Contributions

Commentary

A History of the Ecological Sciences, Part 31: Studies of Animal Populations during the 1700s

The first edition of Malthus' *Essay on the Principle of Population* (1798) may have been the spontaneous product he claimed, responding to writings by William Godwin and Marquis de Condorcet, but a number of other predecessors also influenced him, and he admitted in chapter one that "The most important argument that I shall adduce is certainly not new." Furthermore, he became familiar with even more predecessors before he produced a greatly enlarged second edition (1803). As in the 1600s (Egerton 2005*a*), animal and human population studies in the 1700s were partly separate and partly overlapping. Here the emphasis is on populations of animals and plants, which is a reverse of the emphasis of Malthus and many of his predecessors. This part of my history condenses and updates part of my doctoral dissertation (1967:119–275). Since the writings discussed are mainly un-illustrated, and because it is difficult to find illustrations of particular species that the naturalists did discuss, four natural history illustrations in this part are representative of what one could have seen in university or museum libraries, and are arranged chronologically.

Several naturalists who contributed to population studies were discussed in previous parts of this history. Antoni van Leeuwenhoek (1632–1723) is noteworthy for his calculations of reproductive potential for a variety of species (Egerton 1968, 2006*a*). Perhaps he influenced a French physician and botanist, Denis Dodart (1634–1707), who was a prominent member of the Académie des Sciences in Paris (Grmek 1971). In "Sur la multiplication des corps vivants considerée dans la fécondité des plantes"(1703), his main concern was to provide evidence supporting the *emboîtment* theory of reproduction, but he did so with calculations on the reproductive potential of an elm tree. He cut off an eight-foot branch and counted 16,450 seeds, and saw 10 other branches of about the same size, yielding 164,500 seeds for this young tree. He decided more mature trees produced about 330,000 seeds per year, and they lived about 100 years, which meant they produced 33 million seeds during a lifetime. He thought that this high reproductive capacity was to preserve the species from accidents that tend to destroy them, and he used the phrase "une progression géometrique croissante," which Richard Bradley (1721:110) translated as "a Geometrical Progression of Growth." Earlier, Sir Matthew Hale (1677:205) had used the term "a Geometrical Proportion [of] Increase" in discussing human population. We do not know that Malthus ever read Hale, Dodart, or Bradley, but these examples show that such terms had currency in the 1700s before Malthus used them.

We previously met William Derham (1657–1735) as a later associate of John Ray (Egerton 2005*c*:310–311).

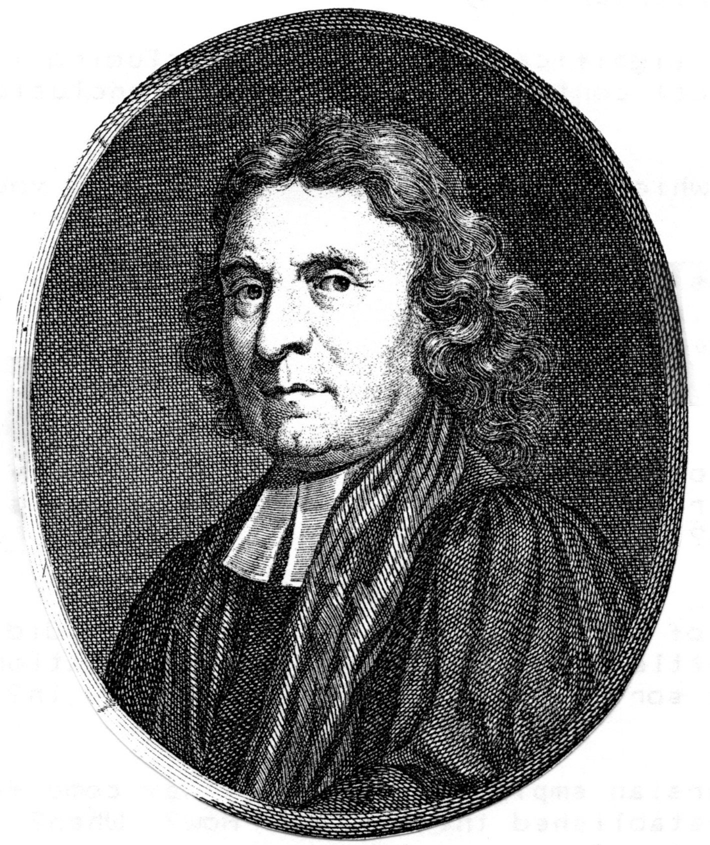

Fig. 1. William Derham.

He was a fellow of the Royal Society of London and published a few original articles in its *Philosophical Transactions*, but he was also a prominent clergyman (Atkinson 1952, Knight 1971, Smolenaars 2004), whose broad influence came from two books on natural theology, *Physico-Theology* (1713) and *Astro-Theology* (1714). His *Physico-Theology* owed a debt to Ray's influence, yet it also contained Derham's own observations and ideas, which are a substantial contribution to animal demography and the balance of nature concept. This book went through 18 editions by 1798 and was translated into French (1732), Swedish (1736), and German (1750).

Derham's most important chapter in *Physico-Theology* concerning population was the 10th in book four, "Of the Balance of Animals, or their due Proportion wherewith the World is stocked." This may be the first time the word "balance" was used in natural history in relation to populations, and his usage conveyed the idea that we call the balance of nature (1716:171, quoted in Egerton 2005*c*:310). However, he made no attempt to reconcile the factors that preserve a balance of populations in this chapter with the phenomena of animal plagues, which he discussed in book two, chapter six. This surprises us, but for him, a balance of populations was how nature normally functions, and animal plagues were God's intervention to punish or discipline humanity, by restraining temporarily those factors preserving a balance. This idea was illustrated in the animal plagues that Yahweh imposed upon the Egyptians when the Pharaoh refused to let Moses lead the Hebrews from Egypt, told in the Book of Exodus. If the balance of nature and plagues were different kinds of phenomena, there was no need to worry about reconciling them.

Derham thought that differential longevity and differential reproductive capacity among species, and also predation, were the means by which animal populations were normally controlled (without God's intervention). However, humans were a special case. In the early history of the earth, he wrote, humans had a longer life span so that the earth could become populated rather quickly. After it was sufficiently stocked, God reduced man's years to about 80. (Derham himself lived 78 years.) His explanation for control of human population in his time was based on vital statistics. Gregory King had found that the ratios of males to females varied in different localities, being 10:13 in London, 8:9 in towns, and 100:99 in villages. Derham supposed that this was about equivalent to the 14:13 ratio that John Graunt had found (Egerton 2005*a*:34). His own parish register at Upminster provided data for 100 years that agreed with Graunt's finding that slightly more males are born than females, and that males die at a slightly higher rate. Derham cited Dr. John Arbuthnot's article (1711) that a balanced sex ratio could not be due to chance, and it therefore indicates divine regulation.

Although Richard Bradley (1688?–1732) had little interest in natural theology, he read Derham's book, since he discussed similar topics that we call ecological and demographic (Bradley 1739:204). He touched on these subjects in a number of his works (Egerton 2006*b*), but his important theoretical discussions were in *A Philosophical Account of the Works of Nature* (1721, edition 2, 1739), and his most substantial practical discussions were in *A General Treatise of Husbandry and Gardening* (three volumes, 1721–1724; new edition, 1726). Theoretically, he suggested that a proportionate relationship existed between the reproductive capacity of a fish and the number of its enemies, and he gave specific data on the average number of offspring of a number of birds and mammals (Bradley 1739:85–87, 119, 132–133). If one also took into account the differences in longevity of different species and the differences in what different animals eat, then one could understand the existence of what we call the balance of nature (Bradley 1739:217, Egerton 1967:149).

Bradley may not have shared Derham's belief that animal plagues were a punishment of people, but confining his discussion of them to *A General Treatise* (1726) had the same effect of separating his discussion of them from his theoretical discussion of the balance of nature in *A Philosophical Account* (1721). On the other hand, his defense of birds as a friend of gardeners and farmers because they eat insects was a practical example of the balance of nature (Egerton 2006*b*:123). However, a modern ecologist could object that he was not considering all the mortality factors when he concluded (Bradley 1726, II:221)

> *…if we consider that every one of these Moths will lay about three hundred Eggs a-piece, which*

will hatch into Caterpillars the Spring following; then the Destruction of an hundred of these Moths, is preventing the Increase of thirty thousand murdering Insects; and so likewise every Caterpillar or Insect that a Bird destroys, is preventing at least three hundred that would otherwise be troublesome to us the following Year.

Some gentlemen of Hoxton had a different idea to control wasps that damaged their fruit: they offered a reward for every wasp nest destroyed. This was supposedly successful in protecting their fruit and Bradley urged others to do likewise. There was no thought that other wasps might expand into the areas where wasps had been eradicated.

Medical statistics began with John Graunt's *Natural and Political Observations* (1662) and was continued by William Petty and Mathew Hale, among others (Egerton 2005*a*:33–36). The subject was given a strong impetus in 1721 when smallpox inoculation was introduced into both England and its American colonies. It was a controversial practice, and its defenders made their case by comparing the death rates from the disease of those inoculated with those who were not. We saw that Francesco Redi invented the controlled experiment in 1668 (Egerton 2005*b*:136), though it was slow in becoming a standard experimental procedure. This controversy over inoculation was a spontaneous controlled experiment, although it was not called by that name at the time. Cotton Mather (1663–1728) and Zabdiel Boylston (1676–1766) introduced inoculation into Boston, and they pointed out that among the inoculated, the death rate was one in 60, but among those infected without inoculation, the death rate was one in six (Barret 1942, Blake 1952, Cassedy 1969:132–136, Finger 2006:52–56). Similarly, in Yorkshire, England, Dr. Thomas Nettleton found that only one of 61 people inoculated had died of smallpox, whereas 20% of those infected and not inoculated died (Nettleton 1722, Miller 1957, Rusnock 2002, Finger 2006:56–57). In 1730 Benjamin Franklin (1706–1790) published similar statistics for Boston and New England in his *Pennsylvania Gazette* (quoted in Finger 2006:57). Tragically, his own son, Francis F. Franklin, died of smallpox in 1736 before his father was able to have him inoculated. Franklin then crusaded for smallpox inoculation for the rest of his life (Finger 2006:58–65). Richard Price (1723–1791), a liberal nonconformist minister, wrote to the Royal Society (1774) about another insight gained from the use of medical statistics: Swiss vital statistics indicated that half of people who lived at high elevations lived to be 47, but that half of those who lived in marshy lowlands lived only to be 25—confirming the ancient suspicion that marshy places were unhealthy.

René Réaumur (1683–1757) built upon Leeuwenhoek and Bradley's insights by going beyond merely calculating potential rates of increase to ask why such potentials did not lead to insect plagues more often than actually occur. His answer was that their numbers were usually limited by their predators, parasites, diseases, and adverse weather, and that it was only when limiting factors weakened that plagues occurred (Egerton 2006*c*:213–215). That was apparently the case in June–July 1735 when a plague of *Plusia gamma* caterpillars occurred. Caterpillars had also been numerous in autumn 1731, spring 1732, and in 1737, but no plague had occurred because flies that lay eggs in the caterpillars had also been numerous.

Unlike some French colleagues, Réaumur was a pious naturalist, and he was a stimulus for Lutheran pastor and amateur naturalist Friedrich Christian Lesser (1692–1754) of Nordhausen to write his popular *Insecto-Theologia* (1738); the natural theology books by Ray and Derham provided Lesser

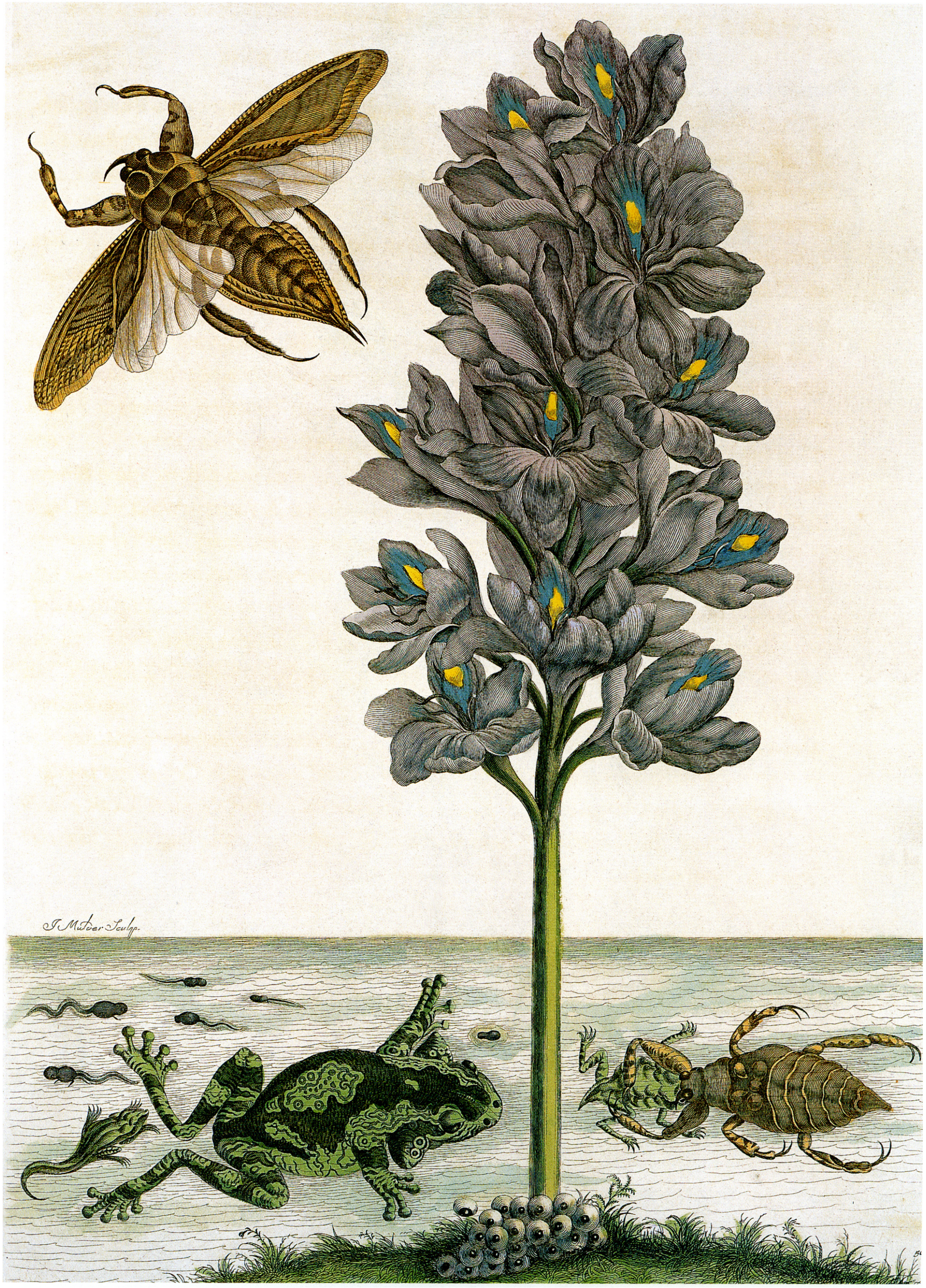

Fig. 2. Aquatic life of Surinam: water hyacinth (*Eichhornia crassipes*) and metamorphic aquatic and land stages of a frog (*Phrynohyas venulosa*) and an insect (*Lethocercus grandis*), by Maria Sibylla Merian (1705). On her, see Todd 2007, Egerton 2008*b*:408–412.

not only with inspiration, but also with specific details and arguments (Egerton 1967:159–163). His first chapter argued against the theory of spontaneous generation. His fourth chapter, "On the Number of Insects, and the Proportion according to which They Multiply," provided a rather familiar example of the rate at which insects could multiply if their numbers were not kept in check. He thought God had provided for the balance of nature, and the abundance of insects partly provided food for other animals. His sixth chapter, on reproduction, emphasized not only the importance of the numerous eggs they lay, but also the shortness of life cycle as contributing to their reproductive capacity. He repeated a common proverb about a flea becoming a grandparent in 24 hours—overlooking Leeuwenhoek's refutation (letter of 5 October 1677; Egerton 2006*a*:53). Although he thought that God used insects as a scourge for humanity, he also believed that God gave man the ability to protect himself against insect ravages. He thought it would be impossible to exterminate insects, but that the study of their life histories could give clues about how to limit their numbers.

Lesser's *Insecto-Theologia* had a second German edition (1740) and was translated into French (1742; edition 2, 1745), Italian (1751), and English (1799). The French edition was expanded into two volumes because of annotations and two plates added by Pierre Lyonet (1706–1789), whom we met in part 30 as the illustrator of Abraham Trembley's treatise (1744) on hydras (Egerton 2008*b*:417–418). Lyonet's attention to the details of hydras, and to insect anatomy in his treatise on the goat-moth *Cossus ligniperda* (1760), also comes across in his annotations of and plates for Lesser's book. Lyonet's training in law must also have sharpened his attention to detail (Van Seters 1962, Pierson 1973, Tuxen 1973:100–101). Lesser discussed in a general way the reproductive capacity of insects and the balance of nature (1742, I:117–120), drawing upon Derham's *Physico-Theology*, but Lyonet felt a need for specifics.

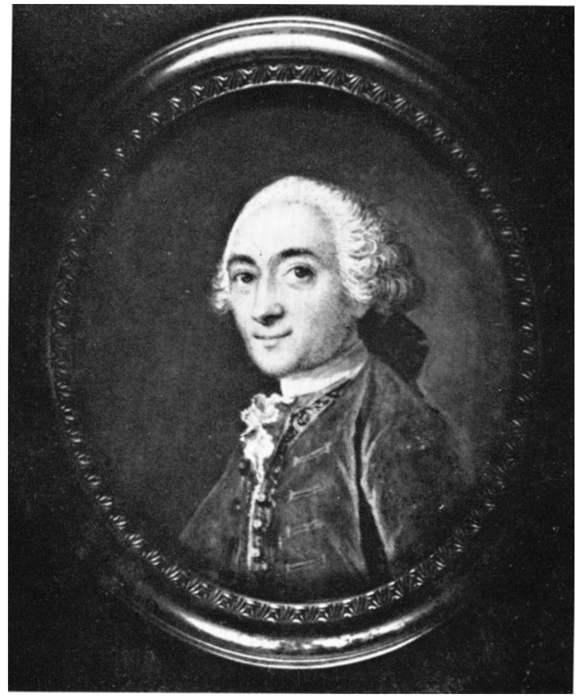

Fig. 3. Pierre Lyonet.

He dismissed Lesser's claim that a louse could become a grandparent in 24 hours. However, his own attempt to be specific was hardly exhaustive. He extracted about 350 eggs from a butterfly, *Orgyia antique* L., which hatched into as many caterpillars. He decided that it was too much trouble to raise them all, so he kept only 80, 75 of which became adults, but only 15 were females. Rather than raise another batch to see if that was typical, he calculated that his original 350 eggs should have produced at least 65 females. These 65 could presumably produce 22,750 eggs, of which 4265 should be females, and they, in turn, could lay 1,492,750 eggs. He also knew of a viviparous fly (unnamed) that carried up to 20,000 young. Assuming a balanced sex ratio, he calculated that the third generation from a single viviparous fly could produce two thousand billion offspring—if Providence had not established measures to control their numbers. These figures were so impressive, Charles de Geer (1720–88), whom we met in part 30 (Egerton 2008*b*:420–421), cited them in his more scientifically prestigious treatise (1752–1777, II:48).

Lyonet's use of the phrase "une progression géometrique" may indicate that he had read Dodart's article. Although Lyonet accepted the idea that the living world was designed to preserve the balance of nature, he did not believe it was a simple matter. He denied Lesser's claim that insect food is so abundant that none ever die of hunger. He thought that when their numbers become unusually large, they could eat all available food and then starve. With high mortality, there would be fewer eggs laid than usual, which explains why there was seldom a large plague of the same species in two successive years (in Lesser 1742, I:273). In several instances where Lesser made vague remarks about predation or parasitism, Lyonet gave more precise descriptions and enumerations (cited in Egerton 1967:253, notes 207–208).

The great importance of Linnaeus (1707–1778) for the history of ecology in general is discussed in part 23 (Egerton 2007*b*). His discussions of animal numbers were substantial (Egerton 1967:170–184). His 1744 *Oratio de Telluris habitabilis incremento* ("On the Increase of the Habitable Earth") explained how plants and animals might have spread from the Garden of Eden to the rest of the world, postulating that the original pair of each sexual species and one individual of each hermaphroditic species increased in numbers every generation. He supported this claim by reporting the large number of seeds from flowers of different species: *Helenium* 3000, *Zea* 2000, *Helianthus* 4000, *Papaver* 3200, and *Nicotina* 40,320. These data led Linnaeus to suggest 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"(Linnaeus 1781:94, 1977*b*).

Since antiquity there had been two different ways to explain the different reproductive potentials of animal species (Egerton 2001*a*, *b*): physiological necessity, and what we now call ecological role or niche (predator, prey). Linnaeus used both explanations in *Oeconomia Naturae* (1749). His example of the former: "*Mites*, and many other insects will multiply to a thousand within the compass of a very few days. While the *elephant* scarcely produces one young in two years," and of the latter: "The *hawk* kind generally lay not above two eggs, at most four, while the *poultry* kind rise to 50" (English translation; Linnaeus 1775:90, 1977*a*). Physiological necessity could not apply in the latter example, because some kinds of poultry are larger than some kinds of hawk. In *Politia Naturae* (1760) Linnaeus repeated some of the former discussion and added that long-lived animals propagate slowly (English translation; Linnaeus 1781:162, 1977*b*). Linnaeus was also impressed by another principle, that we call ecological diversity. He thought this principle ensured that some species do not exterminate others: "If the many thousand species of vegetables grew together in one and the same place, some would infallibly predominate over and extirpate others," and "Every plant has its proper insect allotted to it to curb its luxuriancy, and that it should not multiply to the exclusion of others" (Linnaeus 1781:132, 140, 1977*b*). The principle also applied to relationships between animal species: "the weaker are generally infested by the stronger in a continued series," and "we scarcely know an animal, which has not some enemy to contend with" (Linnaeus 1775:114, 1977*a*). In *Politia Naturae* he emphasized both predation and the role of a species in nature as the chief factors regulating populations. In the case of humans, contagious disorders and war also helped control populations (Linnaeus 1781:159, 1977*b*).

Buffon (1707–1788) included discussions of animal populations in his *Histoire naturelle* (1749–1789), as explained in part 24 (Egerton 2007*c*:148–151), but his discussions can now be viewed within a wider context. Thierry Hoquet (2005:542–554) has already done this for Buffon's discussion of human vital statistics. Buffon attempted to explain differences in animal reproductions only physiologically (1749, II:306–307), without resort to ecological role, in "Histoire générale des animaux" (English translation,

Fig. 4. Camberwell Beauty Butterfly (*Nymphalis antiopa*) metamorphic stages on a *Rosa* sp. (*tomentosa*?), by Benjamin Wilkes (fl. 1690–1749). From Wilkes 1749. On him see Salmon 2000:110–112, 323–324).

1780–1785, II:255–256)

> *In general, large animals are less prolific than small ones. The whale, the elephant, the rhinoceros, the horse, man &c. produce but one, and very rarely two, at a birth. But small animals, as rats, herrings, and insects, produce a great number. Does this difference proceed from the greater quantity of nourishment necessary to support the large animals than the small, and from the former having a less proportional quantity of superfluous nutritive particles, capable of being converted into semen, than the former? It is certain that the smaller animals eat more, in proportion to their bulk, than the large.*

He even applied his physiological theory to explain why women tend to live longer than men (Linnaeus 1749–1789, II:567–568, 1780–1785, II:477–478): "the bones, the cartilages, the muscles, and every other part of the body, are softer and less solid than those of men, [and therefore in women] they must require more time in hardening to that degree which occasions death…" He also generalized about a relationship between the length of time needed for maturation and longevity (Linnaeus 1749–1789, II:569–570, English, 1780–1785, II:478–479)

> *The duration of life may, in some measure, be computed by the time occupied in growth. A plant or animal that acquires maturity in a short time, perishes much sooner than those which are longer in arriving at that period.*

He supported this claim with data on the length of time for maturation compared to longevity for human and dogs, then claimed that "Fishes continue to grow for a great number of years; they accordingly live for centuries; because their bones never acquire the density of those of other animals." However, he did not cite evidence for this. Jean Robine, Hans Petersen, and Bernard Jeune (2009) have examined the data on 56 species in Buffon's "Table of the Relative Fecundity of Animals" (Buffon 1749–1789:XIII, 25–28, 1780–1785, VIII:26–29) which includes age at which the males and females of the species begin to reproduce, gestation period, and age at which the males and females of species cease to reproduce. Much of Buffon's data came from Aristotle's *History of Animals* (Egerton 1975). Robine, Petersen, and Jeune point out that Buffon's table was the beginning of modern statistical studies on biological variables.

In "Histoire naturelle de l'homme" (Natural history of humans) Buffon published vital statistics which a fellow member of the Academy of Sciences had collected in 15 parishes: 12 rural and 3 in Paris. This data included for each parish mortality figures for every age from one to one hundred, and he discussed some reasons why the mortality rate was higher in Paris than in rural parishes. He used these figures to construct a table "showing the probabilities of the duration of human life." This table indicated (Buffon 1749–1789, II:602, English, 1780–1785, II:516–517)

> *That a new born infant, or a child of 0 age, has an equal chance of living 8 years; that a child of 1 year will live 33 more; that a child of 2 years will live 38 more; that a man of 20 years will*

live 33 and 5 months more; and that a man of 30 years will live 28 more, &c.

Although a talented mathematician, Buffon could not apply mathematics to animal populations because of insufficient data, though he could compile a "Table of the Relative Fecundity of Animals" (Egerton 2007*c*:149). He also provided a discussion similar to Dodart's (1703) on the impressive reproductive potential of an elm tree if all its seeds survived (Buffon 1749, II:38, 1780–1785, II:35).

Buffon was interested in animal plagues, and in 1756 expressed his conviction that they never caused permanent alterations of the balance of nature (Buffon 1749–1789, VI:247–248, English, 1780–1785, IV:138–139)

> *We view with terror the approach of those thick clouds, those winged armies of famished insects, which seem to threaten the whole globe with destruction, and, lighting on the fruitful plains of Egypt, or of India, annihilate, in an instant, the labours and the hopes of nations…. We behold, descending from the mountains of the north, innumerable multitudes of rats, which, like an animated deluge, overwhelm the plains, spread over the southern provinces, and, after destroying, in their passage, every thing that lives or vegetates, finish their noxious course, by infecting the earth and the air with the putrid emanations of their dead carcasses…. When men, like the animals, were half savage, and subject to all the laws and excesses of Nature, have not similar inundations of the human species taken place?* * * *
>
> *These great events, these remarkable areas in the history of the human race, are, however, only slight vicissitudes in the ordinary course of animated Nature, which in general, is always the same: Its movements are performed on two steady pivots, unlimited fecundity and those innumerable causes of destruction which reduce the product of this fecundity to a determined measure, and preserve, at all periods nearly an equal number of individuals in each species.*

Buffon never went back and corrected himself when he changed his mind; his belief in the immortality of species that is implicit in the above statement would not last.

The importance of Buffon's work was that it contained both scientific data and generalizations based on the data. Not that he ever had enough data. An example of collecting his own data was, that in trying to protect tree seedlings in his nursery, he set traps for mice and was surprised at the results (Buffon 1749–1789, VII:329, English 1780–1785, IV:288)

> *I desired all the mice that were caught by the traps to be brought to me, and found, with astonishment, that above 100 were taken each day, from a piece of ground consisting only of about 40 French arpents* [one arpent = 13–20 ha]. *From the 15th of November to the 8th of December, above 2000 were slain in this manner. Their numbers gradually decreased till the frost became severe, when they retire to their holes, and feed upon the magazines they have collected. It is more than 20 years since I made this trial, which I always repeated when I sowed tree-seeds, and never failed to catch vast quantities of these mice.*

He may have thought that the reproductive rate of the field-mice was great enough to account for all caught, but a reduction of their numbers by his traps may have led to an influx of others from farther away.

The discovery of fossil bones of elephants raised the possibility that species might become extinct. By 1761 Buffon concluded that Siberian mammoth bones were the remains of an extinct species. Yet the next year, his colleague Jean Louis Marie Daubenton (1716–1800) argued that possible differences due to age, sex, and climate might explain the differences between those bones and Indian elephant bones, and Buffon backed down and assured readers in 1764 and 1765 that species are immutable and immortal. But in 1766 he abandoned his claim for their immutability and by 1778, when he published his greatest memoir, "Des Epoques de la Nature," he had also abandoned his claim for the immortality of species (Egerton 1967:200–203). Hoquet (2005:453–732) argues that Buffon opposed natural theology's basic argument, that nature can reveal a rational plan by God. However, as a state employee whose works were published by the government, he could only argue this in subtle ways, such as ignoring the Book of Genesis when discussing the antiquity of the Earth.

Robert Wallace (1694–1771) was an Edinburgh minister who was friends with the philosophical and religious skeptic David Hume (Cochran 2004). In 1753 Wallace published a *Dissertation on the Numbers of Mankind*, in which he argued that the ancients were more numerous than the moderns. Hume had already published his arguments to the contrary (Hume 1752), having read Wallace's manuscript before publication. Wallace next expressed his interest in population by encouraging the first census of Scotland in 1755. The census was supervised by Rev. Alexander Webster, but "there is no doubt that the actuarial basis of the scheme was largely the work of a colleague of Webster's, the Rev. Dr. Robert Wallace, who also appears to have been deeply interested in the mathematics of population" (Kyd 1952:xiii). Having studied the past and present population, Wallace next turned to the future. The preface to his anonymous *Various Prospects of Mankind, Nature, and Providence* (1761) states that he wrote the book to show freethinkers evidences for a benevolent providence. He may not have read beforehand the manuscript of Hume's *Dialogues on Natural Religion*, since it was not published until 1779, but he had probably heard from Hume many of its arguments. Since arguing in his first book that the ancients were more numerous than the moderns, Wallace must have accepted Hume's counter-arguments, because now Wallace believed that the human population was steadily increasing and would eventually exceed the resources needed to support it (Wallace 1761:115). He hoped that some extraordinary method might be found to support the increasing population, but if not, we will just have to rely on "the superior wisdom of providence" (1761:295).

Another minister, John Brückner (1726–1804), speculated about animal populations. He was from The Netherlands, but immigrated at age 26 to England and settled in Norwich as pastor to Dutch Lutherans there (Smith 2004). His *Theorie du systeme animal* (1767) was a treatise on natural theology. Both it and the English translation (1768) appeared anonymously. Although he obtained information from a wide range of sources, his book contains few, if any, original ideas. Yet, it is an interesting synthesis. Two animal traits, reproductive capacity and predation, were underlying themes of his treatise. He began with an idea that possibly originated with the neo-Platonic philosopher Plotinos (205–270 AD), who argued that the greatest good in nature is the greatest amount of life, which could only be achieved

Fig. 5. Magnificent Frigatebird (formerly named Man-of-War Bird, *Fregata magnificens*). It steals fish from other shore birds. Drawn by George Edwards (1694–1773) and engraved by him on 1 July 1758. From Edwards 1758–1764. On Edwards, see Mason 1992.

with the existence of predators (1962:Ennead 3, chapter 2, section 15, quoted in Egerton 1967:29), and therefore predation is a good, not an evil. Brückner asked what was required to populate the world to its fullest extent? First, create a wide variety of plants that can live in different places and climates. Second, create a corresponding variety of animals to live on the plants. Third, create predators and scavengers (he did not mention parasites) to enable the greatest number of species and individuals to exist and to regulate the numbers of other species (1768:45–46). To add conviction to his justification of predation, he rhapsodized over the continuity of life (1768:66–67).

> *Such is the wonderful oeconomy of nature! Thus it is that by multiplying the species, the living substance suffers no diminution! Its very destruction serves to re-produce it! Thus does the flame of life, after it is extinguished in one class of animals, immediately re-kindle itself in another, and burn with fresh luster and strength.*

His claim that there is no diminution of "living substance" in transferring the "flame of life" from prey to predator was doubtful even at the time. Professor of medicine Santorio Santorio (1561–1636), at the University of Padua, published in 1614 *Ars de Statica medicina* (edition 2, 1615, translated into English, 1676, Italian, 1704, French, 1722, and German, 1736), which included some three decades of data on his weight before and after eating, weight of his food, his excreta, and even calculation of his perspiration (for which he invented the thermometer). His data showed there was a loss of matter in the process (Grmek 1975). The Rev. Brückner may have been unaware of this book and its relevance for understanding predation. Karl Semper in 1881 may have been first to explicitly suggest the loss of matter in predation, and Raymond Lindeman further clarified the matter (posthumously) in 1942 (Egerton 2007*b*:53, 61). Brückner did realize that predators must remain less numerous than their prey, and he rejected reports of wolves being the most numerous animal in parts of America (1768:73).

Being impressed by "Those insects whose immense swarms seem to convert the elements they inhabit into one continual web of life"(Brückner 1768:12), Brückner compiled from literature numerous examples of animal plagues. Animal plagues occurred, he stated, when carnivores were temporarily scarce. He discussed the reproductive potential of deer, rabbits, rodents, insects, and fish, remarking that the progeny of one codfish could quickly fill the oceans if none were eaten. Probably without noticing, he shifted from his claim that the greatest good is the greatest abundance of life to the position that stability in nature is more desirable than abundance of life. He described several food chains and emphasized the fact that when people try to eliminate a link in a chain, unfortunate consequences result. Like Richard Bradley (1726, II:216–217), Brückner (Brückner 1768:131–133) argued that birds in farmers' fields were after insects, not grain, and therefore they deserve protection, not persecution.

In the last few decades of the 1700s no professional naturalists appeared of the stature of Linnaeus and Buffon. Perhaps Peter Simon Pallas, who is discussed in parts 27 and 30 (Egerton 2008*a*, *b*), came close, though he did not have the great influence that they enjoyed. Instead of encyclopedic works that included population studies, amateur naturalists and scholars wrote isolated works that kept interest alive. Malthus was one of them whose work happened to be of more lasting influence than the others. If he did not stand on the shoulders of giants, he at least was the beneficiary of a lively tradition.

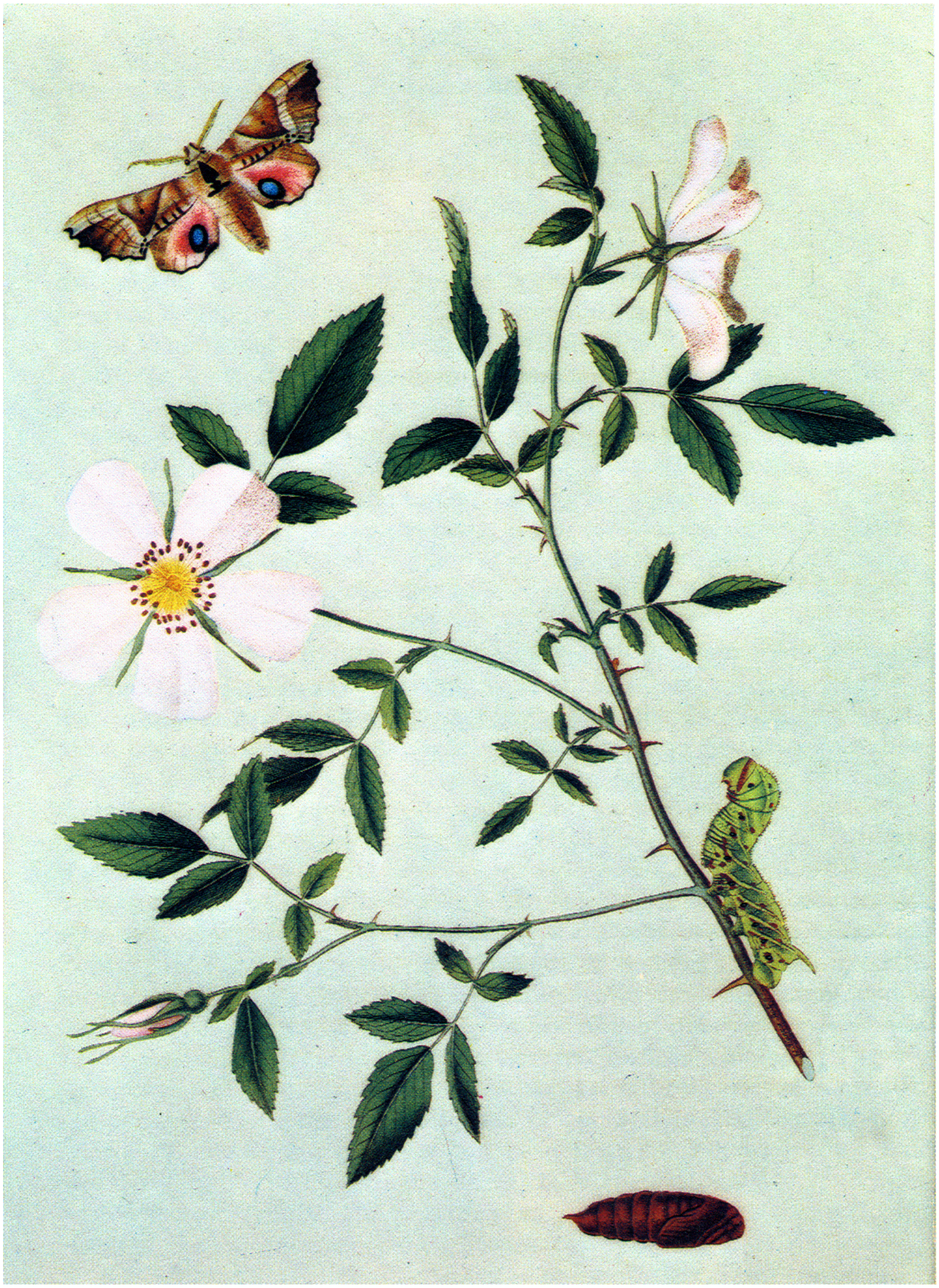

Fig. 6. American eyed hawk moth and Carolina rose. By John Abbott (1751–c.1840). Smith 1797, I: Plate 25. On Abbott, see Mallis 1971:3–9, Rogers-Price 1983, 1997, 1999, Evans 1993:93–110, Gilbert 1998, Fishman 2000:93–110.

Joseph Townsend (1739–1816) was a third British clergyman who wrote an important work on population, *A Dissertation on the Poor Laws* (1786), which first developed the thesis found in Malthus' *Essay* (1798), that supporting the poor without requiring work from them would only lead to their having more children (Egerton 1976, Sherbo 2004). Townsend supported his thesis with an interesting biological example. There is a small Chilean archipelago, the Juan Fernández Islands, 400 miles (650 km) west of Valparaiso, discovered in 1563 by Juan Fernández, who later lived on one of them (named after him during the 1700s, but now named Isla Más a Tierra) for a few years, and there he introduced goats. When the British sailor, Alexander Selkirk, lived alone on that island, 1704–1709 (inspiring Daniel Defoe's *Robinson Crusoe*, 1719), there were goats and cats, but not yet dogs. However, some time before the Spanish admiral Antonio de Ulloa published his memoirs in 1748, he reported, the president of the audience of Santiago of Chile and the viceroy of Peru introduced dogs to the islands to exterminate the goats and thereby deprive pirates of meat (Egerton 1968:235).

If the dogs had been able to eat all the goats, they then would have starved. Townsend retells and then interprets Ulloa's report (1971:38).

> *But as many of the goats retired to the craggy rocks, where the dogs could never follow them, descending only for short intervals to feed with fear and circumspection in the vallies, few of these, besides the careless and the rash, became a prey; and none but the most watchful, strong, and active of the dogs could get a sufficiency of food. Thus a new kind of balance was established. The weakest of both species were among the first to pay the debt of nature; the most active and vigorous preserved their lives.*

Since nature forces animals to scramble for food—Townsend's foreshadowing the struggle for existence of Charles Darwin (1859: Chapter 4)—the poor, he argued, should do likewise.

Following Townsend's anticipation of one key Darwinian idea in 1786, Gilbert White anticipated another one in 1789. As explained in part 26 (Egerton 2007*d*:388–389), White was keenly interested in the natural history of swifts and swallows. He mistakenly lumped them together as *Hirundines*, even though a naturalist whom he admired, Giovanni Antonio Scopoli, had in 1769 placed them in different genera. In *The Natural History and Antiquities of Selborne*, White explained the life history of swifts (in letter 21 to Daines Barrington, 28 September 1774), noting that they lay only two eggs and raise just one brood a year, whereas swallows lay four to six eggs and usually raise two broods a year. In letter 39 to Barrington (13 May 1778), White reported that he found eight pairs of swifts nesting at Selborne every year, and since they produced sixteen young per year, he wondered "What becomes annually of this increase…?" Seventy years later, Darwin (1859: Chapter 3) answered that question.

William Smellie (1740–1795) was a successful Edinburgh printer who, while an apprentice, took courses at the University (Brown 2004). He translated into English both Buffon's general natural history (9 volumes, 1780–1785) and his natural history of birds (9 volumes, 1792–1793). Those projects perhaps inspired him to write his own *Philosophy of Natural History* (2 volumes, 1790–1799, with later reprintings of volume 1). Although he lacked Richard Bradley's first-hand experience studying nature, and his volumes lacked illustrations, his work was somewhat similar to Bradley's *Philosophical Account* *of the Works of Nature* (1721). Smellie's was more detailed, but focused mainly on animals, with an occasional nod to plants. There was much in his book that relates to animal populations (Egerton 1967:221–225), but there was little, if any, originality in either his facts or his conclusions. His explanation for the necessity of predation seems to echo Brückner and Townsend (1790:391)

> *The hostilities of animals, mankind not excepted, give rise to mutual improvement. Animals improve, and discover a superiority of parts, in proportion to the number of enemies they have to attack or evade. The weak, and consequently timid, are obliged to exert their utmost powers in inventing and practicing every possible mode of escape. Pure instinct powerfully prompts; but much is learned by experience and observation. Rapacious animals, on the contrary, by frequent disappointment, are obliged to provide against the cunning and alertness of their prey. Herbivorous animals, as they have little difficulty in procuring food, are proportionally stupid; but they would be still more stupid, if they had no enemies to annoy them.*

Fig. 7. Erasmus Darwin in 1770. By Joseph Wright. Darwin College, Cambridge University.

Smellie doubted that universal peace would lead humans to exceed their ability to provide food for their expanding population (1790:394), as Wallace had feared.

Erasmus Darwin (1731–1802) was one of the most respected English physicians of his time (Garfinkle 1955, Cohen of Birkenhead 1971, McNeil 1987, 2004, King-Hele 1999, Darwin 2003, Smith and Arnott 2005), and a founding member of the Lunar Society (so named because it met on the days of a full moon so members could see their way home at night) about 1765; it met in Birmingham (Schofield 1963, Uglow 2002). During the French Revolution, Darwin was a political radical when most of his countrymen were very conservative. Despite a busy medical practice, he was a productive author of books on medicine, botany, and zoology. He was influenced by Buffon and Linnaeus, but it was the gift of fossil bones that turned his thoughts by 1770 to evolution (King-Hele 1999:297). His contention that all animals originated from "a single living filament" (Darwin 1794:499, 1974) was more comprehensive than any speculations by Buffon or Linnaeus.

Darwin argued that the metamorphosis of insects and frogs during their maturation was evidence of their species histories (Darwin 1968:82–97, Harrison 1972, Bowler 1989:81–82). He was unsure

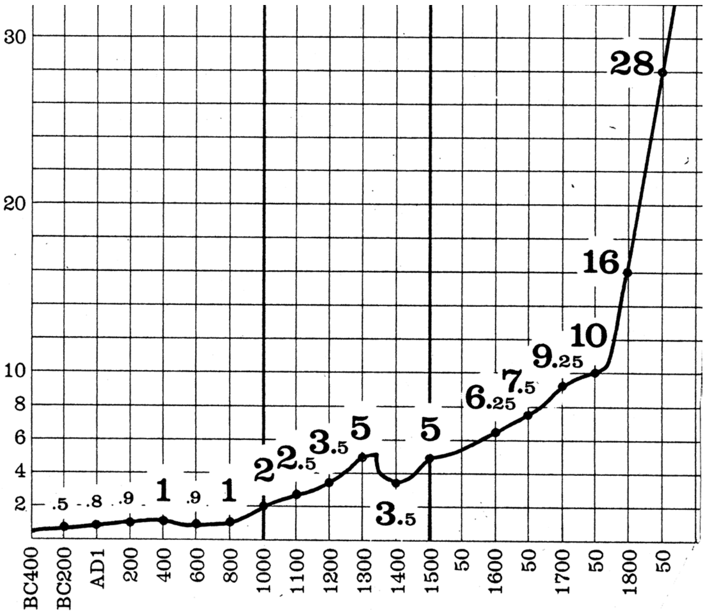

Fig. 8. Population growth in British Isles until 1850. McEvedy and Jones 1978:49. It grew more rapidly than Malthus realized. Britain had no regular census until the 1800s.

whether fossils represented extinct species or species that had greatly altered over time. Although aware of conflict in nature, he emphasized male competition for mates (Darwin 1794–1796, I:503, 1974)

> *As air and water are supplied to animals in sufficient profusion, the three great objects of desire, which have changed the forms of many animals by their exertions to gratify them, are those of lust, hunger, and security. A great want of one part of the animal world has consisted in the desire of the exclusive possession of the females; and these have acquired weapons to combat each other for this purpose, as the very thick, shield-like horny skin on the shoulder of the boar is a defence only against animals of his own species, who strike obliquely upwards, nor are his tushes for other purposes, except to defend himself, as he is not naturally a carnivorous animal.*

He gave similar arguments for stags, and he saw this struggle as leading to the improvement of the species (1794:528–529, 1974). Darwin's evolutionary ideas made little, if any, impression on his contemporaries, but they would be closely studied by his grandson, Charles.

On the practical side, in *Phytologia* (1800) Erasmus Darwin followed the examples of Leeuwenhoek, Bradley, Réaumur, de Geer, and Linnaeus in showing how knowledge of life histories could be used to control agricultural pests. He wondered if, in the previous half-century, water rats had extirpated house rats in England. He suggested that water rats could be controlled by poisons and by altering places where they lived: removal of high grass and weeds around the edge of fish ponds could cause these rats to desert the ponds (1800:368). He was also an early advocate of biological controls of pests (Riley 1931). He thought that parasites might be introduced to control both aphids and rats. He learned from

Réaumur (1734–1742, II: Memoir 9) that aphidivorous flies deposit eggs near aphids, and their larvae suck juices from aphids. He recommended collecting these eggs before winter and placing them in spring on fruit trees one wanted to protect. He read in the American Philosophical Society's *Transactions* that tapeworms limit the numbers of American water rats. One could introduce those rats into Britain and infect native rats (Darwin 1800:356, 583).

Thomas Robert Malthus (1766–1834) had a very liberal, somewhat radical father, and his early education tended in that direction. However, he was influenced by the conservative backlash to the French Revolution and became a clergyman (James 1979, Petersen 1979, Winch 1987, Williams 2000, Pullen 2004). Prime Minister William Pitt in 1796 had introduced an amendment to the poor law to allow larger payments for larger families (Bonar 1924:29). Malthus' most famous book, *An Essay on the Principle of Population* (anonymous, 1798), was an influential argument against church and state support of the poor without a work provision. It is widely assumed that Malthus shared Wallace's worry that population growth would eventually become a difficult problem. After all, the English population was growing rapidly (Fig. 8).

However, this assumption is based upon the fact that many more people discuss Malthus than read him. His Chapter 8 heading states: "Mr Wallace—Error of supposing that the difficulty arising from population is at a great distance." For Malthus, the population problem is always a problem, since population tends to increase at a much faster rate than food production. This is the point of his famous statement in Chapter 1 that "Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio," a geometrical ratio being 1, 2, 4, 8, 16…, and a arithmetical ratio being 1, 2, 3, 4…

His book is a testimony to the excellence of his education, for his thesis is very logically and clearly presented. That, however, did not prevent it from becoming one of the most controversial books ever published. Philip Appleman's Norton Critical Edition (1976) includes a good selection of both background sources (Hume, Wallace, Adam Smith, Condorcet, Godwin) and subsequent commentaries. Karl Marx, among others, complained about the lack of documentation of Malthus' claims about the geometrical and arithmetical ratios (Meek 1954). In subsequent editions (to which he added his name), Malthus did introduce more data than in the first edition, but he never changed his argument about ratios, in which his information on population came from America and his information on agricultural increase came from England (1798, Chapter 2, but shifted into Chapter 1 in later editions). In a valid statistical argument, both data must come from the same region. That he violated this statistical requirement apparently escaped his critics' notice.

Malthus' argument that the American population doubled in 25 years may have come indirectly from Benjamin Franklin's essay, "Observations concerning the Increase of Mankind" (1755, 1987:367–374). Since Malthus cited no source for this figure in the first edition, he probably had none to cite. Since he did cite Franklin's essay in the second (1803) and later editions, he must have learned of it between 1798 and 1803. However, a point of Franklin's essay was that since America had abundant resources and a small population, its population grew much faster than Britain's did. Franklin gave no indication that America had any trouble feeding this rapidly growing population. The use Malthus made of Franklin's essay was merely to document the rapid growth of America's unchecked population growth. When he discussed increase in food production, he turned to Old World populations.

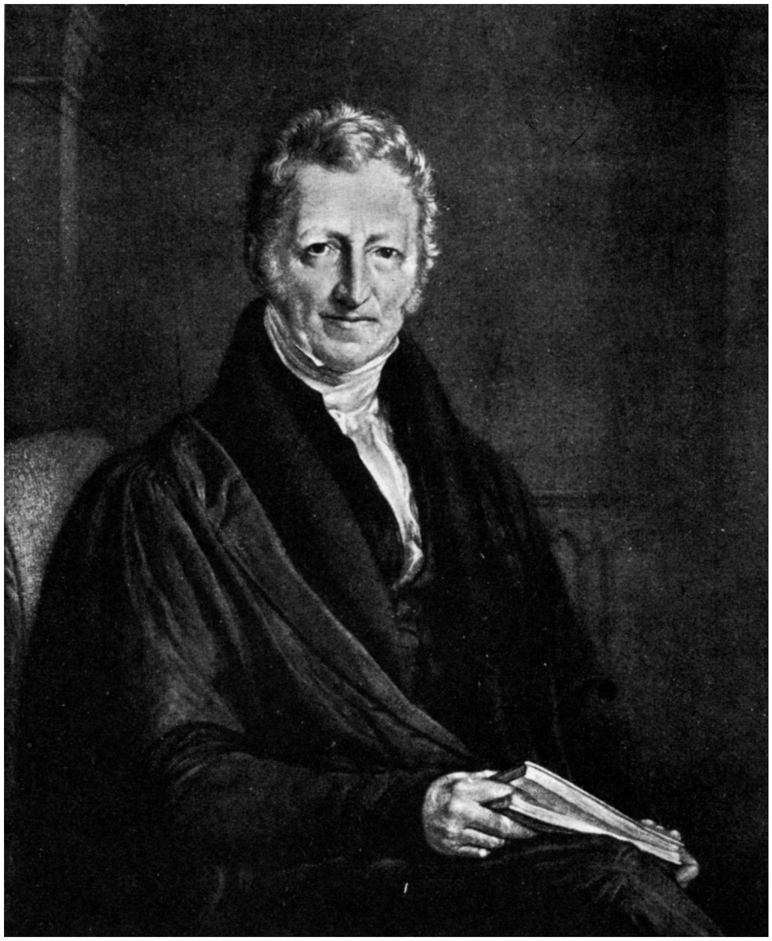

Fig. 9. Thomas Robert Malthus, by John Linnell, 1833. Bonar 1924: frontispiece.

According to Malthus, because of population pressure, there is in human societies a "struggle for existence" (Malthus 1798: Chapter 3). If welfare without work was denied to the poor, they would have to practice sexual restraint or suffer the consequences of not doing so, if they produced more offspring than they could feed. His argument never achieved a consensus in Britain or elsewhere (Hall 2000), but it was nevertheless quite influential. Controversy persisted partly because statistical data were not readily available. The British Parliament had defeated a bill for a regular census in 1753 because it seemed "totally subversive of the last remains of English liberty" (quoted in Buck 1982:32). The United States Constitution (1787) established the first regular census (every decade) in the world, beginning in 1790 (Alterman 1969:164), which was no help for Malthus writing in 1798, since a trend in population growth could only be established after more than one census.

During the 1700s there was progress in collecting and interpreting data on animal populations, but no general theory of population dynamics emerged. Leeuwenhoek and Dodart pioneered calculations of theoretical rates of increase for various species, and such calculations became a popular theme among authors of natural histories. However, there was little attempt to compare theoretical rates with actual rates and to explain the differences. Réaumur noted that it was easier to explain why insect plagues occurred than why they did not occur more often. Knowledge of predation, parasitism, and food chains increased. Awareness of what we call ecological or niche diversity diverted attention from competition between species, though late in the century Erasmus Darwin wondered if the Norway rat (actually from east Asia) had extirpated the black rat from England. Townsend and Malthus speculated about a struggle for existence among humans. The existence of fossils unlike living species led to speculations about species extinction, but Erasmus Darwin also suggested that fossil species might have evolved into different living species.

Progress made in natural history studies during the 1700s enabled separate ecological sciences—biogeography, evolutionary biology, parasitology, entomology, and limnology—to emerge during the 1800s, and also applied ecological sciences— agricultural sciences, forestry, applied entomology, and fisheries biology.

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