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# THE INFLUENCE OF ANIMAL BREEDING ON THE ORIGIN OF SPECIES BY CHARLES DARWIN

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## SUMMARY

Charles Darwin based his theory of evolution on the analogy of 'nature' selecting individuals for reproduction in the same way that plant and animal breeders chose parent stock in their breeding. However, the influence of animal breeding on the theory was all pervasive. The paper illustrates how Darwin used results from animal breeding. Advantages and disadvantages are emphasized.

## INTRODUCTION

Any reader of the *Origin* in this, its sesquicentenary year, will be struck, first, by the metaphor of natural selection. In Darwin's words, '[the] preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. … No one objects to agriculturalists speaking of the potent effects of man's selection; and in this case the individual differences given by nature, which man for some object selects, must of necessity first occur. … In the literal sense of the word, no doubt, natural selection is a misnomer; but who ever objected to chemists speaking of the elective affinities of the various elements? - and yet an acid cannot strictly be said to elect the base with which it will in preference combine.' This metaphor has been explored frequently, notably by Evans (1984), who followed the development of Darwin's thought through his notebooks and correspondence, and concluded that 'Darwin's recognition of the power of selection in changing organisms was almost entirely due to what he learned of plant and animal breeding.' (p. 133)

Darwin's all embracing theory needed data on the nature and origin of variability in natural populations, on the nature of inheritance, on the effects of the environment on variability and inheritance, on the fixity of species and on the effects of crossing species and varieties and on change over time. He recognised that breeders could provide much of this information.

## VARIABILITY, INHERITANCE, EFFECTS OF ENVIRONMENT

**Data**. Darwin corresponded with breeders for over a decade, collecting materials. He wrote: '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 a far better and *more precise* authority; but then his views and facts are scattered through three or four thick volumes. I have picked up most by reading really numberless special treatises and all agricultural and horticultural journals; but it is a work of long years. *The difficulty is to know what to trust.*' (Darwin to T. H. Huxley 29 Nov 1859 (Darwin, F. 1887, vol. 2, p. 281)) Published and privately communicated data were inadequate. Accordingly, he began his own breeding work using pigeons, which had many advantages: small size, low cost, clutch size, generation interval, life pairing, widespread use.

Table 1 shows quantitatively how Darwin drew on information from domesticated species. The different intensity of citation for the two main topics reflects both Darwin's interests and the state of the science at the time.

**Variability**. Darwin was particularly interested in the changes brought about under domestication

and then by selection on the domesticated species, so that, for example, domesticated flying birds such as ducks had reduced wing size and increased leg size compared with their wild progenitors. This showed both how directional selection could occur and its magnitude.

**Table 1. Mention by Darwin of domesticated species in 300 pages dealing with variation, heredity and environmental effects and 60 pages dealing with embryology etc. (in 2nd ed., 475 pages in toto) in the *Origin of Species***

| Species | Variation etc. | Embryology etc. |
|---|---|---|
| Pigeons | 28 | 3 |
| Other poultry | 24 | |
| Sheep | 10 | 1 |
| Cattle | 12 | 3 |
| Other ruminants | 4 | |
| Horses | 14 | 3 |
| Dogs | 15 | 2 |
| Other Mammals | 18 | |
| Bees | 18 | |
| Other insects | 1 | |
| Total | 144 | 12 |

He noted phenomena such as reversion, i.e. appearance of an ancestral type, which we would explain today as segregation of a Mendelian recessive, and prepotency, which we would explain as another aspect of dominance and perhaps epistasis. Here, as elsewhere, Darwin was handicapped by his lack of a workable quantitative model for inheritance (see e.g. pp. 160-1 of Darwin 1859). Thus, he wrote 'The laws governing inheritance are quite unclear; no one can say why a peculiarity in different individuals of the same species, or in individuals of different species, is sometimes inherited and sometimes not so; why the child often reverts to its grandfather or grandmother or other more remote ancestor…' (Darwin 1859, p. 10). He did, however, carefully note reversion to the wild type in pigeons. See also Bartley (1992).

On prepotency, we should note that Yarrell's law (that an older breed would be prepotent when crossed with a newer breed, i.e. the progeny (F1) would resemble the older breed, a concept that interested Darwin: see Nicholls 2009) is a prediction of Fisher's theory of unconscious selection for dominance during the domestication of a species (Fisher 1935, 1938).

Darwin did not spell out details in the *Origin*, which he repeatedly referred to as an 'abstract' of a larger work which he began but did not complete. In later books, he presented much detail but not in the form of experimental results as in his plant hybridisation or earthworm studies. For example, in the lengthy pigeon chapters in Darwin (1890, vol. 1, pp. 166-7), he gave modal numbers of tail feathers for many breeds, but not the range or the shape of the distributions. This reflected both the state of small sample statistical methods and his own preferences for dealing with numerical data (see e.g. Leach and Mayo 2005). He used the same approach for data on number of vertebrae across breeds (Darwin 1890, p. 175). In presenting data on allometric growth, which he regarded as an important constraint on the direction of natural selection, so that human success in changing proportions was strong evidence of potential selective forces in nature, he presented the magnitude of the disproportion using the mode or arithmetic mean, with no indication of within-population variability (p. 181).

Use, disuse, nutrition and other environmental factors Darwin all saw as sources of variability on which natural selection could act. Domestication and breeding led to better nutrition, for example, so that increased fertility was manifested.

Darwin also devoted some space to a consideration of the deleterious effects of inbreeding, to which he returned later, at which later time he demonstrated both these effects and the (converse) beneficial effects of outcrossing (see Leach and Mayo 2005 for discussion and references).

**Speciation**. Though Darwin did not formally use the biological species definition, and indeed recognised many of its problems (Darwin 1859, p. 259, 269, 276), he regarded sterility on crossing as a good indicator of distinct species. He noted that many breeders held, for no good reason, that each major breed of a domesticated animal as having arisen from a different species, and hence used pigeons as a strong counter example. From his own work and that of others, he concluded: 'All the domestic races pair readily together, and, what is equally important, their mongrel offspring are perfectly fertile.' (Darwin 1890, p. 201) In his crosses between pure breeds, Darwin found that the F1 generally resembled one parent, with segregation in the F2. However, as is well known, his model for inheritance was not particulate, let alone Mendelian, and he did not present numerical data on pigeons that others might have been able to analyse.

What he was able to show was that a particular species (*Columba livia*) was highly variable and that the variations had been selected to produce varieties or races that were highly distinctive and could be, given isolation, incipient species. He was also able to reject the widespread confused belief that every major strain of domestic livestock had arisen from a separate species: 'May not those naturalists who, knowing far less of the laws of inheritance than does the breeder, and knowing no more than he does of the intermediate links in the long lines of descent, yet admit that many of our domestic races have descended from the same parents - may they not learn a lesson of caution, when they deride the idea of species in a state of nature being lineal descendants of other species?' (Darwin 1859, p. 29)

Darwin frequently took the word of scientists or breeders whom he had found to be reliable, and this could lead to absurd outcomes as he laboured to condense vast bodies of non-numerical data into a meaningful form. For example, he wrote that the Brahma breed of poultry had arisen recently 'by a cross, which can be truly propagated' (Darwin 1868, p. 258), with additional comments on the origin of the breed which so aroused the ire of a professional poultry man, L. Wright, that he pursued Darwin's 'error' for five pages of his huge book on poultry, even though Darwin corrected the passage to that quoted in his second edition (1875) and had been dead eight years when Wright's volume appeared (Wright, 1890, pp. 245-9). The key unusual evolutionary point, of a 'true-breeding' cross (F1 onwards) was never referred to again, but the fossilized posthumous debate remains in the literature. No usable data were presented by Wright in his discussion, and this contrasts particularly with Darwin's customary practice; he presented data so carefully that they can still be useful and can be analysed with statistical tools that Darwin never dreamt of (see Leach and Mayo 2005, Mayo 2009). In the present context, Darwin (1887, vol. 2, p. 71) presented good Mendelian single factor segregation data from snapdragon without recognising their significance, except insofar as they provided evidence of reversion.

## CONCLUSIONS

Darwin used breeders' information and his own experiments wisely, to strengthen his arguments about the variability of populations, the mutability of species, and the power of selection.

His defective theory of inheritance and lack of statistical tools meant that he overstated some arguments and was wrong on other points e.g. reversion but, overall, evidence from animal

breeding was central to his theory and has been supported by almost all later work.

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