

Darwin's Use of the Analogy between Artificial and Natural Selection

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There are many elements to Charles Darwin's greatness, and one of them is surely the breadth of his scientific knowledge and insight, which has led many disciplines to claim him as their own – as naturalist, geologist, geographer, zoologist, botanist, psychologist, ethologist. His obituary in the *Gardener's Chronicle* referred to him as a plant physiologist who had brought botany and horticulture together, but he could equally be said to have brought biology and agriculture together.

Bagshaw's Directory of 1847 contains the surprising entry "Darwin, Charles, Farmer."¹ Whether this refers to Darwin's eighteen acres at Down(e) or derives from one of his quiet jokes is uncertain, but it suits my purpose, which is to claim him as an agriculturist. It is not my intention to underrate Darwin's debts and contributions to other disciplines; many have already enlisted him to their cause.² His theory was a watershed for controversies in so many areas³ that overemphasis of any one of them has the danger of distorting our understanding of the origin and development of Darwin's ideas. Nevertheless, the extent of his reliance on the domesticated organisms of agriculture and horticulture is often underrated, in spite of Darwin's repeated acknowledgments, so I shall examine his use of the analogy between selection under domestication and that under nature, not only for the genesis of his theory of evolution but also for its development and presentation.

In the introduction to *The Origin of Species* he writes:

At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem.

1. "Darwin Manuscripts and Letters," *Nature*, 150 (1942), 535.

2. J. C. Greene, "Reflections on the Progress of Darwin Studies," *J. Hist. Biol.*, 8 (1975), 243–273.

3. R. M. Young, "Darwin's Metaphor: Does Nature Select?" *Monist*, 55 (1971), 442–503.

Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction of the high value of such studies, although they have been very commonly neglected by naturalists.⁴

Despite the immense influence of Darwin and of his *Origin*, this forceful piece of advice remains neglected.

Writing to J. D. Hooker in 1844, Darwin referred to various other mechanisms proposed for evolution and concluded: "I believe all these absurd views arise from no one having, as far as I know, approached the subject on the side of variation under domestication."⁵ And in another letter he writes: "All my notions about how species change are derived from long-continued study of the works of agriculturists and horticulturists."⁶ In his autobiography he mentions how, following the example of Lyell, he collected "all facts which bore in any way on the variation of animals and plants under domestication and nature . . . by printed enquiries, by conversation with skilful breeders and gardeners, and by extensive reading."⁷ In a later letter to A. R. Wallace, in 1859, he wrote: "I came to the conclusion that selection was the principle of change from the study of domesticated productions; and then, reading Malthus, I saw at once how to apply this principle."⁸

Faced with these comments, historians of science could scarcely ignore the significance to Darwin of the processes of domestication, and indeed they have been more willing to accord them their due than have scientist-historians, perhaps because they are less prone to what Medawar refers to as "intellectual class-distinction" within science.⁹ In his foreword to *Evolution by Natural Selection* de Beer rather disparagingly lists "an English country gentleman's knowledge

4. Charles Darwin, *The Origin of Species*, p. 4. Unless specified otherwise, all references are to the first edition, published by John Murray in 1859.

5. Francis Darwin, ed., *The Life and Letters of Charles Darwin*, 3 vols. (London: John Murray, 1887) [hereafter referred to as L & L], II, 29.

6. L & L, II, 78; cf. II, 116-118.

7. Nora Barlow, ed., *The Autobiography of Charles Darwin, 1809-1882* (London: Collins, 1958), p. 119.

8. Francis Darwin and A. C. Seward, eds., *More Letters of Charles Darwin*, 2 vols. (London: John Murray, 1903) [hereafter referred to as ML], I, 118.

9. P. B. Medawar, *The Art of the Soluble* (London: Methuen, 1967), p. 121.

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of domestic plants and animals and their breeding" among the materials at Darwin's disposal.¹⁰ Wichler and Ghiselin largely accept Darwin's evaluation of the importance of domesticates in the development of his theory,¹¹ and the role of the analogy between artificial and natural selection has also been examined by Vorzimmer, Young, Ruse, and Schweber.¹²

In spite of Darwin's own assessment, and in spite of the lessons that might have been learned from those who earlier claimed that Darwin had overestimated the influence of Malthus on his thinking, several scholars have argued that Darwin did not formulate his theory of natural selection on the basis of an analogy between the processes of artificial selection and those in nature. Limoges¹³ claims that Darwin had no need of this analogy, and Herbert postulates that Darwin did not have "a sufficiently unambiguous notion of artificial selection to have enabled him to anticipate finding, as a mechanism for evolution, a similar process at work in untended nature."¹⁴ Kohn broadly agrees with them,¹⁵ and even Ruse now considers that Darwin was ambivalent about the analogy and that "it did not play the overwhelming role he later implied it did."¹⁶

10. G. de Beer, *Evolution by Natural Selection* (Cambridge: Cambridge University Press, 1958), p. 4.

11. G. Wichler, *Charles Darwin, The Founder of the Theory of Evolution and Natural Selection* (Oxford: Pergamon, 1961); M. T. Ghiselin, *The Triumph of the Darwinian Method* (Berkeley: University of California Press, 1969).

12. P. J. Vorzimmer, "Darwin's Questions about the Breeding of Animals (1839)," *J. Hist. Biol.*, 2 (1969), 269–281; "Darwin, Malthus and the Theory of Natural Selection," *J. Hist. Ideas*, 30 (1969), 527–542; *Charles Darwin: The Years of Controversy. The Origin of Species and its Critics, 1859–1882* (Philadelphia: Temple University Press, 1970); Young, "Darwin's Metaphor"; M. Ruse, "The Value of Analogical Models in Science," *Dialogue*, 12 (1973), 246–253; "Charles Darwin and Artificial Selection," *J. Hist. Ideas*, 36 (1975), 339–350; "Charles Darwin's Theory of Evolution: An Analysis" *J. Hist. Biol.*, 8 (1975), 219–241; S. S. Schweber, "Darwin and the Political Economists: Divergence of Character," *J. Hist. Biol.*, 13 (1980), 195–289.

13. C. Limoges, *La Sélection naturelle. Etude sur la première constitution d'un concept (1837–1859)* (Paris: Presses Universitaires de France, 1970).

14. S. Herbert, "Darwin, Malthus and Selection" *J. Hist. Biol.*, 4 (1971), 209–217; quotation on p. 212.

15. D. Kohn, "Theories to Work By: Rejected Theories, Reproduction and Darwin's Path to Natural Selection," in *Studies in History of Biology*, ed. W. Coleman and C. Limoges (Baltimore: Johns Hopkins University Press, 1980), 67–170, esp. p. 138.

16. M. Ruse, *The Darwinian Revolution* (Chicago: University of Chicago Press, 1979), pp. 172, 177.

While I agree that Darwin's appreciation of this analogy and of its explanatory power continued to grow, and that he developed it actively in the period following his reading of Malthus in the original, I hope to show further that his understanding of it prepared him for his Malthusian insight, as he told Wallace it had.

CHRONOLOGY AND DOCUMENTATION

"When I was on board the *Beagle* I believed in the permanence of species, but as far as I can remember vague doubts occasionally flitted across my mind." So wrote Darwin¹⁷ of the voyage he undertook from December 27, 1831 to October 2, 1836. Nothing in his journal of that voyage hints at evolution.¹⁸ Of the variety of observations on domesticated organisms in the journal, three may be noted.¹⁹ The one on the wild horses of the Falkland Islands was particularly concerned with checks on increases in their number. That on the wild cattle of the Falklands refuted the Linnean view that domesticated organisms quickly revert to their wild form in nature. Finally, there is a perceptive comment on inherited instincts in domesticated animals, inspired by the behavior of birds on the Galapagos Islands and foreshadowing Darwin's later interests.

During the voyage of the *Beagle*, however, several seeds of doubt were sown which germinated in the following year. Darwin noted in his other journal, his "little diary," for 1837: "In July opened first

17. ML, I, 367.

18. Kohn, "Theories to Work By," p. 70. However, in "Darwin's Conversion: The *Beagle* Voyage and its Aftermath," (*J. Hist. Biol.*, 15 [1982], 373 n64) F. J. Sulloway has pointed out that a footnote on the geographic distribution of species on the two sides of the Andes, probably drafted in mid-May 1837, hints at a possible evolutionary interpretation. It is also notable that the first sign of Darwin's evolutionary dialogue with himself, recorded in his *Diary of the Voyage of H. M. S. Beagle* (ed. N. Barlow, Cambridge University Press, 1933) during his trip to Bathurst, was one of the few significant diary passages omitted from his published journal. Contemplating the unique character of the marsupial fauna of Australia, Darwin exclaims: "Surely two distinct Creators must have been at work"; but then, contemplating the predatory technique of the local lion ant, he decides that no two workmen would "ever hit on so beautiful, so simple, and yet so artificial a contrivance" and concludes that "the one hand has surely worked throughout the universe" (p. 383).

19. Charles Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of HMS 'Beagle' round the World* (London: Murray, 1889, ed.) pp. 191, 192, 401.

note book on 'Transmutation of Species' – Had been greatly struck from about Month of previous March on character of S. American fossils – and species on Galapagos Archipelago. These facts origin (especially latter) of all my views."²⁰ During the two and a quarter years immediately following his return to England, Darwin's ideas underwent a remarkable fermentation. He says in his Autobiography that these years "were the most active ones which I ever spent,"²¹ and the entries in his journal, his Reading Notebooks,²² and particularly in his other notebooks, document an exceptionally creative period.

The Red Notebook, edited by Sandra Herbert and largely recovered,²³ begins during the voyage of the *Beagle* and covers the first few months of Darwin's return to England, when Gould and Owen identified some of his Galapagos and South American specimens. Referring to the two South American species of ostrich and their distribution, Darwin notes: "change not progressif: produced at one blow" (p. 127) and adds on p. 130: "if one species does change into another it must be per saltum." Then on p. 133 is the entry: "Dogs, Cats, Horses, Cattle, Goat, Asses, have all run wild and breed, no doubt with perfect success. – showing non creation does not bear upon solely adaptation of animals. – extinction in same manner may not depend. There is no more wonder in extinction of species than of individual." This is the first of several notebook entries in which Darwin uses the success of domesticates in the wild to argue that perfect adaptation is not a prerequisite for either survival or extinction. The last sentence, which derived from Lyell,²⁴ is also repeated in later notebooks (B22, for instance), and even transformed into "it is a *generation of species* like generation of *individuals*" (B63).

The Transmutation Notebooks

The four Transmutation Notebooks (B–E) covering the two years from July 1837 in sequence, and the pages excised from them but since

20. G. de Beer, "Darwin's Journal," *Bull. Brit. Mus. (Nat. Hist.) Hist. Ser.*, 2 (1959), 1–21; quotation on p. 7.

21. Barlow, *Autobiography of Charles Darwin*, p. 82.

22. P. J. Vorzimmer, "The Darwin Reading Notebooks (1838–1860)," *J. Hist. Biol.*, 10 (1977), 107–153.

23. S. Herbert, "The Red Notebook of Charles Darwin," *Bull. Brit. Mus. (Nat. Hist.) Hist. Ser.*, 7 (1980), 1–164.

24. Kohn, "Theories to Work By," p. 77.

recovered, have been edited and commented on by de Beer,²⁵ while those on metaphysics and morals (M and N), and the "old and useless notes," have been edited by Barrett with a commentary by Gruber.²⁶ Of the 902 pages with notes in the four Transmutation Notebooks, Darwin excised 302 for use elsewhere; all except 86 of these have been recovered and published. Thus, Darwin averaged about 1.2 pages per day over the two years, but he wrote as many as 9 pages per day at times in September 1838, just prior to reading Malthus. An earlier burst of entries seems to have occurred in March-April of the same year, although the entries in the C notebook are not individually dated. As we shall see, these two periods were particularly germinal — the first for selection under domestication, the second for selection under nature.

The Transmutation Notebooks have been as productive for Darwin scholars as they were for Darwin himself, to judge by the number of pages he excised. Part of their fascination lies in our being able to watch Darwin gather his facts "on a wholesale scale," connect them in unexpected ways, propose generalizations from them, test these in a variety of ways, reject, refine, or transform them — or, as often happened in his wrestlings with the laws of heredity, remain unsure. A good example of the latter is provided by the changing fortunes of Yarrell's observation that hybrids of older by newer races mostly resemble the older one (B138). This opinion, which haunted Darwin as he sought to understand the laws of heredity, keeps cropping up (for instance, in B140, B171, C1, and C30); seems disposed of as imagination in C121; makes a comeback in C136, D3, and D8; is elevated to a law in D88; but queried again in D91, E35, E112, and

25. All references to Darwin's four Transmutation Notebooks (B-E) are to the page numbers indicated in the versions edited by de Beer and his colleagues, supplemented by the addenda, corrigenda, and recovered excised pages, but using Darwin's original labels (Part I = B, II = C, III = D, IV = E): G. de Beer, "Darwin's Notebooks on Transmutation of Species," Part I. First Notebook (July 1837 — February 1838). *Bull. Brit. Mus. (Nat. Hist.) Hist. Ser.*, 2 (1960), 23–73; Part II. Second Notebook (February to July 1838), *ibid.*, 2 (1960), 75–118; Part III. Third Notebook (July 15, 1838 — October 2, 1838), *ibid.*, 2 (1960), 119–150; Part IV. Fourth Notebook (October 1838 — 10 July 1839), *ibid.*, 2 (1960), 151–183; G. de Beer and M. J. Rowlands, Part V. Addenda and Corrigenda, *ibid.*, 2 (1961), 185–200; G. de Beer, M. J. Rowlands, and B. M. Skaramovsky, Part VI, pages excised by Darwin, *ibid.*, 3 (1967), 129–176.

26. H. E. Gruber and P. H. Barrett, *Darwin on Man: A Psychological Study of Scientific Creativity* (New York: E. P. Dutton, 1974).

E169. Lord Morton's "law" is another example (see B181, B198, D8, D113, D152, D165, D168, E79).

It is not only in relation to the laws of heredity that Darwin's assessment veered from one side to the other throughout the notes: the perfection of adaptation, the relation between form and function, the relation of varieties to species, the relative significance of "monstrosities" and small variations in artificial selection are topics to which he keeps returning with new observations or new interpretations of old observations. We shall see how his opinions developed in the course of the notebooks, but it is important to remember also that these notes record Darwin's continuing dialogue with himself and his unending challenge of his current views. The significance of individual entries must therefore be judged from the overall context.

Fact gathering is prominent in the early notebooks, many having been gleaned from Darwin's wide reading, others from meetings, correspondence, and conversations, in which breeders are prominent. In the later notebooks, while facts still abound, deductions and generalizations become more prominent, and their diversity and originality make exhilarating reading. All nature was of intense interest to Darwin, including observations on animal and human behavior. As he says of an entry on the curiosity of monkeys about women, "These facts may be turned to ridicule, or may be thought disgusting, but to philosophic naturalist pregnant with interest" (D139). Shades of Montaigne! Some of these ideas could hardly be discussed with his more orthodox friends, such as Lyell,²⁷ and had to be worked through in the privacy of the notebooks, whose pace ebbs and flows in relation to that of the other work he has in hand and with the state of his health. The first mention of the Transmutation Notebooks in Darwin's journal is confident enough, but of the next ten entries mentioning his species theory, seven are associated with illness and one with frittering away, as if he felt guilty about it. Did sickness free his imagination, as it has done for others, or did guilt about his species work contribute to his illness during this highly creative period of his life?

Within this period two intervals seem to have been particularly fertile, and in both of them the greatest intensity of note making preceded rather than followed Darwin's major insights. His was a prepared mind! The first, about March 1838, led to his reading the

27. See S. Herbert, "The Place of Man in the Development of Darwin's Theory of Transmutation. Part II". *J. Hist. Biol.*, 10 (1977), 155-227, esp. p. 192.

pamphlets of Sebright and Wilkinson on animal breeding,²⁸ he annotated them extensively and concluded: "Whole art of making varieties may be inferred from facts stated" (C133). The other period of intense note making was the three weeks before he read Malthus' "Essay on Population" in the original on September 28, 1838 (D134–135); during this time he referred to various strengths of "my theory" (D70, D71). Schweber²⁹ has suggested that Darwin may already have been aware of Malthus' conclusions from reading, on September 11th, 1838 (or possibly on September 8th; cf. D73), a review in the *Athenaeum* of Quetelet's book "Sur l'homme." The D notebook entries are confused by the fact that the regular sequence of dates is broken at just this critical juncture, pages 95 and 152 both being dated September 11, and pages 134 and 163–165 both being September 25. The reason for this double series of entries is unclear, but what *is* clear is that any abstract Darwin may have read did not have the impact of that "one sentence of Malthus" (D135) which brought home to him the force of *intraspecific* competition, through its focus on man, and the concept of "population" associated with its title.³⁰

Notebook B. Many of the entries in the first Transmutation Notebook (B) (July 1837 – February 1838) concern the consequences of geographic isolation, but on 19 of the 269 known pages there are references to domesticated organisms. Many, such as those on Yarrell, concern crosses between domesticated varieties and the nature of the progeny (B63, 75, 83, 123, 130, 145, 180, 262, 275). These notes bear on the crucial question of the relation between species and varieties, which Darwin had to resolve before he could be sure of his domesticate analogy. One telling thought in this context was "As man has not had time to form good species, so cannot the domesticated animals with him" (B244), a point that escaped Samuel Wilberforce in his review of the *Origin*.³¹

28. Sir John Saunders Sebright, *The Art of Improving the Breeds of Domestic Animals. A Letter to Sir Joseph Banks* (London: John Harding, 1809), p. 31; John Wilkinson, *Remarks on the Improvement of Cattle. A Letter to Sir John Saunders Sebright* (H. Barnett, 3rd ed., 1820), p. 71. Darwin's own copies of the papers by Sebright and Wilkinson are in the Cambridge University Library where, with the assistance of Peter Gautrey, I was able to consult them.

29. S. S. Schweber, "The Origin of the Origin Revisited," *J. Hist. Biol.*, 10 (1977), 229–316, esp. p. 289.

30. Ghiselin, *The Triumph of the Darwinian Method*, p. 48.

31. S. Wilberforce, "Darwin's *Origin of Species*," *Quarterly Rev.*, 108 (1860), 237; cf. L & L, II, 321–323.

Yet the difference between varieties and species may not be great. For example, "Falkland rabbit may perhaps be instance of domesticated animals having effected a change which the Fr[ench] naturalists thought was species" (B31; see also B54). The first entry on the differences between Indian and European cattle appears here (B132), another case where he eventually concluded (D65, E75) that the differences between domesticated varieties could be quite comparable with those between natural species. Even in this first notebook, therefore, he began using domesticates to throw light on wild species. Amplifying the entry in his "Red Notebook" (133), he wrote: "A Race of domestic animals made from influences in one country is permanent in another. — Good argument for species not being so closely adapted" (B130). And after considering reversion by the offspring of Negro X white crosses, he added, "Now the point will be to find whether know[n] varieties in plants do so" (B180). This quotation illustrates how Darwin not only turned to the known behavior of domesticates for clarification and confirmation of hereditary behavior, but never hesitated to use plants to illuminate observations on animals and humans. A significant example occurs on B63, where he considers the extinction of the horse, elephant, and mastodon and concludes: "They die, without they change, like golden Pippins; it is a *generation of species* like generation of *individuals*." This reference to the degeneration of golden pippin apple stocks under repeated asexual propagation recurs in several later entries, such as B72: "like golden pippins, — if produced by seed, go on, — otherwise all die." As Kohn remarks, this example came to symbolize for Darwin the concept of species senescence.³² His belief in the strength of his transmutation theory was growing, even though he could not understand all the mechanisms involved: "My theory would give zest to recent and fossil Comparative Anatomy; it would lead to study of instincts, heredity and mind heredity, whole [of] metaphysics. — It would lead to closest examination of hybridity, — to what circumstances favour crossing and what prevent it; and generation, causes of change in order to know what we have come from and to what we tend, this and direct examination of direct passages of structure in species might lead to laws of change, which would then be [the] main object of study (B228). Here was an ambitious program of work, based on intimations of a powerful theory which extended even to the relations between monkeys and men (see B214).

32. Kohn, "Theories to Work By," p. 117.

If its reach was now evident to Darwin, its mechanism was not. Many of the late entries in notebook B record the conflicting opinions of breeders of various domesticated animals on the heritability of their characters, their genetic dominance (wild/domesticated, old/recent varieties, mother/father), the results of hybridization, and so on. Faced with this confusion, Darwin's concluding *cri de coeur* is once again "In production of varieties is it not *per saltum*" (B278).

Notebook C. The second Transmutation Notebook, covering the period February – July 1838, has references to domesticates on 29 of the 229 known pages. The emphasis on geographic isolation as a mechanism of evolution in the first notebook shifts in the early part of C to frequent references to the relation between structure and habit (C33, 81, 124, 199). Notebook C opens with Yarrell's theory (C1) and continues with many references to plant and animal breeding and the nature of varieties. It is notable for Darwin's first use of the term "picking" (C17) and the concept of "selection," a word he did not use until after he read Youatt's treatise on "Cattle, their Breeds, Management and Disease" in March 1840.³³ In fact, Darwin's crucial advance through this period was his realization of the power of picking in the formation of varieties, not only of what he referred to as "monstrosities," the frequently abnormal or nonadaptive mutations preserved by horticulturists or pigeon fanciers, but also of sustained selection for much smaller changes. It was the recognition of this latter, brought home to him by reading the pamphlets of Sebright and Wilkinson, that was the prerequisite to Malthus' impact on his thought.

Darwin began to distinguish between two kinds of varieties in C4, "one approaching the nature of monster, hereditary, other adaptation." He had no doubt that the monstrosities were hereditary, although the nature of the adapted varieties is left underfined. The next relevant note is C17: "The changes in species must be very slow owing to physical changes slow and offspring not picked. — as man do when making varieties." Although the punctuation of this first entry to mention picking is confusing, Darwin seems to be drawing a contrast between the formation of varieties by picking and the change in species without picking, associated with slow changes in environmental conditions. No analogue here. The next relevant entry (C33–34) is also ambiguous, partly because its opening is missing: "2. Relation of external conditions, and of succession: the latter is most intimately

33. Cf. Limoges, *La Sélection naturelle*, p. 105.

connected with important structure, which are less obviously affected by external circumstances. These therefore will be chiefly hereditary. — If varieties produced by slow causes without picking become more and more impressed in blood with time. . .” Here Darwin seems to be saying that while those characteristics involved in the succession of species are certainly hereditary, so too may be those of adapted varieties produced over long periods without picking. How the variety changes without picking is not clear, but this entry establishes some analogy between adapted varieties and species.

The next advance is made in C52–53: “The infertility of crosse and cross is method of nature to prevent the picking of monstrosities as man does.” While this rules out any analogy between species and varieties based on monstrosities, it does not eliminate the analogy with adapted varieties established in C33–34, and it introduces the possibility of picking in nature. Moreover “picking” is used here in a positive sense, as it is in the formation of varieties, and not merely as “Nature’s broom.” However, the note goes on to discuss ways in which changes due to such picking can be limited in nature.

Note C106 then refers to “two grand classes of varieties; one where offspring picked, one where not. — the latter made by man and nature, but cannot be counteracted by man. — effect of external contingencies and long bred in.” The first class refers to varieties based on “monstrosities” picked by breeders. The second class presumably includes both adapted varieties and species, since “made by man and nature.” So Darwin is clear about his analogy between domesticates and natural species, but at this stage he considers them both not picked. Likewise in C120 he notes that Yarrell agrees with him: “picking varieties unnatural circumstance.”

All this was changed, however, by his reading the pamphlets of Sebright and Wilkinson in about March 1838. In these the influence of gradual but sustained picking within a variety and without hybridization was set forth. “Sir J. Sebright pamphlet most important showing effects of peculiarities being long in blood. Fully supported by Mr. Wilkinson . . . see mark on pages. . . Whole art of making varieties may be inferred from facts stated” (C133).

Let us look at some of the passages marked by Darwin. In Sebright’s pamphlet *The Art of Improving the Breeds of Domestic Animals*, Darwin underlined the assertion by Bakewell “that a cross was unnecessary” (p. 8), a crucial comment in focusing his attention on intraspecific selection. On p. 11 he marked Sebright’s comment: “I do not believe, that there ever did exist an animal without some defect.”

On pp. 14–15 of the pamphlet Darwin wrote a comment which has already been the subject of some difference of opinion between Ruse and Kohn and need not be considered here.³⁴ In Wilkinson's "*Remarks on the Improvement of Cattle*" (p. 4) we read:

By such procedure animals have at length been produced, so different from the generality of the stock from whence they were originally taken, that none but such as are well acquainted with these matters, could have an idea, that there existed between them the least affinity. The distinction indeed between some, and their own particular variety, has scarcely been less than the distinction between that variety and the whole species. The longer also these perfections have been continued, the more stability they will have acquired, and the more they will partake of nature itself.

Darwin marked this last sentence with double lines, as he did another on p. 32: "Both with respect to the improvement and the decline of breeds, that they are in general gradual, and proceed but slowly through several generations."

It is clear from the annotations that Darwin read these pamphlets several times, and it seems likely that they stimulated him to seek a mechanism in nature equivalent to the sustained gradual picking employed by breeders like Bakewell and Sebright. Sebright's other pamphlet, *On the Instinct of Animals*,³⁵ led Darwin to recognize that instincts were hereditary and could also be picked: "Hereditary tameness as well as wildness – cf. Sir J. Sebright. – Love of man gained and hereditary, problem solved" (C165). Darwin's confidence, indeed elation, is evident in this and other entries (such as C135). Occasional doubts about his artificial/natural selection analogue still appear (C219), but this is true even after he read Malthus (E118) and simply reflects his continuing open-mindedness.

Notebook D. The third notebook, covering the period from July 15 to October 2, 1838, contains the highest proportion of pages referring to domesticates, 39 out of 156 surviving pages, or 25 percent. It was also filled the most rapidly, at an average rate of 2.3 pages per day compared with 1.3 for B, 1.7 for C, and 0.7 for E. Many entries show

34. Ruse, "Charles Darwin and Artificial Selection"; Kohn, "Theories to Work By," note 131.

35. Sir John Sebright, *On the Instinct of Animals* (London: Gossling and Egley, 1836), p. 16.

Darwin still wrestling with the mechanism of inheritance and gathering a wealth of relevant data from all kinds of domesticates, and from crosses between wild and domesticated organisms (see D7, 48, 103, 148). Several are concerned with assessing the relative importance of selection, time, separation/seclusion, and physical conditions in the formation of varieties (D20, 23, 44, 85, 107, 108). D20 suggests that Darwin has again lost confidence in his analogy: "The varieties of the domesticated animals must be most complicated . . . scarcely any breed but what some individuals are picked out, — in a really natural breed, not one is picked out, and few even of local varieties approaches quite to wild local variety. Our European varieties must be very unnatural." In D23/4 and D44 he emphasizes the role of seclusion/isolation: "The very many breeds of animals in Britain shows, with the aid of *seclusion* in breeding how easy races or varieties are made" (D44).

Two weeks before he read Malthus, Darwin made a series of notes concerning domesticates. In D100 he notes the retention by domesticated cattle of a characteristic of their wild counterparts, and also that all the varieties of pigeon were known sixty years previously. Pigeons, cattle, ducks, sheep, and observations by Sebright, Yarrell, and other breeders fill most of the following pages, and in D107 he remarks: "When Macleay says there is no difference between 'permanent varieties' and species, he overlooks those restricted in their range by man and by art." This comment places limitations on the analogy between domesticates and wild species, but certainly does not reject it, since not all are restricted "by man and by art." A week later, having visited Loddiges Garden, he has recovered his confidence in the selection of variation given him by Sebright: "1279 varieties of roses!!! proof of capability of variation." (D118; see also D128). Five days after that entry he read Malthus; his notes recording that crucial insight (D134–135) have been amply discussed by others.

Notebook E. In the fourth notebook (October 1838 – July 10, 1839), 35 of the 162 pages extant mention domesticates. After his earlier doubts, Darwin now seems surer of the analogy between domesticates and wild species (for example, E63, 71, 136): "It is a beautiful part of my theory, that domesticated races of organics are made by precisely same means as species — but latter far more perfectly & infinitely slower. — No domesticated animal is perfectly adapted to external conditions" (E71). Note in passing that this could imply that even after reading Malthus, Darwin continued to believe

in perfect adaptation in nature, as Ospovat has argued.³⁶ Many entries about domesticates are guides to what happens in nature, and Darwin has now grasped quite firmly the view that the variations on which both artificial and natural selection work are numerous, wide, small, and "accidental" (that is, fortuitous, as in E112). Whereas in his previous notebook he was concerned about the limits to variation in domesticates such as pigeons (D100, 104), these now become the flag bearers for variation in nature: "It may be said that wild animals will vary according to my Malthusian views, within certain limits, but beyond them not, -- argue against this -- analogy will certainly allow variation as much as the difference between species, -- for instance pigeons" (E136).

While this entry indicates Darwin's post-Malthusian confidence in the "analogy," an earlier entry (E118) shows him using the analogy creatively, to explore what might happen in nature (as he did with great effect in the following years):

Varieties are made in two ways -- local varieties when whole mass of species are subjected to same influence, and this would take place from changing country: but greyhound race-horse and poulter Pidgeon have not been thus produced, but by training, and crossing and keeping breed pure -- and so in plants *effectually* the offspring are picked and not allowed to cross. -- Has nature any process analogous -- if so she can produce great ends -- But how -- even if placed on Isld. if etc. etc. -- make the difficulty apparent by cross-questioning -- Here give my theory. -- excellently true theory.

Questionnaires to Breeders

The Malthusian insight completed the broad conceptual structure Darwin required for his theory, but highlighted his need to understand the cause of variation in nature and the mechanisms of inheritance by which it was governed. So, possibly under the influence of Quetelet,³⁷ he devised a series of questions for distribution to experienced breeders. A first draft³⁸ was for discussion with Mr. Wynne, who is mentioned several times in the notebooks (B139, B141, C106, C120) -- but not

36. D. Ospovat, "Darwin after Malthus," *J. Hist. Biol.*, 12 (1979), 211-230.

37. This has been suggested by Schweber, "The Origin of the Origin Revisited."

38. See Gruber and Barrett, *Darwin on Man*, pp. 423-425.

during 1839, so the anticipated discussions with him may not have taken place. However, the printed *Questions about the Breeding of Animals*, which were probably composed in mid-March 1839 and distributed in April, received at least two replies (from R. S. Ford dated May 6 and from George Tollet on May 10).³⁹ Still, there is no evidence in Notebook E of much impact from the replies to Darwin's questionnaire, although precursors to the questions are to be seen there (for example, Q3 – p. 113, Q4 – pp. 106 and 112, Q13 and 14 – p. 79, Q18 – p. 118, Q19 – p. 113, Q20 – p. 67, Q21 – pp. 75 and 103). On the other hand, there are many notebook entries at that time about breeding and inheritance in plants, with references to the work of the Rev. William Herbert and of Andrew Knight, which may be associated with replies to a set questions to Herbert, traced by Kohn.⁴⁰ The lack of replies to his animal breeding questionnaire may have led Darwin to rely more on personal letters as a means of obtaining the information he sought.⁴¹

From Sketch to Books, Published and Unpublished

In his autobiography Darwin says: "Here, then I had at last got a theory by which to work; but I was so anxious to avoid prejudice, that I determined not for some time to write even the briefest sketch of it. In June 1842 I first allowed myself the satisfaction of writing a very brief abstract of my theory in 35 pages." It is puzzling, therefore, that Darwin did not continue with his Transmutation Notebooks in the meantime.⁴² Vorzimmer explains this by suggesting that Darwin did in fact prepare an "outline and draft" in mid-1839, when the

39. G. de Beer, *Questions about the Breeding of Animals* (1840) (London: Society for the Bibliography of Natural History, (1968); Vorzimmer, "Darwin's Questions"; R. B. Freeman and P. J. Gautrey, "Darwin's 'Questions' about the Breeding of Animals with a Note on Queries about Expression," *J. Soc. Bibliog. Nat. Hist.*, 5 (1969), 220–225.

40. Greene, "Reflections," pp. 245–246.

41. J. A. Secord, "Nature's Fancy: Charles Darwin and the Breeding of Pigeons," *Isis*, 72 (1981), 163–186.

42. Barlow, *Autobiography of Charles Darwin*, p. 120. D. Kohn, S. Smith, and R. C. Stauffer have recently shown that Darwin did in fact continue making notebook entries on transmutation until the summer of 1842. They have identified and partially reconstructed two such notebooks, referred to as the "Torn-Apart" notebooks. ("New Light on the Foundations of the Origin of Species: A Reconstruction of the Archival Record," *J. Hist. Biol.*, 15 [1982], 419–442.)

E notebook entries stop.⁴³ However, the text Vorzimmer has published, labeled "Chapter 1," deals only with "the principles of variation in animal and vegetable organisms under the effects of domesticity." Despite the importance Darwin attached to that topic, he would certainly not have equated it with his theory. The draft does not include the term "natural selection," which Vorzimmer (p. 206) uses as evidence of its date. But since the subject was not dealt with, there is no reason why Darwin should have used the term. On the other hand, he uses the word "selection" freely (as on p. 213), a word he did not substitute for "picking" until after he read Youatt's pamphlet on cattle in March 1844,⁴⁴ a fact that weakens Vorzimmer's case for an 1839 date.

The next steps in the sequence are, therefore, the "Sketch" of 1842 and the "Essay" of 1844. In his journal Darwin records on June 15, 1842: "During my stay at Maer & Shrewsbury (5 years after commencement) wrote pencil sketch of my Species theory."⁴⁵ The Sketch, like the Essay and the *Origin*, begins with variation under domestication; domesticates are used so frequently throughout the text to illustrate or extend the argument that individual quotations can give no idea of how central the domesticate/species analogy is to Darwin's presentation.⁴⁶

Quite early in the Sketch Darwin considers "whether there are any natural means of selection, and . . . the far more important point whether the characters and relations of animated beings are such as favour the idea of wild species being races descended from a common stock, as the varieties of potato or dahlia or cattle having so descended" (p. 46). Note Darwin's emphasis on the latter as "far more important" than whether there are natural means of selection. As in the *Origin*,

43. P. J. Vorzimmer, "An Early Darwin Manuscript: The Outline and Draft of 1839," *J. Hist. Biol.*, 8 (1975), 191-217; see also Herbert, "The Red notebook," p. 28.

44. Limoges, "La Sélection naturelle," p. 105.

45. De Beer, "Darwin's Journal." Kohn, Smith, and Stauffer, "New Light," have recently reconstructed the sequence of drafts by Darwin of his "Sketch" and "Essay." In doing so, they identify the draft published by Vorzimmer ("An Early Darwin Manuscript") as Chapter I of Draft C of the "Sketch," which became the original version of Chapter 1 of the 1844 "Essay."

46. All references to Darwin's "Sketch" of 1842 and his "Essay" of 1844 refer to the relevant page numbers in the versions published by de Beer, *Evolution by Natural Selection*. The Sketch is given on pp. 41-88 and the Essay on pp. 91-254.

Darwin uses his knowledge of domesticates to elucidate many parts of his overall argument, such as variation in instincts (pp. 54–55), early development (p. 79), and even geographic distribution by clever use of the analogy (pp. 67–68) in a way not employed in the *Origin*.

Between February 13 and April 23, 1844, Darwin's journal records: "In intervals & previously slowly enlarged & improved pencil sketch . . . of Species theory." By July 5 this had been enlarged to about 230 pages, which he arranged to have copied and which he asked Emma to publish in the event of his death, believing it to be "a considerable step in science."⁴⁷ Like the Sketch and the *Origin*, the Essay begins with variation under domestication and the principles of selection and employs the domesticate/species analogy to good effect throughout, with some telling new examples, for instance in relation to classification; these lead to a concluding passage (p. 215) used in the *Origin*. According to de Beer, the *Origin* was elaborated from the 1844 Essay "without much novelty of principle."⁴⁸

Why, then, did Darwin wait another fifteen years before publishing his theory? Remember, first of all, his own autobiographical comment that he now had "a theory by which to work." His notebooks make it clear that he had identified many weak spots that required further support and a number of problems that needed resolving before his theory was likely to convince many, and the progressive exploration and solution of these can be seen by comparing the Sketch, the Essay, and the "Big Species Book."⁴⁹ Some parts of the argument, such as geographic aspects, instincts, and sexual selection become more strongly developed, while others, especially unconvincing parallels, are dropped. Moreover, after 1844, when Robert Chambers published his *Vestiges of the Natural History of Creation*, Darwin would have been acutely aware that only a well-documented and closely argued presentation would do. Darwin also foresaw how pervasive the impact of his theory would be, and what opposition it might arouse, so he

47. Ibid., p. 35.

48. Ibid., p. 26; cf. also Ruse, *The Darwinian Revolution*, p. 184. The opinion expressed by de Beer is thoroughly challenged by Dov Ospovat in *The Development of Darwin's Theory: Natural History, Natural Theology, and Natural Selection, 1838–1859* (Cambridge: Cambridge University Press, 1981).

49. R. C. Stauffer, ed. *Charles Darwin's Natural Selection – Being the Second Part of His Big Species Book Written from 1856 to 1858* (Cambridge: Cambridge University Press, 1975), p. 692; cf. R. J. Richards, "Why Darwin Delayed, or Interesting Problems and Models in the History of Science," *J. Hist. Behav. Sci.*, 19 (1983), 45–53.

wanted to establish his credentials in all relevant areas and anticipate all major objections. He had plenty of other work in hand; some, like his study of barnacles, was useful to the development of his theory. But during this period he was probably as much concerned with *how* to present his “one long argument from the beginning to the end” as with *what* to present.

Ten years after writing his 1844 Essay he was ready to begin again. On September 9, 1854, he recorded in his journal, “Began sorting notes for Species theory” and, on May 14, 1856, “Began by Lyell’s advice writing Species sketch.” The first two chapters, on variation under domestication – about 200 pages in all – were completed by October 13, 1856, and he progressed steadily through the subsequent chapters, completing the piece on natural selection by March 31, 1857.

By June of the following year he was well on the way when he received A. R. Wallace’s letter and manuscript, “On the tendency of Varieties to Depart Indefinitely from the Original Type.” What happened then needs no recounting here. As a result, Darwin immediately began writing what he referred to in his journal as “Abstract of Species book,” that is, *On the Origin of Species*, first published on November 24, 1859. Six weeks later, after preparing the second and third editions of the *Origin*, he recorded in his journal that he “began looking over MS for work on Variation.” Thus he immediately put into effect the strategy he had mentioned in a letter to Huxley “to bring out several volumes in detail – and I shall begin with domestic productions,”⁵⁰ and, as he wrote to Lyell in 1860, “to show that I have not been quite so rash as many suppose.”⁵¹

The two volumes of *The Variation of Animals and Plants under Domestication* were first published on January 30, 1868. After working on *The Descent of Man* and *The Expression of the Emotions in Man and Animals*, Darwin prepared the sixth and final edition of the *Origin* in the latter part of 1871. Four years later he prepared the second edition of *Variation*, in the introduction to which he gave a succinct final account of “natural selection,” and in the concluding remarks of which he took the opportunity of answering various criticisms of the *Origin*, to which he referred readers of his autobiography.

No other sections of the Big Species Book were ever worked up for publication by Darwin, which indicates, I believe, the significance he attached to the presentation in full of his findings on domesticated

50. M.L., I, 131.

51. L & L II, 318.

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organisms. *Variation* is over 300,000 words long, whereas the comparable section in the *Origin* is only 15,000 words, as it is in the 1844 Essay, and only 1,000 words in the Sketch of 1842.

ORIGENESIS

The origins of the *Origin* have been amply visited and revisited.⁵² There were many key elements to be grasped, and the order in which Darwin grasped them was important, because others had recognized several of the elements yet missed the overall significance. Here I shall be concerned only with how Darwin used his knowledge of domesticated organisms.

"A Constant Principle of Change"

The evidence that first suggested to Charles Darwin that species might not be immutable was acquired during the voyage of the *Beagle*; specifically, various South American fossils he collected, the finches and tortoises of the Galapagos Islands, the marsupial fauna of Australia, and the floras of islands visited during the latter part of the voyage. The theme of change is evident in the earliest entries in Darwin's notebooks, but shifts from a "tendency to change" in B16 and B20 to something more potent by B63, where we read "They die, without they change." By C53 Darwin is referring to "the principle of incessant change," and similar phrases are used thereafter. The phrase "a constant principle of change" occurs as an annotation by Darwin on page 32 of his copy of Wilkinson's pamphlet, and a similar phrase is written on page 11 of his copy of Sebright's pamphlet. In fact, although domesticates did not lead him to this view in the first place, they certainly increased his confidence in it and helped him to develop it, particularly to focus on intraspecific change. The entries on pages B63 and C53, and many others in the early notebooks, concern domesticates.

The proposition of change frequently raised the question of intermediate forms: "Opponent will say: show them me. I will answer yes,

52. For example, S. Smith, "The Origin of 'The Origin' as Discerned from Charles Darwin's Notebooks and His Annotations in the Books He Read between 1837 and 1842," *Adv. Sci. (London)*, 16 (1960), 391-401; Vorzimmer, "Darwin, Malthus"; Young, "Darwin's Metaphor"; Herbert, "Darwin, Malthus, and Selection" and "Place of Man"; Ruse, "Charles Darwin and Natural Selection", Schweber, "Origin of the Origin Revisited"; Kohn, "Theories to Work By"; Sulloway, "Darwin's Conversion."

if you will show me every step between bull Dog and greyhound" (B217); cattle replaced dogs in later versions of this argument in the Sketch (pp. 62 and 72), the Essay (p. 204), and the *Origin* (p. 298).

Closely related to the question of immutability of species was that of perfect adaptation. Limoges and others have argued that rejection of this concept was a crucial early step.⁵³ This has been queried by Ospovat,⁵⁴ but here we are concerned with Darwin's thoughts on domesticates. Although there were times when Darwin thought that domesticates were closely adapted (see C175, also C66), for the most part he did not. In his first notebook he used this opinion to argue that wild species might also not be closely adapted (B130). However, the implication of many later entries is that species are formed "more perfectly and infinitely slower" than varieties, whereas "no domesticated animal is perfectly adapted to external conditions" (E71). As Darwin put it in his 1842 Sketch: "Man selects only what is useful and curious — has bad judgement, is capricious — grudges to destroy those that do not come up to his pattern . . . does not select those best adapted to the conditions under which the form lives, but those most useful to him."⁵⁵ However, the last Transmutation Notebook records an important insight: "In the place where any species is most common, we need not look for change, because its numbers show it is perfectly adapted; it is where few stray ones are that change may be anticipated, & thus fresh creation" (E122). The second half of this note clearly implies that Darwin recognized that adaptation would be less perfect at the margin of distribution of a species, and that was where natural selection could lead to change. The first words of the 1842 Sketch extend this theme; it is an area where Darwin's thinking underwent considerable further development, as is evident from his Big Species Book. Here too, insights from domesticated plants were important. As a result of Herbert's work on horticultural plants, Darwin realized that plants often live in sterile soils or dry conditions — not because they prefer those conditions, but because there they can "get a poor livelihood in peace and quiet."⁵⁶

53. Limoges, "La Sélection naturelle"; cf. Kohn, "Theories to Work By."

54. Ospovat, "Darwin after Malthus" and *Development of Darwin's Theory*.

55. De Beer, *Evolution by Natural Selection*, p. 43; cf. Kohn, Smith, and Stauffer, "New Light," p. 431.

56. Stauffer, *Charles Darwin's Natural Selection*, p. 195.

The Power of Selection as an Agent of Change

Darwin's recognition of the power of selection in changing organisms was almost entirely due to what he learned of plant and animal breeding. Simple as this may seem now, it involved a bold and brilliant step, namely comprehending that he could use the facts and insights of breeding to understand species in nature. Sir Walter Raleigh and others had previously made this assumption, but the belief had grown during subsequent centuries that domesticated varieties were quite unlike wild species, being much more variable as a result of better nutrition and care and liable to revert in its absence. Linnaeus was firmly of this view.⁵⁷

As we have seen, Darwin thought domesticates were less perfectly adapted than wild species; we have also noted how unsure he was of the validity of using domesticates as a guide to nature. In part this was because Darwin was aware that some domesticates, such as showy horticultural plants, pigeons, and dogs, involved a perversion of structure, reproduction, or instincts (B197), leading to what he frequently referred to as monstrosities. These had to be maintained by picking, and Darwin recognized that such varieties were not like species in nature — witness his comment, “picking varieties unnatural circumstance” (C120, see also C53). Given the famous aphorism of Linnaeus, Darwin's entry on B278, “In production of varieties is it not per saltum,” clearly indicates that early in 1838 he was dubious about comparing such varieties with species. But over the next few months he began to differentiate between varieties based on monstrosities and those developed by patient, consistent selection over a long period. He grouped the latter, and old land race varieties, with species in nature in many later entries. He notes: “Mr. Herbert does not seem to recognize any difference in crossing between varieties and species” (E141). He became more confident about making such comparisons: “If nature had had the picking she would make such a variety far more easily than man, — though *man's practised* judgement even without time can do much” (E63).

The analogy between artificial and natural selection was crucial to Darwin's recognition of the mechanism of change in nature. Comparing selection under domestication with that in nature, whether in the 1842 Sketch, the 1844 Essay, or the *Origin*, Darwin commented that breeders were often loath to destroy the types they did not want;

57. Wichler, *Charles Darwin*, p. 40.

nevertheless, he knew that successful breeders sometimes practiced quite ruthless selection. As one British peer said of his greyhounds, "I breed many and hang many." Such lordly sangfroid probably helped Darwin to recognize the full power of selection.

The analogy with domesticates may also have played a major role in Darwin's recognition of the importance of sexual selection. The use of only a few males (Sketch, p. 48), and the importance attached to selection for "type" and beauty, may well have led Darwin to look for some analogous process in nature and thereby recognize the significance of sexual selection, which Ghiselin regards as "Darwin's most brilliant argument in favour of natural selection, of which it is a corollary. . . Sexual selection has much in common with artificial selection and can almost be treated as a variant of it."⁵⁸

Darwin's knowledge of breeding was also crucially important to his recognition of the "force of inheritance," for instincts and internal characters as much as for more obvious ones, even though he did not solve the mechanisms of inheritance as he had hoped to do. Nevertheless, the enormous effort he made to understand them resulted in his being able to write in both the *Origin* and *Variation* a succinct and workable account of the behavior of inherited characteristics. After all, seventy more years were to pass before the mechanisms of inheritance operative in evolution were adequately understood. But Yarrell, Sebright, Wilkinson, Youatt, Knight, Herbert, and many other breeders helped Darwin to understand how many characters were strongly inherited. Just as Bakewell and Sebright differed on the relative importance of crossing and selection, so Darwin fluctuated in the significance he attached to hybridization as a source of variation. For example, in the 1844 Essay he emphasized crossing as "a most copious source of new races" (p. 100) and "a most powerful engine, especially with plants" (p. 101), whereas by the time he wrote the *Origin*, he had acquired extensive experience in the breeding of pigeons⁵⁹ and emphasized selection rather than crossing (*Origin*, p. 20).

Related to that question was another, of crucial importance to the argument of the *Origin*. This concerned whether the many varieties of each domesticate descended from one or many different wild stocks. In the Essay he favored "the probability of most of our domestic animals having descended from more than one wild stock" (p. 105).

58. Ghiselin, *The Triumph of the Darwinian Method*, pp. 215 and 218.

59. Secord, "Nature's Fancy."

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In the *Origin*, on the other hand, after agreeing that several wild species of dogs and cattle may have been tamed, he concentrated on pigeons, concluding that they had all descended from the wild rock pigeon (p. 23), a persuasive argument for the power of selection.

A comparable and related shift is evident in his views on the limits to variation and selection. In his third Transmutation Notebook he records: "It certainly appears in domesticated animals that the amount of variation is soon reached — as in pigeons no new races" (D104). But by the time he wrote the Sketch, in 1842, he concluded that "it is impossible to say we know the limit of variation" (p. 58), an opinion repeated in the Essay: "It seems impossible to assign any limit to the complexity and beauty of the adaptive structures, which *might* thus be produced: for certainly the limit of possible variation of organic beings, either in a wild or domestic state, is not known" (p. 242). Earlier in the Essay Darwin said that most authors assume there is a limit to variation in nature, "though I am unable to discover a single fact on which this belief is grounded" (p. 134). Here then is another area in which Darwin's study of domesticated organisms had a profound effect on his understanding of evolution. Moreover, without the breeders' conviction about the strength of inheritance, Darwin's theory could hardly have been developed: without it, selection would have been of little avail, however wide the variation.

Natural Selection

The widespread Paleyan belief in the perfect adaptation of species in nature was coupled with the view that wild organisms did not vary, and just as it took Darwin many years to shake off the former belief, so it did the latter also. In his second notebook he refers to "absence of variates in a wild state" (C176). Eventually, however, he was so impressed by the variation evident in most domesticated species that he considered, by analogy, that wild species must also vary considerably (E136). The Sketch of 1842 opens with variation under domestication, after which Darwin writes: "Let us see how far above principles of variation apply to wild animals. Wild animals vary exceedingly little — yet they are known as individuals" (p. 43) and "Nature's variation far less, but selection far more rigid and scrutinizing" (p. 48). Essentially the same view is taken in the Essay and in the *Origin*, the Essay making the point that the lack of variation in nature may be only apparent "as far as our senses serve" (p. 113).

It was possibly with the object of clarifying the extent of variation

in nature that Darwin undertook his detailed taxonomic study of the Cirripedia, in which, as he wrote to Hooker in 1849, "I have been struck with the variation of every part in some slight degree of every species." However, his observation of this variation in nature was undoubtedly sharpened by what he knew of variation in domesticates. As he explained to Asa Gray in a letter of June 5, 1861: "It is not that designed variation makes, as it seems to me, my deity 'Natural Selection' superfluous, but rather from studying, lately, domestic variation, and seeing what an enormous field of undesigned variability there is ready for natural selection to appropriate for any purpose useful to each creature."⁶⁰

Thus, variation was universal and was being scrutinized daily and hourly, throughout the world, by natural selection – as Darwin put it so eloquently in the *Origin* (p. 84). Or, as he wrote in his last notebook on March 12, 1839, in a passage which is clearly the precursor of the final paragraph of the *Origin*, penned twenty years later: "It is difficult to believe in the dreadful but quiet war of organic beings going on in the peaceful woods and smiling fields" (E114). This passage reveals once again the linkage in Darwin's mind between the mechanisms operating in the agricultural fields and those in the undomesticated woods.

Development of the Theory

With the help of Darwin's Transmutation Notebooks we have seen how domesticated organisms not only provided the central analogue for his species theory, but played a key role in shaping the other concepts he needed to build that theory. Their usefulness to him did not end there, however. Comparison of the 1844 Essay with the *Origin* reveals how significantly Darwin's views on certain topics developed in the interim and how he solved a number of the problems that most concerned him in 1844. So much has been written about the origins of the *Origin* in the 1837–1839 period that there is a tendency to underestimate how much Darwin's ideas developed between then and 1859.

Ruse has discussed this matter and has given some examples of how Darwin continued to make use of domesticates in developing his species theory.⁶¹ In this context, however, the *Origin* is not nearly so

60. L & L, II, 373.

61. Ruse, "Analogical Models"; also Schweber, "Darwin and the Political Economists," pp. 217–220.

useful a source as is the Big Species Book, edited by R. C. Stauffer as *Charles Darwin's Natural Selection* and published in 1975 after Ruse's analysis. The first two chapters of this book have not been located and were presumably used in the preparation of *The Variation of Animals and Plants under Domestication*. Chapter 3, "On the Possibility of All Organisms Crossing, etc.," is heavily based on observations on domesticated organisms, both plant and animal. Chapter 5, on the struggle for existence, begins with domesticates and they are used to lead into various sections of the argument, such as that on the nature of checks on increase (p. 180; see *Origin*, p. 67). The vast differences between nature and agriculture are fully recognized, "but nature raises her crops . . . with this great difference that she is not the determined enemy of any bird; insect or slug, & cares not what or how many plants overmaster the others" (p. 197).

Chapter 6, on natural selection, also refers frequently to domesticates, beginning on the first page (214; cf. *Origin*, p. 80): "If we reflect on the infinitely numerous and odd variations in all parts of the structure of those few animals and plants, on which man may be said to have experimentized by domestication" It is only after illustrating these with a wealth of additional examples that Darwin turns to nature: "See how differently Nature acts! . . . She cares not for mere external appearance; she may be said to scrutinize . . . the whole machinery of the organization. There will be here no caprice, no favouring: the good will be preserved and the bad rigidly destroyed. . . Nature will not commence with some half-monstrous & useless form. . . Nature is prodigal of time and can act on thousands of thousands generations: she is prodigal of the forms of life" (p. 224). The ensuing section on extinction (p. 226; *Origin* p. 109) and the principle of divergence (p. 227, *Origin* p. 111) also begin with domesticates, with examples of the succession and divergence of breeds, respectively, Darwin consistently uses this approach throughout his Big Species Book — that of first seeking light by looking to domestic productions, as he puts it on p. 227; but he varies his presentation much more in its abstract, as he described the *Origin*.

Chapter 7, on the laws of variation, likewise depends heavily on developing "our view, that species are only strongly marked varieties with the intermediate gradations lost" (p. 280). Again and again throughout this chapter Darwin returns to domestic varieties for guidance (examples on pp. 316 and 321).

As in the *Origin*, we then come to three chapters dealing with various difficulties posed by the theory of natural selection, in all of

which he makes use of examples from domesticates. The first (8 in *Natural Selection*, 6 in the *Origin*) deals with the problems of transition and the absence of transitional forms, which Darwin had already partially "domesticated" on pp. 262–269 of *Natural Selection*. The difficulty of accounting for neuter bees and ants particularly concerned him, but "grave as these several difficulties are, do they overwhelm out theory? Let us turn to our best guide, the process of selection by man in our domestic productions" (p. 369). Darwin's use of family selection procedures in radishes and cattle to solve this "gravest difficulty" is masterly.

Chapter 9 deals with the problems posed by hybridism. Here Darwin relies primarily on examples from plants, because of the extensive experiments by Kolreuter, Gartner, and Herbert, but also makes comparative remarks on animals. Primarily domesticates are cited in both cases. The instincts of domestic animals and their inheritance contribute material to Chapter 10 on mental powers and instincts, and serve as a preface to Darwin's consideration of animal migrations (p. 494). On the other hand, domesticates do not figure in the chapter on geographic distribution, which Darwin also completed before he received the letter from Wallace which put an end to his Big Species Book.

CONCLUSION

The central role played by Darwin's analogy between selection under domestication and that under nature has been adequately appreciated, but I have indicated how important the domesticated organisms also were to other elements of Darwin's theory of evolution — his recognition of "the constant principle of change," for instance, of the imperfection of adaptation, and of the extent of variation in nature. The further development of his theory and its presentation to the public likewise hinged on frequent reference to domesticates.

We have seen that Darwin's reliance on the analogy between domesticated varieties and wild species was a bold and original step, in light of contemporary views on the nature of domesticates. However, as Darwin undoubtedly foresaw, his reliance on the analogy created difficulties as well as solving problems, and these began with his Malthusian codiscoverer of the principle of natural selection, Alfred Russel Wallace. Wallace's paper "On the Tendency of Varieties to Depart Indefinitely from the Original Type," presented to the Linnean Society along with the first public unveiling of Darwin's theory, states:

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We see, then, that no inferences as to varieties in a state of nature can be deduced from the observation of those occurring among domestic animals. The two are so much opposed to each other in every circumstance of their existence, that what applies to the one is almost sure not to apply to the other. Domestic animals are abnormal, irregular, artificial; they are subject to varieties which never occur and never can occur in a state of nature.⁶²

Much has been made of the similarity of views of Darwin and Wallace, but this quotation surely reveals how utterly different their views were on what to Darwin was an important matter. Several critics of the *Origin* saw Darwin's reliance on the domesticates as his Achilles heel. As Young has pointed out, Samuel Wilberforce included the following passage in his attack on the *Origin*:

Nor must we pass over unnoticed the transference of the argument from the domesticated to the untamed animals. Assuming that man as the selector can do much in a limited time, Mr. Darwin argues that Nature, a more powerful, a more continuous power, working over vastly extended ranges of time, can do more. But why should Nature, so uniform and persistent in all her operations, tend in this instance to change? Why should she become a selector of varieties?⁶³

Another critic, Fleeming Jenkin, found the analogy a weakness in Darwin's theory because of the limited extent of variation in any one direction in domestic animals and plants.⁶⁴ We have already seen that Darwin had confided a similar view to his notebook thirty years earlier, but changed his mind as a result of his profound study of domesticates. De Beer's reference to "an English country gentleman's knowledge of domestic plants and animals and their breeding"⁶⁵ fails totally to recognize the originality and depth of Darwin's knowledge of domesticates.

Why did Darwin, against the currents of his time, rely so heavily

62. De Beer, *Evolution by Natural Selection*, p. 277.

63. Young, "Darwin's Metaphor," p. 471; Wilberforce, "Darwin's *Origin of Species*."

64. Fleeming Jenkin, "The Origin of Species," *N. Brit. Rev.*, 42 (1867), 277-318; reprinted by D. L. Hull (1973) in *Darwin and his Critics* Cambridge, Mass.: (Harvard University Press), pp. 305-309.

65. De Beer, *Evolution by Natural Selection*, p. 4.

on mankind's experience with domesticated organisms to shape his theory about species in nature? One reason is that only with domesticates was an approach that came close to experimental verification possible. Darwin fully realized the inadequacies of the experiment, as is emphasized by his repeated contrasting of selection under nature and selection by man. Yet the extensive experience and data of plant and animal breeders offered the only reliable base against which Darwin could continually challenge his views. As he wrote in the introduction to *Variation*, with domestication, "man . . . may be said to have been trying an experiment on a gigantic scale."⁶⁶ Given Darwin's high opinion of the quantitative work of Malthus and Quetelet (as emphasized by Schweber),⁶⁷ and his unremitting efforts to secure data by which to test his theories, it was inevitable that he should attach high significance to domesticated varieties. John Tyndall, in his Belfast address of 1874, said: "The strength of the doctrine of Evolution consists, not in experimental demonstration (for the subject is hardly accessible to this mode of proof), but in its general harmony with scientific thought."⁶⁸ Darwin would have agreed with the latter thought, but I think he would have challenged the preceding one on the grounds that long experience with domesticated varieties did provide an element of experimental demonstration. It gave him confidence in his theory, and he used his vast knowledge of artificial selection boldly and creatively.

66. Charles Darwin, *The Variation of Animals and Plants under Domestication*, 2 vols. (London: Murray, 1868); 1905 ed., p. 3.

67. Schweber, "Origin of the Origin Revisited."

68. Quoted by Young, "Darwin's Metaphor."