Darwin and His Pigeons. The Analogy Between Artificial and Natural Selection Revisited

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Abstract. The analogy between artificial selection of domestic varieties and natural selection in nature was a vital element of Darwin’s argument in his *Origin of Species*. Ever since, the image of breeders creating new varieties by artificial selection has served as a convincing illustration of how the theory works. In this paper I argue that we need to reconsider our understanding of Darwin’s analogy. Contrary to what is often assumed, nineteenth-century animal breeding practices constituted a highly controversial field that was fraught with difficulties. It was only with considerable effort that Darwin forged his analogy, and he only succeeded by downplaying the importance of two other breeding techniques – crossing of varieties and inbreeding – that many breeders deemed essential to obtain new varieties. Part of the explanation for Darwin’s gloss on breeding practices, I shall argue, was that the methods of his main informants, the breeders of fancy pigeons, were not representative of what went on in the breeding world at large. Darwin seems to have been eager to take the pigeon fanciers at their word, however, as it was only their methods that provided him with the perfect analogy with natural selection. Thus while his studies of domestic varieties were important for the development of the concept of natural selection, the reverse was also true: Darwin’s comprehension of breeding practices was moulded by his understanding of the working of natural selection in nature. Historical studies of domestic breeding practices in the eighteenth and nineteenth century confirm that, besides selection, the techniques of inbreeding and crossing were much more important than Darwin’s interpretation allowed for. And they still are today. This calls for a reconsideration of the pedagogic use of Darwin’s analogy too.

Keywords: Charles Darwin, evolution, artificial selection, natural selection, domestic breeding, pigeon breeding

Introduction

The analogy between artificial selection of domestic varieties and natural selection in nature was a vital element of Charles Darwin’s ‘long
argument’ in his *Origin of Species*. As Jean Gayon has convincingly argued, Darwin’s use of the analogy was even methodologically essential: “In fact, it is extremely unlikely that the hypothesis [of natural selection] could have been developed without this supporting evidence” (Gayon, 1998, p. 59). Darwin himself, in a letter to Asa Gray, stated that “all my notion about how species change are derived from long-continued study of the works of (¿ converse with) agriculturists & horticulturists.”¹ In his *Variation of Animals and Plants under Domestication* he presented the work of animal and plant breeders as “an experiment on a gigantic scale” that provided empirical evidence for analogous processes in nature (Darwin, 1868, vol. 1, p. 3). Or, as Hans-Jörg Rheinberger and Peter McLaughlin put it: Darwin found his “laboratory” in “the fields and stalls of England” (Rheinberger and McLaughlin, 1984, p. 357).²

The exact role of the analogy between artificial and natural selection in the development and presentation of Darwin’s theory has received ample attention from historians and philosophers of science. Historians have raised doubts about Darwin’s claim that “I came to [the] conclusion that Selection was the principle of change from [my] study of domesticated productions; & then reading Malthus I saw at once how to apply this principle.”³ For instance, on the basis of her analysis of Darwin’s notebooks Sandra Herbert concluded: “it does not seem that Darwin held 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. Rather, it would seem, the discovery of natural selection made the domestic analogy much more

¹ Darwin to Asa Gray, 20 July [1857], Burkhardt and Smith, 1985, vol. 6, pp. 431–433; see also *Darwin Correspondence Project*, http://www.darwinproject.ac.uk/entry-2125; accessed 27 September 2011.
² See also Evans, 1984, p. 140.
³ Darwin to Alfred Russel Wallace, 6 April 1859, Burkhardt and Smith, 1985, vol. 7, pp. 279–280; see also *Darwin Correspondence Project*, http://www.darwinproject.ac.uk/entry-2449; accessed 27 September 2011. A similar statement can be found in Darwin’s private autobiography: “I soon perceived that selection was the keystone of man’s success in making useful races of animals and plants. But how selection could be applied to organisms living in a state of nature remained for some time a mystery to me. In October 1838, that is, fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species” (Barlow, 1958, pp. 119–120).
Philosophers and historians of biology have produced a substantial body of literature analyzing in detail how Darwin deployed the similarities between artificial and natural selection to make his case for the power of natural selection to create new species. Several authors have argued that the analogy served to establish natural selection as a Hershellian *vera causa* in nature. Generally speaking, most commentators have concurred that the analogy was a significant element in Darwin’s reasoning, and a revisionist interpretation that argued that Darwin was *not* arguing by analogy has gained no support.5

Gayon emphasizes that Darwin did not use the analogy between artificial and natural selection as a pedagogic device, yet until the present day the familiar notion of breeders creating new varieties of animals and plants by artificial selection serves as a powerful image of how selection works and what can be achieved by it. The editors of the *Cambridge Companion to Darwin* note that textbook explanations of the theory of evolution “still often include something about the small selectional achievements of the stockbreeder in comparison with the larger outcomes of fitness differences in nature” (Hodge and Radick, 2003, p. 4). The analogy also figures prominently in popular expositions of evolutionary theory. For instance the February 2004 cover story of *National Geographic Magazine* – a spirited defence of Darwin’s theory by David Quammen – starts with beautiful illustrations of “the great analogy” to introduce the readers to the principle of evolutionary change (Quammen, 2004). In *Evolution: Education and Outreach*, a journal that aims to promote “accurate understanding and comprehensive teaching of evolutionary theory,” Ryan Gregory claims that Darwin’s “enduring analogy” remains very useful as “a means of illustrating and clarifying key points about adaptive evolution” (Gregory, 2009). And a BBC documentary presented by David Attenborough made for the 2009 Darwin commemorations includes a tour of a dog and a poultry show to demonstrate what can be accomplished by sustained selection of small individual differences (Attenborough, 2009).

In this paper I aim to show that we need to reconsider our understanding of Darwin’s famous analogy. According to the *Cambridge Companion to Darwin* “Darwin lured readers into his new ways of

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4 Other contributions to the debate on this issue include Limoges, 1970; Ruse, 1975; Kohn, 1980; Evans, 1984; Largent, 2009.

5 The revisionist interpretation was proposed by Richards, 1997. Other contributions to the discussion include Ruse, 1973; Cornell, 1984; Recker, 1987; Sterret, 2002; Gildenhuys, 2004; Alter, 2007.
reasoning by introducing this type of reasoning in the uncontroversial setting of breeding techniques’’ (Waters, 2003, p. 127). Yet as we shall see, however uncontroversial the setting may have seemed, the breeding techniques themselves were anything but uncontroversial, and it was only with considerable effort that Darwin arrived at his interpretation of how domestic varieties were produced. Furthermore he only succeeded in establishing the analogy by downplaying the importance of two other breeding techniques – crossing of varieties and inbreeding – that many breeders deemed essential, besides artificial selection, to obtain new varieties.

Part of the explanation for Darwin’s gloss on breeding practices in the *Origin*, I shall argue, was that the methods of his main informants, the breeders of fancy pigeons, were not representative of what went on in the breeding world at large. Darwin was led to think that their work was typical, or perhaps one should say that he was eager to take the pigeon fanciers at their word, as it was only their methods that provided him with the perfect analogy with natural selection. My analysis thus suggests that Darwin’s understanding of natural selection, while obviously indebted to his study of domestic breeding, in its turn served as a model for the particular angle on breeding practices he presented in the *Origin*.

For an historical analysis of how Darwin arrived at his views on domestic breeding it is of course immaterial whether or not these views are still considered as essentially valid today. From a scientific perspective their validity is not overly important either, as the analogy is no longer needed to argue the plausibility of evolutionary theory. Yet as indicated the pedagogic use of the analogy has lost nothing of its attractiveness, and biologists, teachers and popularisers still readily assume that Darwin was ‘right.’ As we shall see, however, historical studies of the development of domestic breeding in the eighteenth and nineteenth century amply confirm that, besides artificial selection, the techniques of inbreeding and variety crossing were much more important than Darwin’s interpretation allowed for. And they still are today. This calls for a reconsideration of the didactic use of the analogy too.

**Principles of Domestic Breeding**

To begin with, we need a short outline of the development of Darwin’s views on domestic breeding, based on written and other sources we know he was familiar with. It will become clear from this sketch that
these sources did not provide a straightforward exposition of tried and tested breeding techniques that Darwin might have relied upon to develop his domestic analogy. I shall concentrate on animal breeding practices, following Darwin’s example in the *Origin*.6

As appears from his Transmutation Notebooks, Darwin immersed himself in the breeding literature in the late 1830s, and several studies have explored in depth how his reading was connected to his eventual formulation of the principle of natural selection in nature.7 Camille Limoges, Michael Ruse and later historians have singled out two pamphlets on domestic breeding, by cattle and fowl breeding experts Sir John Saunders Sebright and John Wilkinson, as having been of particular importance for his understanding of artificial selection (Limoges, 1970; Ruse, 1975; Sebright, 1809; Wilkinson, 1820).8 Darwin read and extensively annotated these treatises in the spring of 1838. “Whole art of making varieties may be inferred from facts stated,” he jotted down after having studied Sebright (Darwin, 1838, p. 133; Barrett et al., 1987, p. 279).9

Sebright and Wilkinson both recommended scrupulous selection of breeding stock as an indispensable tool for breed improvement. Yet there were also differences between their views, as well as between theirs and Darwin’s as he expressed them in the *Origin of Species*. Moreover, Sebright and Wilkinson also discussed the importance of inbreeding and crossing, and no attention has so far been paid to this discussion. A closer look at their work will at the same time help to get an overview of the main issues that engaged breeders of domestic animals in the first half of the nineteenth century.

A central theme of Sebright’s 1809 pamphlet, *The Art of Improving the Breeds of Domestic Animals*, was that sustained selection of individual differences from generation to generation was an essential

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6 A simple explanation for Darwin’s preference for examples from animal breeding might be that most of his readers were familiar with the (mostly ordinary) domestic breeds he mentioned, whereas the countless varieties of cultivated plants were known only to specialists. Darwin considered his views to be equally valid for animals and plants though.

7 See note 4; see also Hodge and Kohn, 1985. For Darwin’s notebooks on transmutation see Barrett et al., 1987; they are also available online: van Wyhe, 2002, http://darwin-online.org.uk/EditorialIntroductions/vanWyhe_notebooks.html.

8 Sebright’s pamphlet and a short fragment of Wilkinson’s are reprinted in facsimile in Bajema, 1982; the original Bajema used for the Sebright facsimile is Darwin’s own annotated copy.

9 Darwin’s annotated copies of both pamphlets are in the Darwin Pamphlet Collection in Cambridge University Library. Darwin’s marginalia were published by Di Gregorio, 1990.
element of successful breeding. Firstly, selection was indispensable to counteract the tendency of domestic varieties to “degenerate”: without selection, Sebright contended, domesticates would return to their “unimproved” natural state or develop more and more defects. Secondly, selection could be used to enhance a variety’s desirable characteristics, such as “the swiftness of the race-horse, the propensity to fatten in cattle, and the fine wool in sheep” (Sebright, 1809, pp. 5–6). It is not quite clear whether or not Sebright believed that completely new breeds might be created in this way: all he said was that breeds could be greatly improved by selection. He did explicitly mention an alternative route though: new races appeared once in a while as “accidental varieties” – called ‘sports’ by other breeders, Darwin among them – that passed on their new characteristics to at least some of their progeny and could thus be perpetuated. By way of an example Sebright mentioned the sudden occurrence of a completely white pheasant (Sebright, 1809, p. 27).

A second important tool for the breeder was inbreeding, or “breeding in and in.” Here Sebright referred to the impressive results achieved by Robert Bakewell, the eminent Leicestershire farmer and breeder whose pioneering experiments in the second half of the eighteenth century provided the foundation for the new approaches to breeding that began to spread rapidly after 1800. Sebright praised Bakewell in particular for having shown that inbreeding, provided it was combined with meticulous selection, did not necessarily lead to degeneration, as many farmers and breeding experts had long believed. Another important innovation that Bakewell introduced was progeny testing, based on the idea that the quality of breeding stock should ultimately be judged on the basis of the performance of its offspring. Thus for instance Bakewell evaluated his rams by assessing the quality of the lambs they had fathered (Sebright, 1809, pp. 7–10, 28).

Without inbreeding, Sebright noted, “no one could have been said to be possessed of a particular breed, good or bad.” The reason was that a desirable new property normally appeared in only one or a few animals, meaning that these had to be bred among themselves for a number of generations in order to preserve and ‘fix’ the property and thus to create

10 Darwin, in the *Origin*, would dispute that domesticates degenerated or reverted to their wild ancestor without selection (1859, pp. 14–15). Alfred Russel Wallace was among those who believed that domestic breeds were unstable and therefore provided no analogy for natural varieties; for the discussions between Darwin and Wallace on such points, see Kottler, 1985; Gayon, 1998.

a new breed (Sebright, 1809, p. 10). On the other hand Sebright warned against very close inbreeding, as bad characteristics were as effectively passed on by inbreeding as good ones. Bakewell had gone too far in this respect, he felt, and this explained why some of the breeds he had improved tended to grow weak over time. In Sebright’s view it was inbreeding that was responsible for the tendency of domestic varieties to degenerate. Therefore constant culling of animals with defects was needed, and even then an occasional outcross with unrelated animals was needed for a breed to retain its vigor. In nature it was through constant outcrossing that degeneration was prevented. Moreover, weak individuals were destroyed by severe winters, food shortages and the like. Thus Sebright drew a parallel between artificial selection and selection in nature, yet the latter form of selection did not explain species change, as it later would for Darwin, but rather species constancy (Sebright, 1809, pp. 10–17).

Finally Sebright sounded a cautionary note with respect to a third breeding method: crossing of varieties. People seemed to believe, he wrote, that every improvement was due to a cross, when it was actually selection or the occurrence of an “accidental variety” that was responsible in many cases. He did not object to crossing per se, however. Breeders of most regional varieties of sheep might safely put Spanish Merino rams to their ewes for several generations in order to improve fleece quality, for instance. The difficulties only began when two very different breeds were crossed with the objective of combining the good properties of both in a new breed. The first generation offspring of such a cross often looked “tolerable,” Sebright wrote, yet it was “a breed that cannot be continued,” as the “mongrels” that were bred from first generation animals reverted to the parent breeds or were endowed with “the faults of both” (Sebright, 1809, pp. 17–19). 12 Here Sebright was of course describing the phenomena that would only in the early twentieth century be explained as the result of Mendelian dominance-recessive relations and recombination: the variability present in the parent stocks was masked, to a certain extent, by dominance-recessive relations in the first generation, while recombination brought it to light in the second.

Cattle breeder John Wilkinson agreed with Sebright that selection of small individual differences was a powerful tool for the improvement of domestic breeds. He came very close to stating that new varieties might be made in this way: “The distinction indeed between some [animals improved by selection] and their own particular variety, has scarcely

12 The term ‘mongrel’ was customarily used for variety crosses, ‘hybrid’ for species crosses.
been less, than the distinction between that variety and the whole species. The longer also these perfections have been continued the more stability will they have acquired, and the more will they partake of nature itself” (Wilkinson, 1820, pp. 4–5).

Wilkinson did not share Sebright’s pessimistic view of variety crossing though, and this was one of his motives for entering the discussion. He concurred that it was virtually impossible to combine the best properties of two varieties through crossing without some unwanted characteristics also creeping in. Perfection was unattainable, yet it did not follow that crossing different varieties was not useful: “it may very much be so” (Wilkinson, 1820, pp. 23–24, 28–29, 34–35).

By way of an example Wilkinson mentioned the widespread use of Shorthorn cattle for this purpose, after the breed had been improved by the Colling brothers, who had followed in Robert Bakewell’s footsteps. There “is scarcely any breed in the kingdom,” Wilkinson wrote, “where individuals have not been crossed with them” (Wilkinson, 1820, p. 41). Often, in implementing such crosses, farmers had not wanted to lose all the characteristics of their own breed and had consistently bred from carefully selected crossed animals that conformed best to their standards, in this way creating new, intermediary varieties. For instance breeders of Longhorn cattle who had crossed their animals with Shorthorns had preferred offspring that was intermediary between them and had created a new breed they called ‘half horns.’ Similarly breeders of Alderney cows, a breed that produced small quantities of extremely rich milk, had used Shorthorns to obtain a new variety that produced not only more (though less fat) milk but also better meat. It was judicious selection among the offspring that provided the key to such successful crossbreds. Wilkinson cautioned however that there were limits to what might be achieved in this way: it was useless, for instance, to try and improve the hardy and sober cattle of Scotland by an infusion of Shorthorn blood, as beefier animals could not survive the unforgiving Scottish climate and soil (Wilkinson, 1820, pp. 36–38, 42–43).

In a nutshell Sebright and Wilkinson’s pamphlets thus conveyed the main principles of the art of breeding as they were spreading among well-informed breeders in the early decades of the nineteenth century, after the example of the path-breaking work of Bakewell and his followers. Yet there was still ample room for discussion, as their writings also make clear. Furthermore, though the basic principles might be fairly simple, successful breeding required long experience and limitless

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13 For the improvement of the Shorthorn see, for instance, Youatt, 1834, pp. 226–266. See also Derry, 2003, pp. 17–47.
patience, and it was no exception that attempts to improve a breed ended in failure. Such experiences continued to fuel the discussion over breeding techniques in the early nineteenth century.

In Britain, for instance, crossing with Merino sheep was tried on a wide scale from the late eighteenth century onwards, but many farmers considered it as unrewarding. Some believed that wool of Merino quality deteriorated under adverse circumstances. Incidentally, not inbreeding was generally taken to be the main cause of this degeneration, as Sebright had claimed, but the direct influence of climate and soil. To maintain the qualities of an imported breed, it was often assumed, repeated fresh imports were needed. Bakewell, on the other hand, and Sebright after him, had argued that selection and a high standard of feeding and care prevented deterioration (Sebright, 1809, pp. 19–20, 25). In his *Sheep: Their Breeds, Management, and Diseases* of 1837, veterinarian and well-known breeding expert William Youatt documented how farmers in several European countries had indeed succeeded in preserving or even improving the Merino and its crossed offspring’s fleece by giving the animals high quality care (Youatt, 1837, pp. 157–183). English breeders however were not prepared – as Wilkinson had warned they should be – to pay the price of crossing. Meat production was important in Britain, and the Merino’s carcass quality was poor. It proved impossible to create a crossed animal that combined superior meat production with superior fleece quality. “The first crosses promised well,” wrote agriculturist David Low in his *Domesticated Animals of the British Islands*, yet “in breeding from the mixed progeny, it was found that, while the wool had become inferior to that of the Spanish stock, the hardy qualities, the goodness of form, and the aptitude to fatten, of the English breed, were impaired” (Low, 1853, p. 158).

Yet many other domestic breeds were successfully crossed with other, improved varieties. Besides Shorthorn cattle Bakewell’s renowned New Leicester sheep and John Ellmans’ equally well-known Southdown sheep, both bred for early maturing and the production of meat and fat, provide examples. Both breeds were used widely for crossing and “either superseded the pre-existing varieties, or [have] been so mingled with them in blood, as to have modified all their characters,” Low wrote (1853, p. 166). Crossing not only led to breed improvement in many local strains but also to new sheep breeds. Youatt wrote that the

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Southdowns had “penetrated to almost every part of the kingdom,” and had been used to improve countless local breeds. Bakewell’s New Leicester had played a comparable role, and Youatt even considered this the breed’s principal value (Youatt, 1837, pp. 237–238, 322–328).\(^\text{16}\) There was a similar story to be told about dogs, horses and cattle. Low mentioned a host of dog breeds that had recently been created or improved by cross-breeding (Low, 1853, pp. 700–753).\(^\text{17}\) Youatt found that all types of heavy draught horses in Britain, such as the Scottish Clydesdale, had been improved by crosses with horses from the Low Countries. And a cross with a Galloway had been at the basis of the improvement of the Shorthorn (Youatt, 1831, pp. 40–41; 1834, p. 230).

Inbreeding, as a method for improving stock, was no less controversial than crossing. Some breeders saw it as unnatural, and the delicacy and impaired fertility of heavily inbred animals were known to all. Again Bakewell’s New Leicester and the Collings’ Shorthorn provided ample evidence of both the advantages and the disadvantages of inbreeding (Youatt, 1834, pp. 234, 239, 525; 1837, pp. 314, 322, 494–495). Sebright, while accepting that a modicum of inbreeding was indispensable to create and preserve new varieties, deplored the use of sustained close inbreeding in new pigeon breeds to enhance their fancy points, as extreme frailty was the result (Sebright, 1809, p. 13). Youatt agreed:

The breeding from close affinities – the breeding *in and in* – has many advantages to a certain extent. It may be pursued until the excellent form and quality of the breed is developed and established. It was the source whence sprung the cattle and the sheep of Bakewell, and the superior cattle of Colling; and to it must also be traced the speedy degeneracy and the absolute disappearance of the new Leicester cattle, and, in the hands of many an agriculturist, the impairment of constitution and decreased value of the new Leicester sheep and the short-horned beasts (Youatt, 1834, p. 525).

We know that Darwin was aware of these discussions. He heavily annotated Sebright and Wilkinson’s pamphlets and paraphrased their main points in one of his notebooks (Darwin, 1838, p. 133). He also read Youatt and Low’s works, besides a host of other articles, pamphlets and books on breeding (Darwin, 1838–1858). Moreover, the two respondents to his *Questions about the Breeding of Animals*, which he


\(^{17}\) See also Ritvo, 1997, pp. 104–120.
circulated among breeding experts in 1839, also pointed out the ins and outs of crossing and inbreeding to him, such as the use of crossing with improved breeds to transfer desirable properties to local varieties, the difficulty of breeding from mongrels, the use of inbreeding to fix properties, and the harmful effects of prolonged close inbreeding (Freeman and Gautry, 1969).

**Darwin on Domestic Breeding**

It will be clear by now that breeding practices were more diverse and complicated than suggested by Darwin’s rendering of domestic breeding in 1859. For in the *Origin of Species* he claimed that sustained selection of small, almost imperceptible differences was the predominant method used by breeders to create new domestic varieties.

In an earlier attempt at committing his evolutionary thoughts to paper, however, Darwin had fully acknowledged the role of crossing in the practices of breeders. In the manuscript known as the Essay of 1844 he wrote that besides artificial selection of small differences, there was a second method: “namely repeatedly procuring males with some desirable qualities, and allowing them and their offspring to breed freely together; and this in the course of time will affect the whole lot” (Darwin, 1909, p. 65). Put differently: breeders might also profit from strains or varieties that already possessed a valuable character by crossing and (possibly) inbreeding consecutive generations of their animals with males from such a strain until all individuals had the desired quality – a method now known as ‘breeding up’.

Next he discussed breeding from the mongrel offspring of a cross between different varieties:

When once two or more races are formed … their crossing becomes a most copious source of new races. When two well-marked races are crossed the offspring in the first generation take more or less after either parent or are quite intermediate between them, or rarely assume characters in some degree new. In the second and several succeeding generations, the offspring are generally found to vary exceedingly, one compared with another, and many revert nearly to their ancestral forms. Much careful selection is requisite to make intermediate or new permanent races: nevertheless crossing has been a most powerful engine, especially with plants … (Darwin, 1909, pp. 68–69).
Where animals were concerned, Darwin added a reservation that echoed Sebright’s view of the matter: “with animals the most skilful agricult-uralists now greatly prefer careful selection from a well-established breed, rather than from uncertain cross-bred stocks” (Darwin, 1909, p. 69).

The Essay of 1844 was published after Darwin’s death by his son Francis, and in a footnote to the passages just quoted the latter re-marked: “The effects of crossing is much more strongly stated here than in the *Origin*. See Ed. i. p. 20, vi. p. 23, where indeed the opposite point of view is given” (Darwin, 1909, p. 68). The passage in question in the first edition of the *Origin* reads:

Moreover, the possibility of making distinct races by crossing has been greatly exaggerated. There can be no doubt that a race may be modified by occasional crosses, if aided by the careful selection of those individual mongrels, which present any desired character; but that a race could be obtained nearly intermediate between two extremely different races or species, I can hardly believe. Sir J. Sebright expressly experimentised for this object, and failed. The offspring from the first cross between two pure breeds is tolerably and sometimes (as I have found with pigeons) extremely uniform, and everything seems simple enough; but when these mongrels are crossed one with another for several generations, hardly two of them will be alike, and then the extreme difficulty, or rather utter hopelessness, of the task becomes apparent. Certainly, a breed intermediate between *two very distinct* breeds could not be got without extreme care and long-continued selection; nor can I find a single case on record of a permanent race having been thus formed (Darwin, 1859, p. 20).

Further on, referring to the substantial improvement English breeders had achieved in their domestic breeds in recent years, Darwin added:

The improvement is by no means generally due to crossing different breeds; all the best breeders are strongly opposed to this practice, except sometimes amongst closely allied sub-breeds. And when a cross has been made, the closest selection is far more indispensable even than in ordinary cases (Darwin, 1859, pp. 31–32).

Thus in the *Origin*, as compared to the Essay of 1844, Darwin down-played the role of crossing as a source of new stable varieties by qualifying attempts to mix distinct breeds as hopeless, adding, moreover, that breeders disapproved of the technique anyway. He did not mention
the crosses involving, for instance, Shorthorn cattle, Flemish and Friesian horses, and New Leicester and Southdown sheep, which according to Wilkinson, Youatt and other authors had resulted in the creation of new, intermediary breeds. Furthermore, Darwin did refer to Youatt for an example of how two experienced breeders, by selecting in different directions for years, had produced two very different strains of Bakewell’s New Leicester sheep, yet he did not mention the many crosses for which Youatt said the New Leicester was used (Darwin, 1859, p. 36). Similarly he did remark on the pivotal role that selection played in the breeding of Merino sheep in Saxony, yet he did not record that the breed was also used to improve the local flocks (Darwin, 1859, p. 31). At the end of the chapter on variation under domestication in the Origin Darwin simply repeated that “the importance of the crossing of varieties has, I believe, been greatly exaggerated” (Darwin, 1859, p. 43).

Whereas he still saw a significant role for crossing in the Essay of 1844, Darwin presented inbreeding as a purely detrimental technique, in the Essay as well as in the Origin. In the Essay he stated that “injurious consequences follow from long-continued close interbreeding in the same family,” and in the Origin he merely repeated this verdict in various formulations, mentioning in particular reduced vigor and impaired fertility as ill effects (Darwin, 1859, pp. 111, 267, 270–271; 1909, pp. 70–71). There was no mention of Bakewell and other breeders’ positive evaluations of the method as a tool for fixing varieties. It was selection that was “by far the predominant Power” in creating varieties, Darwin summarised his chapter on domestication in the Origin (Darwin, 1859, p. 43).

After having drawn attention to his father’s different appreciation of crossing in the Origin as compared to the Essay, Francis Darwin speculated: “His change of opinion may be due to his work on pigeons” (Darwin, 1909, p. 68). He was right, as we shall see.

**Fancy Pigeons**

If Darwin had taken a special interest in cattle, pigs, sheep or chicken instead of fancy pigeons, the drift of his discussion of domesticates in the Origin would doubtlessly have been different. Pigeon breeding was not the domain of farmers but of fanciers. Pigeon fanciers did not breed their animals for utility but for perfection of conformation, and – unlike most farmers, as we shall see – they worked with clearly differentiated and standardized breeds.
As Jim Secord has shown in his papers on Darwin’s pigeon work, the English pigeon clubs arose in the eighteenth century. The most renowned early organisation, the Columbarian Society, was founded in 1750. By 1850 there were four societies in London, and the fancy had become part of an excited movement for poultry improvement that was termed the ‘fowl mania’ or ‘hen fever’ by contemporary commentators. At the height of the mania, in 1855, after ornithologist William Yarrell had persuaded him to take up pigeon breeding as a case study, Darwin had his own dovecot built in his garden at Down. He became a member of two pigeon fanciers societies and attended a number of poultry and pigeon shows (Secord, 1981, 1985).18

The shows and breed competitions organized by the societies enabled the fanciers to test their breeding skills against other club members. The main pigeon varieties had been in existence since the early eighteenth century at the latest; in 1735 James Moore had described them in his Columbarium (Moore, 1735).19 A century later their conformation and characteristic properties had been set down in detail in standards of excellence that were employed by show judges to assess an animal’s merit (Secord, 1981, pp. 169–172).

Understandably, absolute breed constancy or ‘purity’ was of the utmost importance to the breeders of fancy pigeons. A fancier who bought an expensive bird bred from prize-winning stock expected it to breed true, that is to beget uniform offspring that approached the breed standard as closely as possible. As poultry journalist and expert William B. Tegetmeier, Darwin’s main adviser on pigeons, explained to the readers of his Profitable Poultry (1854), crossbreds, however beautiful their looks might be, were “worthless for stock purposes, as they do not breed true to any particular character” (Tegetmeier, 1854, p. 32).

Darwin himself provided a splendid example of the indignation that the surreptitious use of crossing aroused among fanciers. In 1859, in a letter to Huxley, he wrote:

For instance I sat one evening in a gin-palace in the Borough amongst a set of Pigeon-fanciers, – when it was hinted that Mr Bult had crossed his Powters with Runts to gain size; & if you had seen the solemn, the mysterious & awful shakes of the head which all the fanciers gave at this scandalous proceeding, you would have recognised how little crossing has had to do with improving breeds, & how dangerous for

18 See also Feeley-Harnik, 2007; Derry, 2003, pp. 51–55.
19 Moore, 1735. An annotated and extended version was published anonymously in 1765. An earlier work that contained descriptions of several breeds was Willughby, 1678.
endless generations the process was. – All this was brought home far
more vividly than by pages of mere statements &c. 20

We shall have to return to the question of the trustworthiness of Dar-
win’s informants, yet this anecdote reveals, if anything, that Darwin was
willing to believe the fanciers’ protestations of their abhorrence of
crossing as a breeding method. With respect to inbreeding in fowl he
may, besides Sebright, have taken Tegetmeier as his guide, who warned
his readers that close inbreeding for more than a few generations, while
it might help to preserve special characteristics, resulted in “diseased
and weakly offspring” (Tegetmeier, 1854, pp. 18, 24). 21

Darwin’s readiness to attach credit to these breeding experts’ state-
ments is understandable: pigeons were his prime example of the power
of artificial selection in the *Origin of Species*, and if crossing and
inbreeding had been unimportant, it was selection, and selection alone
that had been responsible for the creation of such spectacularly different
varieties as the Tumbler, the Pouter, the Jacobin and the Runt, out of a
single wild ancestor, the rock pigeon. (The fact that *Columba livia*, the
rock pigeon, could convincingly be shown to have been the only wild
ancestral species, had been an important reason for Darwin to choose
domestic pigeons for his special study of domestication.)

However, there was no lack of evidence that crossing of varieties had
played a role in the original creation of the main pigeon breeds. Several
examples were given in *A Treatise on Domestic Pigeons*, an annotated
version of Moore’s *Columbarium*, published in 1765. For instance the
so-called Dragon, it was suggested, was a pigeon variety that was
“beyond doubt, a bastard strain, being bred originally from a horseman
and a tumbler.” The Horseman in its turn was said probably to be a
crossbred too, and it had also been used, in combination with the
Cropper, to produce the English Pouter. 22 Darwin did not mention
these examples in the *Origin*.

It should be added though that nothing conclusive was known about
the origin of the main pigeon varieties. In this respect pigeons were no


21 Although Darwin clearly valued Tegetmeier’s opinion, he did not see him as an
equal: “we cannot be said to be working at all together,” he wrote to his cousin W.D.
Fox in 1856; quoted in Secord, 1981, p. 175. For the intricacies of the relations between
gentlemen-naturalists and artisans see, for instance, Secord, 1994.

22 Moore gave more examples than mentioned here: Anonymus, 1765, pp. 69, 89, 93,
106, 114, 131. Moore’s *Columbarium* was included in Eaton, 1852. Darwin owned a
copy of Eaton’s work and also read the *Treatise*. 
different from most other domestic species: public record keeping by means of stud or herd books and pedigrees did not develop until the late eighteenth and nineteenth century. Being buried in mystery, the origin of most domesticates could not plead against Darwin’s view that crossing had been unimportant. Stephen Alter has shown how Darwin exploited this lack of evidence about the origin of domestic breeds to make a negative inference with respect to his proposed mechanism of evolutionary change (Alter, 2007). In Darwin’s own words:

All that we know, and, in a still stronger degree, all that we do not know, of the history of the great majority of our breeds, even of our more modern breeds, agrees with the view that their production, through the action of unconscious and methodical selection, has been almost insensibly slow (Darwin, 1868, vol. 2, p. 244).

The reason was that “the chance will be infinitely small of any record having been preserved of such slow, varying, and insensible changes” (Darwin, 1859, p. 40).

For a proper understanding of Darwin’s perception of breeding practices it is also important to realize that he was not an experienced pigeon breeder. Charles Darwin has become an icon of science because of his singular dedication to his research and the depth of his involvement in any subject that he deemed relevant for his theory of evolution. The fact that he was prepared to go deeply into the breeders’ world is a clear illustration of this dedication. Nevertheless some qualifications with respect to his involvement in pigeon breeding may not be superfluous.

To begin with, Darwin bought his first pigeons in May 1855, and by September 1858 he had done away with all of them (Secord, 1981, pp. 165–166; Bartley, 1992, p. 329). Becoming an experienced practical breeder takes the better part of a lifetime, as Darwin himself acknowledged; three or four seasons are definitely not enough (Darwin, 1859, p. 32). Obviously Darwin’s excursion into practical pigeon breeding was also too short to find out whether or not artificial selection could create new stable varieties. Nor did Darwin have the same intentions as the regular pigeon fancier, whose aim it was to breed animals that approached the official standard as closely as possible. As Malcolm Kottler and Mary Bartley have shown, Darwin bought his pigeons because was interested in a number of quite different questions, concerning heredity.

For instance in order to provide proof that the modern pigeon breeds indeed shared a single wild ancestor he dissected specimens of the various breeds, searching for anatomical clues to their genealogical relations. For the same reason he investigated the interfertility of the breeds and the appearance of reversions to the ancestral type in crossed animals. He also crossed varieties in order to test ‘Yarrell’s law,’ according to which older breeds impressed their properties more strongly on the offspring than more recent ones. Incidentally, these experiments confirmed his misgivings about crossing as a breeding method, as some combinations produced highly variable offspring (Darwin, 1859, pp. 20–29; Bartley, 1992; Kottler, 1985)\(^2\).

Clearly then, Darwin did not undertake his pigeon work in order to provide direct experimental confirmation for his claim that domestic varieties were created by artificial selection. For information on breeding methods he could not but rely on the specialist literature and the breeders’ testimonies, meaning that he constantly had to weigh the often contradictory evidence. The end result of his balancing of the data available to him was the familiar picture of domestic breeding presented in the *Origin*, which took artificial selection to be the principal mechanism and thus provided the perfect analogy with natural selection.

At this point one might perhaps begin to think that Darwin wilfully suppressed good evidence for crossing in the *Origin*, but there is no cause for suspicion in my view. For one thing Darwin wrote the *Origin* in a great hurry, after having been surprised by Wallace’s paper on evolution, and he restricted his treatment to the essentials. The much bigger manuscript on evolution (his ‘big species book’), that he had been preparing for several years when Wallace’s paper reached him, suggests that he had planned to give more detailed information on crossing in this work. The chapter on domesticates of this manuscript has not been preserved, but in a later chapter Darwin wrote: “By the aid of some selection several intermediate mongrel breeds of sheep, as the Oxford & Shropshire Downs have been firmly established, & amongst cattle a breed, before mentioned from Wilkinson between Long & Short-Horns” (Stauffer, 1975, p. 455).

Furthermore Darwin demonstrably struggled with the information obtained from his reading. A letter to Huxley from November 1859

\(^2\) For the development of Darwin’s views on heredity, see Hodge, 1985; Olby, 2009. In the 1860s Darwin had Tegetmeier execute more crosses of various fowl varieties. As Kottler has shown, these experiments were sparked by his debate with T.H. Huxley over the latter’s claim that sterility barriers should arise between domesticates in similar fashion as between incipient species in nature, and by his debate with A.R. Wallace over the latter’s conviction that inter-species sterility was a product of natural selection. Incidentally, Olby (2009) is one of the very few authors who noted Darwin’s rejection of crossing as a breeding method in the *Origin*. 
nicely illustrates this. In the letter Darwin responded to a question about his sources on crossing and breeding:

Gärtner grand – Kölreuter grand, but papers scattered through many volumes & very lengthy […] For animals no resume to be trusted at all: facts have to be collected from all original sources […] About Breeding I know of no one Book. – I did not think well of Lowe, but I can name none better. Youatt I look at as far better & more practical authority; but then his views & facts are scattered through 3 or 4 thick volumes. I have picked up most by reading really numberless special treatises & all Agricultural & Horticultural Journals; but it is work of long years. The difficulty is to know what to trust. No one or two statements are worth a farthing, – the facts are so complicated. I hope & think I have been really cautious in what I state on this subject, though all that I have given, as yet, is far too briefly.25

The matter of ‘what to trust’ in relation to breeding matters is a recurrent issue in Darwin’s correspondence. More generally, as Anne Secord and others have shown, it was a problem that nineteenth-century gentlemen-naturalists were well familiar with. Many of their informants and correspondents were no gentlemen, meaning that their moral status and credibility were unknown (Secord, 1994).26 Thus Darwin had to try, as best he could, to establish the trustworthiness of the breeders and fanciers he consulted. For instance in a letter to Tegetmeier he asked: “Can you tell me what sort of man Ferguson the author of a Poultry Book is? Has he had much experience? Is he honest?” And in a letter to Hooker he wrote: “By the way, thanks about Beaton […] I can plainly see that he is not to be trusted. He does not well know his own subject of crossing.”27 What Darwin presented in the chapter on domestic breeding in the Origin, I would suggest, reflects the decision he had made with respect to ‘whom to trust’: he had decided to trust the pigeon fanciers, whose testimonies were fresh in his mind and fully supported the analogy between artificial and natural selection.


26 For Darwin’s interactions with the pigeon fanciers see Secord, 1981, 1985.

Darwin did not leave it at this however; in the 1860s, after the publication of the *Origin*, his grappling with the data on domestic breeding continued. A review of the *Origin* by naturalist John Duns, a protégé of Richard Owen, may have spurred him on ([J. Duns], 1860).28 Believing that species were products of divine design, Duns, it seems, was so hostile towards Darwin’s evolutionary ideas that he made no bones about disclosing how pigeon breeding really worked. After having noted that Darwin saw the accumulative selection of successive spontaneous variations as the key to making new breeds, he wrote:

…is it a fact, as Mr Darwin alleges, that even his favourite “pigeon argument” warrants the conclusions which he has come to in conducting it? Has man’s intelligence gone out in seeking variation by selection only? If the author had only given us a few facts from his treasures in reserve, which tell only one tale, we would have felt obliged. But he has not done this, and we are left to seek out the truth for ourselves. After more than twenty years’ observation in regard to pigeons, we are shut up to acknowledge the influence of cross-breeding in modifying structure, and in varying ornamentation, to an extent which is destructive of the conclusions from Mr Darwin’s “facts.” So is it with cattle. Cross-breeding, and breeding in-and-in, under man’s watchful care and discriminating intelligence, can alone give the key to variation ([J. Duns], 1860, pp. 472–473).

Duns gave more examples, for instance from dog breeding.

Whether he was affected by Duns’ review or not – in a letter to Lyell he called it “clever”29 – in the years after the publication of the *Origin* Darwin came across new evidence for successful variety crossing in domestic animals, and in his *Variation of Animals and Plants under Domestication*, published in 1868, he slightly shifted his position. For instance in 1857 he had still been asking around if any intermediate pig breeds had ever been created by crossing.30 In the *Variation* he acknowledged their existence on the basis of new publications by

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30 C.R. Darwin to W.D. Fox, 30 April 1857: “Whenever you write, as you are, I know, very learned in Pigs, pray tell me, whether any breed, known to have originated or to have been greatly modified, by a cross with the Chinese or Neapolitan Pig, whether any such crossed-breed, breeds true or nearly true.” Burkhardt and Smith, 1985, vol. 6, pp. 385–386; see also Darwin Correspondence Project, http://www.darwinproject.ac.uk/entry-2085/; accessed 27 September 2011.
Youatt and the German agriculturist Hermann von Nathusius (Darwin, 1868, vol. 1, pp. 78–79). A detailed article by veterinarian Spooner (1859) on the cross-breeding of sheep varieties convinced him of the possibility to obtain intermediate breeds in this way (Darwin, 1868, vol. 1, pp. 99–100; vol. 2, pp. 95–97). He reached similar conclusions with regard to dog and cattle breeding, and it was probably Tegetmeier (who performed several breeding experiments for Darwin as a paid assistant) who opened Darwin’s eyes for the feasibility of creating new fowl varieties by crossing (Darwin, 1868, vol. 1, pp. 42–43, 83, 93; vol. 2, pp. 95–97). In a book on the varieties and management of fancy pigeons published in 1868 Tegetmeier deferred, perhaps diplomatically, to Darwin’s authority by stating that the author of the *Origin of Species* had established that artificial selection had produced the main pigeon varieties (Tegetmeier, 1868, pp. 27–28). Yet in a new edition of his *Poultry Book* published a year earlier Tegetmeier wrote that many poultry breeds had been improved by crossing. He noted, moreover, that crossing pigeon breeds in order to obtain new varieties, while considered improper in Britain, was quite common in Germany (Tegetmeier, 1867, p. 65).

Thus in the *Variation* Darwin felt compelled to concede that breeding from mongrels was not as impracticable as he had suggested in the *Origin*. “Until quite lately,” he now wrote, breeders had indeed been convinced that the task was “hopeless.” Yet “it appears that patience alone is necessary,” as after “six or seven generations the hoped-for result will in most cases be obtained,” provided rigorous selection was applied in every generation (Darwin, 1868, vol. 2, pp. 96–97). He now also accepted that old domestic races “have often been intentionally modified by one or two crosses, made with some allied race,” adding again that particularly in such cases sustained selection was needed in order really to improve a breed (Darwin, 1868, vol. 2, p. 173).

Darwin’s acknowledgement of the feasibility of crossing in the *Variation* did not imply, however, that he had changed his mind on its importance in any fundamental way. He remained convinced that only a small number of breeds owed their origin to crosses. It was a technique, moreover, that breeders had mastered only recently, Darwin believed. In most cases breeds had merely been modified by an occasional cross,

31 Darwin referred to Youatt, 1860 and von Nathusius, 1864.

32 An unbound copy, annotated by Darwin, is in the Darwin Library (CUL); the book was published in ten parts in 1866 and 1867; see W.B. Tegetmeier to C.R. Darwin, 1 February 1864, Burkhardt and Smith, 1985, vol. 12, pp. 36–37; see also Darwin Correspondence Project, http://www.darwinproject.ac.uk/entry-4761/; accessed 27 September 2011.
and selection had always been crucial. In the *Variation* Darwin again suggested that the main breeds of domesticates had a long history. Some pigeon breeds, he stated, had been well characterised as early as around 1600 and had probably been in existence for much longer (Darwin, 1868, vol. 1, pp. 207–209). In a letter to Charles Kingsley he speculated that the formation of domestic races was “the work of centuries, probably in some cases of 1000s of years.” In his overview of the origin and development of domesticates at the end of the *Variation*, selection was again presented as the principal method, working slowly over thousands of generations.

That Darwin had modified his views on crossing only marginally during the 1860s is confirmed by the sixth and last edition of the *Origin* prepared by him, which appeared in 1872. There are hardly any changes as compared to the first edition. Breeding from crossbreds was no longer said to be utterly hopeless but “very difficult,” and Darwin now wrote that “hardly anything,” instead of “nothing,” was known about the origin and history of domestic breeds (Darwin, 1872, pp. 15, 29). For the rest he left the information on crossing as it was.

The same can be said with respect to inbreeding. There is only a single statement in the *Variation* that acknowledges the role of inbreeding as a breeding technique: “It should, however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour.” Yet this remark is immediately followed by: “In relation to the subject of domestication, the whole question is of some importance, as too close interbreeding interferes with the improvement of old races, and especially with the formation of new ones” (Darwin, 1868, vol. 2, p. 114). From these rather circumspect formulations it appears that Darwin acknowledged that inbreeding might help preserve desirable characters in a breed, yet that he still could not believe that a procedure that affected the fertility and vigor of breeding stock had played a significant part in the production of the immense variety of domesticated breeds. In this case too pigeon fanciers such as Sebright and Tegetmeier, who worked with breeds that had long been well-established and who considered close inbreeding to be ill-advised, may have been Darwin’s guides.

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Historical Studies of Domestic Breeding

So far, in order to obtain a better understanding of the backgrounds of Darwin’s views on domestic breeding, I have only discussed sources of information on the subject that we know Darwin was familiar with and that he used or might have used to shore up his rendering of domestic breeding practices in the *Origin* and the *Variation*. Historians of animal husbandry and domestic breeding have by now gathered much more information on breeding practices in the nineteenth century and before. This information, that Darwin may or may not have had at his disposal, sheds additional light on the difficulties he experienced in finding out ‘what to trust.’ Besides supporting my point about his reliance on the information obtained from pigeon fanciers, these historical studies also underscore the need for us to be aware that Darwin forged his analogy between artificial and natural selection in a nineteenth-century context, and that the uncritical use of the analogy in contemporary biology to illustrate the nature of evolutionary theory is unwarranted.

In their detailed analysis of Merino breeding on the European continent in the late eighteenth and early nineteenth century Roger Wood and Vítězslav Orel have shown that crossing and inbreeding were very much part of the new breeding practices that developed at the time, and that the best breeders knew exactly how to handle these techniques in order to improve their local sheep breeds. While it was still widely believed that climate and soil determined an animal’s properties, it was becoming increasingly clear that good food and proper management helped to prevent ‘degeneration.’ Skilled breeders, who often took Bakewell as their example, controlled the amount of Merino blood they introduced into their local herds so as to improve the fleeces while at the same time making sure that the animals remained adapted to the local environment. Inbreeding was not merely used to fix desirable characteristics but also to make undesirable ones visible, so that they could be weeded out. The judicious combination of crossing (which produced new combinations of properties), inbreeding (which helped to fix desirable ones) and selection was the key to their success. Deterioration of improved flocks also occurred regularly though, mainly when they came into the hands of less experienced breeders (Wood and Orel, 2001, 2005; Wood, 2007).

As already indicated, similar efforts were undertaken in Britain where Merino crossing fared less well. Yet Bakewell’s New Leicester 34 Here I shall focus again on animal breeding. Historical studies of the vast literature on plant hybridisation include Roberts, 1929; Zirkle, 1935; Olby, 1985; Müller-Wille and Orel, 2007.
and Ellman’s Southdown sheep were at the basis of well-established new sheep breeds such as the Hampshire Down, the Suffolk and the Oxford Down. An example of successful crossing that preceded Bakewellian practices is the creation of the Thoroughbred. This horse breed, that now represents the epitome of a purebred race, was actually a product of prolonged cross-breeding, combined with inbreeding and selection, of Arabian horses and British mares. When horse racing became popular in the eighteenth century it was found that particular Arabian-British crosses produced exceptionally good racers, and breeders then started to breed these crossed animals among themselves. By prolonged selection for speed among this mixture of animals a ‘thoroughly-bred’ type of racing horse was produced that was no longer crossed with its two parent breeds and thus, ultimately, became a ‘purebred.’ To provide warrants for this purebred status, the Thoroughbred stud book, the first of its kind, was created in 1791. Bakewell probably thanked his innovative insights at least in part to the skills of the Thoroughbred breeders (Russell, 1986, pp. 60–65, 85–86, 98, 218–220; Cassidy, 2002).

What was new in these examples of successful breeding was the controlled use of crossing, inbreeding and selection, to create uniform breeds that conformed to well-defined standards. There were few breeds of this kind among farm animals before the nineteenth century. Contrary to what Darwin was inclined to believe, most breeds were not at all of ancient origin. Horses, cattle, sheep, pigs and fowl were kept in local strains (called landraces on the European continent) which their owners saw no need to breed on the basis of generally accepted standards. There were no standards; utility was all that mattered. “The great majority of eighteenth-century animals,” according to Nicolas Russell, “as in previous centuries, were literally ‘workhorses’ of no particular breed or merit.” They just represented the stock found in a particular geographical region and their characteristics shaded into those of adjacent regions as a consequence of frequent intermixture. Natural selection and adaptation to local circumstances were often more important than artificial selection (Russell, 1986, pp. 60, 160–162, 165, 197, 218–220).

For instance pig strains, as Julian Wiseman has shown, were named after the geographical region where they were kept, and their name might well be all they had in common. In the early nineteenth century the Berkshire pig, for example, “was anything but an established

35 Quotation on p. 60. The Romans began selectively to breed some of their farm animals and pets, yet in medieval times most Roman breeds probably dissolved again into local strains; Trow-Smith, 1957, pp. 38–42, 165; Clutton-Brock, 1987, p. 26; Russell, 1986, p. 37; Wood and Orel, 2001, pp. 16–23; Leach, 2007, pp. 75–85.
breed,” as the name “described a whole host of animals of different shapes, sizes and colours” (Wiseman, 2000, pp. xii–xiii, 21, 27–30).  

As Harriet Ritvo has argued there were even few well-defined dog breeds until the nineteenth century. Names such as bulldogs, greyhounds, beagles and spaniels did not refer to animals that shared accepted breed characteristics, but to utility categories. Bulldogs were intrepid dogs suitable for bull baiting, whatever their looks, and any small dog that was kept as a pet might be called a spaniel. The characteristic Bulldog as we know it represents a fancy breed created from what was left (or believed to be left) of the bull baiting dog strains several decades after this type of public entertainment had been banned in 1835. The dog fancy took off in the mid-nineteenth century, and many breeds then began to be produced as entirely new creations (Ritvo, 1987, pp. 82–115; 1997, pp. 104–120).

The sources of the wide range of variation shown by local strains were many. Descriptions of breeds are very scarce until the nineteenth century, but there is ample documentation for the importation into Britain, from the Renaissance onwards, of horses from the Near East, Turkey, Italy, Spain, Flanders and Friesland, and of dairy cows from the north-western European countries. Shorthorn cattle and horses such as the Shire and the Clydesdale – not well-defined as breeds either until the late nineteenth century – thanked their mixed origin to these imports. Pigs of Asian origin may have been introduced in Europe as early as Roman times (Trow-Smith, 1957, p. 52; Wiseman, 2000, pp. 21, 27). Chinese, Indian and Italian pig varieties, valued for their early maturing qualities, definitely made their entrance in Western Europe in

36 Quotation on p. 37. See also Moncrieff, 1996, pp. 229ff.
37 For a provocative view of dog domestication and breed formation, see Coppinger and Coppinger, 2001.
38 Different varieties, as shown by recent studies based on new genetic techniques, came into existence virtually simultaneously with the process of domestication. Domestic varieties may have been formed from several geographically separated subspecies of the wild parent species, and early domesticates may have been backcrossed with their untamed progenitors in geographical areas where they were introduced by humans. Since Neolithic times groups of humans roamed the world in wave after wave, taking their domestic animals with them, which may have mixed with the local strains they encountered; see Zeder et al., 2006; see also Herre and Röhrs, 1990. It seems that even a hybrid origin of domesticates from parents belonging to different wild species cannot be excluded: see for instance Eriksson et al., 2008.
the late eighteenth and nineteenth century. As in the case of the Merino, there was hardly any local variety that was not affected by these imports. About 1800 the result, according to Robert Trow-Smith, was an “inchoate mass of regional varieties of which only one or two yet bore the semblance of breeds.” In the nineteenth century the Yorkshire breed, for example, was developed from a melting pot of Chinese, Italian and regional British pig types such as the Berkshire and the Lincolnshire (Trow-Smith, 1959, pp. 154–156, 288).⁴⁰ In that period fowl breeders experienced a similar invasion of animals of Asian origin that strongly stimulated the breeding of fancy varieties (Derry, 2003, pp. 51–55).

For the pioneers of the widespread movement toward breed improvement that started in the late eighteenth century, finding ways to reduce the enormous variability of local strains and the concomitant unpredictability of their performance was the main challenge, one might say. Bakewell and his followers used very close inbreeding and selection as the most reliable methods to obtain uniform breeds. Thus we can understand why Sebright approvingly noted that Ellman had produced his Southdown sheep without resorting to crossing: what he had been after was more uniformity, not more variability (Sebright, 1809, p. 26). Ellman and Bakewell’s trustworthiness, however, is a different matter. Even though they never divulged the nature of the foundation animals from which they created their new breeds, it is now generally accepted that they did in fact start their experiments with a highly variable group of animals, possibly even different strains from a wide geographical area. They must have crossed these animals until some individuals appeared that combined the characteristics they were looking for. By consistently breeding these in and in, in combination with scrupulous selection, they obtained sheep in which all the desired characters were fixed (Russell, 1986, pp. 196–215; Wood and Orel, 2001, pp. 57–94). Thus they did in fact accomplish what according to Sebright was virtually impossible: the creation of a uniform new breed from highly diverse parental stock.

Obviously the notorious secretiveness of leading breeders such as Bakewell about their foundation animals – or, as Sebright phrased it, “the mystery with which he [Bakewell] is well known to have carried on every part of his business” – was motivated by the need to protect their trade interests (Sebright, 1809, p. 9). Moreover, in the course of the nineteenth century, as uniformity and predictability were becoming the central aims of rational breeding, breeders became increasingly reluc-

⁴⁰ Quotation on p. 154; see also Wiseman, 2000, pp. 21–26, 47–56.
tant to acknowledge their use of crossing, as it might raise the suspicion that their seemingly uniform animals were directly descended from animals of mixed origin and might for that reason produce highly variable, less valuable offspring in the next generations. The Colling brothers for instance vehemently denied allegations that they had out-crossed their Shorthorns with the Scottish Galloway as a counterweight to their intense use of inbreeding (Trow-Smith, 1959, pp. 61–62; 237–238). Pigeon breeders – like the ones Darwin met at the gin-palace – provide another example of such secretiveness about crossing and many more could be given, for instance from dog breeding. When dogs became pets, and when shows and breed competitions became popular in the mid-nineteenth century, the ‘purity’ of an established breed became sacrosanct. Purity implied quality, and compromising it became an offence (Ritvo, 1987, pp. 82–115; 1997, pp. 104–120; Derry, 2003, pp. 48–102). Thus it is not surprising that attacks on Darwin’s work such as the one by John Duns, who acknowledged that new pigeon and dog breeds were produced through crossing and inbreeding, were exceptional.

It was also in this context that standards, recorded pedigrees and stud books were introduced, after the example of the Thoroughbred stud book. These record keeping devices had to provide the guarantees that buyers now demanded of the purity of their acquisitions. Pedigrees even became an obsession in some circles. The ‘barons of beef,’ the breeders of cattle among the landed gentry, tried to give their animals’ pedigrees the same distinction as their own by tracing it backwards in time, hoping to find a lineage that had not been ‘contaminated’ by ‘common’ blood for as many generations as possible. The longer the pedigree, the more prestigious the breed. As Trow Smith noted: “It was as though a pure descent from some mythical, indigenous Old Adam of a beast was a sine qua non of a perfect performance in the pail or upon the butcher’s block … [A] passion for pedigree ran mad through the world of Shorthorn breeders” (Trow-Smith, 1959, pp. 235–236). Not surprisingly, it was in circles such as these that the most extreme forms of inbreeding were employed to preserve purity – with dire results, sooner or later, which confirmed other breeders in their opinion that the method was inadmissible.

In some cases, the prestige attached to a lineage might be such that the possibility of a less distinguished descent was flatly denied. For instance Youatt, when discussing the Thoroughbred – the textbook example of a breed derived from cross-breeding – found it impossible to believe that this noblest of British breeds had not originally been of pure
Arabian descent. It must have been the combination of Arabian blood, the British climate and soil, and selection, he confidently stated, that had been responsible for the creation of the Thoroughbred (Youatt, 1831, pp. 43–44).

At the other extreme were the breeders of utility stock for whom only performance mattered and who used the prestigious high-breeds merely to improve their local strains of cattle, sheep, pigs and fowl. Yet the advantages of predictability and the increasingly controlled use of crossing, inbreeding and selection ensured that the utility breeds became more and more uniform too, and that the highly variable local strains and landraces began to disappear by the end of the nineteenth century.

Against this background we can understand the difficulties of interpretation that Darwin faced even better. Crossing and inbreeding were recommended by some experts and condemned by others, while still others discouraged, played down, or denied their use. It is also clear what set the fancy pigeon varieties apart from sheep, pigs, and other utility breeds: they were different in that the best known breeds had been in existence and well-defined for a comparatively long time. When Darwin entered the field of pigeon breeding, the cult of purity and uniformity had been in place for a longer period than most fanciers could remember. Many pigeon fanciers, Darwin noted ruefully, even believed that their stunningly different appearance proved that the main varieties derived from separate wild species (Darwin, 1859, pp. 28–29). So while breeders of utility stock were improving their local strains by means of crosses, Darwin dwelled in circles of fancy breeders for whom cross-breeding was anathema or at least couldn’t bear the light of day, and who professed that their varieties had a long history of pure descent. Assuming that what was true for pigeons was true for all major breeds, and projecting his reading of contemporary pigeon breeding technique back onto the past – in Lyellian fashion, one might say – Darwin concluded that it was sustained selection of small individual differences that must have created the domestic breeds.

**Darwin’s ‘Enduring Analogy’**

The only way to overcome the constant problem of knowing ‘what to trust’ would have been for Darwin to become a breeder himself. Yet despite his various experimental investigations of pigeons and other animals he never became a breeder in the sense required here. So he could not but rely on the experience and testimony of others. Darwin’s deepest
thoughts on breeding methods remain inaccessible to us – we can only speculate for instance that private worries about his consanguineous marriage with Emma Wedgwood may have made him extra sensitive to the aversion to inbreeding in some circles of breeders (Hodge, 1985, p. 223; Olby, 1993, vol. 1, pp. 423–424). Yet it seems safe to conclude that Darwin devised an interpretation of breeding practices that tried to make the best of the evidence at his disposal while it suited his purposes at the same time. Thus he sided with Sebright on inbreeding, not with Bakewell; he conceded that new breeds might be produced from crosses, yet considered the procedure to be too complicated to have been widely used; he took pigeons as his prime example, not sheep or pigs; and finally, knowing very little about earlier periods, he assumed that the main domestic breeds were of ancient origin and that the pigeon fanciers’ breeding technique had been used in their creation.

Arguing that Darwin’s ideas on natural selection cannot have been directly derived from his study of domesticates, Sandra Herbert noted: “Rather, it would seem, the discovery of natural selection made the domestic analogy much more clear to Darwin than it had been before” (Herbert, 1971, pp. 212–213). My analysis supports the idea that Darwin’s understanding of natural selection influenced his interpretation of breeding practices. Yet the domestic analogy did not simply become ‘clear’ to him after Malthus’ Essay on population had provided him with the foundation for his thoughts on natural selection in September 1838. There was no ready-made, pre-existent domestic analogy to become clear. Over a period of two decades, of which the years he associated with pigeon breeders were particularly important, and with considerable difficulty, drawing selectively on a wide range of often contradictory sources, Darwin skilfully moulded the domestic analogy into what was to become one of the pillars of his argument in the Origin. I agree with Mark Largent’s suggestion that trying to pinpoint the exact chronology of both insights is less rewarding than studying their development and interaction during the whole period between their first conception in 1838 and their presentation in 1859 (Largent, 2009).

Not only popularisers of evolutionary theory, but also biologists have, to this day, endorsed Darwin’s interpretation of domestic breeding practices for didactic purposes. James Secord, among others, has noted that nineteenth-century naturalists tended to look down on domesticates, and whether or not this is still true today, my suspicion is that many evolutionary biologists still know little about the methods of domestic breeders, and even less about the history of breeding practices (Secord, 1981, pp. 167–168). The same can be said about historians and philoso-
phers of evolutionary theory. It is not our job, of course, to evaluate the accuracy of Darwin’s scientific claims, yet at the same time it seems not unreasonable to think that the philosophers’ continuing interest in the analogy between artificial and natural selection is not purely academic and at least partly inspired by their silent assumption that it is a valid analogy. And it is quite clear that, where nineteenth-century breeding techniques are concerned, Darwin scholars can learn a lot from historians of animal husbandry and of animal and plant breeding.

That the practical methods of breeding domesticates today – leaving the very recent introduction of genomic selection apart – do not differ essentially from those used in the nineteenth century and do not merely revolve around selection, is made painfully clear by recent publicity about what unrestrained inbreeding has done to popular dog breeds (Harrison, 2008). Breeders still use inbreeding to preserve and enhance desirable properties, and some of them ignore the dangers of taking this too far that Sebright warned against as early as 1809. New breeds – fancy varieties as well as utility breeds – are still routinely made by means of the techniques of crossing, inbreeding and selection, the basics of which were explained by Bakewell, Sebright and Wilkinson. The sheer number and diversity of new domestic varieties that have been created over the last two hundred years suffices to make one realize that breeders must possess much faster means of producing novel races than mere selection of very small chance variations. Cross-breeding produces variation by recombination, and inbreeding and selection help to curb variation, so that only the desirable properties remain. Thus a new breed can be created in a limited number of generations. New breeding techniques were developed in the twentieth century, yet these also involve artificial selection, crossing and inbreeding: for instance the modern chicken and pig breeding industries are based, like hybrid corn breeding, on the hybridisation of carefully selected, highly inbred lines.

There is an obvious interest in our illustrating the theory of evolution and the history of its development only by means of examples and analogies that hold water. Darwin’s analogy between the production of domestic varieties and the production of species in nature does not qualify without qualification.

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