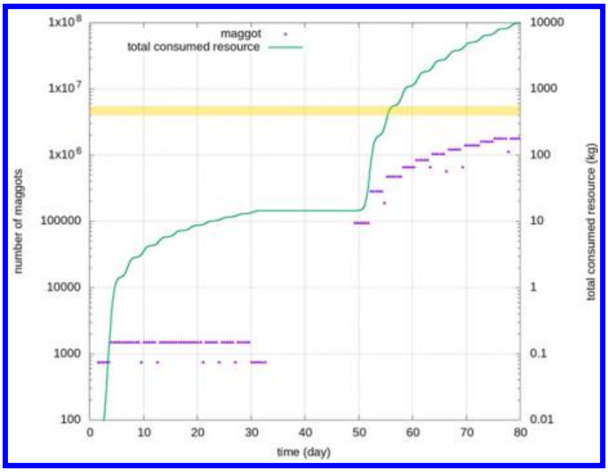

Figure B2. The total number of maggots (red triangles) and the total consumed resource (green line). The yellow band corresponds to the weight interval of 400–550 kg.

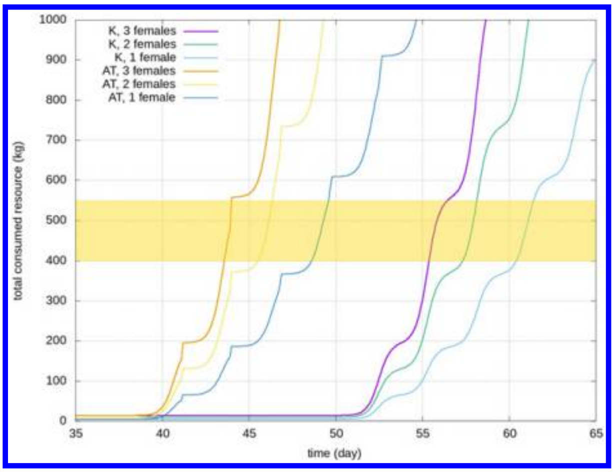

Figure B3. Time courses of the total consumed resource based on parameters from Kamal (1958) (denoted by K) and Ames and Turner (2003) (denoted by AT), with 1, 2 or 3 females at the beginning. The yellow band corresponds to the weight interval of 400–550 kg as in Figure B2.

$$m[t] = \frac{m[0]Ke^{rt}}{K + m[0](e^{rt} - 1)},$$

where $m[0] = 0.1$, $K = 1930$, $r = 0.3$ and d measured in 0.1 day units (partly following Shah *et al.* (2015)). In this case, the initial phase of growth is exponential, and then growth is mitigated.

The resource $R[t]$ consumed by maggots between time periods (t–1) and t can be calculated as follows:

$$R[t] = 2\sum_{\tau=1}^{55} (m[i] - m[i-1])\, p_{i+11}[t]$$

in which prefactor 2 refers to the 1:1 sex ratio. (Note that this simple form is valid only if there is no degradation between life stages, i.e., all sub-diagonal elements are 1.) The total consumed resource until time t ($R_{\text{sum}}[t]$), which is the relevant quantity for our investigation, can be calculated easily:

$$R_{\text{sum}}[t] = \sum_{\tau=1}^{t} R[\tau]$$

The number of maggots (red triangles) and their total resource consumption (green line) is shown as a function of time (Figure B2). As seen, the total consumption is in the interval of 400–550 kg between days 55–56.

Next, we have analyzed the change of the time course of the total amount of food if we use the parameter set from Ames and Turner (2003) or assume one or two females at the beginning. The original parameter set of Kamal (1958) with three females was the reference; see the thick red line in Figure B2. With the second parameter set, starting with three females, the total consumption reaches 400–500 kg on the 43rd–44th days. Starting with one or two females extends the time period by approximately 2 and 5 days, respectively (see Figure B3).