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PERSPECTIVES IN ORNITHOLOGY

CHARLES DARWIN'S FANCY

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CHARLES DARWIN WAS not much of an ornithologist. Although in boyhood he spent much of his spare time hunting birds and collecting eggs, by the time he returned to England on the *Beagle*, at the age of 27, he was finished with studying birds in the wild. After writing up his work on the voyage of the *Beagle* (Darwin 1839, 1838–1843), Darwin devoted his in-depth studies of organisms first to the barnacles (Darwin 1851), then to plants (Darwin 1862, 1875, 1876, 1880) and earthworms (Darwin 1881). Of more than 150 letters and short papers that he published, only six were about birds and none was in an ornithological journal (*The Ibis* began publishing, coincidentally, in 1859, and *Journal für Ornithologie* in 1853). Nor was he elected to any ornithological society of the day, and his passing was not marked with an obituary in any of the ornithological journals. The names of his contemporaries John Gould and Alfred Russel Wallace figure in the present-day common names of six and nine bird species, respectively (Gill et al. 2009), whereas Darwin's name is in only two: Darwin's Nothura (*Nothura darwinii*) and Darwin's Rhea (*Rhea pennata*).

"Darwin taught us lessons about experimental evolution that have been ignored by ornithologists for too long. It took biologists more than a century after Darwin (1859, 1871) to fully appreciate the nature of adaptation (Williams 1966) and the importance of sexual selection (Andersson 1994). It is time for ornithologists to pay attention to his lessons about the study of domesticated animals (Darwin 1859, 1868)."

Ornithologists can be a cliquish lot, sometimes treating with disdain those who pursue other kinds of natural history—and, thus, are not completely devoted to the study of birds—even though those naturalists make significant contributions to ornithology. Haffer (2001:28) defined an ornithologist as "any person who studied birds from a scientific point of view, and wrote up (and published) his or her research results," and Darwin did all of that. It seems to me that we should recognize, in this bicentennial year of Darwin's birth, his generally underappreciated ornithological work. Here, I outline some of Darwin's ornithology, focusing particularly on his studies of domesticated pigeons (*Columba livia*), a species, coincidentally, held in low regard by most ornithologists. Darwin taught us lessons about experimental evolution that have been ignored by ornithologists for too long. It took biologists more than a century after Darwin to fully appreciate the nature of adaptation (Williams 1966) and the importance of sexual selection (Andersson 1994). It is time for ornithologists to pay attention to his lessons about the study of domesticated animals (Darwin 1859, 1868).

DARWIN'S ORNITHOLOGY

Like many boys of his generation and social class, the young Charles Darwin spent much of his spare time roaming the woods and fields near his home, hunting birds and mammals, observing

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nature, and making collections of plants, animals, fossils, rocks, and minerals (Desmond and Moore 1991, Browne 1995). He clearly liked hunting birds, watching their habits, and collecting their eggs, but his real passion in natural history was reserved for collecting beetles (Desmond and Moore 1991). By age 17, though, after reading Gilbert White's (1789) *Natural History of Selborne*, he began observing birds more closely, recording his observations in a pocket notebook, and wondering "why every gentleman did not become an ornithologist" (Desmond and Moore 1991:29).

At Edinburgh University, while studying to be a doctor, Darwin attended a few meetings of the Wernerian Society where he interacted regularly with William MacGillivray (1796–1852), arguably the leading British ornithologist of his day (Huxley 1888). MacGillivray has been called the first professional ornithologist (Bircham 2007), and his *A History of British Birds* (MacGillivray 1837–1852) is a brilliant compilation of both detailed species accounts and lessons on "practical ornithology." At the Wernerian Society, Darwin also heard MacGillivray's friend and collaborator, John James Audubon, speak about the birds of the Americas (Steinheimer 2004), and he could only have been inspired. At the Edinburgh Museum, Darwin took weekly lessons in preparing study skins of birds from John Edmonstone, a freed slave who had accompanied the eccentric explorer Charles Waterton (1752–1855) on his travels in South America—lessons that would prove invaluable on the *Beagle* voyage (Steinheimer 2004). Waterton was renowned for his collections of birds, Joseph Banks himself having remarked (Waterton 1825:vii) that he was

> sorry you did not deposit some part of your last harvest of birds in the British Museum, that your name might become familiar to naturalists, and your unrivalled skill in preserving birds, be made known to the public.

Clearly, Darwin was well prepared for ornithological work when he stepped aboard the *Beagle* in the last days of 1831.

Darwin began making notes on birds at the ship's first landing, on the Cape Verde Islands, where he recorded the habitats and behavior of the kingfisher *Dacelo Iagoensis* (now called the Grey-headed Kingfisher [*Halcyon leucocephala*]) near Porto Playa on 16 January 1832 (Darwin 1839). Although he observed many birds (Haupt 2006) and accumulated a reasonable collection of study skins during the ship's long sojourn in South America (28 February 1832–7 September 1835), his main interests were geology and, possibly, entomology. In a letter to his cousin William Darwin Fox on 23 May 1833, only 17 months into the voyage, he wrote (Burkhardt and Smith 1985:316):

> You ask me about Ornithology; my labours in it are very simple — I have taught my servant to shoot & skin birds, & I give him money.—I have only taken one bird which has much interested me.

There is now pretty good evidence that this servant, the cabin boy Syms Covington, actually collected and prepared most of the 486 skins and various other specimens of birds that Darwin brought home to England (Steinheimer 2004).

In South America, Darwin "discovered," observed, and collected a new species of rhea that now bears his name. John Gould originally called this bird *Rhea darwinii*, in those days known locally in Argentina as the "Avestruz Petise"—but it had already been named *Pterocnemia pennata* in 1834 on the basis of observations alone, without any specimens being preserved. The recognition that this was a different species from the Greater Rhea (*R. americana*), which Darwin found to be a common bird in northern Argentina, appears to have been an important milestone in the development of Darwin's ideas about evolution and the origin of species. At first, Darwin mistook *R. pennata* for a juvenile Greater Rhea (Barlow 1963:273):

> which I looking slightly at it pronounced to be a young one of the common sort, —that is it appeared to be 2/3 size of the common one. I also saw some live ones of same size, but entirely forgot the Petise.

Later, having reflected on local information and his own observations, he concluded that it was a distinct species. Unfortunately, by the time Darwin realized this, the crew had already cooked and eaten the birds, but he was able to recover various parts that were later combined to make the passable composite specimen that Gould described (Steinheimer 2004). Darwin's notebooks document his epiphany as he came to realize that these two very similar, largely allopatric species must have arisen from a common ancestor and that this geographic pattern of slight differences in closely related species must mimic the temporal pattern seen in the fossil record. Toward the end of the voyage, he wrote in his notebook (Barlow 1945:264; these are notes to self and not the polished prose of published work):

> Speculate on neutral ground for 2 Ostriches: bigger one encroaches on smaller.—change not progressive: produced at one blow, if one species altered: . . . The same kind of relation that common ostrich bears to (Petise—& difft. kinds of Fournilli[?] extinct Guanaco to recent: in former case position, in latter time (or changes consequent on lapse) being the relation, as in first cases distinct species inosculate so must we believe ancient ones: not gradual change or degeneration. from circumstances: if one species does change into another it must be per saltum—or species may perish . . . When we see Avestruz two species. certainly different. not insensible change:—yet one is urged to look to common parent? Why should two of the most closely allied species occur in same country?

He is clearly onto something here and is beginning to put the pieces together.

On the Galápagos Islands, Darwin famously failed to appreciate the variation and relations among the finches on the different islands (Sulloway 1982a), focusing instead on the obvious differences and similarities among the mockingbirds on several of the islands (Sulloway 1982b). Darwin was ready for the Galápagos mockingbirds (now *Mimus parvulus*, *M. trifasciatus*, *M. macdonaldi*, and *M. melanotis*; Gill et al. 2009), having already collected some of their closest relatives (now *M. saturninus*, *M. patagonicus*, and *M. thenca*) in Uruguay, Patagonia, and the Chilean coast, respectively (Sulloway 1982b, Steinheimer 2004). For whatever reason, the Galápagos visit apparently marked the end of Darwin's interest in birds on the *Beagle* trip, and he collected only six more bird specimens on stops in Tahiti, New Zealand, Australia, and South Africa (Steinheimer 2004).

Upon settling in London in 1832, Darwin got busy putting together his popular account *Journal of Researches* (Darwin 1839; usually referred to as *The Voyage of the Beagle*) and a comprehensive, multivolume *Zoology* of the trip (Darwin 1838–1843). Part 3

of the *Zoology* is devoted to birds and was written by John Gould on the basis of Darwin's collections, notes, and correspondence. While in London, he also made some remarks on both the rheas of South America (Darwin 1837a) and the finches of the Galápagos Islands (Darwin 1837b) at meetings of the Zoological Society of London, which were later published in the *Proceedings* of that Society.

Throughout the remainder of his life, Darwin amassed facts about birds through correspondence with ornithologists and explorers around the world, including A. Newton, P. L. Sclater, C. H. Merriam, R. B. Sharpe, and F. D. C. Godman (to name a few), all of whom were authorities on avian natural history, behavior, or systematics. Certainly, bird examples figured heavily in *On the Origin of Species* (Darwin 1859), *The Descent of Man, and Selection in Relation to Sex* (Darwin 1871; with four full chapters on birds), and *The Expression of the Emotions in Man and Animals* (Darwin 1872). Despite his early interest in birds and his teenage aspirations to be an ornithologist, Darwin does not seem to have made any serious study of birds after the *Beagle* voyage—except for his work on pigeons.

Darwin's Fancy

By the mid-1800s, the pigeon fancy—the hobby of breeding, raising, and showing domesticated pigeon breeds—was in full flower in Europe but had just begun in North America, where formal publications and societies devoted to the birds did not appear until the 1870s (Levi 1941). "Fancy" pigeons had been bred and raised by humans for centuries, but the activity developed into a fascinating social phenomenon in 18th-century England. By the middle of the 19th century, pigeon breeding dominated the public interest in birds until it was surpassed by bird watching in the mid-20th century. During the 1800s, major pigeon-fancier clubs sprang up all over Britain, often dividing along social lines—for example, the Philoperisteron Society of London (established in 1847) restricted membership to the wealthy and could be joined only by invitation and election. Major shows populated the social calendar of fanciers every year, and at the main poultry show in London, held twice a year in the Crystal Palace, several hundred pens were devoted to pigeons (Secord 1981). Similarly, the huge annual Birmingham cattle and poultry show attracted pigeon breeders from all over Britain to show their birds and compete for prizes. In addition to the breeding hobby, literally thousands of dovecotes were constructed in household and estate gardens throughout the British Isles to attract feral pigeons for the simple pleasure of the landowners or to provide a ready supply of tasty squabs in season. Even the young Queen Victoria had her own dovecote built on the grounds of Windsor Castle (Haupt 2006).

By the 1850s, Darwin had completed his amazingly comprehensive work on the barnacles (Darwin 1851) and was well into his magnum opus on natural selection and the origin of species. Possibly seeing the need for analogy to explain the action of natural selection, and keen to do some "evolutionary" experiments of his own, Darwin decided to raise fancy pigeons. There has been much debate (see Gregory 2009) about the role of analogy in Darwin's thinking, but he said that his views and those of Alfred Russel Wallace "differ only, that I was led to my views from what artificial selection has done for domestic animals" (letter to Charles Lyell, 25 June 1858; Burkhardt and Smith 1992:117). And it was the study of domesticated pigeons that gave Darwin his own first-hand look at artificial selection and the nature of variation.

Darwin had a dovecote built in his garden at Down in the spring of 1855 and quickly began accumulating a breeding flock of various fancy breeds. By 26 November of that year, he already had breeders of 10 varieties and was expecting 2 or 3 more within a week (letter to T. C. Eyton; Burkhardt and Smith 1990a:508). Darwin was enchanted by the distinctive breeds (which he called "races")—pouters, carriers, runts, scanderoons, murassas, barbs, fantails, turbits, tumblers, frill-backs, jacobins, trumpeters, laughers, nuns, spots, and swallows—but also by the "eye of the fancier," the breeder's ability to recognize the subtle differences among individuals that would improve a fancy pigeon breed (Secord 1981). Pigeons had been domesticated since at least 3,000 BC, and by the 1850s more than 155 distinct morphs were recognized—more than for any other domesticated animal of the day, including dogs. At the height of his pigeon work, Darwin had more than 90 birds in his flock and regularly attended fanciers' meetings and pigeon shows to learn more about the processes of artificial selection.

Darwin obtained most of his pigeons from fanciers in London, sometimes lovingly carrying the birds in a box on his knee during the hour-long coach ride home. Interestingly, he joined both the elite (and elitist) Philoperisteron Society and at least one much more open society of working-class men—probably the National Columbarian Society—who showed pigeons all over Britain. Darwin was keenly interested in the methods used by the best fanciers to select breeding stock, and he sensibly realized that such ability had nothing to do with social class. He was wary of the fanciers, though, and did not make many friends among them. Indeed, he thought them "a strange set of odd men.—Mr Brent was a very queer little fish . . . (N.B. all Pigeons Fanciers are little men, I begin to think)" (letter to W. D. Fox, 29 November 1855; Burkhardt and Smith 1990a:508). Darwin had a long and productive association with William Tegetmeier, a prominent journalist and amateur pigeon fancier, but even that relationship was sometimes strained, and Darwin really treated him more as a paid assistant than as a scientific collaborator. Tegetmeier once wrote in the periodical *Cottage Gardener* that he and Darwin worked together on a project, which prompted Darwin to note rather haughtily in a letter to his cousin: "Mr. Tegetmeier is a very kind & clever little man; but he was not authorized to use my name in any way, & we cannot be said to be working at all together" (letter to W. D. Fox, 15 March 1856; Burkhardt and Smith 1990b:56). Nonetheless, Tegetmeier introduced Darwin to many important fanciers from whom he obtained most of his pigeons, and they continued to interact and correspond about pigeons until 1881.

Darwin's first task in his pigeon work was to establish a phylogeny of the domesticated breeds. Fanciers (e.g., Dixon 1851), on the one hand, were convinced that the breeds had arisen from different wild species, long extinct, whereas ornithologists of the day (e.g., Yarrell 1837–1843) were certain that all domesticated pigeons had come from a single wild species, the Rock Pigeon (*C. livia*), that was native to the Middle East. Darwin applied his signature blend of hypothetico-deductive reasoning, logic, and fact-gathering to the problem and concluded definitively that the ornithologists were correct. He was fortunate to have more than 300 years of written records of pigeon breeding available to assist his research, but some

of his key insights came from his own experiments. In the end, his conclusions about pigeon origins derived from six arguments, as follows (Darwin 1868, chapter 6). He argued that it was odd that (1) all of the putative aboriginal species were now extinct and (2) all of those species had taken readily to breeding in captivity. He also wondered (3) why none of the fancy breeds had later become feral like other domesticated animals and (4) how some of the aboriginal species could have survived in the wild if they were anything like their descendents, which possessed bizarre behaviors and morphologies. In addition, he noted (5) that it was highly unusual that all the races could interbreed and have fertile offspring if they came from different ancestors and (6) that all the breeds shared many traits with the wild Rock Pigeon. Today, we know that none of those arguments would be enough to solve the problem, but taken together they make a very strong case, the argument about hybrid fertility being particularly insightful. As a result of his investigations, Darwin constructed a phylogeny of the pigeon breeds (Fig. 1), the only phylogenetic tree that he ever published (Darwin 1868).

Darwin eventually solved this problem of pigeon phylogeny to his satisfaction, though it took him several years as he pored over the written records, corresponded with fanciers far and wide, collected his own data on pigeon morphology and behavior, watched fanciers at work, and conducted his own breeding experiments. His morphological work was focused on the skeletons of different breeds in an attempt to quantify the fundamental differences between them. To do this, he bought and was given dead birds that he prepared as both skins and osteological specimens, often to his own and his family's considerable displeasure:

> I wished to clean the skeleton of a bird, which had not been sufficiently macerated, and the smell made my servant and myself (we not having had much experience in such work) retch so violently, that we were compelled to desist. (Darwin 1872:261)

The result was a fine set of specimens from at least 21 "breeds" (Fig. 2) that he then measured and compared. As a standard for comparison, he used two specimens of feral pigeons from the Hebrides, where the wild Rock Pigeon had been introduced centuries earlier. From today's perspective, it seems incredible that he would have thought that two specimens were enough to characterize the population of wild birds, particularly given that his main focus here was the study of variation (Darwin 1868). He then characterized several traits from each breed in comparison with the feral bird, standardizing for body size, using proportions, and designating each character as "too short" or "too long" accordingly (Fig. 3). We now know that this method does not properly account for allometry and is especially inconclusive given Darwin's small sample sizes, but he correctly decided that there was no consistent pattern from one breed to the next—some, like the short-faced tumblers, had smaller bills than expected from their body size, and 25 of 35 specimens of various breeds had wings that were relatively long (Darwin 1868). These measurements confirmed his suspicion that such differences were the result of selection by fanciers for specific traits and not simply for variation in body size.

From his study of artificial selection on the pigeon breeds, Darwin concluded that there are two kinds of artificial selection: methodical and unconscious. The distinction seems unclear today, but here is what Darwin (1868:214) wrote:

> When a bird presenting some conspicuous variation has been preserved, and its offspring have been selected, carefully matched, and again propagated, and so onwards during successive generations. . . . This may be called *methodical selection*, for the breeder has a

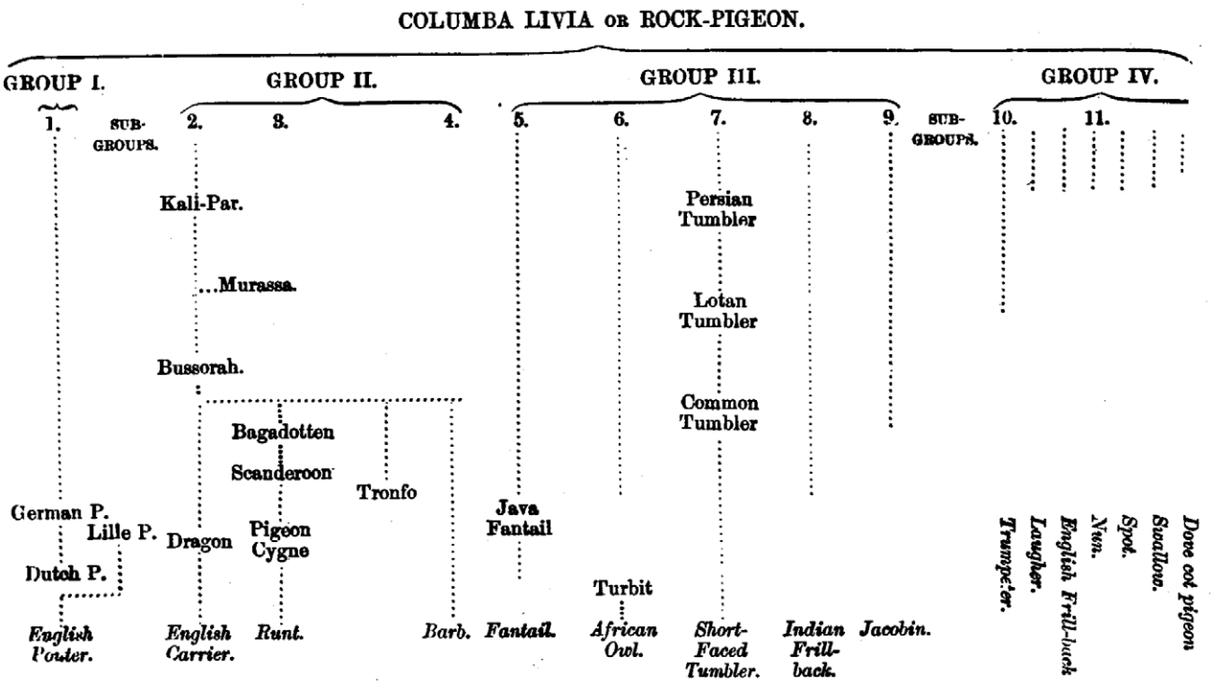

FIG. 1. Darwin's (1868) phylogeny of the various fancy pigeon breeds.

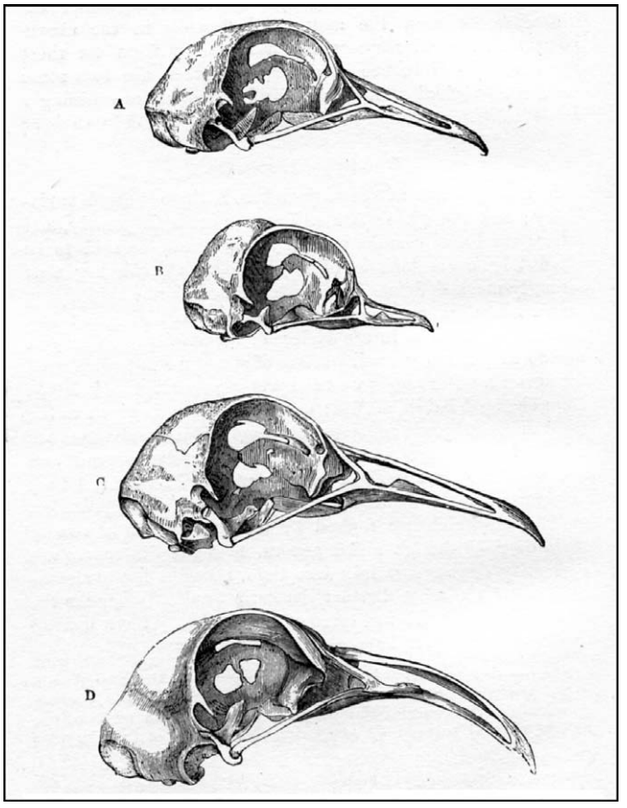

FIG. 2. The skulls of pigeon breeds prepared and measured by Darwin (1868) for his work on the role of artificial selection in shaping the morphology of fancy pigeons.

TABLE. I.

Pigeons with their beaks generally shorter than that of the Rock-pigeon, proportionally to the size of their bodies.

Name of Breed.	Actual length of Feet	Difference between actual and calculated length of feet, in proportion to length of feet and size of body in the Rock-pigeon.	
		Too short by	Too long by
Wild rock-pigeon (mean measurement) ..	2·02		
Short-faced Tumbler, bald-head	1·57	0·11	..
„ „ almond	1·60	0·16	..
Tumbler, red magpie	1·75	0·19	..
„ red common (by standard to end of tail)	1·85	0·07	..
„ common bald-head	1·85	0·18	..
„ roller	1·80	0·06	..
Turbit	1·75	0·17	..
„	1·80	0·01	..
„	1·84	0·15	..
Jacobin	1·90	0·02	..
Trumpeter, white	2·02	0·06	..
„ mottled	1·95	0·18	..
Fantail (by standard to end of tail) ..	1·85	0·15	..
„ „ „	1·95	0·15	..
„ crested var. „	1·95	0·0	0·0
Indian Frill-back „	1·80	0·19	..
English Frill-back	2·10	0·03	..
Nun	1·82	0·02	..
Laugher	1·65	0·16	..
Barb	2·00	0·03	..
„	2·00	..	0·03
Spot	1·90	0·02	..
„	1·90	0·07	..
Swallow, red	1·85	0·18	..
„ blue	2·00	..	0·03
Pouter	2·42	..	0·11
„ German	2·30	..	0·09
Bussorah Carrier	2·17	..	0·09
Number of specimens	28	22	5

FIG. 3. Darwin's (1868) summary of his measurements of the bills of various fancy pigeon breeds, compared with those of the wild Rock Pigeon.

> distinct object in view, namely, to preserve some character which has actually appeared; or to create some improvement already pictured in his mind.

And the other form of selection

> may be called *unconscious selection*, for the breeder selects his birds unconsciously, unintentionally, and without method, yet he surely though slowly produces a great result . . . He does not wish permanently to modify the breed; he does not look to the distant future, or speculate on the final result of the slow accumulation during many generations of successive slight changes; he is content if he possesses a good stock, and more than content if he can beat his rivals.

Thus, he reasoned that methodical selection involved the deliberate choice of interesting "sports" or "mutations" by breeders seeking to start a new line or breed, whereas unconscious selection resulted from the breeder choosing the birds of highest quality, with no objective criterion to define "quality." Unconscious selection relied on the fancier's eye, which fascinated Darwin. Not surprisingly, he found it difficult to specify exactly what was being selected by this unconscious process, and why, but he was certain that this form of artificial selection molded the breeds into their present form. It is perhaps instructive that he used terms like "handsome," "elegant," "beautiful," and "noble" to describe the finest pigeons in his own flock and those he saw at shows and in the flocks of other breeders; this suggests to me that cultural traits, possibly including those associated with human mate selection, influenced the breeders' unconscious choices. Indeed, there was a certain arrogance in calling the English pouter so much more worthy than its German equivalent. This would be a fascinating research topic for a sociologist with interests in ornithology.

Darwin's pigeon-breeding experiments were designed both to test some of his ideas about pigeon phylogeny and to give him some first-hand experience with hybridization. In a series of at least 12 experiments crossing different breeds—a fine male nun with a female jacobin, for example—Darwin (1868) noticed a striking pattern that helped his argument on origins, though he was at a loss to explain it comprehensively (because he knew nothing about genetics). From each cross, he occasionally got an offspring that had traits of the ancestral Rock Pigeon, traits not present in either of the parental breeds. He immediately ruled out the possibility of extrapair paternity involving a wild bird as father:

> Pigeons, differently from any other domesticated animal, can easily be mated for life, and, though kept with other pigeons, they

> rarely prove unfaithful to each other. . . . I have bred in the same aviaries many pigeons of different kinds, and never reared a single bird of an impure strain. (Darwin 1868:206–207)

It would be another 60 years before Sewall Wright's experiments investigating the coat colors of Guinea Pigs (*Cavia porcellus*) revealed the action of epistasis as the most likely cause of such "throwbacks," as Darwin called them. Most important for Darwin, though, this consistent result was his best argument for a common progenitor in the Rock Pigeon.

In *The Variation of Animals and Plants under Domestication*, Darwin (1868) devotes two full chapters to his pigeon studies, the first (chapter 5) on his morphological measurements and experiments and the second (chapter 6) on his arguments for a common origin and the relevance of this work on pigeons to his study of variation. No other animal or plant gets this much ink in *Variation*, the second half of his treatise that began with publication of *On the Origin of Species*. Recall that the latter was rushed to print as an "abstract" of his magnum opus, in response to his correspondence with Wallace about natural selection and their joint publication in the *Journal of the Proceedings of the Linnean Society of London* (Darwin and Wallace 1858). *On the Origin of Species* begins with two chapters on variation, including some reference to the pigeon studies, but he reserved almost all of the details for the *Variation* volumes (Darwin 1868). It is instructive to read *Variation* today for the insights it gives into the ways that Darwin gathered data on, and thought about the analogies between, natural and artificial selection (Gregory 2009). Much of it reads as if Darwin was well aware of what we now know about genetics, and there is more than one indication that he almost stumbled upon Mendel's principles.

The end of Darwin's pigeon fancying came rather abruptly in the spring of 1861 after a trip with his daughter Henrietta to Wales, where he became intensely interested in orchids (Desmond and Moore 1991). Right after that trip, he got rid of his pigeons and immersed himself in the care and breeding of orchids. I wonder, though, whether another incident may have precipitated the fall from grace of his pigeon research. Earlier, he had discovered that Henrietta's cat had eaten a few of his pigeons, including a couple of his prized birds (Haupt 2006). On discovering this, he surreptitiously killed the cat and told Henrietta that it must have run away, but the perceptive Henrietta clearly knew what had happened. The trip to Wales may well have brought that incident to an embarrassing head. Although pigeons had absorbed him for almost six years, Darwin directed most of his subsequent experimental work toward plants. His transformation into an orchid biologist even resulted in a book (Darwin 1862) that was published before the pigeon studies were detailed in *Variation*.

Eulogy

The Auk did not begin publication until 1884, two years after Darwin died, but an obituary would still have been timely for that first issue. Had I been asked to write it, I would have praised Darwin's uncanny knack for ferreting out little-known facts about birds in support of myriad arguments about the action of selection and the nature of variation (Darwin 1859, 1868, 1871). I would also have marveled at how all of my understanding of bird behavior and ecology made so much sense in the light of natural and sexual selection—it all seems so obvious in retrospect.

In that eulogy, I would have predicted, correctly, that an appreciation of natural and sexual selection would guide much of ornithology over the next century, at least, and that the study of birds would likewise contribute much to our understanding of evolutionary patterns and processes. The key advances made in the study of evolution and evolutionary and behavioral ecology by ornithologists like Mayr, Lack, Wynne-Edwards, Ricklefs, Krebs, and Davies, to name just a few, are a testament to the value of bird studies to 20th-century evolutionary biology. Bird research still dominates many aspects of evolutionary biology, far out of proportion to the number of extant bird species (even as a percentage of all vertebrates). For example, in 2008, almost 5% of the papers published in the four major ecology and evolution journals and almost 10% of the papers in the three main behavior and behavioral ecology journals were about birds. In North American universities, at least, ornithologists undoubtedly outnumber all other taxon-specific scientists. Darwin, of course, had nothing to do with the popularity of ornithology as a discipline, but it does seem that ornithology has had a lot to do with the success of evolutionary biology.

On the other hand, I would have mistakenly predicted that studies of pigeons, in particular, and domesticated or captive birds, in general, would have dominated 20th-century ornithology, following on Darwin's lead and insights. Judging from his work described in *Variation* (Darwin 1868), I would have thought that pigeons were an ideal study species for exploring many facets of natural and sexual selection. It is striking, for example, how many of the sexually selected traits that we see in birds arose through artificial selection during the breeding of fancy pigeons: delayed plumage maturation, colors, songs, wattles, long tails, crests, elongated secondaries, plumes, and so on. We could learn a lot about the genetics and evolution of such traits by studying pigeons.

Pigeons are readily kept in aviaries, can be induced to breed several times a year, have simple and interesting courtship displays, have short generation times (for a large bird), and are docile and easy to handle (Levi 1941). Thanks to psychologists, there is a wealth of information available on the perceptual and cognitive abilities of pigeons and a rich literature on design of experiments and experimental apparati for studying pigeon behavior. Pigeons should be a model organism for the study of avian evolutionary and behavioral ecology. The pigeon has not, of course, been ignored by behavioral ecologists, especially with respect to navigation and homing (Wallraff 2005). On a smaller scale, Nancy Burley (1981) did some nice work on pigeon mate choice, Luc-Alain Giraldeau and colleagues have used them in their pioneering work on social foraging (summarized in Giraldeau and Caraco 2000), and Richard F. Johnston (1984) did extensive research on their reproductive ecology, to name just a few. Surprisingly, though, the pigeon has not become the species of choice for experimental ornithologists.

We ornithologists also have been slow to embrace the study of domesticated species (Birkhead and van Balen 2008). The Zebra Finch (*Taeniopygia guttata*) and Domestic Chicken (*Gallus gallus*) are notable recent exceptions that have become model organisms for the study of sexual selection with respect to mate choice (e.g., Burley et al. 1982, Zuk et al. 1990) and sperm competition (e.g., Birkhead et al. 1995, Pizzari et al. 2003). There also have been many groundbreaking studies of birds bred in captivity—Indian Peafowl (*Pavo cristatus*; e.g., Petrie 1994), Japanese Quail

(*Coturnix japonica*; e.g., Bateson 1982), and various finches (e.g., Pryke and Griffith 2009), to name just a few—but the highly domesticated species that show tremendous variation as a result of artificial selection have largely been off our radar (Price 2008). I think they have much to tell us about the evolution of bird behavior and morphology, just as they informed Darwin about the nature of variation.

Further Reading

In preparing this essay, I have relied heavily on the excellent popular book on Darwin's bird studies by Haupt (2006), Steinheimer's (2004) treatise on Darwin's bird work during the voyage of the *Beagle*, and Secord's (1981) paper on Darwin's pigeon research. The biographies by Desmond and Moore (1991) and Browne (1995) are excellent and essential accounts of Darwin's life and times. In addition, the websites "The Complete Works of Darwin Online" (darwin-online.org.uk/) and "Darwin's Pigeons" (darwinspigeons.com/) are invaluable sources of scholarly information.

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