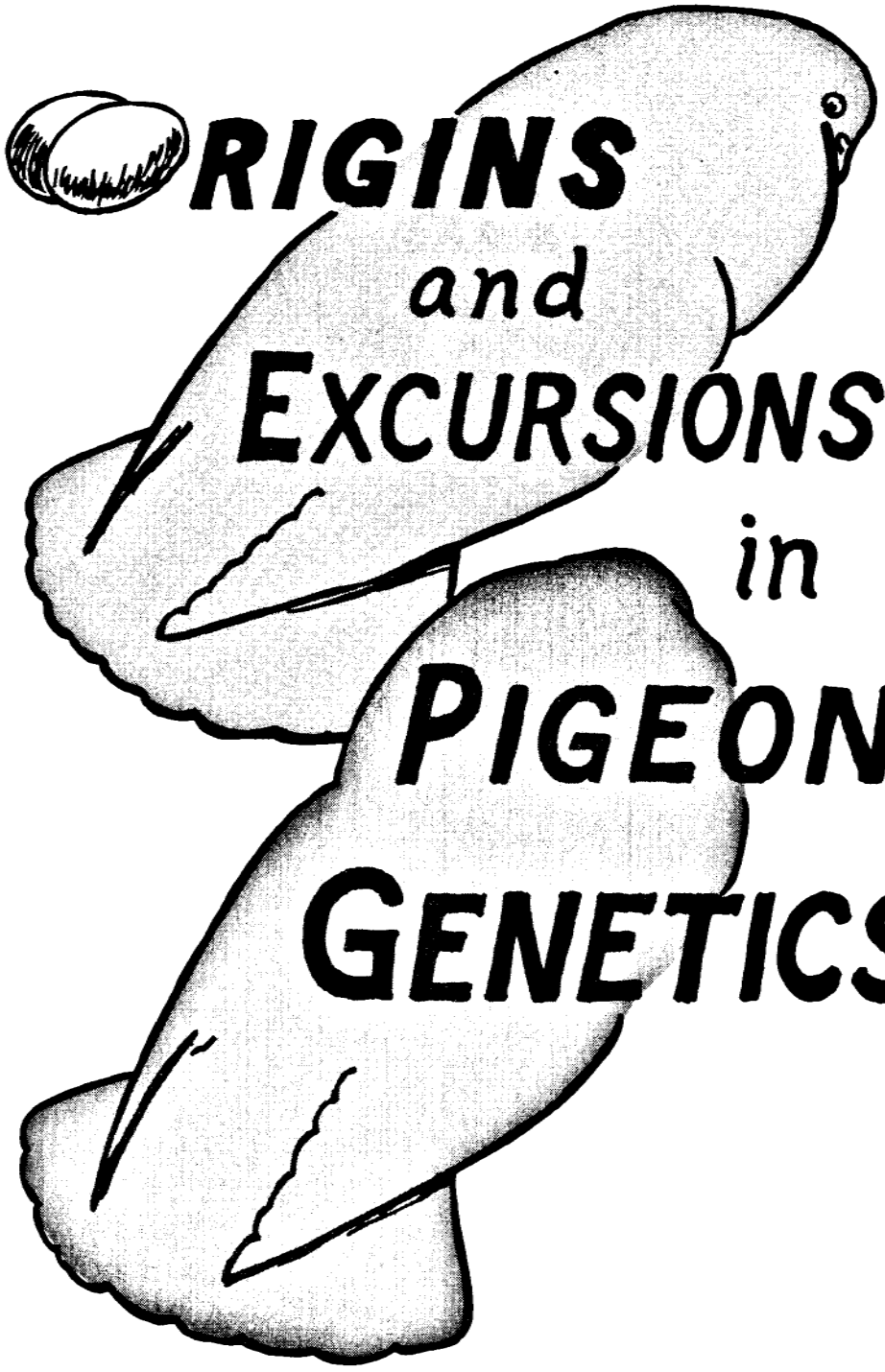
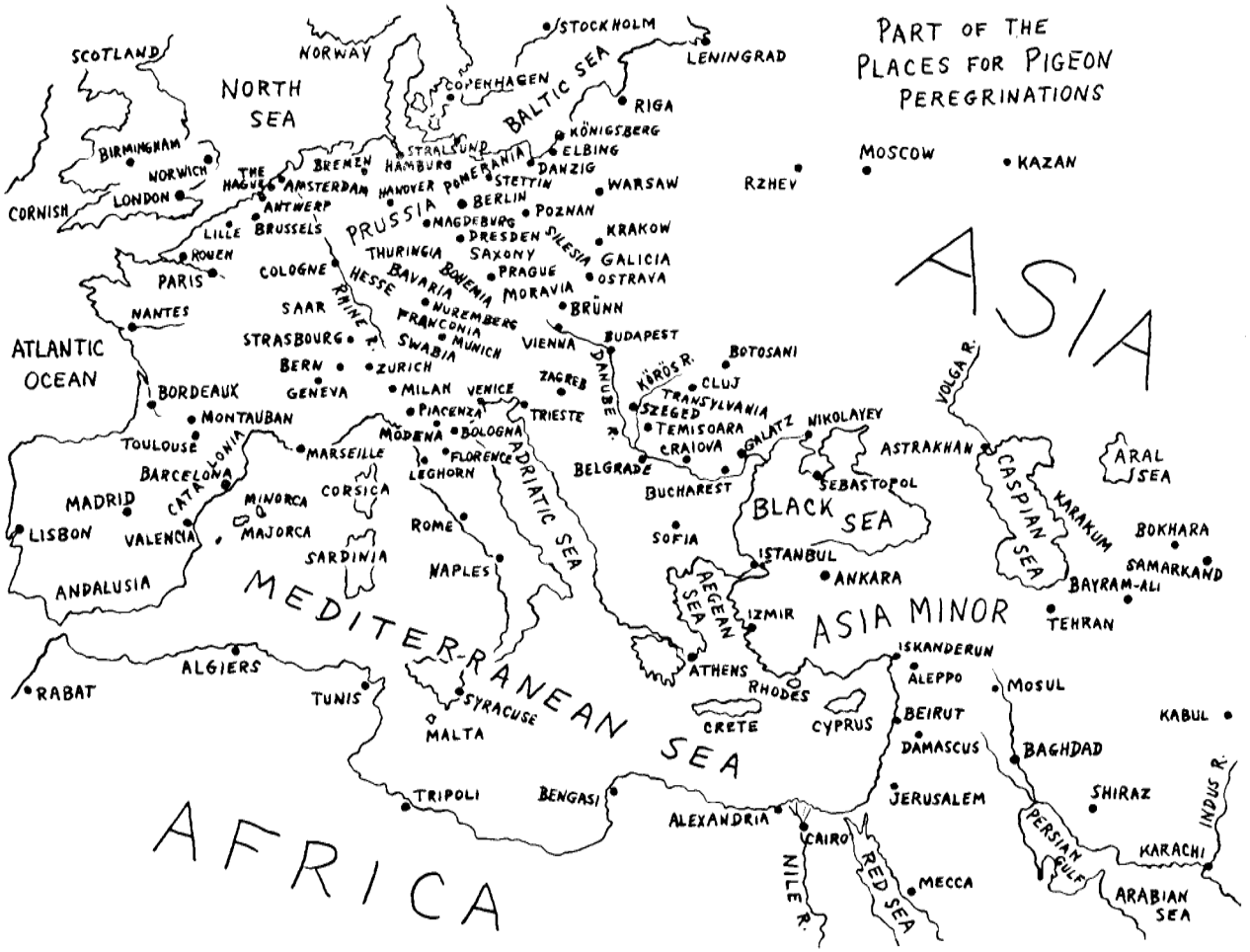


W. F. HOLLANDER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KÖNIGSBERG
ELBING
DANZIG
STRALSUND
POMERANIA
STETTIN
WARSAW
MOSCOW
KAZAN
RZHEV
BIRMINGHAM
NORWICH
THE HAGUE
AMSTERDAM
BREMEN
HAMBURG
HANOVER
BERLIN
POZNAN
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CORNISH
ANTWERP
BRUSSELS
PRUSSIA
MAGDEBURG
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KRAKOW
LILLE
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HESSE
BAVARIA
BOHEMIA
PRAGUE
OSTRAVA
RHINE R.
NUREMBERG
FRANCONIA
MORAVIA
BRÜNN
NANTES
SAAR
SWABIA
MUNICH
VIENNA
BUDAPEST
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STRASBOURG
BERN
ZURICH
ZAGREB
DANUBE R.
KÖRÖS R.
BOTOSANI
CLUJ
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BORDEAUX
GENEVA
MILAN
VENICE
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SZEGED
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CRAIOVA
GALATZ
NIKOLAYEV
MONTAUBAN
PIACENZA
MODENA
BOLOGNA
TOULOUSE
MARSEILLE
FLORENCE
LEGHORN
ADRIATIC SEA
BELGRADE
BUCHAREST
SEBASTOPOL
BLACK SEA
ASTRAKHAN
VOLGA R.
ASIA
ARAL SEA
CASPIAN SEA
KARAKUM
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CATALONIA
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CORSICA
MADRID
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ROME
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ISTANBUL
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INDUS R.
ALEXANDRIA
CAIRO
PERSIAN GULF
KARACHI
NILE R.
RED SEA
MECCA
ARABIAN SEA
AFRICA

ORIGINS
and
EXCURSIONS
in
PIGEON GENETICS

A compilation by W. F. Hollander

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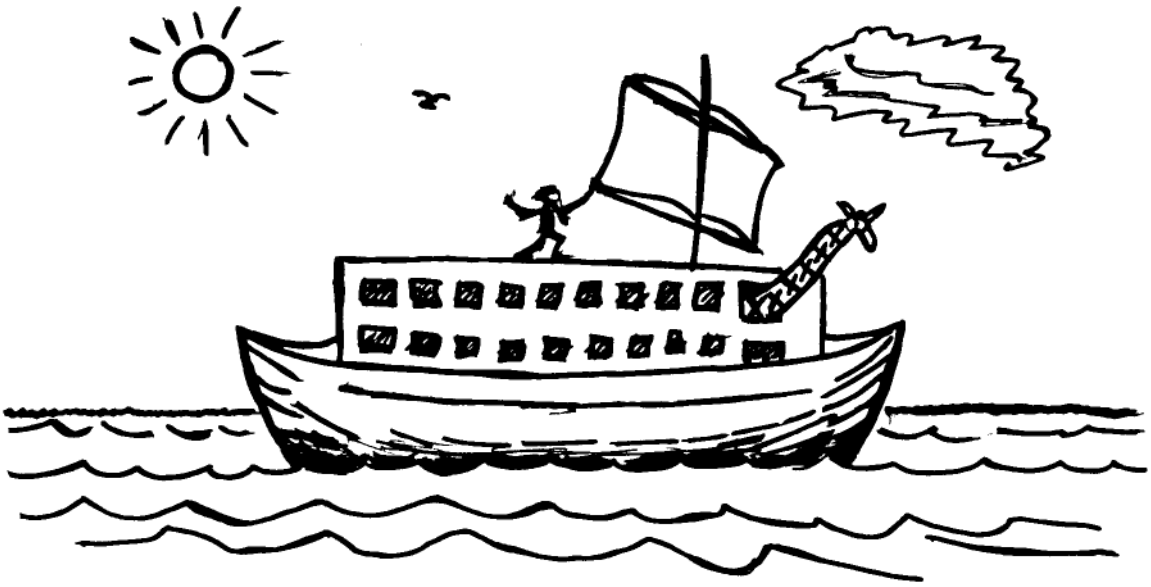

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FOREWORD - 1982

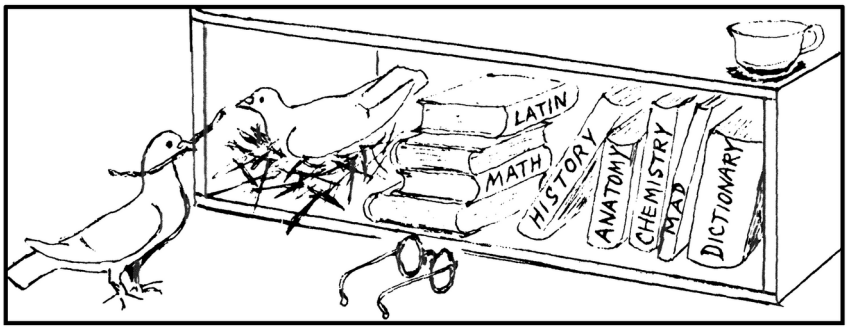
Genetics: William Bateson of England coined the word in 1906 and defined it as “the physiology of heredity and variation.” A nice, scientific-sounding word, and a nice, simple-sounding definition. Ah, but it is tricky. That nice little word and the neat definition now seem to engulf most of Biology. And the technologies and methodologies and the lines of reasoning have become astoundingly complicated. It is practically impossible for the layman or fancier to comprehend formal reports any more, even when the subjects should be highly interesting.

Over the years I have tried to build a bridge over the chasm between the fancier and professional scientist. Rickety, wobbly, and not too well aligned, to be sure, but it has allowed a lot of cross-communication, even fraternization. The present compilation of essays is the essence of that bridge, though not complete. The arrangement is to some extent rational, but not chronological. Informality is the key.

We cannot say that expertise in Genetics is essential to success in showing, racing, or even squab farming. Some understanding however can be helpful and gratifying. But like all science, Genetics is never finished: the pigeons will continue to give us new mysteries for solution. Any fancier may discover something that is beyond our knowledge, and the fancier may even discover the answer. Generally we are not adequately prepared to pursue the myriad problems that arise, but perhaps collaboration will develop. Pigeon Genetics News Letter, and its successor, Pigeon Science and Genetics Newsletter, have been leading the way, trying to keep up communication. Other periodicals have also been helpful.

At the end of each essay its date and place of previous publication are given. The following abbreviations may be used: N. P. A. = National Pigeon Assoc.; P. G. N. L. = Pigeon Genetics News Letter; P. S. & G. N. = Pigeon Science and Genetics Newsletter; A. P. J. = American Pigeon Journal; A. G. H. A. = American Giant Homer Assoc. For further background information and bibliographic references the reader should consult the big books by Wendell M. Levi: “The Pigeon”, and “Encyclopedia of Pigeon Breeds.”

Willard F. Hollander



SO YOU THINK YOU KNOW WHAT'S A DOVE

The 1966 "Birds of North America"? by Robbins et al. (Golden Press, N.Y.) includes the Rock Dove. You would call it just plain common pigeon. But the authors of this book are not uneducated or stuffed shirts. So who is right? Both. Now ain't that a mess?

Blame it on the old English language. If you lived in Mexico, for example, there would be only one name: paloma. And in Sweden, only one word: dufva. Those languages make no distinction. But English grew not in isolation but by mixing. First the ancient Celts, then Roman invasion, Germanic invasions, (Angles, Saxons, Jutes), Scandinavian invasions (Vikings), Norman French invasion, religious and trade terminology, and probably Shakespeare's influence all contributed to the richness of our language. Richness, but also some confusion. We got the word dove from the North countries, and the word pigeon from the French, both meaning the same birds.

But that isn't the worst of the mess at all—as the exploration of the globe proceeded after the Middle Ages, the sailors went around Africa, to India, China, the New World—both North and South America—and the Caribbean islands, New Guinea and Australia. Great: everywhere they went, they discovered new sorts of pigeons or doves. Hundreds of kinds, never imagined to exist. Even that gigantic flightless wonder, the dodo (dove-dove?), which was so good to eat that pretty soon none were left alive. All sorts of pigeon and dove names were casually assigned, such as quail-dove, green pigeon, nutmeg pigeon, diamond dove, bleeding-heart dove, bronzewing pigeon, passenger pigeon, etc. etc.

To make sense of this superfluity of diversity, scientific names were gradually worked out, so that each kind would have a fixed monicker that everybody agrees on. The latest compilation is a big volume (over 400 pages): "Pigeons and Doves of the World'? by Derek Goodwin, publication No. 663 of the British Museum of Natural History. It hit the bookstores in 1967, and few dove breeders bought it because it cost almost as much as a pair of doves. Anyway, this book uses the name Rock Pigeon instead of Rock Dove, and our old pal the common pigeon has the dignified scientific name *Columba livia*. The first part of the name is the genus, and the second is the species. All together, some 40 different genera have been identified, including around 400 species. Memorizing all of them is a challenge. Many of these species are terribly wild and hard to satisfy in captivity.

Now where does the silky dove fit in this scheme? Well, we know the history of this critter—it was found as a mutation among ordinary ringneck doves (*Streptopelia risoria*). So it is not another species but rather a subdivision, and such subdivisions do not rate a scientific Latin label. We can call established mutant types breeds or varieties within a species. New breeds and varieties can also be bred by crossing previous ones. So we have such combinations as rosy silky, pied silky, white silky, etc., just as we have silver Fantail pigeons, black Fantails, white Fantails, etc., all in *Columba livia*. It helps to remember that species are our interpretation of natural divisions, while varieties and breeds are human contrivances.

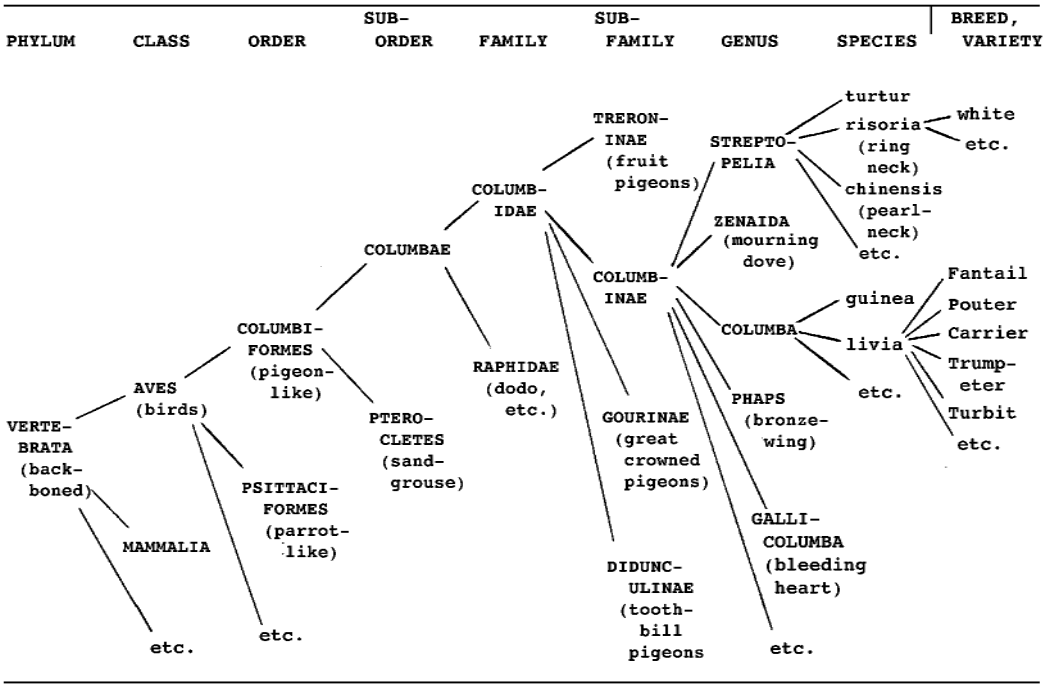
So now you know? Like the Dove of Peace, man?

—American Dove Association Bulletin, June 1975

PIGEONS — DOVES

Greek:	Peristera, Peleia, Phassa, Phatta, Treron
Latin:	Palumbus, Columba, Turtur
French:	Pigeon, Biset, Palombe, Turturelle
Italian:	Piccione, Palomba, Tortora
Spanish:	Paloma, Tortola
Dutch:	Duif
Danish & Norwegian:	Due
Swedish:	Dufva, Skvabb
Scotch:	Doo
English:	Dove, Pigeon, Turtle, Squab
Portuguese:	Pombo
Polish:	Golab
Rumanian:	Porumbel
German:	Taube
Hungarian:	Galamb, Gerle
Russian:	Golub
Czech:	Holub
Turkish:	Güverçin, Kumru

TAXONOMY = CLASSIFICATION



DEREK GOODWIN'S BOOK "PIGEONS AND DOVES OF THE WORLD"

Though this book is nearly as big as Levi's "The Pigeon", it has practically no other similarity, and Goodwin even refrains from citing Levi in his references! Issued December 1967 as Publication No. 663 by the British Museum of Natural History (London), it has 446 pages plus 3 color plates (paintings), and costs 6 pounds 6 shillings (over 15 U.S. 1969 dollars). There are no photographs, but numerous pen-and-ink drawings and distribution maps. The illustrations are credited to Robert Gillmor, but many are based on Derek's sketches.

Goodwin is not a fancier or even an aviculturist but an ornithologist especially interested in natural behavior. In this aspect of taxonomy he is a true disciple of C. O. Whitman. The bulk of the book consists of individual treatments of the hundreds of species of the pigeon-dove Order. Each species has for its heading first the chief common name, then its genus and species name, and the original taxonomic reference. Following these are paragraphs on description, distribution and habitat, feeding and general habits, nesting, voice, display, other common names, and finally a few selected references. Shading shows the species distribution on a sketch map. The birds are pictured simply standing or perching, not in display.

For the first 50 or so pages, Goodwin discusses general topics, including nomenclature, adaptive radiation, eggs, plumage sequences, and much on voice and habits. Of special interest to me are his "dendrograms"—tree-like diagrams showing his ideas of the evolutionary relationships of the species and genera.

Interestingly, Goodwin gives no weights or measurements but uses the feral common pigeon and Barbary (ringneck) dove as familiar comparisons. Probably weights are not available for many species, but measurements must be. Goodwin is usually frank to state "No information" if other data are lacking, and he desires to point out the extent of ignorance.

I find the book a long-needed compendium. Years ago Marvin Emery set out to prepare a magnum opus something of this sort but never completed it, much to my disappointment. It is a huge job. Other available books on the wild species are mostly fragmentary (Naether), or regional (Baker, Delacour, Mayr, etc.), or lacking descriptive detail (Peters).

Like most naturalists, Goodwin hardly touches on Genetics. He casually mentions species hybrids in his treatment of the Barbary dove, but seems unaware of sex-linked inheritance of the color: ". . . hybrids usually show no trace of the pale creamy tint of the domestic parent". He also has an aversion for mutants: "Pink-eyed albinos and birds with 'silky' and otherwise abnormal feathering have been produced in laboratories in America and elsewhere but are, happily, not yet commonly distributed.' But Derek, as far as I know all the mutants so far originated outside of laboratories! We have simply seized on them as grist for our Miller! And some of them are far from repulsive, even if not competitive in the wild. Incidentally, he also casually mentions "pink" mutant Wood Pigeons (*Columba palumbus*) existing in the wild, though at a disadvantage (page 8).

Goodwin has little appreciation for Immunogenetics—he refers to “biochemical studies of the blood antigens”, just once. But on behavior he expatiates. Strangely, he says he has not seen use made of the preen gland by pigeons. I have.

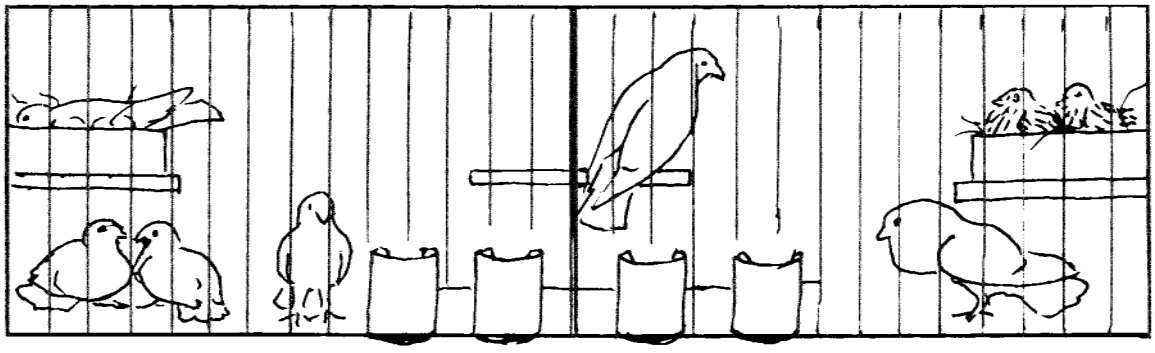
Speaking of the preen gland, did you know that the Crowned Pigeons (*Goura*) of New Guinea have no oil gland and have 16 rectrices? (Sounds like the Oriental Roller!) But try to find Crowned Pigeon in the index; despite the fact that the index is exclusively for names of the birds, that one got omitted. A fair number of typographical errors occur, for example “J. W. Miller” on page 24 (instead of W. J.). Well, maybe Derek was in a hurry to beat Emery. But don’t let these little things deter you from appreciating this really impressive work. Pigeons and doves of the world are not all in lofts, yet.

—P. G. N. L. No. 52, pages 30-31 (1969)

P.S. 1982: A second edition of Goodwin's book has been issued, but the errors noted remain.

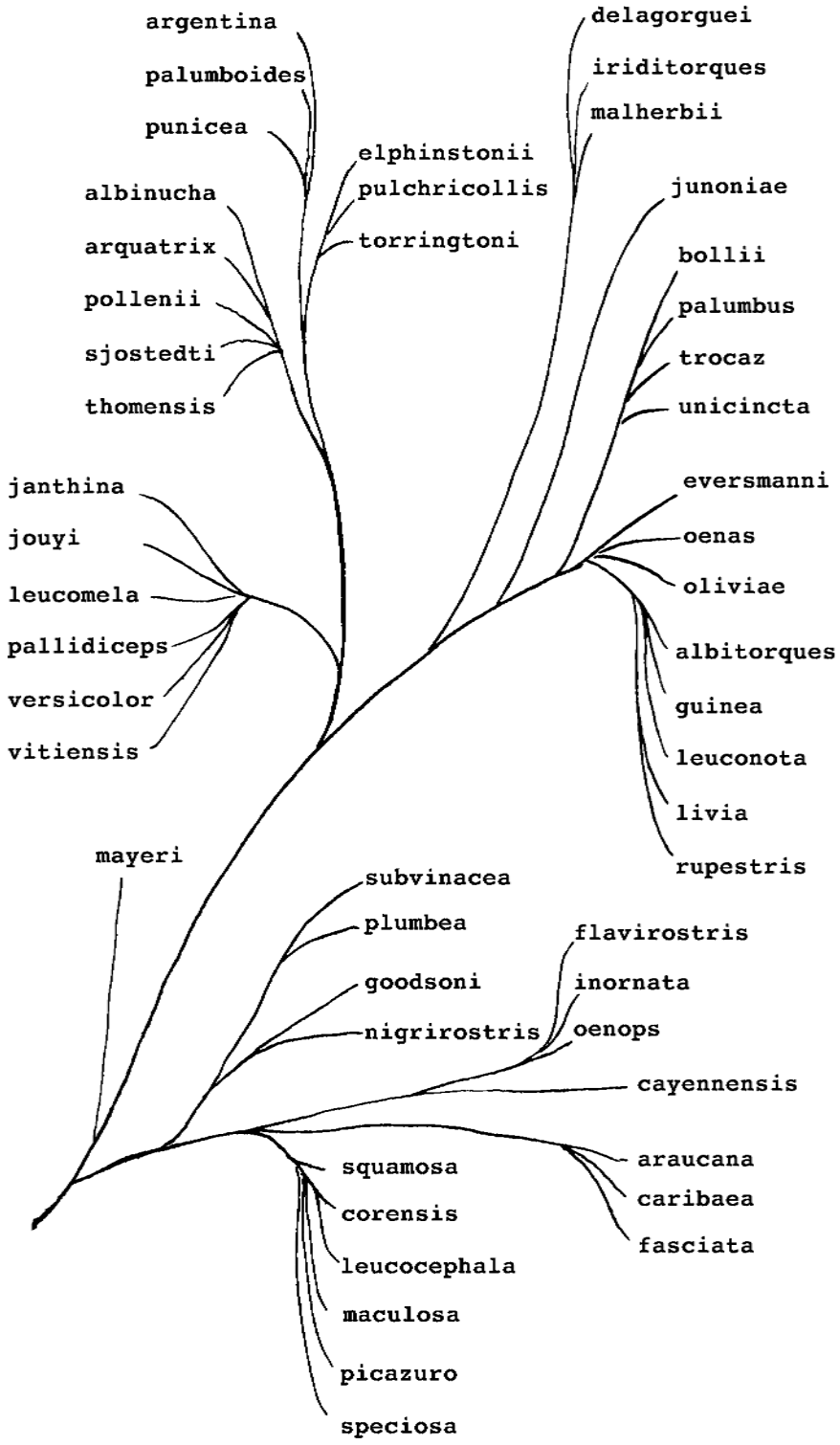
In 1969 a paperback of 74 pages by Jürgen Nicolai was published in Stuttgart, West Germany (Kosmos, Frankh Verlag) entitled (Care, Breeding and Species of Ornamental Doves). It has good sketches of 50 species, plus a color photo on the cover, and is a mish-mash of information about habitats, food requirements, cold-tolerance, and breeding. Common names are given only in German.

In 1975 Gerhard and Ruth Rösler produced a more extensive treatise: published by VEB Deutscher Landwirtschaftsverlag, East Berlin (DDR). It is 288 pages with sketches, some photos, distribution maps, taxonomic information, and common names in German, English, and Russian. There are several pages on reported hybrids and much information on care of wild species in captivity. Good bibliography.

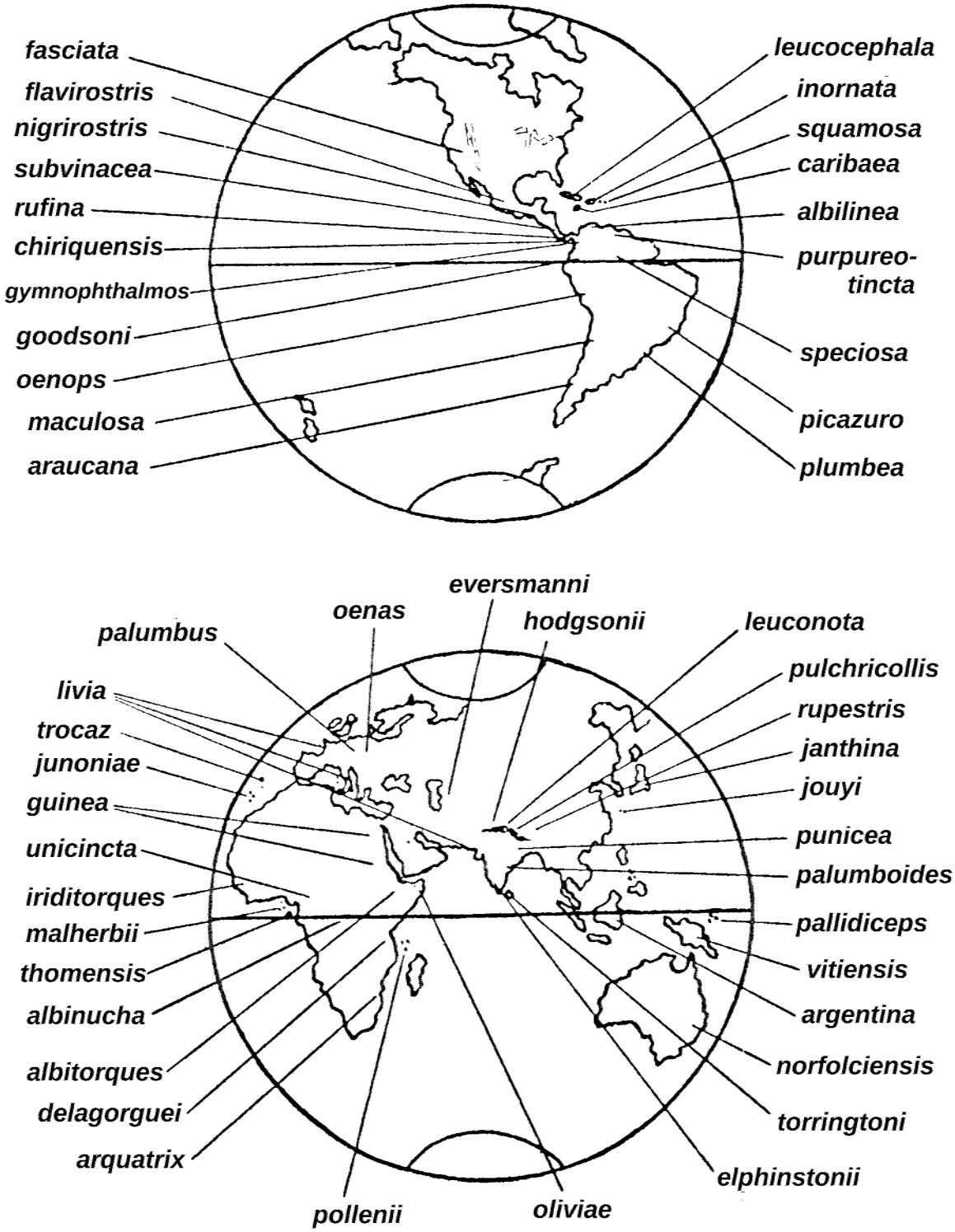


DENDROGRAM OF SPECIES RELATIONSHIPS IN GENUS *COLUMBA*

(modified after Goodwin 1970)



SPECIES OF *COLUMBA*



LIKE BEGETS LIKE — OR DOES IT?

Me: Here is a white egg in my hand. What will hatch from it?
You: How should I know?—maybe a turtle. What laid it?
Me: A bird laid it.
You: Well, naturally you'll get a bird from it.
Me: But what kind of bird?
You: Well, the egg is white, so it wouldn't be a robin's or a crow's or a killdeer's or—maybe a kingfisher?
Me: No, a pigeon laid it.
You: Well then, it'll produce a pigeon. Satisfied?
Me: No—what kind of pigeon?
You: For Pete's sake! Anything except a stool pigeon. What laid it?
Me: A Fantail laid it.
You: Well then, it will naturally hatch a Fantail.
Me: But what kind of Fantail?
You: Ye gods. Whatever kind they were that laid the egg.
Me: They were white with big tails.
You: O.K., it'll be white with a great big tail. Anything else?
Me: Will it be more like the father or the mother, or a blend?
You: I thought you said they were just alike.
Me: No, the father has 42 tail feathers and the mother 29.
You: Why didn't you ask me for a photograph of this future bird?! I guess it will be in between.
Me: You don't know?
You: No—I'm no magician.
Me: But you have already given me a much more definite prediction about what this egg would produce than a scientist using the most refined techniques of chemical analysis could have given.
You: But anybody knows that like begets like.
Me: Then as far as the parents are alike you can predict, but when they are different you can't?
You: That's it. Up to that point it's simple.
Me: Then if both these parent Fantails had 42 tail feathers, you'd say the squab would also?
You: Probably—I'm not sure.
Me: What makes you uncertain now?
You: Well—tail feathers in Fantails are sort of variable——.
Me: First you say like begets like and now you say sometimes it doesn't. Where is the dividing line?
You: Say, you're running me ragged. How do you expect me to know all the details of those questions?
Me: How can we find out more about those details?
You: Well, we could hatch the egg and see, I guess.

So we hatch the egg, and what do you know, the bird grows up to be a white Fantail all right, but it has 43 tail feathers and a crest on its head.

Scientific studies of cases where like fails to produce like have revealed three common reasons and a fourth which is less common. First, it is practically impossible to find two birds exactly alike in any trait: careful measurements reveal hair-breadth differences, at least. Such differences are often meaningless in heredity, as they may be due to feeding, climate, etc., or obscure fluctuation in the expression of a gene. This may account for some of the unpredictability of feather number in the Fantail, for example.

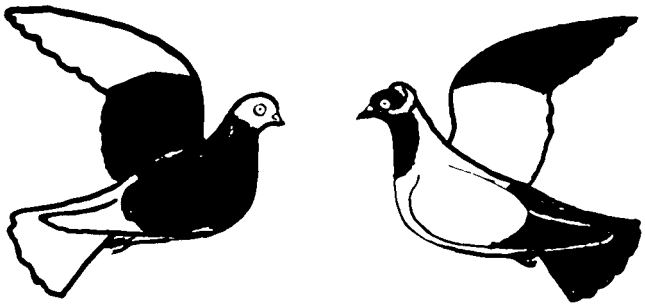
Second, the parents, although identical in appearance, may "carry" a trait derived from a previous ancestor, and this will appear in a certain proportion of the young according to Mendel's laws. For example, two black Owls may produce some solid red squabs; or two blue check Homers may produce some blue bars. Certain sex-linked colors behave somewhat similarly: a pair of blacks may produce some dun daughters, or a pair of red checks may produce some blue daughters.

Thirdly, there may be a case of mistaken identity. There are two very similar genetic types of red, which when crossed will produce some blacks; and two similar types of silver which when crossed will produce blue. A red Turbit hen mated to a red Tumbler may give some blacks, and a Silver King crossed with a silver Giant Homer may produce some blues.

The fourth and rarest cause of new or unlike types is mutation or sporting. Cases of sporting are hard to prove, as a rule, but proof has been available in a few cases. Sporting is rare because it is due to a break-down in the vital machinery or to some other unpredictable change in the otherwise routine processes of reproduction and growth.

These four causes tending to make like not beget like make it a bit dangerous to predict in detail just what would come out of that little white egg. And that's where the fancier's fun begins!

—American Pigeon Journal, December 1940, page 409



EYES FRONT

Fanciers constitute an army of attentive specialists around the world. Observation and trial and error are their forte, and an almost incredible register of experience is at hand. But most of these people do not realize that they are amateur scientists, and unlike amateur astronomers they are not under any coordinating arrangement. Perhaps they can be convinced that there is dignity in their "widow's mites" and that science cannot be entirely the realm of professionals. There is no need to flaunt jargon; the laboratory has no monopoly on clear eyes and minds. But there is need for communication.

SPLITTING BLOOD

Fresh blood! Good blood! Paternal, maternal, and thicker than water! But there has been bad blood among friends concerning the channeling thereof.

Whatever breeding system or lack of one is used, a pedigree results. According to the sages, a bird gets half his blood from the father and half from the mother. What could be fairer? Except that the mother seems to get less credit than she deserves, considering her greater labors in the matter.

Following this elementary calculation, the sages figure that a quarter of a bird's blood is from each grandparent. And an eighth from each of the eight great-grandparents. Continuing this pleasant train of thought, we note that there were 16 great-great-grandparents; further back, doubling the ancestors each generation, we get 32, 64, 128, 256, 512, and in the tenth generation 1024. Then each of these 1024 ancestors contributed 1/1024th of the blood of our bird?

This is all very delightful until we push further back. If we figure that it took about 20 years to get those ten generations, then a century ago would have taken us back 50 generations. To calculate the number of ancestors 50 generations back is a bit laborious with pencil and paper, but easy on a desk calculator. I reckon it at some trillions more than a quadrillion. If that number doesn't seem impressive, just think that there probably have not been so many pigeons in all since the landing of Noah's Ark!

Continuing these absurd calculations we soon reach fractions of blood more numerous than the number of atoms in the bird's body. That does it. I can't split blood that fine! Somewhere along this crazy path a lot of ancestors somehow must get canceled out. But that seems impossible too, since each ancestor was contributing 1/2 to its progeny!

What a bloody mess! But the paradox is easily resolved, by saying that *chromosomes* instead of "blood" are passed on. Our bird has let's say 35 pairs of chromosomes per cell; one of each pair from the sire and the other from the dam. Those from the sire were a presumably random-picked half of his 35 pairs, and the same idea for the distaff side.

By such figuring we can show that some ancestors even three or four generations back may be unrepresented in our bird, chromosomally. Such ancestors, and most of those further back, are merely ciphers, only of historical significance.

Maybe it's just as bloody well.

—N. P. A. News, May 1962, page 6.

LOISEL et MENDEL

Soon after 1900 and the re-discovery of Mendel's studies on heredity, a Frenchman, G. Loisel, tried to apply these new ideas to pigeons. He used official breeding records of Racing Homers, and classified the matings by colors and patterns. For example, blue X blue, checker X red, grizzle X blue, etc.

The results of these matings were confusing. They did not show any of Mendel's ratios, and they seemed to permit no simple rules. Therefore Loisel reported to the world that Mendel's laws do not apply to pigeons. Perhaps because of his strong opinions other Frenchmen were discouraged from further thinking about Mendel, and that is sad, because Loisel was mistaken.

Why was he fooled? Well, he was a newcomer in a new field, and the procedures had not been clearly established. He used incorrect methods. What was wrong?

(1) Mendel started with tested pure-breeding types for his crosses; Loisel did not.

(2) Mendel made careful assurance of correct pedigrees; Loisel's data involved flocks of pigeons where infidelity and other errors could occur.

(3) Mendel dealt with clearly-defined opposites; Loisel dealt with a number of colors and patterns.

(4) Mendel tested his conclusions by further breeding; Loisel did not.

Loisel's errors were recognized and corrected in England and the U.S.A. It was demonstrated clearly by careful breeding tests that Mendel's laws apply very well to pigeons. Some characteristics are however more complex than others, and it is sometimes difficult to classify. Experience is helpful.

Modern breeders can profit from these studies. They can ask what is known and what is yet unknown, in the scientific literature, and they also can ask the pigeons for answers, if the questions are clearly and simply asked: the progeny may settle the questions. Sometimes there are surprises.

Careful records are very important. A good notebook is needed, and it should be protected from damage (water, mice, etc.). If possible, test matings should not permit error: a single pair of birds in one cage is desirable. Many breeders have been fooled in flocks.

Mendel's clearly-defined opposites should usually be abnormal vs. normal. Pigeon breeders often dislike to consider large body size or pearl-colored eyes as abnormalities, but they are. We must recognize the truth of Darwin's argument that all of our domestic types are descended from the wild Rock Pigeon (*Columba livia*), and that it is the only normal type for us. A domestic breed may be abnormal in having a crest, and normal in other respects, while another breed may be abnormal in color only, and so on.

Each abnormality consists of one or more unit differences from the wild type. For example, Loisel's checker is such a unit, and in Mendelian terms it is dominant. His red is another. Pearl eye color is a recessive unit. Many such units have been identified; try them yourself to see how they work, alone and together.

—This article was translated into French by Mr. Bernard Cau
of Marseilles, for the French Mondain Club (Paris), March 1972

GENETICS, QUO VADIS?

Well, I made it to the St. Louis National, and do you know what one bird there got the biggest crowd of admirers? It had a white ground color, but the wings had lovely purple, yellow and green bars. Lots of gawkers wrote down the owner's address and the name of the pigeon. A funny name; in German it means "Hoax". Yep, George Kleinpell done it with his little palette.

If the gawkers had known it was a paint job, wouldn't they have been disgusted! That's sort of ironic, because most fanciers will carefully trim, bathe, and train their birds for the show. Why not paint 'em too? But no, that's too artificial. Better bred than dyed!

What are the great color achievements of pigeon breeders? I would name Archangels, Swallows and Ice Pigeons, Modenas, Lahores, and Oriental Frills as outstanding. All were produced before the science of Genetics was established after 1900. Their creators were artists in flesh and blood, bone and feather; theirs is a sort of craft union.

But some modern fanciers have let their gaze stray over to what goes on in Genetics, and have seen revelations. Sometimes there are revelations of hope, sometimes of ignorance or awe. But they often cause ructions in language. When fanciers begin talking about "homozygous dilute recessive red", their brethren know the science bug has been biting. When the bite is bad, the victims develop delusions of intelligence and a messianic urge to change color-class names on show tags.

The fact remains that nobody has bred a domestic pigeon with scarlet, green, canary-yellow, or sky-blue plumage color effects. But that cynosure of the St. Louis show proves that such colors would sell if we could ever breed them. It must be possible—not only parrots have such colors, but also a number of wild tropical "fruit pigeons". Real flamboyance.

Oho! you say, let's cross 'em! But the scientist is pessimistic. Can you cross cats with dogs? No, a mutation must be the key. And what do we know about such things?

Well, we know that mutations are tiny changes in the chromosomes. We are beginning to learn how such changes are produced, and we hope to learn how to produce the ones we want. Meanwhile we shoot blind, and get mostly freakish effects.

Visitors looking at my birds are often horrified. One commented "Why do you keep those poor things—blind ones, featherless, wobblies, toeless, and so on? It's cruel to keep them alive." Well, there's a point all right—something like Hitler's point in putting the poor

Jews out of their misery. But there's a different point to my "cruelty"—if each kind of genetic freak is due to a changed spot on a chromosome, my breeding tests can help locate those sites. It is a slow and difficult job, but no one has found a better way to get such knowledge. Maybe after a century or so of such "cruelty", with hundreds of freak types, we will begin to master the complexities of these "blueprints of heredity."

To a breeder infected with the Genetics virus, breeds are like makes of cars to a mechanic; familiar, fairly reliable, but not sacred. He begins to imagine all sorts of new combinations, such as a Cadillac motor in a Jeep, or Volkswagen wheels on a Ford. He may even go beyond imagining and start tinkering, and the result may be a sad mess indeed. But a good mechanic can become an engineer.

Working backwards, we may be able to deduce how our present breeds were developed. I remember once having a conversation with Jay Brushart, the late great fanfarer for the Trumpeters. As I recall, it was at a National in Camden, N. J., and we were having a bit of midnight refreshment. Jay thought he could make a Trumpeter fancier out of me.

"Doc," he said, "now don't you agree that the Bokhara is the acme of the breeder's art, the pinnacle of perfection? But its origin is lost in limbo. The breeders that nurtured it over the centuries never heard of Mendel's laws or read Levi's book, and maybe it was a good thing. What's so all-fired wonderful about Genetics, then?"

"Jay," I replied, "if the Bokhara were to become extinct tomorrow, as it has often threatened to do, we could build a reasonable facsimile in a few years with the aid of Mendel's laws. Just take the muffs, the crest, the rose, the long loose feathering, and the voice from other breeds and slap 'em together."

Brushart leaned back and wiped beer head from his mustache, his eyes wide with what I took to be admiration. But it wasn't. "Doc," he said sibilantly, "you are just a plain damned coldblooded scientist. If it weren't that I have a morbid fascination in seeing how the other half live, I wouldn't have any more truck with you."

Ho hum, and they say they aren't appreciated in their own country. Well, East is East, and West is a fur piece; to each his own, but on the other side of the zig zag date line there is the lure of strange music, spicy aromas, visions of loveliness, riches, and an exotic philosophy. Surfeit can bring revulsion again, but opposites can attract and complement. I can use your freaks, and maybe you can use my crude blueprints.

Heigh ho, back to the show!

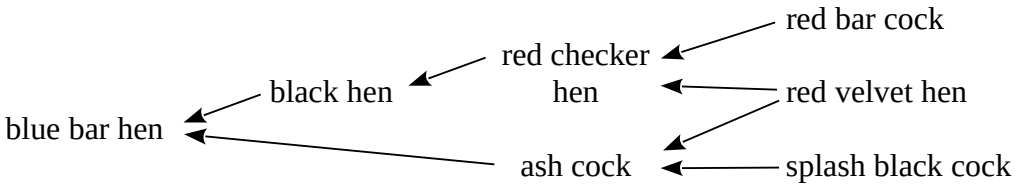
—American Pigeon Journal,
July 1963, page 203

YOU GOTTA BELIEVE THE BEGATS?

How valuable is a pedigree? Partly it is a matter of faith. Who can tell if something has been hoked? Who has a secretary to double-check all the records? And if the pedigree includes errors, is it better or worse than nothing?

If we have faith in the writer of the pedigree, it may still be possible to find errors, and if we are suspicious, it is worth looking for hokes. For example, in the pedigree of a supposedly top bird in a reputable loft I noticed there was a red checker grandmother out of a pair of blue bars. According to all we know about color Genetics, something is screwy here: red checker is the combination of two dominant genes compared with wild-type blue bar, so the parents could not have been hiding them. Possibly the bird's coloration had been described wrong? But that hen's son in the pedigree was mealy red bar, by a blue cock. Looks to me as if she had been the result of one of those things—wrong cock treading. Anyway, a big hole is blasted in that pedigree.

In our laboratory breeding we use individual pens to preclude such errors. Generation after generation in such pens can produce pedigrees that are really reliable, even if they sometimes are astonishing. Look at this gem:

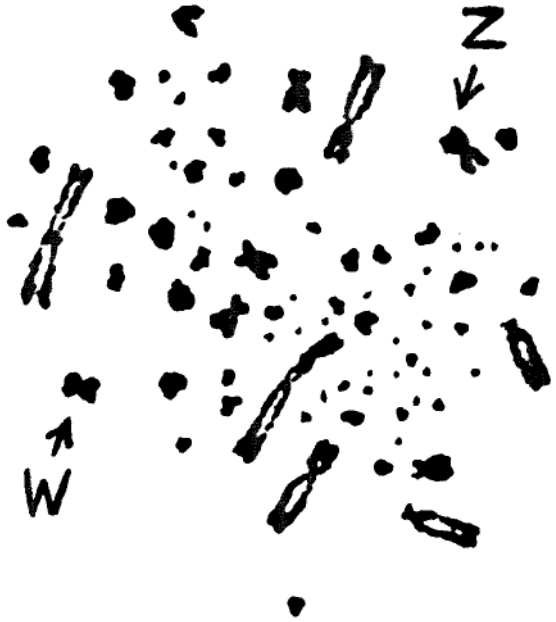


Yes, that's a complete pedigree. Only three great grandparents in this case instead of eight. We don't fill in printed forms—just any writing paper or even bigger sheets, one generation after the other and connected with arrows. Each arrow represents an egg or sperm so a bird must have one from each parent. But a lot of eggs or sperms (arrows) could come from a particular bird. The ash cock, for example, served as grandsire and as sire.

That's four generations with no two birds alike, but we know it is correct. And the thing does make sense. There are five dominant genes to follow, none of them pure, so it is a 50-50 chance for a progeny to get the one that is in a parent. The blue bar hen is a beautiful example of reversion—Darwin's famous "reversion to the wild type," at least for color. What happened? She just happened not to get any of those genes. It didn't have to result; and actually she has a sister that is a red checker.

With the arrow method it is not too difficult to put an entire strain on one big piece of paper, so that each bird has its place and the arrows intertwine as best they may. It is easy to spot the really influential birds—the ones with the most arrows. To my way of thinking, such charts are almost indispensable guides. Since I make my own, I trust them. If you make your own, and if other breeders see your trust, they will be convinced too. But without individual mating pens, errors can happen.

—American Racing Pigeon News, October 1971, page 17



PIGEON CHROMOSOMES

Magnification over 1000X. This is a spread of the chromosomes at metaphase of mitosis from a female embryo; they have started to divide, leaving connections at the centromeres. More than 70 chromosomes are visible, but only the larger ones are easily recognizable. Arrows indicate the Z and W sex chromosomes. Reference: Galton and Bredbury, 1966, Cytogenetics 5: 295.

Another example of metaphase chromosomes (in mitosis). These were from a cell of an adult female pigeon; they have not yet shown the beginning of division. Magnification about 1500X, stain preparation by Stock et al., 1974, Cytogenetics and Cell Genetics 13: 410. As in the preceding figure, one can see three pairs of relatively long chromosomes, while the rest grade down to tiny dots so that accurate counting is very difficult.

GENETICS—MUST IT BE ALL GREEK TO ME?

Some of the explanations of Genetics that I have tried to read in All-Pets may have been well intentioned but they certainly failed in their purpose. What good is it for me to learn what syngamy means? Or apomixis? Or zygotene? Or even parthenogenesis? Maybe the author thought such language would be professional, or perhaps good for the soul, but a breeder wants something more practical, down to earth. Now I realize that atom bombs and television were not invented by “practical mechanics”. But the practical mechanics that build and service such things have to get their training in straight-forward language, or else.

But language isn’t the whole trouble either. If I want to know what will be the prospects from crossing a White Leghorn hen with a White Silkie cock, for example, I don’t exactly get up and cheer when I’m told that ABCDEFG X QRSTUV theoretically should give LMNOPDQ. Anybody can mumbo-jumbo with the alphabet, but what is it all about? Genes, maybe, but are genes like tiddlewinks, marbles, or baby’s blocks? And how can you tell one from another if you can’t even see them?

There is a solution, and I think the budgerigar breeders are closer to it than most of the rest of us. They were sort of lucky, I think, in starting to breed them only a century ago, so that the origin of the breeds or rather varieties is not such a mystery as in the case of chickens or dogs or goldfish. The budgies started with a monotonously uniform type, which was about all that could be got, since they were wild birds. And then what happened? Sports appeared occasionally, and they were the foundation of strains of the same new sort. And then what happened? These new types were crossed together, and combinations were produced. The mathematics of this is simple enough: one sport gives one new strain; two sports give two new strains plus one combination; three sports give three new strains plus three new combinations of two plus one new combination of three; and so on. If no interference occurs, every new sport doubles the potential number of varieties. With only ten sports, over a thousand varieties are possible. But building all of them may not seem worth while; a breeder can sort of visualize that certain combinations would not have much appeal even before he makes them, so many of the potential varieties are never used. Anyway, a thousand varieties would be a zoo all by themselves. So the varieties that hang on are usually the original sport types and a few of the most interesting combinations.

For the budgerigar breeder, Genetics boils down to this: an intimate knowledge of all the single sport types. For they are what he is using in combinations; they are his building blocks, but no two are the same even if they look quite alike sometimes. Some of the sport types are dominant to the original wild type, others are recessive. These are essential facts to know about them. Some may be sex-linked, others not. Some may be linked with each other, more or less, and others not. Such information doesn’t come from guessing or books but from actual breeding, careful recorded tests of the sport with the wild type and with every other kind of sport. But even the budgerigar breeders have not made up comprehensive lists of the accumulated information. They haven’t even finished accumulating it.

Perhaps I have conveyed to you a glimmering idea of how simple and orderly a system these budgie breeders have nearly latched onto, even if I haven’t used any Greek. Butyou will say, we don’t know the original sports in cats, or chickens, etc. That’s fine for the budgie breeders, but what about the rest of us? And that’s just the point—we should

ANALYZE, take our breeds and varieties apart by crossing with the wild type, and work out what these original sports must have been. After all, the essential feature of a sport is that it is a unit difference from the wild type; it does not split into several types when tested, the way most breeds will.

Sure, I have eased over some rough spots; some sport types are clear-cut, some are not so clear. But the principle holds anyway. Of course, the idea of such tests with the wild type may be abhorrent. “I wouldn’t think of bringing a mangy old alley tabby into this cattery, much less mating it with any of my prize-winning Persians!” Well, there is logic in that; and anyway, maybe George will do it. And what’s more, maybe he has already done it and we just haven’t read all the literature to learn about it. But I see no other way to make a coherent scheme. Genetics doesn’t apply only to Persian cats, but to all.

A beginning of this sort has been attempted for chickens by F. B. Hutt in his book (1949) on the genetics of the fowl. But it can stand improving. I’ll attempt to illustrate what can be done, with a good list of sports, or primary mutant types if you like that term better. The color of the wild-type fowl is the common black-breasted red, like in “Brown” Leghorns, etc. Okay, one of the analyzed primary mutants is the well-known “silver”, as in Games, for example. Another is the “pile” color, also found in Games. But names aren’t enough. We must know more about these types. Okay, let’s study them. Silver chickens differ from the wild-type color in lacking most of the red or gold color—nothing else different. In crosses with the wild color, silver has been found to be dominant, and also sex-linked. Well, that is enough on silver for most purposes. Now about pile: these birds are red and white; they differ from the wild color in lacking practically all the black—no other difference. Crossing with wild color shows pile also to be dominant, but not sex-linked. Now look ahead to what may happen when these two primary mutants are combined by crossing them together: can we predict what a silver-pile chicken will look like? We can, quite accurately. It should lack most red and yellow (the silver effect), and it should lack practically all black (the pile effect). Result: the bird should be practically all white. And it is.

Going back to the question about White Leghorn X White Silkie, if we know the mutants making up each of these breeds, predictions should not be too hard. Well, the White Leghorn has the silver and pile mentioned above, and also usually a couple more for color, blue, and barring. The Silkie also has silver, but a different pile type (a recessive white), and a lot of others: black skin, crest, beard, extra toes, rose comb, short tail, feathered shanks, and of course the silky feather structure. A list of all these with what is known about them individually would help vastly in figuring out just what sorts of combinations we can get. But in the first generation the color should be white.

Perhaps it doesn’t seem the fancier’s job to do all the work of compiling such lists. Maybe it is a job for a big organization. But I think every breed should be so analyzed, and the facts published. Genetics may not be simple, but it certainly doesn’t need to be all Greek.

All Pets Magazine, March 1956, pages 61-64

THE INHERITANCE OF BLUE

At least a hundred times I've been asked to explain the inheritance of blue. If you don't know the answer already, I hope you will be shocked. Blue is not inherited. Inheritance implies transmission from parent(s) to offspring by eggs and sperms. As every school child knows, the parents keep their color, at least until they molt, and even then they don't transmit it to the squabs. Look in any egg and you'll never see a bit of blue—just white and yellow.

Now that we are straight on that point, somebody will of course ask, "Well then where *does* the squab get the blue?" Get it?? No, he doesn't get it; he grows it. And next somebody will ask, "Isn't there some inheritance at all?" Sure there is—chromosomes. But chromosomes aren't naturally blue.

Next question: "But I thought it was genes that are inherited. Aren't they?" Hmmmm. Well, it is theorized by the pundits that chromosomes are long chains of genes. However, it is so far impossible to see these hypothetical units, whereas chromosomes are visible enough.

"Then we shouldn't talk about genes?" Oh, did I say that? Sorry, talk all you like about 'em. "O.K., I'll talk about a blue gene." "Talk away, but I won't listen."

"You mean you don't think there is a blue gene?" Blue jeans, yes; blue gene no. Not any more than a blue chromosome.

"But there must be one so the pigeon can be blue!"

"I'm blue too because you are missing my point. You think because you use the word gene that you are on the verge of understanding blue pigeons. Alas, not so."

"O.K., you explain it. That's what I wanted in the first place."

"It's too complicated for me to understand."

"You're a big help."

"I hope so. It was really nothing."

"Even less. All I've learned is that you think blue isn't inherited and there isn't even a gene for it."'

"Exactly. But I didn't say blue has no inherited basis. The basis is probably so complex that the whole story would take a book to explain."

"I don't see why you make it so difficult. Don't you talk about a gene for recessive red, or a gene for dilution?"

"Indeed we do. Those are units identified by being different from blue. Blue is the wild type, normal, standard of reference. Recessive red or dilution are departures, changes, single and identifiable. Many other mutants are also known."

"Then blue isn't single and identifiable?"

"Correct! If you want a crude analogy, blue is health, while recessive red is a specific disease, so to speak."

"My red birds are just a healthy as my blues."

Well, I tried.

—National Pigeon Assoc. News, December 1965

MUTATION — DID YOU REALIZE

1. That prior to 1900 the word for sudden change in heredity was "sport"?
2. That Hugo de Vries about then proposed that such a "mutation" could be the origin of a new species?
3. That later studies indicated species differences to be less simple.
4. That analysis of heredity in domestic types is typically the demonstration of what differences (mutants) exist from the normal or standard wild type of the species.
5. That the demonstrated mutants are probably only a small fraction of those which have occurred, the rest mostly having been culled as worthless or worse, or having escaped analysis yet.
6. That mutation was not controllable until H. J. Muller proved the efficacy of X-rays in producing them, in 1927.
7. That most mutations produced by X-rays were found to be lethal (causing early death), and involve chromosome damage.
8. That the war gas, nitrogen mustard, was proved to be as effective as X-rays in mutagenesis, about 1942.
9. That radioactive substances such as fall-out from atomic fission can be strongly mutagenic.
10. That many other non-radioactive chemicals are now known to be mutagenic, such as urethane, trypoflavin, nitrous acid, aflatoxin, etc. New ones are being found effective, and also may induce cancer.
11. That dominant mutants are easier to get rid of than are recessives because the latter can be hidden.
12. That each new mutant retained theoretically doubles the possible number of combinations from crossing.
13. That the more mutants, the more genetics, the more work, the more mysteries, the more—

—P.G.N.L. No. 70 page 20 (1974)

Q&A re +, or Lost in the Wild

Q 1. What's so special about wild type?
A 1. It was made by natural selection.

Q 2. But aren't there lots of wild types?
A 2. Not in one species; taxonomists have a "species type".

Q 3. What about sub-species?
A 3. For convenience these can be regarded as variants.

Q 4. Is convenience a sensible argument in science?
A 4. Yes: consider the standard meter, for example.

Q 5. But should convenience hide the fact there there is variation in a species in Nature?
A 5. Who is hiding it? Having a reference type, preferably that which is most frequent, makes it more feasible to evaluate the variation.

Q 6. Then can't some of the variants found in Nature be the same as those of domestic breeds, etc.?
A 6. Certainly, for example albinos. Generally it is not difficult to see that natural selection will not favor them.

Q 7. How about checker in pigeons? What's wrong with it?
A 7. I don't know; perhaps the bar pattern has some camouflage value in the Rock Pigeon *Columba livia*. In *Columba guinea* however checker is wild type.

Q 8. But you use the letter *C* for the checker gene and + for bar, don't you?
A 8. In *Columba livia*, yes, checker is regarded as a mutant or non-standard allele.

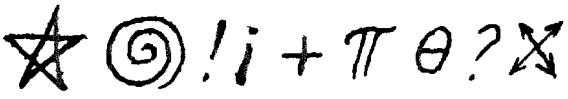
Q 9. You mean that in *Columba guinea* the bar gene would be *c* and the wild type checker would be +?
A 9. If you are not considering the relationship between species, that would be logical.

Q10. Then if you crossed wild *Columba livia* with wild *Columba guinea*, you would be crossing + with +?
A10. Ah, now you are demanding a consideration of the species relationships, and a different symbolization is required. We could use one species as the standard of reference and consider the other as the variant type, or we could identify all the differences by a species tag.

Q11. Wowee, Doc, are you sure that doesn't get too messy?
A11. No.

Q12. What about wild type for people?
A12. I think we better stick to pigeon Genetics here. . .

—P.S. & G.N. No. 2 page 15 (1976)



DARWIN'S MYSTERY—MENDEL'S SOLUTION

Atavism, regression, reversion to ancestral type. Or, to use less refined language, throwbacks. These were impenetrable mysteries before 1900. Galton tried to explain with his statistical Law of Ancestral Inheritance, but even he could not account for a cross of two pure breeds giving progeny all like the wild ancestor, perhaps a thousand generations before. Magic? But no! Mendel, yes! And so simple.

Let's take a simplified example: a purebred Damascene cock with a purebred barless Coburg Lark. Both of these are highly selected types, and presumably have no common ancestry for perhaps a thousand years. But all their cross progeny look practically like wild Blue Rocks, and even behave like them. We can say that all the cherished characteristics of each parent disappeared. And that is precisely the Mendelian answer: each breed has essentially recessive characteristics. Not recessive to each other, but to the wild type. Each parent has different recessives, and is otherwise still wild type. The Lark is barless and dilute but the Damascene is neither—it is iced, while the Lark is not. So the hybrids are not going to show any of these characteristics. Bingo—they look like Adam and Eve.

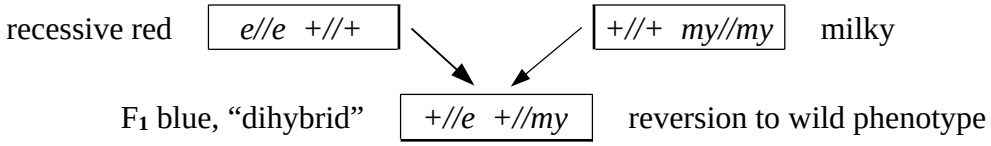
Those hybrids are beautifully alike in appearance, but if we mate them together, what will they produce? Variety, man. Those recessives ain't lost—they are just hiding, and they may sort out in any combination. Maybe even a throwback to pure Lark. And maybe something new—a barless Damascene?

Some crosses don't give reversion in F_1 but maybe later. Take a Black Barb X White Fantail. Hybrids from these are likely not to look like Blue Rocks, but in F_2 some young may revert all the way. Mendel to the rescue again: the characteristics of the pure parents are not all recessive, but they are different in each. Recombination in F_2 may eliminate them.

Knowing the recessiveness or dominance of the various domestic characteristics and the composition of each breed or variety, we can predict quite reliably what to expect from most crosses. We can plan, we can dodge, we can make Mendel jump through hoops. The only trouble is, we do not yet know all about each domestic characteristic.

Atavism is generally considered the opposite of progress. But not all progress is panacea—we can sometimes advance into a rose garden and find it full of thorns from which we may want to retreat. And from atavism we may also have a better understanding of our directions.

—Rare Breeds Pigeon Club Bulletin, March 1974, page 38



DELUSIONS OF GENETICS

During the last 15 years numerous fanciers became convinced that genes and Mendelian laws of heredity exist. What's more, they have made genetics a sort of new indoor sport. It has the pleasures of solitaire, and also some possibilities of competition.

One breeder complained to me though that he produced more "pot pie" than the family could eat. Another said that his cross matings were squeezing out his show birds. But the biggest trouble of all is results that seem to violate the rules, or are incomprehensible. This is often the case in color crosses. I have had scores of letters about this. Sometimes I can clear up the problem easily, other times not.

The application of Mendel's laws is easy if classification is clear. But if the distinctions are foggy, or if graduated differences exist, the whole basis of Mendelism crumbles. Usually the trouble arises from careless observation, or prejudicial names for classes, but there are plenty of "mimic" types to puzzle anybody.

Let's look at cases. An enthusiastic new fancier wants to see for himself about this "recessive red" business, so he crosses a rich red Carneau hen to a blue bar Homer cock. According to the book, he figures all the squabs will be blue bars. Comes the dawn: he gets a mess of dusky reds and bronzed black checkers. Wow! the laws don't work! Call the experts and give 'em razzberries!

So the expert tries to wiggle out. He says the Carneau had three kinds of red, not just one, and also pattern genes to be dealt with. Sad to say, this seems to be a sort of rule—the "better" or richer a color, the more likely it is to be a compound affair.

Here's another example. The Dutch pigeon genetics student, Bol, back in 1926 thought that "storked" grizzles were of the barless pattern. But in his tests he never found barless blues coming out. Reason? His assumption was wrong.

The classic case of "look-alikes" of course is "dilution" and "brown". These have both been classed as "silver" in most shows.

A lot of fellows expect me to be able to look at problem colors in the show, or at feathers they send me, and give a final decision as to what gene is there. Well, I can be fooled almost as easily as anyone else. A microscope is no help in such judgments.

What's a person going to do in such a case? How can a decision be made? The answer is simple: progeny tests. Of course, progeny tests take a bit of time; but one just can't rely entirely on one's eyes.

Suppose we have a hen that looks to be ash-red, but we want to be sure. Cross her to a blue bar cock. If she is ash-red, then the result should be a sex-linked "criss-cross", sons ash-red, daughters blue. But suppose all the squabs (four of them) are red. What does that mean? Maybe no daughters were produced yet. The test should go on, to rule out this chance. Or suppose we get all squabs (a dozen of them) intermediate in color. This would suggest that the hen was not ash-red but pure indigo. Or, a third possible result, suppose all the squabs

(12) are ordinary blue. That would point the finger of suspicion at some recessive gene, say opal.

A single test may not give the answer. Some of my tests are more intricate and time-consuming, going on for several generations. Here one gets the thrill of exploration into unknown territory, of discovery. One must keep an open mind, make cautious judgments, and not leave records just to memory. We mapmakers must show our routes.

The "stencilled" effect of Oriental Frills is an example of another sort of difficulty. Here we are pretty sure that the character is not confused with any others, but it seems to go to pieces in crosses. All the first-cross progeny are plain blue. If it were merely a single recessive gene effect, then in the second generation about 25% of the progeny should show it again. But the percentage is not nearly so high—More like 5%, and not very obvious at that. What's wrong? Well, maybe the character should not be classified until the bird is two years old? Or, maybe there are two recessive sets of genes, not one, needed to produce stencilling. More tests are still needed.

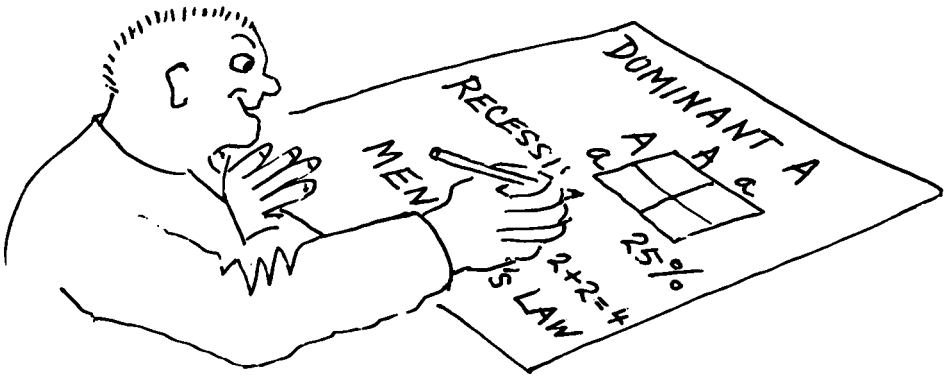
Still another problem is posed by the "powdered" effect of the Damascene. The cross progeny look sort of intermediate, and later generations show no clear-cut divisions between grades of powdering. The gene (or genes) involved here can't be readily grasped as a unit. Better classification must be devised.

The biggest headache of this sort is the white and pied effects. Not only is each of these a slippery customer, but the relationships among them are very tedious to work out. The solitaire game here isn't enough—a large-scale exploring expedition needs to be equipped!

A lot of genes have been "nailed" by fanciers, and some of these are being put into shows in new combinations. Al Westling is introducing barless (blue) and the "reduced" color into Tumblers. Irvin Goss and Ed Blaine have introduced indigo into Giant Homers. And many other seeds are sprouting.

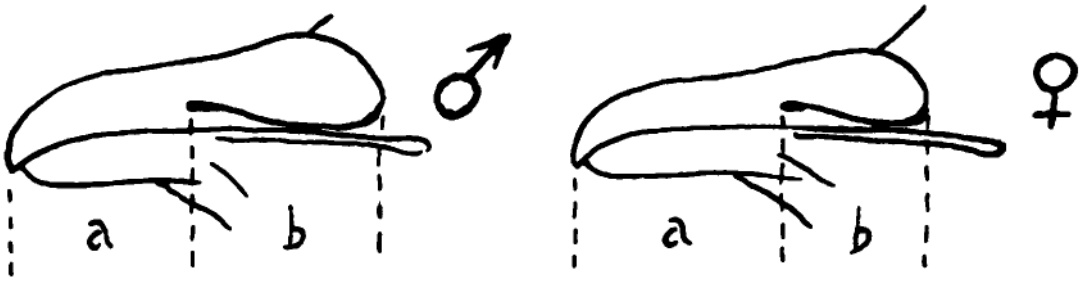
These are mere scratches on the surface compared to the possibilities. The fun is just beginning, and the pot pie will never end.

—National Pigeon Assoc. News, March 1957, pages 11-13.



NOTES ON SEX DIFFERENCES

With a pocket ruler and pencil I think I have found a reliable sex difference in the relation of beak to nasal cere (wattle) length in common pigeons:



I also measured a lot of Racing Homers and King crosses etc., and unfortunately (?) the difference was either slight, absent, or reversed. I haven't measured any other breeds—hope you specialists will take up where I have left off. Anyway, I am wondering if these peculiarities are related to the body-weight phenomena reported by Riddle (1947); his Magpies for example showed no sex difference. Probably sex hormones are not involved.

I was looking up castration effects recently in connection with Riddle's work. Levi cites several studies, but there were earlier ones: T. H. Morgan 1918 American Naturalist 52: 26; A. Lipschütz and O. Wilhelm 1928 C. R. Soc. Biol., Paris 99: 691; A. Lipschutz 1931 ibid. 108: 690.

Herman Smith informed me some years ago that he had experimented with male hormone effects. Injected into squeakers of either sex it resulted in rapid development of adult masculine behavior and mating. He should present more details in PGNL, don't you think so?

—P. G. N. L. No. 50 page 9 (1969)

FLECKS AND SEX

Probably every pigeon fancier who has looked around a little bit has seen and wondered about black flecks, specks, "ink-spots", or the like, which often occur in light-colored birds. The flecks are well known to breeders of Racing Homers, in mealy or red checker birds. These color varieties exist in many other breeds also, of course, and are now collectively known in pigeon genetics by the term "ash-red."

Charles Darwin in his great work "The Variation of Animals and Plants under Domestication", published in 1868 and a second edition in 1875, has almost 100 pages on pigeons. The flecking puzzled him too. He wrote: "The existence in France of a wine-coloured variety of the Pouter, in which the male is generally chequered with black, whilst the female is never so..... Dr. Chapuis also remarks ('Le Pigeon Voyageur Belge', 1865) that

in certain light-coloured pigeons the males have their feathers striated with black, and these striae increase in size at each moult, so that the male ultimately becomes spotted with black."

Breeders of almond or magnani colors also realized long ago that sex and age differences in the spotting or mottling of those varieties are important. Attention was called to these facts in 1908 by the Italian scientist Ghigi. He said (translated): "In spite of the most rigorous and accurate selection, mating among them the males and females best characterized (most marked with black) it is not possible to obtain in the females the variety and intensity which can be obtained in the males." Ghigi then theorized: "Evidently we do not have true and real variations in tint, but only a mosaic of colors existing in the progenitors with the predominance of one tint rather than another. The magnani is derived as a result of complicated hybridization in which the colors of the progenitors appear one next to the other ..... dominance is imperfect..... the influence of the testis determines the dominance of the strong colors and most of all the formation of the mosaic."

By 1925 it had been established that ash-red and almond were both dominant and sex-linked factors (Cole and Kelley, 1919, at the University of Wisconsin, and Christie and Wriedt, 1925, in Norway). At the University of Wisconsin careful studies were made of ash-red. Steele (in an unpublished thesis,1926) concluded that (1) males more often exhibit any flecking than do females;(2) flecked males generally show more flecks than do flecked females; and (3)flecks in females are "dunnish", not as dark in color as those in males. Ghigi's idea that the testis is a controlling agent was tested by Hawkins (1931), who castrated flecked males and pulled feathers repeatedly. No decrease in the flecking resulted. Hawkins further demonstrated that the brown color (for example in Silver Kings) is caused by a recessive sex-linked gene and that it seemed to bean alternative (allele) of ash-red. Males having both the ash-red and the brown genes were ash-red with brown flecks only, not black ones. Males having two ash-red genes (homozygous) had no flecks at all. Hawkins did agree with Ghigi's idea of incomplete or mosaic dominance; he said: "Flecking is merely a result of a heterozygous condition." Unfortunately, Hawkins somehow never saw a fleck in an ash-red hen's feathers. As a hen has only one sex chromosome, transmitted from her sire, and none from her mother, she cannot have two sex-linked alleles heterozygous. Therefore, Hawkins' theory was easily demolished by proof that ash-red hens do often have *brown* flecks.

It is generally stated that to use ash-red in sex-linked matings, the hen must be ash-red and the cock blue-black or brown. Then the squabs will be the reverse:ash-red sons, daughters other color. Advice is usually given not to mate ash-reds together, as only the blue or brown squabs from such a mating will be of known sex (female). But by means of flecking, one can sex the ash-red squabs fairly well even from matings of ash-red cock X blue hen. Almond is a different story,because the flecking in almond hens looks about the same as in cocks.

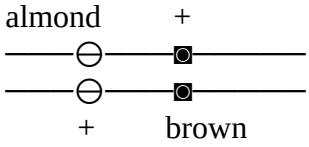
In 1926 Serebrovsky of Russia reported his studies of the genetics of chickens, in the Journal of Genetics. He noted that purebred Plymouth Rock hens(sex-linked dominant barred gene) often had black flecks, and that "blue"(Andalusian) fowls had black flecks. Blue is not sex-linked, but incompletely dominant. Homozygous "white" Andalusians have blue flecks, plentiful. Serebrovsky suggested that flecking is loss of the light-color gene, here and there, in the plumage.

Further studies of such phenomena were also carried out with fruit flies and with plants, where the term ‘variegation’ was applied. More than one mechanism was discovered to be involved in different situations—there might be real loss, or the gene might be unstable. In cases of instability, the gene seemed to undergo mutation, changing to another allele.

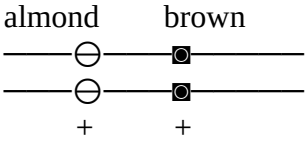
In 1940 I got into the flecking study, with Dr. L. J. Cole at the University of Wisconsin. Our 1940 report concerned ash-red, almond, and faded (a new allele of almond). We decided that there was one big series of alleles: almond, ash-red, faded, wild-type (blue-black), and brown, in descending order of dominance. To explain the flecking we suggested that the almond gene is very unstable, ash-red somewhat unstable, and faded a little less so. Each might change to a lower allele in the series. One particularly interesting thing that we discovered was that an almond cock out of brown X almond has both brown and black flecks.

Our beautiful theory of 5 alleles collapsed in 1943 with the discovery of a faded brown hen. She was out of back-crosses to Silver Kings during the development of auto-sexing Kings. According to the sex chromosome set-up, a hen could not have two alleles. Therefore, the genes for brown and for faded must not be alleles, and a new theory of two series was required. Series (1) then consists of ash-red, wild-type, and brown; series (2) includes almond, faded, and a different wild-type gene. According to this, it should be possible to produce three more new combinations in hens: faded ash-red, almond brown, and almond ash-red. A multitude of cross combinations should also be obtainable in cocks. (Reference: a review paper by me, 1944.)

In 1948 I finally obtained the almond-brown combination. Unlike ordinary almond hens, almond-brown hens show only brown flecks, and almond-brown sons of such hens X brown cock have also only brown flecks. And now a striking fact appeared: an almond son of an almond-brown hen X blue cock has only blue-black (no brown) flecks, in contrast to the almond son of almond X brown, which has both brown and black flecks. Evidently the arrangements of these genes in the two sex chromosomes makes a big difference in fleck color. Here is a diagram of the two chromosomes of contrasting cocks: (+ signifies wild-type gene)



flecking here is both brown and black;



flecking here is only black.

Careful examination of flecking in comparable arrangements of the faded and brown genes has shown the same phenomenon.

About 1952 the faded red-ash hen combination was achieved, by C. M. Gottfried of Stamford, Connecticut. This became the basis of his “copper-white” auto-sexing Kings, and later the basis of the Texan Pioneer breed developed by Delwin James in Houston. And about 1954 Carl Graefe in Cuyahoga Falls, Ohio, succeeded in getting almond ash-red, thus completing the predicted possible combinations. Almond ash-red cocks out of almond ash-

red X blue generally have plenty of blue-black flecks and some ash-red flecks. In almond ash-red hens, however, all the flecks are ash-red. Therefore sexing the squabs in the nest is usually not difficult: just look for black flecks.

Some of these many color combination types may be commercially useful; almost all have light skin color. But at present they are more decorative curiosities, for amusement and instruction.

That is about the present status of the knowledge about flecks and sex, but nobody knows all the answers yet. And we must remember that some genes that are not sex-linked also show flecking, for example indigo. We are still wondering what makes some birds densely flecked and others less or very little; why flecking tends to increase in amount with age; why ash-red hens have almost exclusively brown flecks—almost never blue-black. Perhaps some experiments will shed new light on the dark spots before too many years.

—somewhat revised; original in NPA News, June 1960, pages 21-23

GENETICS À LA QUINN

Interest in pigeon Genetics has increased tremendously in the last 20 or so years, and breeders are continually bringing up problems not fully covered in any of the books. Joe Quinn, the energetic editor of the Pigeon Genetics News Letter, saw that a new book was needed. The result was “The Pigeon Breeder’s Notebook”—copyright 1971 (price $4.50 ppd., Q. B. & Q., 2817 Sanford Rd., Atwater, Ohio 44201). Debbie Ban Drosky and Joe’s daughter Patricia helped edit the work, which is styled like a large notebook and mimeo-printed, with lots of diagrams.

This book doesn’t read like a novel, and even Joe’s vast sense of humor doesn’t show, but I think breeders will like it and keep it handy to dip into time and again. It is an exhaustive refresher course, not to be swallowed all at once. Joe has sifted the literature and uses good examples, many from his own experience.

Still, I expect many breeders to say, “This stuff is all technical and we don’t have time to study it—after all, we have to keep the show on the road, and anyway, this is supposed to be a hobby, not a science project.” This attitude is exactly what Joe is trying to correct. He points out in the introduction that the dignity and challenge of a hobby are largely dependent on the complexities and technology involved, and that old muddling and mysticism must go. Certainly Joe has smoothed the road.

No book is free of errors, and Joe admits to at least one. I found a couple of others, but they won’t bother the majority of readers. There are even some problems that Joe didn’t cover. Try to find one. No, I don’t refer to biochemical details or electrophoresis or karyotyping—maybe in another 20 years?

—American Pigeon Journal, May 1972, page 267

BELATED BOOK REVIEW

> Regenstein, F., 1970. "Vererbung bei Huhnern und Tauben" (Heredity in poultry and pigeons). Published by Verlagshaus Oertel & Spörer, Reutlingen, West Germany. 143 pages, 16 plates (partly in color), 27 diagrams and text-figures. Price 14.80 DM.

Pigeon breeders probably do not realize the enormous flood of reading material pouring out of the world's presses. I have long since acknowledged. the futility of trying to keep abreast, even of literature in my own scientific area. Even with the aid of Joe Quinn's vacuum-cleaner bibliographies, I expect to miss many items, and I missed this one for several years.

In his preface, Regenstein states that the publishers asked him to prepare a book on heredity in fancy pigeons, but there was so little known concerning pigeons that he decided to include poultry also. He says he has had many years of breeding experience but has lacked the facilities and equipment of the technical institutes, and consequently mistakes are possible. He writes for fanciers, and uses a minimum of genetical lingo. In this review I shall limit comments to pigeons.

Well, like me, Regenstein has been unable to keep up with the literature. Unlike me, however, he lived not far from that phenomenal bibliographer of pigeons, Herr Werner K. G. Moebes. So far as I can discover, there was no contact between them. (How else can one explain that Regenstein makes no mention of my efforts?)

Few fanciers outside Germany are likely to study this book, unless it will be translated from German, an event I would not favor. We have enough difficulty with English writers already. Regenstein's symbols are mostly his own, such as *R* for dominant red, *TR* for Tumbler red (which he says is recessive to black but dominant to yellow), *Schi* for grizzle (Schimmel), and *v* for dilute (verdünnt). Unfortunately he includes the "silver" (lavender) Lahore as dilute of black, in figures 21-22.

On page 33 Regenstein states that he worked out the sex-linked inheritance of dominant red by 1941, and in the Preface he says Levi plagiarized from his book "Die Brieftaube"' (The Homing Pigeon). I don't know just when Regenstein's first edition appeared, but very little German literature was available in U.S.A. from about 1938-1945 (World War II). Levi's first edition of "The Pigeon" was published 1941, so that Levi could not have plagiarized. Moreover, the elucidation of sex-linked dominant red had been accomplished long before by Cole and Kelley (1919), as noted by Levi.

Regenstein credits the late C. S. Th. van Gink for his present illustrations, mostly drawings rather than photos. Six of these (figures 5, 8, 11, 23 and plates VI and XIII) are strangely similar to illustrations in Levi. It doesn't take Sherlock Holmes to figure out which came first.

Regenstein is original in some other areas. For example, on pages 36-37 he describes a young bird that was blue bar on the left side and a testis on the right. A true hermaphrodite, he calls it, and says this demonstrates the influence of sex hormones in sex-linked

inheritance. The fact that hormones circulate in the blood and are not limited to left or right is conveniently ignored. Mosaic wilderness!

—P. G. N. L. No. 70 page 11 (1974)

RED AND WHITE IN BLUE

Doc Horn asked me why he can't get good red eye ceres in his blue Kings. I told him to try applying some lipstick.

Blue is the color of the wild *Columba livia*. Of course it really isn't blue, it's black and gray, with some decorations like white underwings and rump, edge of tail, and nose, and of course orange-yellow eyes and red feet. The pigment in the feathers is called melanin, and under the microscope you can see it is finely granular. The white areas lack the pigment and reflect light the way snow does.

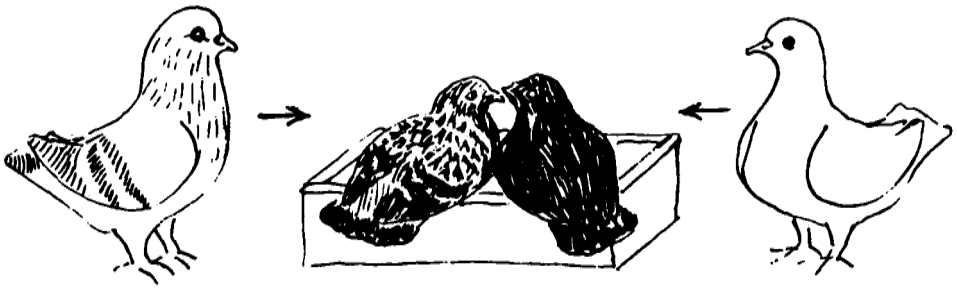
In the blue squab's feet there is also melanin, giving a blackish or brownish color. This gradually gives place to a completely different kind of pigment, that is not granular, and is called carotenoid. Similarly, in other parts of the body the skin may have melanin and carotenoid pigments, especially where not feathered. It is interesting to watch the darkening to blackish or reddish skin color in an area that has been plucked and exposed to the sun for some days.

The eye cere, having both black and red pigments in the exposed skin, looks purplish, not very red. Not much we can do to change that. By contrast, a White King lacks melanin in feathers and skin; therefore the only pigment developing in the skin is carotenoid, and it shows gorgeously. (Red.) The typical White King also lacks the yellow-orange pigment in the iris, leaving the outer surface transparent, so that we see the black pigment inside. The only way I know to keep the yellow pigment in the iris of a white pigeon is to use a different kind of white factor, which I call "tiger grizzle". This factor is commonly found in orange-eyed white Carneaux, Modenas, etc. It does not eliminate all pigment in the first plumage, but whitening occurs with the molt. This factor also leaves the melanin in the skin.

I've often been asked why a cross of a blue King with a white gives other colors. The questioner often has the notion that a white bird lacks not only melanin pigment but also color genes. Well, the pigment is the only thing missing. The cross reveals the genes that were latent in the white bird. Sometimes a cross of blue cock with white hen will produce ash-red sons, showing the presence of that sex-linked dominant gene in the white.

These observations are easy to test in your own loft—you don't have to rely on my opinions. Maybe you can disprove something I've said. Anyway, until you do, I still recommend lipstick for those eye ceres.

—American Pigeon Journal, September 1973, page 554



ESCUTCHEONS ASKEW, or BLUE BAR SINISTER?

Often times the mailbag brings in questions that are slightly difficult to answer. Like telling what disease a bird has a thousand miles away, or what color a squab is without enclosing feathers, or where can somebody buy Swiss Crescents in this country.

But some of the problems are not too bad. Here's one: "Dear Doc: how can this be? This year I had an extra English Trumpeter hen. Usually too many cocks but this time the other way. Well this hen, a nice solid red, was making a nuisance of herself so I got a blue check Racing Homer cock from a friend here to mate with her.

"I should of used them for feeders but didn't need to, so they raised four squabs. Well, they were all half-muffed like I expected, but here's the funny part. One of them was solid black with a crest like a Swallow. Another was near-black with blue tail, a third was red with plum tail and flights, and the last one is plum color all over, more reddish in the shield, and there are lots of black ink spots. This last one has a crest too. I gave them to neighbor kids and they lived somehow. The first two hens and the others cocks. Now what I want to know is how come this explosion of odd stuff?"'

I answered that one like this: 'Dear Jack: your English Trumpeter cross seems explainable as follows. The red she shows is recessive red, but she carries sex-linked ash-red and also the *S* factor. These are masked by the recessive red. The Homer carries a crest factor —it is not too rare among Homers, probably a hand-me-down from Turbit in ancient ancestry. In case you are interested in the mechanics of the chromosomes and genes, here's the set-up for color and crest:

Hen	$\frac{B^A}{\cdots\cdots}$	$\frac{S\ C^T}{=\!=}$	$\frac{e}{=\!=}$	$\frac{cr}{=\!=}$	Cock	$\frac{+}{=\!=}$	$\frac{+\ C}{=\!=}$	$\frac{+}{=\!=}$	$\frac{+}{=\!=}$
	(sex)	$+\ C^T$	e	cr		$+$	$+\ +$	$+$	cr

Eggs (4 kinds): Sperms (4 kinds):

1.	$\frac{B^A}{}$	$\frac{S\ C^T}{}$	$\frac{e}{}$	$\frac{cr}{}$	5.	$\frac{+}{}$	$\frac{+\ C}{}$	$\frac{+}{}$	$\frac{+}{}$
2.	$\frac{B^A}{}$	$\frac{+\ C^T}{}$	$\frac{e}{}$	$\frac{cr}{}$	6.	$\frac{+}{}$	$\frac{+\ C}{}$	$\frac{+}{}$	$\frac{cr}{}$
3.	$\frac{\cdots\cdots}{}$	$\frac{S\ C^T}{}$	$\frac{e}{}$	$\frac{cr}{}$	7.	$\frac{+}{}$	$\frac{+\ +}{}$	$\frac{+}{}$	$\frac{+}{}$
4.	$\frac{\cdots\cdots}{}$	$\frac{+\ C^T}{}$	$\frac{e}{}$	$\frac{cr}{}$	8.	$\frac{+}{}$	$\frac{+\ +}{}$	$\frac{+}{}$	$\frac{cr}{}$

"According to this there are 16 possible kinds of matchings of eggs and sperms. You did pretty well with your sample of 4. For example that last squab 'all-plum' would be the matching of No. 1 and No. 6 or No. 8."

So much for Jack—at least my theory works. Here's another letter, just in: 'Dear Mr. Holander: They tell me you know about color breeding well I got a real intresting one for you, can you explain it? This is the mating, I crossed a Silver cock and a yellow hen and they have raised a black, 2 blue bars, and a self dun. No they wasnt in with other birds, they has there own individual pen. Also I dont switch eggs. Theres a blue cock in the next pen, but he can't do nothing about it because the partition is half inch galvanized hardware cloth. No blacks or duns anywheres, but I had a black cock last year for a while. Do you believe it is long distance effect like Everet Milsted says? Sounds like magic to me but I got the best Kings in the county and it never happened before.'

Shall I give Mr. King-breeder genes and chromosomes? Shall I tell him his "Silver" is not dilute but brown? that his self dun is really chocolate, and that his yellow carries the *S* factor? Or is telekinetic breeding the easier out?

I guess I'll give him the genes and chromosomes, and hope for the best:

Hen	*d* +	*S*	*e*	Cock	+ *b*	+	+
	_ _ _ _						
	(sex)	+	*e*		+ *b*	+	+

Eggs (4 kinds):

1.	*d* +	*S*	*e*
2.	*d* +	+	*e*
3.	_ _ _ _	*S*	*e*
4.	_ _ _ _	+	*e*

Sperms (only one kind):

5.	+ *b*	+	+

So Mr. King-breeder got three out of the four possible combinations. The one he didn't get (yet?) is No. 4 with No. 5. That would be a "silver" (brown bar). The black he got was No. 1 with No. 5, and the blues were No. 2 with No. 5. Such a blue would have to be a cock (2 sex chromosomes). All the marker genes are recessive, matched with wild-type alleles, so they can't show. Result blue bar. Reversion to wild color.

d +	+	+
+ *b*	+	*e*

Dear Reader: do you have a problem too? If so, remember the mailbag brings me tougher ones than yours!

—N. P. A. News February 1962, pages 19-20

NEW WRINKLES IN SEX LINKAGE

Several of my ~~patients~~ readers have complained that I've been dishing up too much hash lately and not enough meat. It used to be the other way around. But don't stew, boys—in spite of austerity and high taxes, here's a change: a serving from the sex pot. Let's call it a Midwest exposure.

What's the latest about sex-linked factors? Well, not a thing that you couldn't get from Levi's books, really. We seem to have leveled off with four sets of these factors—hardly anybody is trying to discover more. Let's list these sets of mutants:

(1) the ash-red and brown set, B^A and *b*
(2) the almond and faded set, *St* and St^F
(3) the dilute and pale set, *d* and d^P
(4) the reduced set, *r*

Note that the members of a set are given the same base letter, and this is capitalized if the factor shows dominance to the wild type. There may be other members of these sets, but identifying them isn't progressing very fast (for example "sandy" for the second set).

Locating these factors with relation to one another in the sex chromosome is only partly resolved, because it is a long hard job and George hasn't worked at it enough. We do know that sets (1) and (2) are close together, and (3) and (4) likewise. The chromosome map can be tentatively diagrammed thus:

(1) (2) (3) (4)

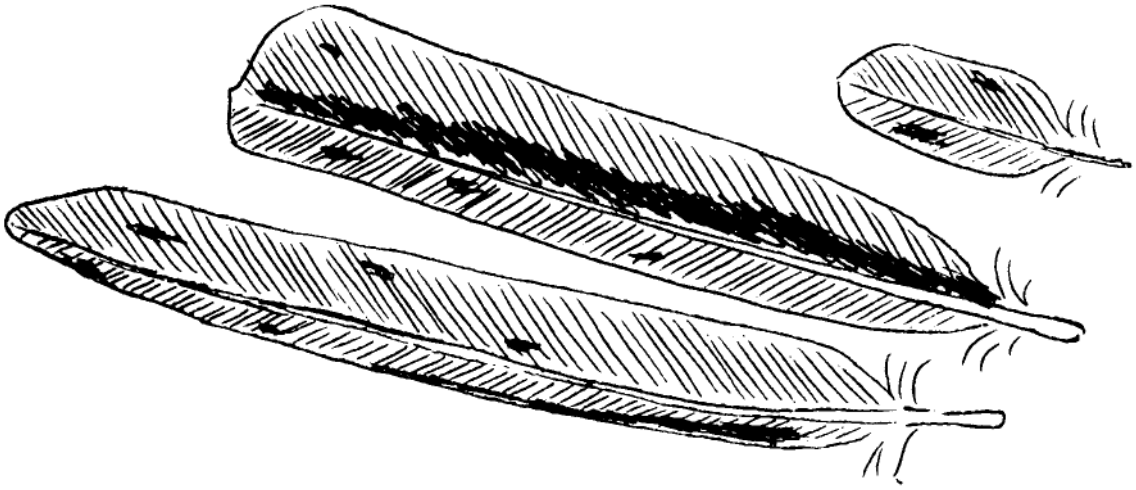
The essential principle of sex linkage, as most fanciers have learned (?), is that a hen has only one of these chromosomes, and she inherits it only from her sire. To utilize this idea in sexing squabs we use a cock having a recessive in his sex chromosomes, preferably homozygous, and a hen having a corresponding dominant. Examples are dun-barred silver (*d//d*) cock X blue hen. From such matings we get a "criss-cross"—the sons look like their mother, daughters like their father. Exceptions to the rule are sometimes found in flock pens, where fidelity is problematical.

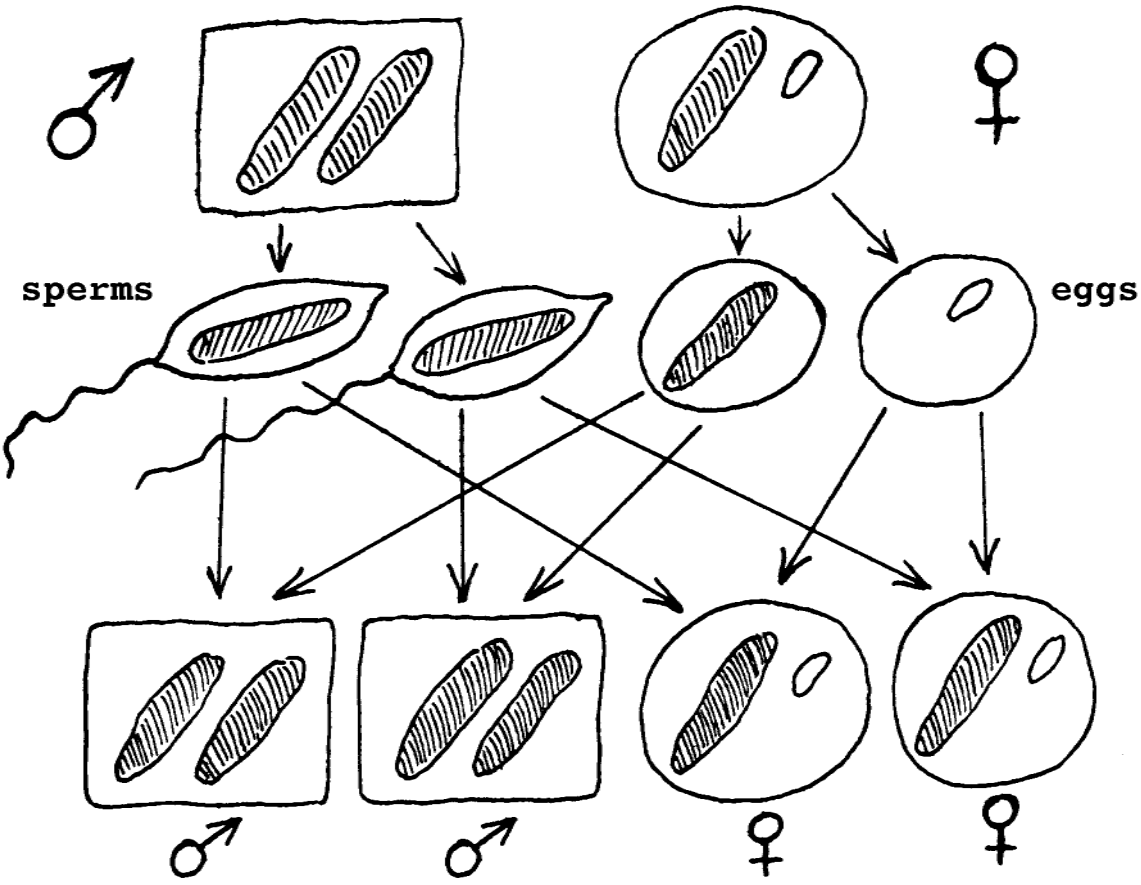
The criss-cross is simple and handy, but what do you do next? Well, let's consider the original mating of a blue cock X ash-red hen. The blue daughters from this could be mated to several recessive types of males (e.g., silver, brown reduced). The ash-red sons from the original mating can be mated with faded or almond hens. So we can go on for a while longer, criss-crossing happily. But eventually we seem to run out of combinations.

In this apparent blind alley there is still another escape—the use of certain double-factor colors that are still not very widely available. One of these is almond-ash-red. Now, suppose we have a nice khaki hen (*d, b*) with no cock for criss-cross. If we mate her with an almond-ash-red cock (*St* B^A*//*?), lo! we can sex some of her squabs. Both sons and daughters can be almond ash-red, but if we examine these for flecks or splotches we find that the sons have usually a good many, and their color is brown, while in the daughters the flecks are ash-red and scarce. So off we go again with a criss-cross for the young hens, and a cross to blue for the young males.

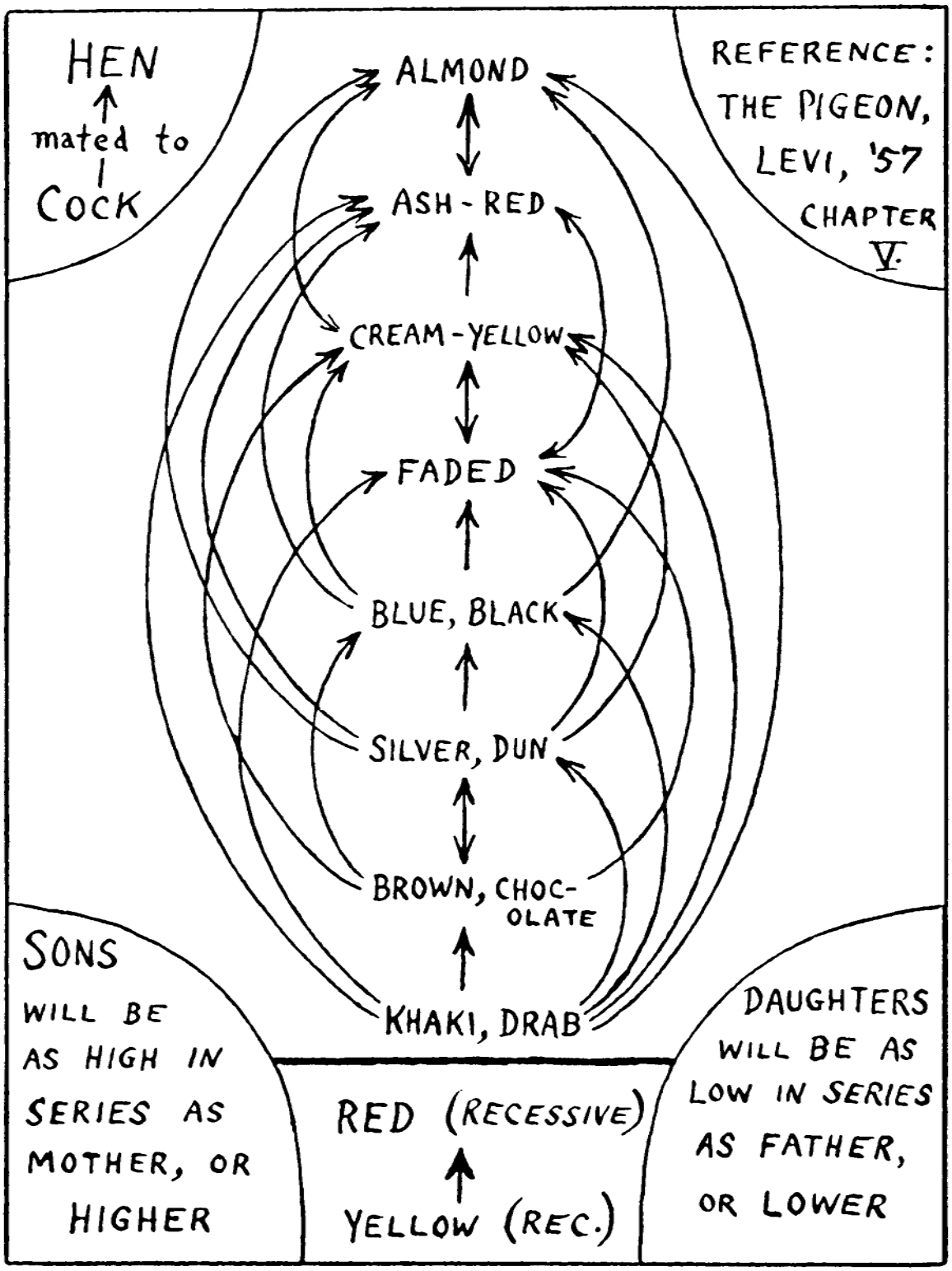
Other double-factor colors of value are almond-brown, faded-ash-red, and faded-brown. When we get into triples or quadruples, it takes an expert to tell what's going on, and the puzzlers require breeding tests for analysis. Even so, some of the simpler ones can't get into a show except A.O.C. And of course a lot go into the pot. Sex pot, eh wot?

—A. G. H. A. Bulletin, July 1967





SOME COMMON SEX-LINKED MATINGS



TESTING..... TESTING .....

In Genetics, eye-balling is very useful, just as it is in the show room. The expert can deduce things that the novice must consider magic. But eye-balling can not give all the desired answers. For example, looking at a champion show bird will not tell whether it carries a lethal factor or some other heterozygous recessive. And looking at a bull-eyed white bird won't tell what other color factors it is masking. And two persons eye-balling the same bird may differ violently in interpretation.

So—tests are needed, hopefully good (decisive) tests. Usually the breeder can run his own breeding test, but the question is how willing he is to do it.

Our tests are somewhat like qualitative analysis in Chemistry. Some reagents (tester birds) will be needed, and the analytical steps depend on the unknown. But if we have reliable pedigree information, the test may be partly or completely finished already. Let's look at some cases (simple ones).

1. Question: I have a blue checker hen that had a recessive red grandmother. How can I find out if she carries *e*?

   Answer: Mate with recessive red. If any *ee* squab results, she carries *e*, so stop the test. If no *ee* shows up in say half a dozen squabs, she probably doesn't carry *e*.

2. Question: I have a male red checker cock out of a blue checker X yellow mating. How can I test whether the red checker carries the dilute gene?

   Answer: the pedigree is the test—he had to get *d* from his yellow parent.

3. Question: I have show Red Carneaux. Do they have the *S* gene?

   Answer: Testing Red Carneaux with wild type (blue) I haven't seen any *S* progeny.

4. Question: My lavender Lahores look barless. Are they?

   Answer: Probably not—more likely *S* in there. To test, you might try crossing with blue barless.

5. Question: What is this strange pearly color?

   Answer: I don't know. How about some pedigree information, and if possible cross with wild-type (blue bar) and let's see what results. Further tests may then be indicated.

6. Question: My best pair of Homers produced this freak-foot squab. Is it genetic?

   Answer: If they can produce another, probably yes. If the freak can breed, get F_1 and F_2 to see whether it reappears. Freak X freak matings should tell a lot too, if you can get any.

AMERICAN RARE

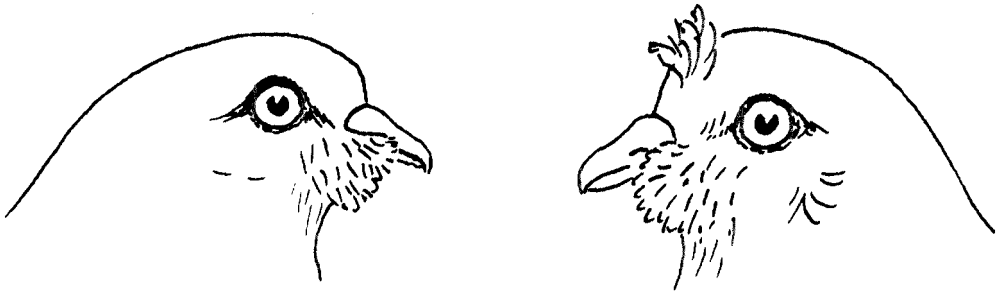
Everybody knows by now (I hope) that America had no domestic pigeons until they were imported by the settlers. But Americans have been claiming for many years that there are strictly American breeds—new creations, especially the King (being a democracy, it's logical we gotta have royalty). And the American Giant Homer, American Carneau, the Saint, the Swerdna, and others (such as the "Indian Fantasy"). Anybody in this free country can make his own breed and plaster his own nutty name on it, right? No patent required. Unlimited!

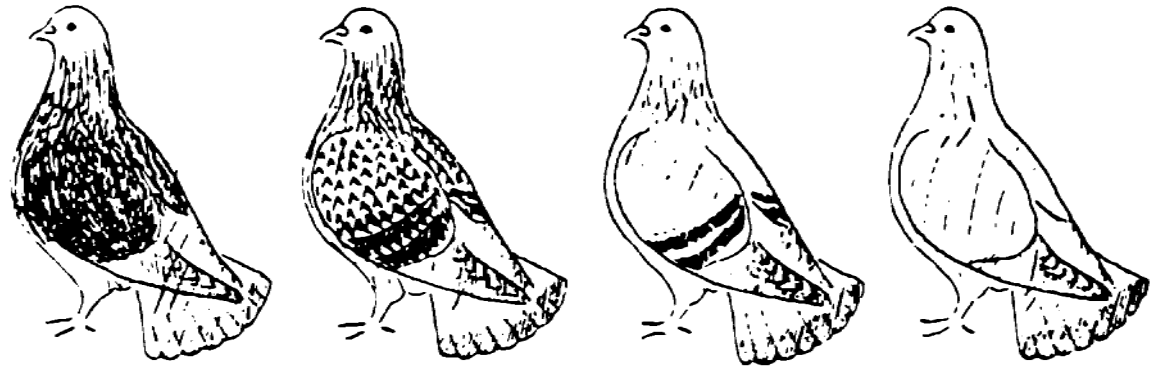
After you make a new breed, usually by scrambling some older ones, you find that it is rare. To get it out of the clutches of RBPC, you gotta get a good publicity man, beat the drums and bushes, wangle sales and shows, set up competing clubs, and argue about standards. Pretty soon, whoopee! You're in the big time, right up there with American Domestic Flights and Giant American Crests and American Pie. Popularity is the key to not being rare.

Sooner or later there are gonna be thousands of breeds competing. It's inevitable, unfair, and the American Way. I'm agin it. I say, brethren (and sistern?), this word *breed* is leading us to destruction. What we call a breed is just a particular batch of genes. We don't have to sanctify any particular assortment: the important thing is to know what genes are in the mess. And the question can then be, what genes are rare? Are there any in danger of being lost? And how do we ride herd on a flock of rare genes without using the word *breed*?

Maybe you'll say I'm just being destructive, but I'm not. And as an example of Americana, consider my strictly American mutant gene, "sideburns". I've given it to a lot of fanciers, and the typical comment I get is "Is it a breed?" Hell no! It's a mutation, a new gene. It can be put into almost any breed. Just cross it in. Being a dominant gene, it shows up in about half the youngsters. Like crest and other "ornaments" its expression is variable and selection can be effective in breeding differences. So for hevvin sakes let's not start a club for Giant American Sideburns or Chinese-American Double-Whiskered Owls or American Bearded Nuns or such. Don't even think about going in for "pure" sideburns. Just enjoy scrambling, and let the judges tear out their coiffures. And if you can think of following my heretical lead, how about just giving birds away instead of hassling over prices?

—Rare Breeds Pigeon Club Bull., Vol. 9, No. 2, 1981.





MULTIPLE-ALLELIC SERIES

Mendel never used the words gene or allele—they were coined years after he was dead. Still, he had the idea: that there are contrasting unit determining factors which go in pairs. For example, AA or Aa or aa. A and a are now called alleles, a contraction of the original “allelomorphs”, meaning alternatives.

But must alleles be limited to 2? Mendel thought so, but later studies discovered examples of more. One of the earliest and best known is the multiple-allelic series of human blood-groups, A, B, O. A person can have any 2 of these allelic factors: you can be AA, AB, AO, BB, BO, or OO.

Actually, the symbols A, B, O are obsolete. Modern symbolization for multiple alleles uses the same base letter, with other distinguishing differences, usually superscripts: I^A, I^B, i respectively for those blood-group factors (I here referring to isoantigen). And for most series one allele is usually recognized as the wild-type or standard, and therefore given a + symbol.

In 1930 L. J. Cole reported triple alleles in ringneck doves: white, blond, and dark (wild type). This series was later found to tie in with the *d* (dilute) series in pigeons (Cole and Hollander, 1950).

In pigeons multiple alleles were first reported by Hawkins, also at the University of Wisconsin, by 1931: the sex-linked ash-red, wild-type, and brown factors, now symbolized B^A, B^+ (or +), and *b*. Hawkins had been trying to map the positions of ash-red and brown in the sex chromosome, and found no crossing-over at all between them in the breeding tests. That of course meant that there was zero distance on the map, and by definition genes which are at the same map position (locus) are allelic. Carl Graefe believed that with more testing a little crossing over would be found, but so far none has appeared, and there is one other fact pointing to allelism: ash-red females have usually brown flecks (if any), which can be interpreted as somatic mutations from B^A to *b*.

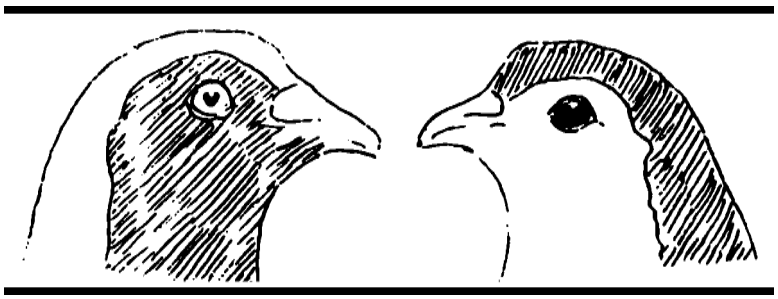
About the same time Bjaanes reported an intermediate allele of dilute which he called pale. The symbols we now use for the series are *d*, d^P and D^+ (or +).

By 1937 I had discovered another multiple-allelic series—this with at least 4: barless,

bar (wild type), checker, and T-pattern, with symbols *c*, + (or C^+), *C*, and C^T. I also had some evidence for at least two additional: dark checker (C^D) and light checker (C^L).

Another series that I worked out was almond, faded, and wild type. For a time Cole and I thought (1940) these were also allelic with the B^A-*b* series, but later some crossing over was demonstrated. Therefore almond was symbolized *St* (the prior German symbol used by Christie and Wriedt) and faded St^F. (See my review 1944, and also "Origins" articles.)

That's 4 series of multiple alleles already. Are there more? Yes, but evidence is slow to come in. The "tiger" type of grizzle seems to be another allele of *G*, and the usual self-white with bull eyes seems allelic with gazzi. Extra-outer-toe polydactyly (*t*) seems to have a lethal "Hasz" allele. Different sorts of webbed toes may be allelic. Different sources of albino, of silky, of ..... we have probably only scratched the surface. And pigeons and doves have blood types too!



SHORT DOWN

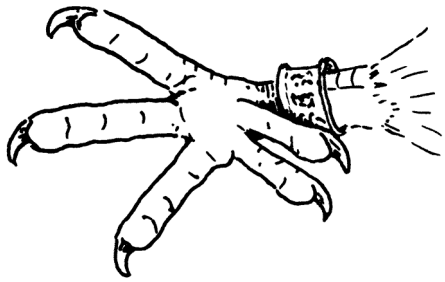
"Mr. Tegetmeier has informed me of a curious and inexplicable case of correlation, namely, that young pigeons of all breeds which when mature become white, yellow, silver (i.e., extremely pale blue), or dun-colored, are born almost naked; whereas pigeons of other colours are born well-clothed with down." Thus wrote Charles Darwin in Chapter V of his 1868 book, The Variation of Animals and Plants under Domestication. He was right, in general, except that the ordinary white pigeons have normal down.

In the 100-plus years since then we have learned more about the "almost naked" condition. It seems to be shortness of the down plumules rather than absence. The degree of shortening is variable, but hardly anyone has bothered to get precise measurements, or to report them. Short-down birds also develop short filoplumes.

At first the dilution factor was considered the only cause of the short-down condition, but as other color factors were studied it became clear that *d* had no monopoly. Short down is typical in squabs of the almond, homozygous faded, faded brown, albino, pink-eyed-dilute, and perhaps some other color classes. White and albino ringneck doves are similarly short-downed. Also lethal-polydactyl (*py*) and homozygous silky squabs are short-downed, a less unexpected condition because the later plumage is also very abnormal.

Short down has been thought related to "low vigor" and increased mortality of squabs, but careful studies have not been made.

Maybe we haven't progressed really far since Darwin!



ONE TOE OR TWO, OR WHAT CAN GENES DO?

There is no such thing as a black gene. Or a white gene. Or even a red or a blue one. Have you been guilty of such unsemantics? Many of my correspondents enjoy flinging their ignorance around—"the gene for racing ability", "the gene for intelligence", "the barred gene", "the gene that makes feathers on the toes", and so on. Perhaps the cap of the climax is "the gene for death". Next we'll have a gene for life?

Sad to say, nobody really knows what a gene is, and just because it is an easy word to pronounce and looks so definite is no excuse for over-confidence. Look in the books and you will find all sorts of definitions. How do you like this recent one: "the DNA-coding sequence for a particular polypeptide." Or this one: "a cistron". Or this: "a locus on a chromosome''. Or this: "a unit of heredity, variously comprising a number of mutons or-and recons." See what I mean? Nothing about color or feathers or death at all.

So, on guard! What can we say that will not be easily shredded by logic or facts? Let's start with wild type. Does it have any genes? Whatever they are, yes indeed, but we really don't know much more by saying that. Maybe we could get someone to catalog all the different sorts of proteins (polypeptides) produced by the wild type in its life, and postulate that each has a gene responsible for it, but that would not give us any idea of loci on chromosomes. And we still would not know really that our postulation is right.

Everybody thinks he is sure of certain genes. How about *d* for dilute? Here we have a definite unit and we know it is on the sex chromosome. But what do we mean, "for dilute"? Well, maybe you will respond, "it causes lighter color or pigmentation". Ah so, but lighter than what? Certainly not lighter than white! Well, if you have been following my lead, you will answer "lighter than wild type'. Very good, we need that reliable normal standard of reference. All we know then is that dilution is a sex-linked recessive mutant. It is not a gene but an altered condition from the normal. It behaves as a unit, yes, but a broken windshield on a car could also be called a unit, with a definite position. Maybe we don't know what broke it, but we can recognize its effects in great detail. And knowing those effects, we can more vividly appreciate the normal. If we must call *d* a "gene", let's at least preface it with the word *mutant*.

Mutant "genes" are our keys to further knowledge. Without them, Genetics is extremely limited, frustrated. Maybe the mutants are "good", or more often "bad" or ugly, but in any case they are our chromosome markers and our tools for unlocking the secrets of heredity and physiology.

Everybody realizes that “genes” do something, even if we aren’t clear what. Can we be clear? I think there is hope. If we can’t get down to a strictly chemical level, we can at least nail down the mutant effects more precisely. For example, just how much is pigmentation reduced; is it a uniform effect, involving all pigment in the body and eyes? Just how much shorter is the nestling down, and the filoplumes? Is there really a lessening of vigor, and if so what organs are involved (muscles? liver? or ?). And so on. After compiling a summary, we may be able to say that the *d* mutant causes all those alterations from normal—directly or indirectly. Perhaps an underlying chemical difference will be found as the ultimate basis. And perhaps the *d* effects can be prevented or counteracted by some as yet unknown injection or feeding.

This same sort of approach can be applied in other cases just as well. Some mutants’ effects are not as consistent as those of *d*, however, and recognition of inconstancy or variability is necessary. Perhaps there is a sensitivity to environmental variables, and these can be tested. Why, for instance, is polydactyly so varied? We should not say “sometimes *py* causes one extra toe and sometimes two”—even a mutant can’t cause a toe. Maybe it would be better to say “*py* tends to multiply the clefts in the embryonic limb bud, so that digit formation is in excess of normal”. Or maybe a still more accurate statement is possible.

As we clear up the understanding of how the unit mutants are operating, we can then get a better insight into what happens when two or more mutants are working together.

Who said Genetics is simple?

—P. G. N. L. No. 65 pages 14-15 (1973)

BAD GENES? MERCY ME!

You may never have seen a naturally naked adult pigeon, but a whole family of such handicapped Homers has been studied. Simple recessive gene was the report. Same story for several types of blindness—“clumsy,” “feed-blind,” and complete blindness. Same story for such feather conditions as “porcupine” and “scraggly.” Same story for albinism, in which vision is very poor because of lack of pigment in the eyes. Same story for “ataxia,” a brain defect resulting in poor coordination. These are some of the KNOWN genetic abnormalities that were originally discovered in Racing Homers. No other breed of domestic pigeons has such a record!

Most fanciers finding such a specimen would have a negative reaction, very likely resulting in rather early death (of the bird). The tender feelings that we are supposed to have for the weak, the suffering, the crippled, seem to evaporate readily when we think of visitors to the loft seeing eyesores like that. Pride in our stock makes us want to hide such skeletons in the closet, or rather, get rid of them completely. Seldom do fanciers realize, however, that the appearance of such a recessive condition implies that both parents carry a hidden gene for it. And since these abnormal birds often come out of the “best” breeding pairs, culling the

undesirables only scratches the surface of the problem.

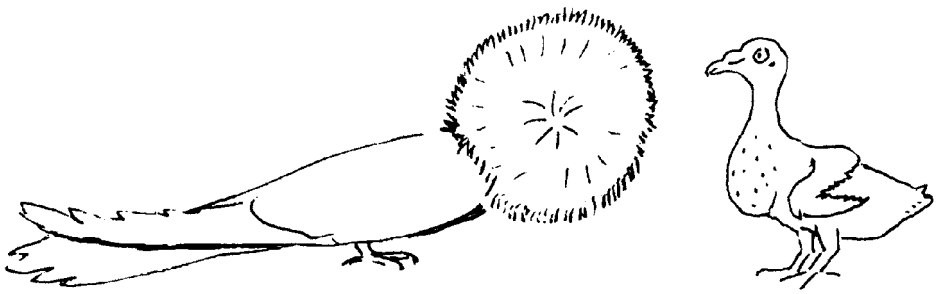
Well, any stock may carry such genes hidden until two birds that both carry the same one are mated. Then about a fourth of their young may inherit it from both parents and show it. The obvious solution is to avoid such matings. A bird carrying such a gene should be mated with one that doesn't carry it; then none of their young can show it (though half will carry it). The only problem is to know which birds do NOT carry it. One way to find out is make a breeding test—mate the bird in question to one which shows the abnormality or one known to carry it, and see whether any of their young show it. If a dozen young from such a mating include no affected specimens, the tested bird can be pretty safely classed as free of the "bad" gene. But that's quite a bit of time and work. And, of course, the "tester" birds may not even be breedable, or not easy to get, or maybe the wrong sex. But to top all of the problems off, just having proof that a particular bird is free of a particular "bad" gene is no proof that the bird is free of some other(s), especially if the bird is from some other stock.

Abnormal recessive young almost never are produced when different stocks are crossed, even if each parent carries a "bad" gene. Why? Because they almost never the carry the same kind. Some of the young may even carry both kinds but not show either one.

Furthermore, this method of hiding the "bad" gene works even when two frankly abnormal types are crossed: for example, an albino with a feed-blind. All the progeny come normal though all carry both "bad" genes. Theoretically much more complex crossing is possible without any abnormality showing, and a bird carrying a whole flock of hidden "bad" genes would probably have as good racing potential as a bird carrying none. Perhaps systematic crossing of this sort (say 4-way) where none of the parent stocks can race, may become more respectable in the future, just as modern field corn is routinely produced by hybridizing inferior (but pure) strains. Breeding best with best is not always the ideal method! Matching is both science and art.

How many "bad" genes are there? Nobody knows. Mutations are thought to be continually occurring, and there seems to be no limit to the possible types. Why have so many been found in Homers? I think it is simply that Homers outnumber all other breeds, and the fanciers have been willing to report the most interesting to researchers. And interesting they are! It is a challenge to work out the genetics of such difficult types. But it is also rather thankless, not to mention costly, when most fanciers would just as soon butcher them all off. Anyway, if you think you have a scientific eye-popper, I hope you will stay the axe until you have informed me. Merci!

—American Racing Pigeon News, January 1980, page 34



MOSAICS

When you think you have just about got an understanding of Genetics, watch out, because the more you learn, the less you know. But if you don't get too scared, it can be fun, sort of like a roller-coaster ride.

Mosaic pigeons break all the rules. They are individuals but they are composites, as if two birds had been melted down and made into one. Maybe you have never seen one, but if you keep looking, you probably will. However, the chances that you'll raise one are pretty slim, so look in other lofts, and in dealers' flocks. For the past 25 years I have kept a record of examples that I have seen and found reported in the magazines, etc. The total is over 150, so that one can estimate the frequency of these freaks in a very rough way—perhaps half a dozen a year from maybe a million pigeons? But probably a lot never got noticed or reported.

Mosaics break the rules, such as the rule that a hen must be either blue or ash-red or brown. A mosaic hen may be blue in one wing and ash-red in the other, for example. And it is a rule among mosaics that no two are just alike. Also it is a rule that mosaics can occur in any breed, any place, any time of year. And as a general rule you can't breed mosaics from mosaics. They seem to be strictly accidental.

The most striking mosaics are those called "half-siders"—the differing parts being almost completely right vs. left and looking as if they have been sewed together down the middle. These have most usually involved the *S* (spreading) gene. Mosaics involving color genes such as recessive red, dilute, etc., are usually slap-dash crazy-quilts. We can hypothesize that the half-siders maybe are formed as two embryos fused together on a single yolk. But the crazy-quilt birds might also have such an origin—we can invoke the wandering behavior of pigment cells. Apparently the *S* gene works not in the pigment cells but in the non-wandering tissues (skin). Anyway, some sort of embryonic fusion does seem involved.

Breeding tests and pedigrees are our main sources of further information about particular cases. If a hen is say blue and brown, mate her with a brown cock and see whether she can produce any blues. And was her father a blue heterozygous for brown, or what? If he was a brown, where could the blue have come from? Maybe another cock in the same coop? Once in a while the evidence is good enough to incriminate two different fathers for the same bird. I have used the term "bipaternity" for such a situation. My idea is that sometimes an extra sperm that gets into the egg may survive and produce cells which are incorporated into the embryo like a graft.

Mosaics are so rare and surprising that they are always news. When you find one, don't keep it a secret. Get photos, in color if possible. Report it in the club bulletin or the magazines. Maybe even tell me about it. Who knows what more we will learn!

References:
(1) Hollander, W. F. 1949 "Bipaternity in pigeons," Journal of Heredity 40: 271-277.
(2) Cock, A. G. 1955 "Half-and-half mosaics in the fowl." Journal of Genetics 53: 49-80.
(3) Levi, W. M. 1957 "The Pigeon." Second edition. Levi Publishing Co., Sumter, S.C.
(4) Levi, W. M. 1965 "Encyclopedia of Pigeon Breeds." Levi Publishing Co., Sumter, S.C.
(5) Hollander, W. F. 1975 "Sectorial mosaics in the domestic pigeon: 25 more years." Journal of Heredity 66: 197-202.

—American Pigeon Journal, August 1975, page 554

A SECOND LOOK AT BLAINE'S BRAINSTORM

Blaine started something new at the National this year. Some 30 birds were entered in this "Rare Color Exhibit", and I was asked to decide which had the rarest color.

Four of these modern marvels were mosaics—patchwork or crazy quilts. I was all ready to pin the prize on one of these but objections were raised: "Mosaics are just accidents, so the award should go to another color, one you can breed for.'' Being a judge of a rather rare color myself (green), I picked another rainbow fragment for the winner.

Later I gathered comments about the exhibit.
(1) The bird that I picked wasn't over half Giant Homer; unfair.
(2) That color may be rare but it ain't much to look at.
(3) Whose brainstorm was that exhibit anyway?
(4) Color ain't what we want—gotta have better squab production.
(5) Oh, was there a color exhibit?

That got me to thinking. Is Blaine a menace? Is he one of those eggheads— well cracked? Is rarity a virtue? Just because parakeet breeders have gone crazy over new color mutations, and pay outrageous prices for them, should we? Should innocent, contented fanciers be bombarded with supersonic genetic mumbo-jumbo? Should we forget that the Giant Homer is in the competition for squab production honors?

Maybe some argument should be developed in the Bulletin about all that. Anyhow, if Blaine wins and another exhibit is to be held next time, I certainly will be excited to see it.

—A. G. H. A. Bulletin February 1954

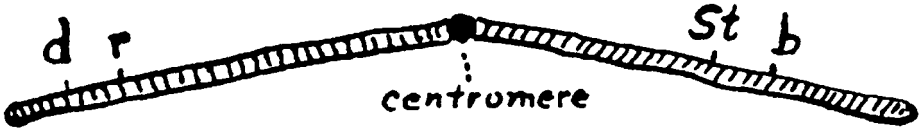
WHY ARE WE STYMIED ON THE SEX-CHROMOSOME MAP?

The cytologists now seem agreed that the pigeon sex chromosomes are of the "Z-W" type. That is, the male has two of the Z kind, while the female has one Z and one W. The Z usually looks V-shaped because of median spindle-fiber attachment (centromere), but the W chromosome is merely a small rod.

Sex-linked mutants go with the Z. We make a map of the chromosome by setting up linkage-test matings, raising a lot of young, classifying them, and calculating cross-over percentages. There's no trick to that—it's just a matter of planning, work, time, expense, and some luck. Sometimes we can dovetail a linkage test along with producing show birds, or squabs for the table, or both. Anyway, if we keep good records and get a fair number of progeny, say between 50 and 500 (!), we should be well on our way to a reliable map of the chromosome, at least as far as those particular mutants are concerned, and there is a remarkable satisfaction in the accomplishment. Here is a picture of gene positions that even the best microscopes can not provide, but we did it with paper and pencil.

By such laborious testing, not always as well documented as might be considered necessary, various breeders have found that *d* (dilute) and B^A (ash-red) give somewhere around 40% cross-overs, and are therefore not close together on the map. By contrast, *d* and *r* (reduced) have given only about 5% cross-overs: therefore these are close together on the map. Similarly, B^A and St^F (faded) give few cross-overs, probably about 3%, so that these also are close together on the map. Other tests, such as *d* with St^F or B^A with *r*, have given confirmation. Also other alleles such as *b* instead of B^A, or *St* (almond) instead of St^F agree.

It seems likely, though we can't prove it yet, that these loci (positions) are in the two "arms" of the chromosome rather than the middle. We might visualize the map thus:



Well, that's all very nice except that we really don't know whether *d* is to the left of *r* or vice versa, and the same sort of problem applies with the other loci. So the total map is not so good after all. What we need is more linkage data. Why not set up a big linkage test with all 4 loci at once? Theoretically that will reveal the relative positions, but unfortunately theory crashes into a practical roadblock: many of the color combinations are too difficult to classify accurately, and map reliability is dependent on the classifications. If the mutants were not all involved in colors, we wouldn't have so much confusion. Maybe.

How about using three loci all together instead of 4? Still some classification problems. And even if that were not discouraging enough, we are faced with more trouble: where two loci are far apart and the third close to one of the others, it will be almost as easy to get double-crossovers as singles. Therefore the map order will still be elusive, even if we get hundreds of test progeny.

And that isn't all. Differential mortality is very likely to occur—for example, dilute almond seems a weak type at early ages. It would not require much loss of this sort to make the classifications unreliable.

All in all, the refinement of our map seems practically unachievable with the mutants available. Perhaps we should be satisfied with what we have, or even happy with it, but I'm not. All we need is more mutants to plug into the tests, preferably not just color mutants. However, for some strange reason, no new sex-linked mutants have been discovered (or at least reported) for 25 years. Here is a wide-open field for sharp-eyed breeders. Who will be the next to gain such fame (durable fame, too) instead of winning second prize at the Podunk Pigeon show?

But new mutants are not too likely to be loitering around one's own loft. Finding them means search, exploration, maybe in a show, maybe in a dealer's flock, even in some other country..... Ah, I think I'll try Holland.

—P. S. & G. N. No. 5 pages 42-43 (1977)

P.S. 1982: the new web-lethal mutant, *wl*, may help with mapping. (See American Racing Pigeon News, Oct. 1982, p. 50.) See also Sittman's study, PGNL 67:5 (1973).

THE QUEST FOR LINKAGES

(This article was written by Wilmer J. Miller and W. F. H.)

Characters which do not assort independently in F_2 are in violation of one of Mendel's great principles, and are said to show linkage. By 1920 independent assortment was recognized to indicate that characters were controlled by genes on different sets of chromosomes, while linkage indicates that genes on the same chromosome (pair) were involved. Further, since some genes seemed tightly linked but others not, linkage maps of the chromosomes could be deduced. That is, the tighter the linkage, the closer the genes are to each other on the chromosome map. For pigeons we have so far only rather sketchy maps of two chromosomes, one of which is the sex chromosome:

sex chromosome	first autosome
d r ——— *b St*	*S* ——— *C o*

Discovery of a new linkage is an exhilarating experience, but along with such success usually there are many vain searches and bad luck. To hunt for years without finding anything exciting is discouraging, for sure, but some of us deluded souls keep trying. Anyway, by accumulating data we get more and more "feel" of the genetic machinery.

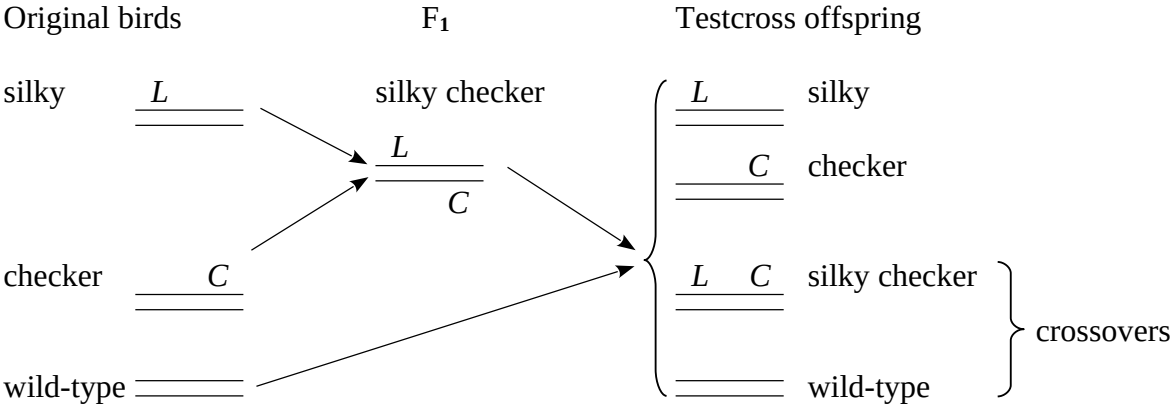
If you are gambling-minded and care to take a chance in this numbers game, how do you start? Let's assume that you are equipped with "facilities"—breeding coops (preferably

one per pair of birds), a record book (with at least one page for each pair of birds), some cash for expenses, a good eye, common sense, patience, and a touch of insanity. Next you choose two characters (mutants) whose genes seem adequately established, and start to get F_1.

Right there already problems arise: why not three or more characters? O.K.—fine, but remember that the project is basically a search for linkage between any two. And how about the best way to cross? It can be done in more than one way. For example, one mutant may be in the cock, the other in the hen, or both may be in one parent and neither in the other. Sometimes there is a preference, but usually not. And then the question hits you: how many F_1 should be raised? (Answer: It depends; maybe a couple, maybe a dozen?)

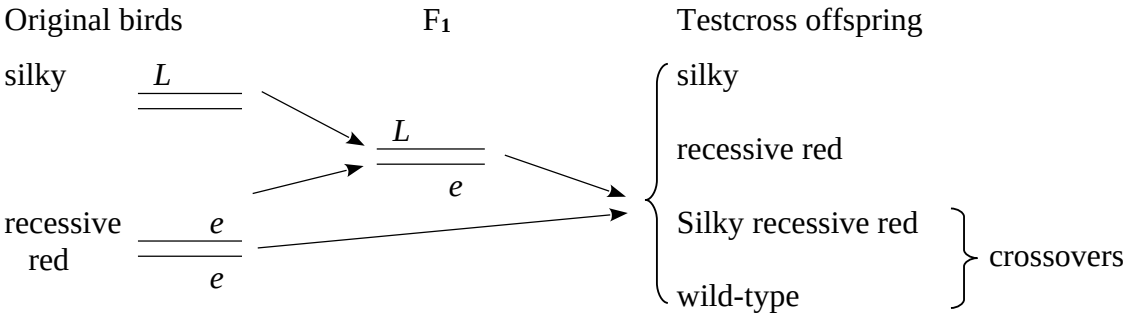
After getting some F_1 birds, the obvious next step is to go for F_2—obvious, but often inefficient. It is much better to get "testcross" matings where possible. Let's examine some examples.

(1) Suppose we want to work with two dominant (or partially dominant) mutants, such as silky and checker. If we start with a silky bar X checker, some of the F_1 birds will be the desired silky checkers. To make a testcross, we simply mate these with wild-type birds (that is, having neither mutant). To diagram the project, let's assume that there is really linkage—only one pair of chromosomes involved:

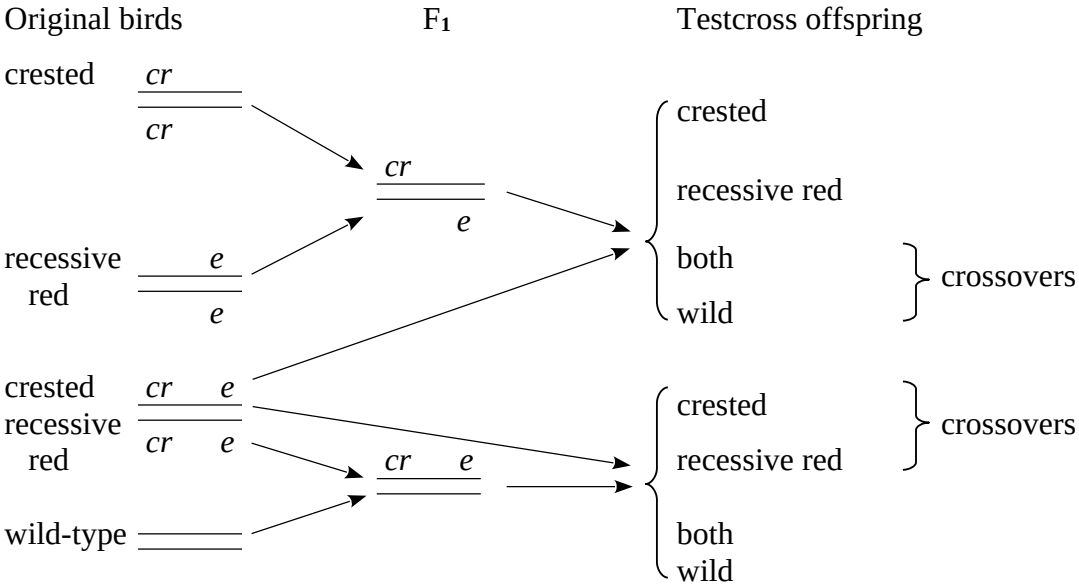


Crossing over of the chromosomes in meiosis of the F_1 birds is necessary for the production of silky checker and of wild-type progeny in the testcross. If linkage is very tight, there will be few or no crossovers. Therefore, we count. Suppose we get a dozen squabs and find that only one is a crossover. That is good grounds for believing we have linkage (8% crossing over). But not proof— we might have simply had a statistical fluke. So, more testing is needed. However, if the first result had been the reverse—only one "non-crossover" in the dozen squabs—there would be no good reason to suspect linkage any more, and we could consider the test complete; independence indicated. Of course, usually the counts are not so clear as that. After some 50 squabs have been classified, and recorded, we may sometimes still be undecided. Anyway, make a report! (See a similar example by Miller, 1964, "First linkage of a species antigen in the genus *Streptopelia*," Science 143: 1179-1180.

(2) Suppose we want to work with one dominant or partial-dominant character and one recessive. In this case the testcross can be a back-cross:



(3) Suppose we want to work with two recessive mutants, say crest and recessive red. Either or both of two procedures can be used here:



In the above examples the double-recessive (crested recessive red) can be obtained readily, maybe by purchase. But for some other examples, the double recessive may not yet exist anywhere, such as crested albino. For such birds we have to obtain F_2. If these mutants are independent we can expect approximately 1/16 of the F_2 squabs to be the double recessive type. If we don't get any in say 50 squabs, suspicion of linkage is strong, and testing would be worth continuation. If any double-recessive young appear, they can then be used for testcrosses.

Sometimes linkage tests are not so simple. If one of the mutants is lethal or sterile when homozygous, or if both mutants are affecting related phenotypes, serious difficulties face us. Testing linkage of albino with any other color or pattern mutant, for example, give only half the testcross progeny classifiable as crossovers or non-crossovers, and F_2 is hopeless.

Considering all the headaches, and the rare delights, it would seem sensible for such projects to be run in a coordinated, cooperative way. So who will join us?

—P. S. & G. N. No. 8 pages 13-14 (1978)

MORE ABOUT MULES

There is something strangely enticing in species crossing so that many otherwise sane (?) breeders have a fling with it. Maybe it's scientific curiosity, or a perverse urge to flout Mother Nature, or maybe even a hunch that hybridizing can lead to desired blend or novelty. I remember one deluded fancier who thought he could bring back the extinct Passenger Pigeon (*Ectopistes migratorius*) from crosses of mourning doves with Racing Homers. Well, after a bit of experience with such unnatural matings, most of us recognize that Mother Nature doesn't look favorably on them, and we go back to sensible breeding.

Still, there is much to be learned from mules, and the scientific experimenters have found the Columbidae uniquely favorable subjects. C. O. Whitman was a leader in this sort of research around 1900, and he had many followers, especially Ghigi in Italy and Oscar Riddle in the U.S. Then Leon J. Cole at the University of Wisconsin started a big hybridizing study which dominated the field for years and was joined by M. R. Irwin for blood-typing analyses. Other outstanding investigators are A. M. Taibel, who was an associate of Ghigi's, and W. J. Miller who studied under Irwin and is at present at Iowa State University (Ames). Miller has been particularly interested in "Hybrid substances" of the red blood cells.

One can spend days reading the many and voluminous reports from these and other hybridizers, but it is a bit depressing—the extensive infertility, early mortality, intermediate phenotypes, and other seeming blind-alley results. There are several generalizations or rules which may be deduced from hybridization data: (1) "success" or failure depend on the closeness of relationship of the parent species. For example, we can predict that crossing fruit pigeons with domestics will be impossible. (2) Female hybrids are more likely to die early or be sterile than males. This is an example of "Haldane's Rule" and is explained by sex-chromosome "imbalance". (3) Male hybrids may show sterility or poor fertility because of failure to produce sperms or because the sperms are highly abnormal. Hybrids between pigeon and ringneck dove occasionally produce offspring in backcrosses to dove, probably from double-size (diploid) sperms. These backcross birds have always been totally sterile and may be triploids.

Surviving species hybrids may be vigorous and long-lived, good examples of heterosis. But there are plenty of examples of the opposite, where the hybrids are delicate and prone to die young. There are some unsolved mysteries here about how the chromosomes from the different parents work together in development.

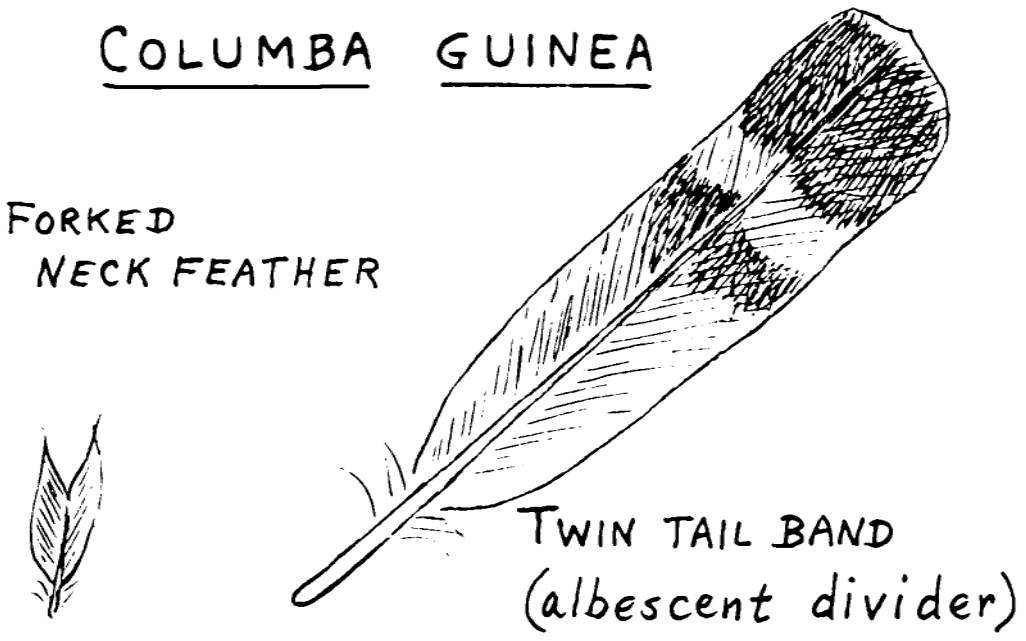
Anyone interested in plowing through the literature in this field up to 1958 will find a book by Annie P. Gray extremely useful: "Bird hybrids: a check-list with bibliography," Commonwealth Bureau of Animal Breeding and Genetics, Edinburgh, Technical Communication No. 13. A good percentage of the references are in foreign languages. I will mention only one more recent report: Dr. Dieter Harmuth of Berlin, Germany, raised a Wood Pigeon (*Columba palumbus*) squab by hand; it was a female, so he mated her with a blue-barred (self) Danzig Highflier cock. They produced 2 hybrids in 1972 which had the whitish wing bows like the Wood Pigeon and two bars on the wing shield; rather long tail, no crest, and look otherwise intermediate, healthy. (Personal communication to WFH.)

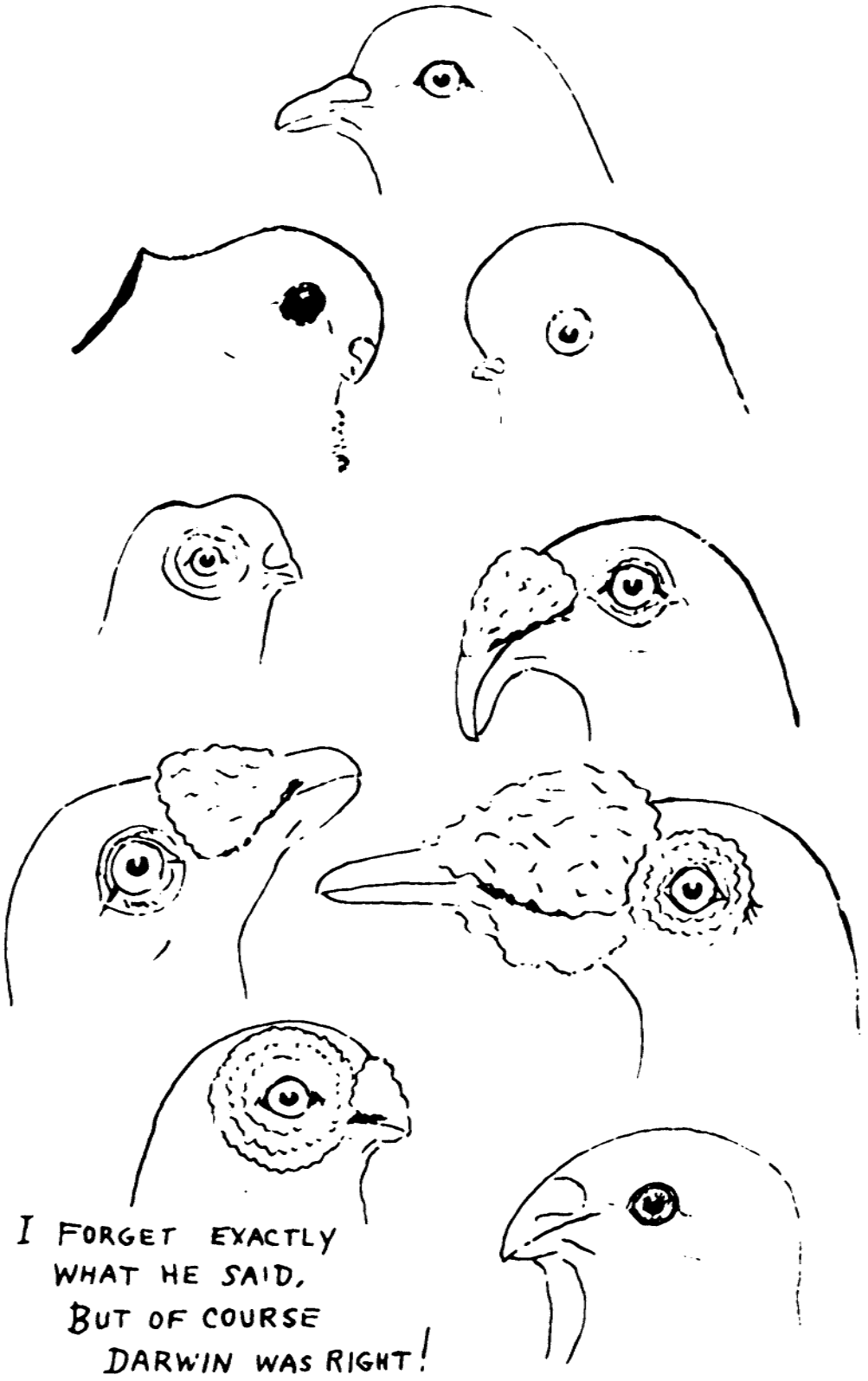
Color photos of two pigeon X ringneck dove hybrids are printed in Levi's Encyclopedia of Pigeon Breeds (figures 798 and 799). Colors of the hybrids can be various, depending on the mutants brought into the cross. Evidence of this sort has shown that the fawn (blond) mutant of the dove is allelic with dilution of the pigeon. Also, the true albino mutant in the dove is allelic with true albino in pigeons (W. J. Miller, 1971, PGNL No. 59 page 2).

Ghigi was confident that domestic breeds of pigeons originated in large part from species hybridization in the distant past ("polygenesis"). It is easy to imagine such possibilities: the gazzi pattern might trace to *Columba leuconota*, the Snow Pigeon of the Himalayas; large size and barless pattern might come from *Columba palumbus*, the Wood Pigeon of Europe; naked eye cere and checker pattern might derive from *Columba guinea*, the Triangular-spotted Pigeon of Africa; and so on. However, the evidence for such origin is slim or absent, and the wildness of those species is a big obstacle. Also only the male hybrids can be bred from further, as a rule. Therefore it seems easier to assume that the multitude of domestic types originated in *Columba livia* by mutation and recombination, with man's selective efforts.

In spite of the failure of the experimenters so far to produce even one new breed or variety from hybridizing, I think they could have. Transferring the wing shield color pattern of the European turtle dove, *Streptopelia turtur*, into ringneck doves should be relatively easy, for example, and attractive. The forked neck feathers of *Columba guinea* could be introduced into domestic pigeons such as the Damascene, perhaps, to give a novel and beautiful effect. Such possibilities may be successfully exploited by able fanciers rather than scientists.

—P. S. & G. N. No. 5 pages 9-10 (1977)




I FORGET EXACTLY
WHAT HE SAID,
BUT OF COURSE
DARWIN WAS RIGHT!

ON THE ORIGINS OF DOMESTIC GENES

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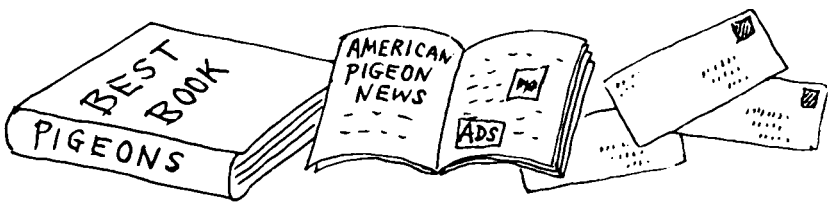
ON THE ORIGINS OF DOMESTIC GENES (PREFACE)

"Genes" have been classified in various ways by various persons; actually the classifications pertain usually to the effects, the phenotypes, so that we need to know about physiology, embryology, growth, psychology, and the like. But another aspect of classification is evolutionary: natural selection over the eons has resulted in those marvelous entities we call species, beautifully adapted to their environments. It is almost a truism that man's interference in the evolutionary scheme has produced types unfit to survive in Nature. Artificial selection has obviously been effective in propagation of genes which seem not to exist in the wild. I realize that classifying such genes as "domestic" may be even more artificial than they are, but that is the general direction in which we need to look. Not to make a mental distinction between what man has fancied and saved versus the primordial and natural—that is to misconstrue the world.

The series which follows was written over a period of 20 years; it was put together in no logical order, and the coverage is very uneven. I have added 1982 postscript information to help update some of the articles. The reader should have access to Wendell Levi's books (The Pigeon; Encyclopedia of Pigeon Breeds) for background information and bibliographic references. Also some genetics aid may be obtained from the Information Booklet on Genetics published 1951 by the NPA (National Pigeon Association) and reprinted 1980 by the Ink Spot Co., and from Joe Quinn's "Pigeon Breeders' Notebook" as well as other texts.

My impression of the history of domestic pigeons is that agriculture and architecture were fundamental. Probably the wild *Columba livia* found man's fields and buildings very convenient from the beginning of civilization—in Asia Minor, Egypt, Persia, etc. Probably religion and the tendency of people to make pets and to value them were important in allowing aberrant types to multiply. Eventually trading probably became important in spreading and mixing the new types, for example from Egypt to England. And finally the development of clubs, competitive showing, racing, and squab farms became influential. The geneticist is a late-comer in the history, but perhaps his seed will grow. Certainly he propagates a lot of new and unfit genes, and he may conjure up a vista of novel possibilities.

I hope the readers will be encouraged to correct my errors and report their own discoveries.



I. BROWN

Is it possible at this late date to figure out when, where, and how the peculiarities of our domestic types came into existence? Historical data are scanty or absent; we know only a little about ancient trade in pigeons, or of their intercrossing. Possibly the particular peculiarity we are interested in did not originate only once, or in only one country of the world.

Maybe it is impossible to get a reliable answer, and probably many people consider the matter of no consequence anyway. But just for the fun of it let's look into a few examples and see what comes of it.

As the first peculiarity to investigate, I am choosing the "brown" or "chocolate" color factor, which is a sex-linked recessive. This gene must be fairly ancient but was first recognized as different from the sex-linked "dilution" factor in 1924, by Metzelaar at the University of Michigan. How can we say then that it is ancient? Simply because it is common—this state of affairs could hardly have arisen rapidly without special selection.

So far as I am aware, no one has found brown popping up in a breed where it had never been seen previously, unless introduced by a cross. Not that a mutation could not occur; but at best it would probably be rare. Therefore in trying to trace the origin of this gene, let's see where it is now, and try to figure out how it got there by cross-spreading. We must assume, I think, that some intercrossing occurred, but not indiscriminately; also, it seems likely that deliberate selection of brown birds in such crosses, over other colors, did not occur. In other words, we may reasonably assume that the spread (if such it was) occurred slowly and without direction (i.e., randomly).

Brown is common in large breeds, such as Runts, Mondains, Hungarians, Strassers, and of course Kings. It also seems prevalent in Oriental Frills and Owls. And finally it is found in Barbs, English Carriers, Pigmy Pouters, and Mookees, If it occurs in any other breeds, I have never seen or heard of it, except extremely rarely in Racing Homers and Carneaux (hidden). Quite possibly my information is deficient, but readers can perhaps fill me in? Apparently brown does not occur at all in such huge groups as Tumblers, Rollers, Highfliers, the Nun, the German Toy or Field pigeon group, Trumpeters, Jacobins, Fantails, Continental Pouters, and Modenas. And I have never seen it in Dragoons, Scandaroons, Damascenes, Dewlaps, Lahores, Lynx, or Archangels. By contrast, in the groups where brown is absent we find dilution usually common.

Is this breed distribution of brown completely haphazard? Not much. The only significant breed having brown but not geographically or historically connected with others seems to be the Mookee. The Mookee stands out as a little "island." Otherwise brown seems very likely to have originated in the Mediterranean region, perhaps Egypt, and spread by introgression into most types except those used in the flying sport, around that sea. The Pigmy Pouter may be another "island" type, but its known crossbred origin suggests introduction.

One other possibility as to origin should be considered. Brown is known to be an allele (alternate) of the very common ash-red factor. Ash-red birds generally have flecks or "ink-spots" in their plumage, which have been attributed to instability of the ash-red factor. In hens these flecks are almost invariably brown. It is conceivable that this instability is not limited to the feathers—that mutation to brown could occur occasionally in the germ cells. And when we look at the large breed groups where brown is not found, it seems that ash-red is not particularly common either. But ash-red is also not found in Barbs, Carriers, Strassers, or Hungarians; and it is rare in Oriental Frills.

Putting our ignorance and guesses all together, it looks as if the introgression idea is more important. However, who knows?? Readers' comments will be welcomed.

—NPA News, April 1958, pages 6-7.

P.S. 1982: After the above was written I was soon informed that brown does exist in Nuns and LFCL Tumblers. Also I have seen it in English Pouters and Modenas, and it has been introduced into Rollers, Saxon Ice Pigeons, and Fantails. In the Modena the "brown family of colors" has been given a fancy nomenclature for show purposes.

The "khaki" mutant in common domestic ducks, and the "chocolate" mutant in the Muscovy duck seem genetically the same as brown in pigeons (Poultry Science 49: 594).

II. INDIGO

At the rate we are publishing, the series will go on forever, because new genes are discovered or dug out of more complex associations nearly every year.

We reasoned in the first article that the gene "brown" had a moderately ancient origin. It still seems to be missing in a number of breeds; the list of these as given was not too accurate, since later George Neuerburg and others have given me some evidence that Nuns, Modenas, and a few Tumbler varieties may also have this color gene.

In this second article a much less common gene is up for scrutiny. Indigo was not recognized as an entity before 1936. Wendell M. Levi discovered it and named it at the Palmetto Pigeon Plant. It first appeared in some hybrids from White Carneau cocks x blue Racing Homer hens, perhaps 2% of the crosses. Test matings with blue Racing Homers showed that the new color was not sex-linked. Pure (homozygous) indigo birds out of indigo x indigo matings were almost "dead ringers" for ash-red in appearance, except for darker "cushion" (tail coverts).

Crosses with solid black Racing Homers produced a novel color type, spread indigo. This remarkably resembled what chicken fanciers call “Andalusian blue”, and many pigeon fanciers consider it beautiful. First publicized in Levi’s book THE PIGEON in 1941, the color is now widespread in the U.S., particularly having been introduced into Giant Homers.

Introduction of the color into a different breed is very easy, and it may become popular in many others. However, the fancier must realize that the “Andalusian blue” or indigo is a heterozygous effect and will not breed true. Only half the progeny, on the average, can be expected to resemble the desired parent type.

Obviously the indigo gene did not originate from the Racing Homer, as it had never previously been seen in that breed. We therefore trace the gene to the White Carneau. Beyond that the trail is lost. Suggestive cross results indicated that Red Carneaux may also carry it. More testing would be desirable—Red Carneau hens x blue cocks. If any *daughters* look indigo, that would be good evidence. In the 1957 edition of Levi’s book it is suggested that perhaps the Carneau could have got the gene from the *miroité* Lebanon. That seems to have been a wrong guess, since my subsequent crossing tests of the miroité have not yielded indigo.

One other breed that I have observed seems certainly to have the indigo gene -- the Syrian Swift. Still another, that I have not seen, is the Batschka Tumbler, where the “schiefer grau” (slate gray) color is probably the same as our “Andalusian blue”. Possibly the gene lurks unknown in a few other stocks, to be ferreted out by some future experimental crossing.

What else can be said for indigo? Is it good for commercial squabs? I don’t think it has any advantages in that line, as the skin color is not affected. This gene will probably remain a fancier’s gem, to be tried in various new settings. For example Earl A. Klotz has produced an “all-blue” Show Racer, a combination of indigo and barless, that is a delight to the eye.

—NPA News, April 1960, pages 25-26.

P.S. 1982: Indigo has now been introduced into a number of other breeds, including Modena, Fantail, Chinese Owl, LFCL Tumbler, Oriental Roller, and Jacobin.

Homozygous indigo generally shows darker head coloration than that of ash-reds. Vigor has been good.

III. REDUCED

(This article was written by Carl F. Graefe)

I know of no proof as to when or where or in what breed the mutation now called "reduced" first occurred, but it was no doubt somewhere in the great Tumbler tribe, which has probably been the longest and most widely bred, and certainly is the most varied in color and type of any class of domestic pigeons. At any rate, it was first recognized as something distinct or unusual, in 1945 at Cuyahoga Falls, Ohio, in a pair of pied Birmingham Rollers, ancestry unknown, and derivation rather hazily going back to "Rollers from Baltimore."

Colored feathers of the original pair were lighter than normal shades of bluish to blackish, with some reddish in the wing pattern, and rather ashy in the tail. The cock was T-pattern, the hen barred. Offspring of the original hen with normal-color cocks were all normal. The original cock mated to normal hens produced daughters all of his color, sons all normal. The original pair mated together produced all offspring like themselves. These and further tests demonstrated that the new "color" is inherited as a sex-linked recessive which can modify all the normal colors. The only other sex-linked recessive genes known are "brown", "dilute", and "pale." Since the new color had no resemblance to them, but still always seemed to reduce pigmentation, I named it "reduced." (Not a very attractive name but the best I could think of, so now we are stuck with it.)

When cocks carrying dilute from one parent and reduced from the other are bred from, the new combination of dilute with reduced appears in only a very small fraction of the squabs, compared with the number expected if the assortment were free. This means that dilute and reduced have closely linked positions (loci) on the sex chromosomes.

Some reduced-blue pigeons are very pretty, for instance when with T-pattern they are attractively laced on light gray. The *S* (spread) factor also encourages some tendency to lacing, on a dusky ashy background, when the underlying pattern is T. Some barred reduced ash-reds are soft pastel in ground color with bars modified to pinkish or soft gray. Reduced recessive reds are variable, yellowish to pinkish. Reduced browns, so far scarce, haven't shown anything very attractive. The only reduced dilute recessive red I ever saw, which was my first cross-over here, was a very pale pretty shade of yellow. There are many other combinations still to be tried out, some of which might be attractive and unique. There is usually an interesting difference between nest feathers and adult, the baby plumage being lighter.

Since reduced has never been discovered in other stocks, it has been bred in by crossing from these Birminghams. So far, it has been transferred to Show Racers, American Giant Homers, Show Tumblers, and Domestic Flights, and maybe some other breeds. Some breeders have remarked that reduced hens have a tendency to lay eggs with poor shells, but this has not been our experience in Ohio. However, for commercial squab production reduced birds may not be quite as rugged as necessary, and skin color is hardly lighter than in blues. There is also some evidence that dilute-reduced birds are lacking in vigor, though pretty.

This is one of the few examples where the origin and dispersal of a new gene are reasonably well known. The future progress of the reduced color will be interesting to watch.

—NPA News, April 1960, pages 26-27

P.S. 1982: Reduced has also been introduced into Fantails, Modenas, Swing Pouters, and Chinese Owls.

IV. BARLESS

The first genetic study of the barless pattern was by Sarah van Hoosen Jones at the University of Wisconsin. Her report in 1922 gave results of crossing a barless Racing Homer hen with a normally barred (wild-type) Racing Homer cock. Four offspring survived, all showing normal bars. Another mating was also made, a black crossbred cock with a barless Swallow hen. Three youngsters were obtained: two normal blue with bars, and one black "with blacker bars." Miss Jones concluded from these results that barless is a recessive condition.

In 1926, C.J.A.C. Bol reported his breeding tests with colors and patterns of Racing Homers, in Holland. He assumed that mealies without bars were comparable to barless blues in pattern, but made no actual breeding tests of this. Similarly, he assumed without valid breeding evidence that light grizzles, showing mostly whitened wing shield, were barless. Both of these assumptions have been found subsequently to be unjustified, but many breeders still are fooled in the same way. Actually, the so-called "barless mealies" are usually comparable to solid black in pattern.

In 1938, I reported my studies of barless at the University of Wisconsin. My start was the blue barless Strasser. Crosses with other patterns never gave barless in the F_1 squabs, so that I agreed with Miss Jones that it is recessive. Backcrosses to barless, and F_2 progeny showed that barless is alternative (allelic) to checker as well as to T-pattern. For example, a blue checker out of blue checker X barless was mated back to barless. This backcross produced about equal numbers of checker and barless squabs -- never any barred. From these results, I concluded that barless was here the effect of a gene which I symbolized *c*, checker on the other hand having *C*.

Few breeds have the barless pattern in their repertoire. It is fairly common in Swiss breeds—the Eichbuhler, Berne, Zurich, and Lucerne types; and in "German Toy" breeds—Archangels (Gimpel), Ice Pigeons, Monks, Priests, and Swallows. It is also common in Coburg Larks and in the Crested Soultz, both of these breeds probably of recent origin from crosses involving Toy breeds. Strassers, of course, commonly are barless. The only Pouter type which I have heard of being barless pattern is the Bohemian. Barless blue Racing

Homers in Wisconsin, according to comments I got at shows, appear to have been developed from Strasser crosses. Whether independent sources of the pattern exist is not certain, but rarely such a bird has appeared in other Racing stocks,

Up to 1940, so far as I know, barless blue was non-existent in all the Tumbler breeds, Fantails, Modenas, Oriental Frills, Runts, Maltese, Kings, Mondains, and numerous less ordinary breeds. Barless seems then to be primarily of Central European origin. Probably it was deliberately crossed into the Strasser, Larks, and Soultz, although their origins are not very clear. My guess then is that the mutation to barless occurred relatively recently—that is, less than a thousand years ago, rather than in extremely ancient times.

At present, some enterprising color breeders have been introducing barless into various new settings, such as L.F.C.L. Tumblers, Rollers, Show Racing Homers, and others. With a little planning, this can be done very easily. For example, here is one method: suppose one desired to create a barless blue Modena. If the Gazzi pattern is desired, the Strasser is a good source of barless. Cross it with a T-pattern Modena ("Bronze" will do) and get a T-pattern ("black check") hybrid. Cross this back to a checker (tricolor or "arrow-point" is OK) Modena. Select a checker progeny; this is 3/4 Modena. Backcross to a barred Modena and select several good barred progeny (7/8 Modena). Mate these together and about a fourth of their squabs should come out barless. Note how the patterns are used in sequence, so that barless is not seen at all until the final step.

Barless is a distinctive pattern, easy to manage in crosses, so that it may soon be very widespread. Certainly it is attractive and a desirable addition to the bars and checkers so common in the shows.

—NPA News, October 1960, pages 19-20.

P.S. 1982: Narrowness of wing bars is a common condition in pigeons heterozygous for barless, so that this gene may be considered incompletely recessive.

Dr. Dieter Harmuth of Staufen, East Germany crossed a hand-raised female Wood Pigeon X smoky blue bar Danzig Highflier cock and obtained an F_1 showing definite wing bars. (Personal communication and photos.) This result suggests that the barless wing pattern of the Wood Pigeon is genetically the same as that of barless domestic pigeons. The same argument applies in crosses of ringneck dove (*Streptopelia risoria*) X barred domestic pigeons, as the F_1 shows a faint tendency to wing bars.

A strange relation between barless and defective vision (semi-blind, or "foggy vision") has been repeatedly observed in some derivatives of crosses; for example see PS & GN 4:48.

I have obtained the crossover combination of barless with recessive opal.

V. MILKY

One day about 25 years ago I was walking downtown from the University of Wisconsin campus, and passed a flock of common pigeons on a lawn. One of these was a pale color that was new to me; the bird had a "pin-wheel" leg (sticking out at one side like an oar), but he was hobbling around gamely. I forgot my errand and traced this flock to its loft, an old 2-story barn behind an apartment house.

Inquiry revealed that the pigeons were supposed to belong to a boy living in the apartment house. When he arrived, I found that he was only about twelve years old. He readily agreed to sell the crippled pigeon for the good price of 10 cents. He had no idea as to the origin of the bird, and his pigeons apparently were simply street vagrants.

This crippled pigeon was a cock, and in an individual coop had no trouble breeding. Crossed with an "opal" hen, he gave only blue squabs. Next, he was crossed with a T-pattern blue hen, and produced again only blues. The young from these two matings were paired, and produced Mendelian assortment (about three times as many blues as of the new color). These and some other data indicated that a previously unrecognized simple recessive gene was responsible for the new color, and I gave it the name "milky" (symbol *my*). The reason for this foolish name was that the color looked like a blue pigeon that had been soaked in milk. It is quite different from grizzling—no white specks, and the wing bars are clear but faint.

A few years later, I saw "powdered silver" Fantails for the first time, and realized that this color was a ringer for my milky. Later, a cross-breeding test proved that they were genetically the same. Furthermore, the so-called "lavender" color in Lahores proved to have the milky factor, and apparently the same thing has been found in Mookees. So far as I know, no other breed has shown such colorations.

Since the Fantail, Mookee, and Lahore are all of Persian or Indian origin, it seems likely that the original milky mutation occurred in that region of the world. Being recessive and not sex-linked, it would be difficult for breeders to handle in crosses, so that the actual origin may have been many centuries ago. My own original specimen may well have had some Fantail in his ancestry, though he showed no other evidence.

I have tried numerous combinations of milky with other genes. The only one of much interest is with recessive red: milky is not hidden as most other color genes are with recessive red, but gives a pinkish effect to the red, with neck feathers a beautiful pearl. This combination, of course, will breed true.

Milky by itself does not give light skin color in squabs, and the pinfeathers are fairly dark. Otherwise, I have seen no undesirable feature for its use in squabbing stock. With smoky or recessive red these drawbacks are eliminated.

To introduce milky into other breeds should be a bit time-consuming but otherwise not difficult for anyone who feels like tackling the project. For example, suppose a milky King was desired. Cross a milky (lavender Lahore?) hen with a blue King cock. Since most

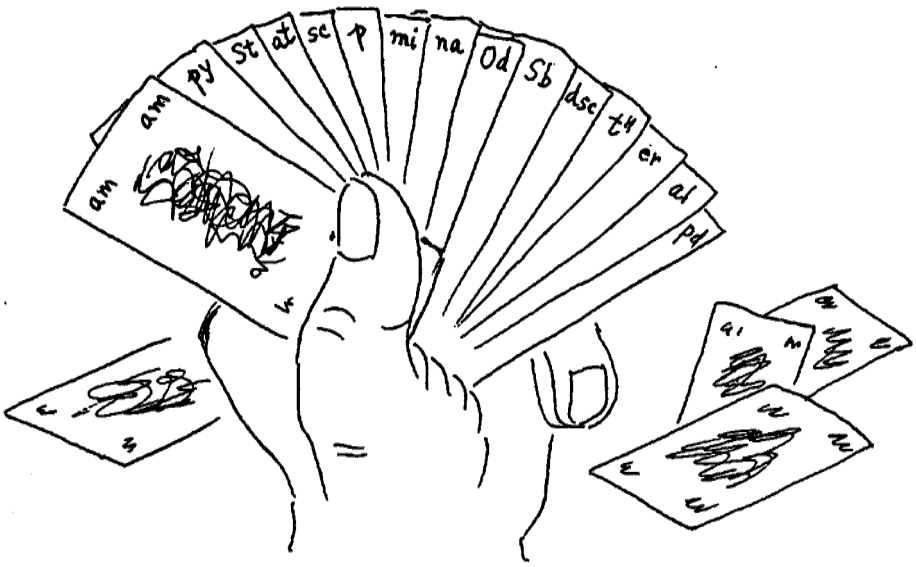
lavender Lahores carry the ash-red and the *S* (spread) genes as well as milky, the squabs from this cross will most likely be black hens and ash sons. The latter are confusing so get rid of them. Now mate several (half a dozen) of the black hens back to blue King cocks. Raise a good many young (20?) and pick out the blues or blacks with best size and type. These are of course three-quarter King: each of them has about a 50-50 chance of carrying the *my* gene. It is necessary to make a test to find out which birds do carry it. The test is whether they can produce a milky squab. So mate the cocks to the first-cross hens; if no milky squabs appear in say five clutches of squabs, presumably the test is negative—the cock is of no use. If a milky squab does appear, the sire is tested. The milky squab may be useful later as a tester, so better hold on to it.

The next step is to backcross tested cocks to blue King hens, and produce seven-eighths Kings. It should be rather easy now to pick out young which are indistinguishable from pure blue Kings. These must again be tested to see which got the *my* gene. When the tests are completed, the final step is to mate tested birds together. About a quarter of the squabs should be milky and of King type. And then the proud creator can advertise. Of course other breeds could be "milkified" in similar fashion, and the gene would be pushed further from its origin.

—NPA News, April 1962, pages 4-5.

P.S. 1982: Milky has been found in Modenas without known outcross origin.

I have seen occasional milky ferals caught on farms in Iowa and neighboring states, so that a possible Fantail source of my original milky common pigeon seems less likely.



VI. ALMOND

(This article was written by W.F.H. and Carl F. Graefe)

What is almond? Ever since 1735, when John Moore described it in his "Columbarium", the word has been associated with English Show Tumblers. But does that mean it originated in England? Other European countries also have Tumbler varieties, and the same coloration is known in them, by indigenous names. Tumblers probably originated in Persia, not Europe, and the Oriental Roller from that area of the world is very commonly of the almond color.

Most breeders know almond as a scrambled patchwork of colors—yellowish, blue, black, brown, red, whitish, etc. It is the variegated effect which impresses us, not really the almond (yellowish) portion of the effect. The German names "gesprenkelt" (sprinkled), "vielfarbig" or "harlekin" (varicolored), and the Danish terms "Stipper" and "stankede" (speckled) convey the same thought. In Italian the term "magnano" (plural, magnani) has the same meaning, but is applied to Modenas of such coloration. The original meaning of magnano is clear; it also means "coppersmith". (The French term "magnan" may be a clue —"silkworm"; silkworms have a variegated color pattern, and Italians also raised silkworms.

It is well known among breeders of such colors that the dark component of the scrambled effect increases with age, and also that males tend to become much darker than females. These peculiarities distinguish almond (and related color types) from such superficially similar colorations as "tiger", "grizzle", "splashed", and "mottled", where the light component is more likely to increase with age, and there is no sex difference. Probably the first scientific attention to the phenomenon was by A. Ghigi of Italy, in 1908. Among other observations he stated that the sex difference is most prominent in the *Gazzi* Magnani.

The first genetical study of almond (gesprenkelt) was reported in 1925 by Wriedt and Christie of Norway. They found that almond Tumbler hens mated to blue-black cocks produced almond sons but never almond daughters. From this and other tests they concluded that a sex-linked dominant gene was responsible, to which they assigned the symbol *St*. They also noted that almond squabs have much shorter down than normal, in this respect resembling dilutes.

Almond breeders generally have frowned on mating almonds together. Fulton, for example, in the latter part of the 19th Century, stated ("Book of Pigeons") that the progeny from such matings were often "bladder-eyed", blind, with white plumage. Wriedt and Christie also found such results and other eye abnormalities (coloboma or fissure of the iris) However, they found that not only "pure almonds" (*St St* males) were so affected but also some dilute-almond squabs. These studies further indicated that the dilution gene was situated not at all close to *St*, on the sex chromosome,

Subsequent studies (including our own) have confirmed most of Wriedt and Christie's conclusions. For a time almond was considered an allele of brown (and of ash-red),

but later a small amount of crossing over was found by us and others. Our tests with Magnani show agreement with those involving almond of Tumbler derivation.

Wriedt and Christie used the symbol *St* for "gesprenkelt", referring to the variegation. But the *St St* ("pure") birds show very little or no speckling or flecking, being almost pure white. It is thus evident that the essential action of *St* is to inhibit pigmentation. The increasing of dark areas with age may be considered a "recovery" or reversion toward normal pigmentation. The modern genetic theory to explain such variegation is instability of the abnormal factor. The exact nature of the process is unknown, but for convenience we may use the idea of mutation, *St* changing back toward its normal allele, here and there. The theory does not explain why females and heterozygous males differ, but as the process continues, we should not be surprised that the bird gets darker with age. (See "Flecks and Sex", NPA News, June 1960.) In birds with double dose (*St St*) both would have to mutate before recovery can occur.

The multiplicity of colors in "standard or classical almond" seems best explained by assuming that the *St* factor is operating there on a "kite" base. Kites (bronzy-black T-pattern, usually heterozygous for recessive red) are generally used as mates for show almonds. Such almonds start life with ashy tail band and flight tips, and yellowish elsewhere. Mutation of *St* back toward normal allows the residual kite base to be exposed.

Similarly, "agate" or "DeRoy" colorations seem to be the operation of *St* on a recessive red base. Fulton mentions and figures also "red agate splashes or mottles", which are white in ground color, red flecks increasing with age. Such an effect has not been much analyzed; possibly it is *St St* on recessive red, or the grizzle factor or ash-red may be included.

When *St* is operating on a spread black or dun base, the result in old birds may imitate "tiger" grizzling. Knowledge of the birds' history, or a breeding test, may be needed so that their counterfeit nature can be recognized, though an expert may be able to distinguish them (more even mottling with *St*).

After this lengthy prelude we may now return to the matter of origin. A number of breeders are at present developing almond strains in Fantails, Show Racers, English Show Homers, American Giant Homers, Kings, Blondinettes, and even Danzig Highfliers—breeds that were presumably never almond previously. In these cases we know that the *St* gene has been introduced dilberately by crossing, the origin being some variety of Roller or Tumbler. So far as we have been able to learn, *St* has otherwise been nonexistent in most breeds: the German Toy and Swiss groups, the Pouter group, the Oriental Frill-Turbit-Owl groups, the Carrier-Barb-Homer groups, the Fantail-Mookee-Lahore group, Maltese, Hungarians, Strassers, Larks, and so forth.

The chief source of *St* seems most probably the old Oriental Roller. From it most probably have been derived the other kinds of Tumblers (including Parlor Tumblers) and Rollers. Possibly it even contributed to the origin of the Triganini of Modena, since both were valued for their flying skill. But this is only a guess.

At the World's Poultry Congress Exposition in Cleveland, 1939, a pair of Sottobanca pigeons (Mondains) from Italy showed typical almond coloration. Also in other Mondain stocks almonds have apparently been common at times: a hundred or more were seen in George Hughes' loft of squabbers near Bridgeton, N.J., in 1910; about 45 years ago (1916) some were observed in a stud in Sandusky, Ohio; and at the 1955 National Show at Atlantic City a number of apparently almond French Mondains (notes by C.F.G., and by B. Petersen). In show-type White Kings nearly downless squabs have occasionally been observed; while this might indicate the presence of the "dilution" gene, it could equally well be the effect of *St*. From the cross of a White King cock with a blue Homer hen in 1940 an almond-like ("Sandy") bird was bred (by W.F.H.). "Sandy"-colored birds are often produced in almond stocks, and differ from standard almond in having relatively little flecking, even at advanced ages. It may be a more stable form of *St*. However, such birds are generally culled.

Whether *St* exists in other breeds at all we are not sure. There may be examples in Bokhara Trumpeters and in Jacobins, but confusion with "tiger" grizzle is easy. Conceivably if *St* is present it could have been introduced long ago from Tumbler crossing.

This is as far as we can carry the study at present. No one seems to have caught almond recently originating *de novo* from blue. But in view of the interesting genetics, as well as the intriguing color combinations, it seems likely that *St* will increase its domain.

—NPA News, October 1961, pages 3-5.

P.S. 1982: The article "Flecks and Sex" is reprinted in this booklet. (Much remains to be learned.)

The crossover combinations of almond with brown (produced by WFH) and with ash-red (produced by CFG) are being introduced into various breeds.

Joe Quinn discovered a mutant more or less intermediate between almond and blue in a feral flock in Ohio. Tests indicate that it is an allele of almond. It has been introduced into several breeds under the names "Quinn's mutant" and "qualmond", with gene symbol St^{Q} (PGNL 41:4; PS & GN 3:43).

VII. FADED

If we *know* the origin of any color genes in pigeons, that honor should go to "faded", because it has literally been seen originating—from almond. Dr. H. W. Feldman at the University of Michigan had taken over the pigeon Genetics research there after the death of Jan Metzelaar, and about 1933 was puzzled by a peculiar new color. The bird was a male bred out of an almond hen X kite cock (Parlor Tumbler X Tippler origin).

According to sex-linkage of almond, the son should have been almond, but he wasn't —the color was more of a washy kite. Feldman tested the bird, and out of him got more of the same but no almond. In 1934 he gave up pigeons, and sent these birds to me at the University of Wisconsin. For a couple of years, I called the new color "Feldman's opal". In my first report, in *Genetics* 1938, I first used the name faded, but a symbol suggestive of Feldman's opal, *Of.*

In 1938 Wendell M. Levi showed me some novel color types which had appeared at the Palmetto Pigeon Plant when White Carneau cocks were crossed with blue Racing Homer hens. In addition to indigo, there was one we referred to as "frosted" which I helped test out. This proved to be identical with my faded. But there was no possible connection in origin, so far as we could see.

In *Genetics* 1940 further test results were reported. By this time it was clear that faded was sex-linked, and its origin was interpreted to have been mutation from almond. The evidence then indicated that almond was an allele of brown and ash-red; therefore, the symbol was changed to B^{of},

In 1940 I discovered that males homozygous for the faded gene were quite different from ordinary faded males and females. The homozygotes were practically white, with a slight sandy effect in the tail band, the ends of the flights, and the neck. Also traces of reddish showed up in the neck and sometimes in the wings. Often flecks of faded color were scattered in the plumage, especially the neck, so that these birds sometimes looked remarkably similar to almond, even to having rather short nestling down.

The difference between faded females and homozygous faded males suggested the possibility of commercial utilization. That is, one could distinguish cocks from hens in the nest without special sex-linked crosses. George Stearns of Wilmington, N.C., obtained a Wisconsin-stock faded bird from me to introduce into his Giant Homers, while Palmetto Pigeon Plant began to introduce their faded gene into Silver King stock, Racing Homers, and Red Carneaux. For a while these sex-marked stocks were called "dual-colored", but a similar set-up in chickens had been named "autosexing" and this term has been preferred by pigeon breeders also. These developments were reported in the *Journal of Heredity* in 1942.

The auto-sex types were first offered for sale about 1944, and they zoomed in popularity. The gene was introduced also into several other breeds, but interest died down as the color became widespread. Prices quickly plummeted to those for any other color. Commercial utilization for squabbing was dampened when records at Palmetto Pigeon Plant

demonstrated somewhat poorer squab-rearing by auto-sex birds than by other colors, on the average. Also, the faded gene proved not entirely adequate to prevent some skin darkness in female squabs.

Meanwhile I had discovered in 1943 that it was possible to get crossing over between the faded and the brown genes (reported in *Genetics* 1943). An auto-sexing brown type was consequently started. Manfred Gottfried of Stamford, Conn., obtained a bird of this type from me about 1944 and began to develop it in large Show King stock selected for production. The result was called "Amber-whites", since the females were more or less yellowish in color and the males white. Gottfried also developed a comparable cross-over type of faded with ash-red, and the resulting stock was called "Copper-whites". Birds of these stocks have been distributed widely, and being more attractive than ordinary auto-sex colors may become more popular.

The final revision of symbols to show allelism of faded and almond was in the NPA Genetics booklet (1951): St^{F}.

Mutation from almond to faded has been observed at least twice again since Feldman's original case. Apparently this must occur rather easily. My estimate is that the frequency is in the neighborhood of one squab out of about a hundred from matings of almond hen X blue cock. As long as we have almond, then, we can rely on it as a source of new origins for faded.

Finally we must note one other old source: the Reehani Dewlap of Syria. This apparently ancient auto-sexing breed first came to the attention of the Western world in 1955. My breeding tests show that here again the gene responsible for the auto-sex feature is our familiar faded. Whether this could have come from almond originally is completely a matter of speculation, but who knows?

—NPA News, May 1962, pages 4-5.

P.S. 1982: Delwin James of Houston, Texas, also produced faded ash-red (crossover) Kings and developed an auto-sexing stock from mixture of these with French Mondain which he named "Auto-sexing Texan Pioneer" for squab production. It was admitted as a new breed in 1962 by the National Pigeon Association.

John Roddey of Rock Hill, South Carolina, developed a stock of auto-sexing Giant Runts out of white X blue crosses (Amer. Pigeon Journal, July 1978, p.423).

The faded factor apparently is fairly common in varieties of Dewlaps, Bagdadi, and Swifts which I observed in Turkey and Egypt.

VIII. SMOKY

Breeders of Racing Homers apparently first named the peculiar coloration “smoky”. In some strains it never occurs, while in others (including some long-distance record winners) it is often seen. I first began to study it in this breed, and reported the tests in *Genetics*, 1938, A recessive gene was found responsible, and I proposed the symbol *sy* for it.

It is important to distinguish smoky from other superficially similar variations such as “sooty”, “dirty”, and “dusky”. Comparing smoky with wild-type blue I was impressed that this is not just an indefinite darkening effect. Rather, the smoky condition has several distinctive features: (1) the outer tail vanes are not white as in the wild type, but dark blue; (2) the rump and underwings tend to be bluish instead of whitish; (3) the wing bars or checks are blurred or weakened, especially in squabs, so that against the darker blue ground color the pattern is not clear; (4) the blue tipping of tail feathers is more obvious than in the wild type; (5) there is a tendency to whitening of feather bases, usually most obvious in the flights; and (6) the skin and all except the tip of the beak of smoky squabs (and of smoky adults protected from sun-tanning) is much lighter than in the wild type.

When smoky is brought into combination with such genes as brown, grizzle, ash-red, and so forth, the above constellation of features is less obvious. Experience helps in detecting them, but breeding tests may be necessary to settle the dubious cases. In solid blacks smoky only has a darkening effect except for skin color, so that breeders may unconsciously select for it (unless the breed standard also demands black beak).

Smoky probably came into the Racing Homer from the old Carrier blood in its ancestry. Smoky is common in Bagdadi from Syria, and practically 100% in English Carriers, where a waxy-white beak is desired. Similarly it is almost universal in Barbs, modern Magpies, and dark Archangels. Breeds that I have not tested which appear to have the smoky factor commonly are the Domestic Flight, Hamburg and Hanover Tumblers, Parlor Tumblers, and Oriental Rollers. I have seen unmistakable smoky blue Fantails, Runts, and Kings, and the gene has been demonstrated to occur to some extent in different varieties of Carneaux.

Breeds in which smoky apparently is non-existent are Oriental Frills, including Owls and Turbits; German Toy breeds (except Archangels); Trumpeters; Pouters; Dragoon, Maltese, Lynx, Strasser, Hungarian, and Modena.

Probably fanciers have more or less consciously selected for or against the smoky features, especially the light beak, for many centuries. This selection undoubtedly can account for the erratic breed incidence. About all that we can conclude is that the smoky gene is quite ancient; my guess is that it probably originated in the region of Persia, perhaps even 1000 years B.C., before breeds there had become clearly separated.

There is a question whether the smoky gene may also exist in wild species of *Columba*. At least some of them have light beak and indistinct wing pattern—for example for the Wood Pigeon, *C. palumbus*, and the European Stock Dove, *C. oenas*. Crosses to answer

this question have not been made. Until we get the answer a slight possibility remains that this "domestic" gene might have been introduced anciently by species hybridization.

—NPA News, June 1962, pages 7-8.

P.S. 1982: The smoky gene is common in Swing Pouters. Also I have found it present though not common among feral pigeons in the middle-Iowa farm area.

IX. SILKY

Let us interrupt the series of "color genes" for a change and consider a so-called "structural gene". Silky pigeons are unable to fly more than a few feet and are therefore able to propagate only under domestication.

The silky condition, also referred to by Fantail breeders as "lace", has existed for centuries, and many pigeon writers have discussed it. A rather comprehensive review was presented by D. G. Steele in the Journal of Heredity for 1925, though he failed to include at least one significant early writer—Charles Darwin (1868).

Steele utilized some breeding records of Fantails as furnished to him by an Ohio fancier, and concluded that silky was sex-linked and recessive. He proposed the symbol *l* (for lace). Later breeding tests at the University of Wisconsin disagreed—the character was neither sex-linked nor recessive. The data were presented in the Journal of Heredity for 1939 by Cole and me. Steele's conclusions were based on presumably erroneous and inadequate observations. At any rate, the new tests revealed two grades of silkiness, one ordinary and the other extreme or "fuzzy". The latter has proved to be homozygous, while ordinary silkies have proved heterozygous. The symbol therefore was revised to *L*.

The essential feature of silky feathers is softness, lack of strength, with a tendency for the barbs to twist. They readily become water- soaked, and in the homozygotes much shattering occurs, so that the flights in a few months become reduced to bare shafts.

Perhaps the first recorded observation of silky arising by mutation was by F. M. Gilbert in his book "Pigeons and all about them" (1898): "The best one I ever saw came from a pair of sound whites (Fantails) that never before, and never afterwards, bred another silky." Another possible case of mutation was mentioned by Spruijt in his book "De Structuurduiven" (1931). The bird was a Dutch Cropper with mostly silky plumage but some patches of normal feathers also. Mated with a sister he produced only normal young. Levi (1941, The Pigeon) recorded a clear case of mutation. The parents were a White Carneau cock and a blue Racing Homer hen. The silky hybrid male gave rise to a large number of silky descendants, some of which I still possess. Levi also noted a silky mutant in purebred White Carneau stock and another in purebred Racing Homers, at the Palmetto Pigeon Plant,

but these were not progeny tested.

In the Journal of Heredity for 1956 W. J. Miller reported a silky mutation in the ringneck dove. The structure and inheritance appeared to be identical to the condition in pigeons.

In 1960 I received reports of three more mutations (Pigeon Genetics News Letter #15 and 16). The first was a Brünner Pouter, sex not reported, but it did produce some progeny that were silky. The second case was a Racing Homer hen; mated with a normal cock she also produced some silky squabs. The third mutant was a male hybrid from a pigeon X ringneck dove mating (H563 S) at the University of Wisconsin.

No doubt other cases of mutation have occurred and never been reported, or have escaped my attention. It seems clear that even if all the existing silkies in the world became extinct overnight, we would not have to wait many years before new ones would pop up. I will hazard an estimate that the mutation rate is somewhere near one in fifty thousand squabs.

However, far be it from me to encourage extinction of this gene. At least in white Fantails it is most attractive, and at least a few breeders seem interested in keeping these alive (Pigeons and Pigeon World, May 1959, page 7). Silky is an ideal “marker” gene in genetics experiments.

From one point of view silky might be vexing to some fanciers because the desired feather texture, intermediate, does not breed true. The homozygotes are too ragged most of the time to show. On the other hand, the heterozygous nature of ordinary silky can just as well be considered advantageous, since a single specimen can produce many more without any inbreeding, from matings with normals.

In 1956 I discovered a “slightly silky” squab from a cross I had been following (Racing Homer cock X Black Dewlap hen). The bird turned out to be a cock, and in several matings produced many more slightly silky progeny as well as about an equal number of normals. Some of these I turned over to W. J. Miller for study.

When we mated the slightly silky birds together, we obtained at least two young which resembled ordinary silky. These appear to be homozygotes, according to progeny tests. Miller has also been testing slightly silky with ordinary silky in crosses, to find out whether they are genetically related (allelic); preliminary results indicate that they are not.

We therefore have the prospect of breeding intermediate-type silky birds for show which will produce no normal-feathered young. Will this new gene start to spread?

—NPA News, March 1963, pages 6-7.

P.S. 1982: Reports of new silky or similar mutants continue to appear (PGNL 30:3; 39:4 in LFCL Tumblers; PGNL 46:27 in Modena; PS & GN 6:42 in Tumbler; and PS & GN 7:34 in Arabian Laugher).

My “slightly silky” mutant is not an allele of silky. It has been renamed “frayed”, with gene symbol *F* (Iowa State Journal of Research 53:109).

Dr. Miller found linkage of silky in the ringneck dove with an erythrocyte-antigen factor (Science 143:1179).

A recessive mutant which has been named “frizzy” has been found in Chinese Owls (PS & GN 7:16; 9:17). The defect is most evident in juvenile plumage and affects mainly the proximal portions of the larger feathers. Breeding tests by Wilmer Miller and WFH indicate little variation. The symbol *fz* is proposed.

X. OPAL

About 1930 I began breeding Racing Homers, and soon became intrigued with a peculiar “washed-out” color type. Nobody seemed to know the proper moniker for it, and it wasn’t the same as the familiar red checker and mealy types, so I decided to name it myself. With my mother’s assistance, the name “opal” was chosen.

Studying how this color behaved in breeding tests proved more interesting to me than racing. My rather extensive results wer¢ finally reported in *Genetics* in 1938. In brief, they showed that opal is a single recessive to wild-type color, and that the opal gene (which I symbolized *o*) is closely linked with the pattern genes (checker, etc.).

In spite of this basic simplicity, opal is rather tricky. There is a great deal of variation: one extreme is almost like blue, with some washing-out of the tail band, while the other extreme is similar to red checker or mealy, except for a tendency to pencil-edging of the flights. Sometimes there is considerable change during the molt. I got some evidence that these variations might be related to thyroid gland activity—reddish with high, and bluish with low thyroid function. Also there was a tendency for females to be more bluish than males, in general, though there were plenty of exceptions. The opal females tended to have somewhat poorer average hatchability of eggs than blues; apparently this failing was most prominent in the case of “reddish” hens.

Since 1938 I have learned a bit more. Opal seems very widely distributed among Racing Homers both here and in other countries, but in no other breed. (A similar color type found in other breeds proved to be dominant to blue and therefore not related.) I have seen opals from numerous strains: Trentons, Barkers, Sions, Bastins, Hansennes, etc. In Europe the coloration is frequently referred to as “mosaique”, probably a Belgian term. In this country I have heard it called various names, most often “chocolate”, quite a misnomer.

Opals are uncommon; probably among Racing Homers not over one percent of the birds hatched are of the color. However, considering the vast numbers of Racing Homers in

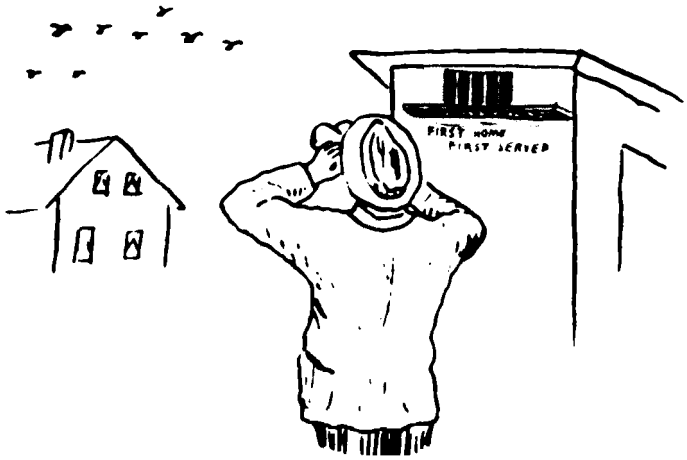
the world, this “rare-color” gene must be recognized as actually one of the most abundant pigeon mutants now available. We can calculate this way: the relative frequency of the opal gene as compared with its normal allele is the square root of the percentage of birds. If opals occur at the rate of 1%, the square root is 10%. (If this seems queer, brush up on your arithmetic!) Assuming random breeding here, that means that nearly a fifth of all Racing Homers carry this gene hidden. If the world population of Racing Homers is fifty million, ten million should carry this gene!

How can we explain the limitation of opal to Racing Homers? My best guess is that when Racing Homers were created in Belgium, less than 150 years ago, one of the key stock birds had a mutation and passed it on to various descendants. As the breed’s popularity caused great expansion, the opal mutant was automatically multiplied too. Offshoots such as the Show Homer, the Exhibition Homer, the Giant Homer, the Schautaube, and the Showpen Racer seem not to have included opal, or may have deliberately weeded it out. However, the “Genuine Homer” does sometimes produce opal progeny, according to data of Al Westling. This breed is supposed to have been derived strictly from English racing stock, probably since 1900.

It is possible that some selection for opal may have occurred in Racing Homers in an indirect way: in combination with ash-red, it tends to make a light or “bright” red checker or mealy that is quite attractive. However, selection for opal this way may well have been balanced by culling out of the less attractive bluish opals.

At present I am breeding opal in barless pattern, a rather unique and interesting combination. Whether this will increase is dubious—more likely opal will continue to be an unobtrusive camp follower of the Racing Homer legions.

—NPA News, June 1963, page 5.



XI. DOMINANT OPAL

A color somewhat resembling opal (see previous article) has been known for many years in Florentines, Hungarians, and Strassers. Usually it has been called “white bar” or “white checker”, though the “whiteness” here is generally not clear but light gray with a little yellowish-reddish mixture. The tail band is washed out.

My first encounter with this color type was in 1934 at the National Pigeon Show in Springfield, Illinois. A Strasser cock with smeary whitish checkers was shown by W. F. Hanselman. He was willing to sell the bird, and showed me the parents—a rather weak-colored red and a blue barless hen.

Testing this cock with various hens—blue, opal, red, etc.—I soon found that unlike the opal of Racing Homers this color is dominant, and I therefore gave it the name dominant opal, and gene symbol *Od* (1938). It acted quite independent of the other opal.

What appears to be the same type, from photos and breeding data, was used early in this century by C. O. Whitman, in Brünner Pouters. It seems then that the Brünner may have two different “white-bar” genes, the other being the familiar “stencil” type which affects only the wing pattern.

More recently “white bar” and “white checker” Birmingham Rollers have been bred in various parts of the country, and breeding tests by Carl Graefe, Ted Smith, and others indicate dominant opal is responsible. The origin of these Rollers is unknown. However, some “white-barred” Prague Highfliers in New Jersey studied by Ben Cichinski apparently are dominant opal, and it is possible that the Rollers had some mesalliance in their background.

Dominant opal popped up unexpectedly in a wide cross made by Joseph Cavaliere about 1949: a black Scandaroon cock with a blue bar Tippler hen. The only squab produced was a dominant opal checker with white flights. This bird, a hen, in turn produced a number of other dominant opals. This stock is probably no longer in existence.

The dominant opals at present being bred in Showpen Racers and Giant Homers trace to some of my own birds, out of the Strasser cross. Earl Klotz, Carl Graefe, Gerhard Hasz, George Schroeder, David Bruce, and others have been experimenting with combinations. One that seems rather attractive is dominant opal with ash-red, giving an orange bar or checker.

Dominant opal, like recessive opal, can be highly variable. Occasional birds are so little bleached that they are easily mistaken for blues, while at the other extreme are birds so light as to approach ash-red. Yet all of these are heterozygous. Nobody has had a proved homozygote.

If the dominant opal in Birmingham Rollers really involved Prague Highflier infusion, then it is easy to surmise that all dominant Opals trace to a single source in Central

Europe. The Scandaroon x Tippler source would apparently be the exception that proves the rule. At any rate, dominant opal seems to be a rather recent mutation—probably within the last two or three centuries.

—NPA News, May 1963, pages 4-5.

P.S. 1982: Search for the elusive, possibly lethal, homozygous dominant opal has been carried on by a number of fanciers. In Rollers and Modenas no homozygotes have been recognized (PGNL 57:51; PS & GN 3:42; 7:28). In several other breeds presumptive homozygotes have been reported with a variety of defects: whitish plumage color, ragged feathering, poor growth and small size, crippled feet, poor eye-sight, and often severe tremor (PGNL 23:3; 24:3; 28:2; 29:2; PS & GN 4:52; 7:27; 7:36; 9:9; 9:16). Melvin Ziehl tells me that in his Brünner Pouters the homozygotes have been white with poor growth and subcutaneous air puffs, but no tremors. Most reports indicate short life spans for the homozygotes, usually death before maturity. A few of both sexes have survived and tried to breed (eggs typically infertile).

XII. WEB-FOOT

While the average fancier has probably never seen a pigeon with webbed toes, this unusual condition has been reported many times, in many breeds. Apparently the first good commentary was that of Charles Darwin in his book "The Variation of Animals and Plants under Domestication", published in 1868:

"The rock pigeon has no sensible amount of skin between its toes; but I possessed a Spot and a Nun with the skin extending for a space of a quarter of an inch from the fork, between the two inner toes. On the other hand....pigeons with feathered feet very generally have the bases of their outer toes connected with skin....when the feet are much feathered, the roots of the feathers are connected by a web of skin, and apparently in correlation with this the two outer toes become connected for a considerable space by skin. I have observed this in very many specimens of Pouters, Trumpeters, Swallows, Roller-Tumblers (likewise observed in this breed by Mr. Brent), and to a lesser degree in other feather-footed pigeons."

J. C. Lyell in 1887 noted webs between inner and middle toes of some Altenburg Trumpeters (a clean-leg breed).

In 1896, William Bateson described three "common blue Antwerp pigeons, lent by Mr. F. Doggett of Cambridge, England, showing webbing between the toes. All the birds were the offspring of a single pair which were absolutely normal. Mr. Doggett states that he had seen one or both birds with more or less webbing in four different pairs of young reared by the same parents." One of the three birds described by Bateson had complete attachment

of inner, middle, and outer toes, but not a loose web like a duck's. A second bird had a complete outer web on the left foot, and partial outer web on the right but no inner webs. The last bird had partial inner and outer webs on both feet.

Another bird from this family was reported in 1902 by E. S. Montagu in the Bulletin of the British Ornithological Club, vol. 12, page 41. This bird had really duck-like webbing.

In 1905, Richard Staples-Browne, a student of Bateson's, reported breeding tests of web foot. He introduced his paper thus: "The (web-footed) character has been found in the Dovecot Pigeon and Working Homer, also in the Show Homer, Dragon, Magpie, Tippler, Tumbler, Jacobin, and Pouter. I have myself bred birds in the F_4 generation of a cross between a Barb and a Fantail, which showed this character to a considerable extent. So far as I can at present judge from specimens recorded by breeders, the most common type is a web between two digits only on each foot, and it is more unusual to find the development of the web nearly symmetrical in the two feet. It sometimes occurs between digits 2 and 3, sometimes between 3 and 4, and sometimes between all three. The instances in which it reaches the bases of the claws between all the digits on both feet are rarer. It has occurred on one foot only.

"Though this character has been observed to occur in the offspring of normal-footed parents, I have never heard of an instance in which all the young so bred were webbed. It has been found in a pigeon bred from parents of two different strains, and I have also heard of cases in which it occurred from time to time in the same strain."

Staples-Browne crossed the most completely webbed Antwerp described by Bateson with a Nun hen. Six squabs were produced, all normal. The webbed sire was mated to two of the crossbred daughters; one mating produced five normals and four webbed, and the other produced four normal and five webbed. Three matings of the crossbreds with one another produced no webs out of 12 squabs, no webs out of 11 squabs, and 3 webs out of 12 squabs, respectively. (The 3 webs all died very young.). That is a total of 3 out of 35, not a very good fit to the expected ratio. Four matings of web birds with each other produced no normal squabs in a total of 19. However, Staples-Browne commented that some of the webs of these squabs were quite small. (Anything less than a 1/4-inch web was called normal.).

In all, Staples-Browne produced 37 birds which he classed as webbed, of which fourteen died before hatching or soon after, a surprisingly large proportion. His detailed descriptions of the 37 webbed birds show that only one lacked an inner web, and this was lacking on only one foot. On the other hand, seven of the birds lacked <u>outer</u> web on both feet, and eight more lacked outer web on one foot.

I give Staples-Browne extended mention because his was the first breeding analysis. He concluded that in spite of the poor F_2 ratio, web-foot could be considered a simple recessive Mendelian character, though the possibility of occasional mistaken classification of a web bird as normal was recognized.

The next person who studied web-foot was James L. Bonhote, also in England. He writes in 1911: “In the spring of 1905, Mr. Staples-Browne kindly gave me a pair of his webbed birds, and during that year and the two subsequent years this pair produced nothing but webbed birds. In 1907 Mr. F. W. Smalley wrote to me in regard to some webbed birds” in his study of Dragoons. Pedigree data supplied by Mr. Smalley confirmed simple recessive Mendelian inheritance. Smalley gave Bonhote a male from his stock, and it mated with a hen from the Antwerp stock. Bonhote continues:

“My object was merely to get a change of blood...The result of this mating was five birds, of which four were normal. For the past three years I have carefully mated these five birds and their descendants.” He got very erratic results, with all sorts of webs as well as normals. One bird actually had “all four toes fully webbed.” He tried to explain the results, without much success: “the webs when mated with normals behave as recessives, but when mated with other webs of either the mixed or of Staples-Browne’s strain, they produce normals to webs in a ratio closely approximating 3:1. Such a result in the case of no less than five matings seems to show pretty conclusively that the joining of the two strains has produced a factor disturbing the normal course of Mendelian inheritance. It must be carefully noted that each strain by itself breeds true...Mention should perhaps be made of a suggestion by Prof. Bateson, to whom I wrote on the subject. This was that the webbed foot was possibly a double character, and that the web between digits 2 and 3 had a separate inheritance from that between digits 3 and 4.” This explanation however failed to fit some matings. Bonhote finally settled on a single “factor composed of two parts”.

In 1915 Bonhote reported some further breeding results with the same stocks, in his book “Vigour and Heredity.” A possible relation of increased webbing to reduced vigor was indicated. Drawings of the feet from a pertinent mating were included.

Since Bonhote’s work—nearly 50 years!—practically no serious further study has been reported. Additional examples of web-foot in numerous breeds have been mentioned in various pigeon books and magazines from time to time, the majority being webbed between middle and outer toes. Breeds not previously included are Racing Homer, Modena, Birmingham Roller, Fantail, Archangel, Zitterhals, Swallow, Magpie Pouter, Vienna Highflier, and Stralsunder Highflier.

So far then it would appear that web-foot has not been found in any Mondain, King, Runt, Carneau, Maltese, Hungarian, Carrier, Barb, or Oriental Frill, to consider the more popular breeds. Perhaps the wide scattering among other breeds indicates merely repeated sporadic mutations; or to some extent there may be common origin very anciently. Bonhote’s study suggests independent origins even in the Dragoon and Antwerp.

Certainly the occurrence of web-foot is not evidence that pigeons evolved from a web-footed type of bird such as gulls. The nearest any of the Columbiformes comes to aquatic tendency is the love to bathe in water. Webbed fingers and toes are found as freak types even in man. The technical term, to cover our ignorance, is syndactylism.

Most fanciers seem not to care for web-foot pigeons, but who knows—perhaps some day such a variety will catch on.

—NPA News, August 1963.

P.S. 1982: Another early example of inner-middle-toe webs in a clean-leg breed (Fantail) seen in 1891 was reported by F. Finn in England (see PGNL 52:31).

An extensive new study of web-foot has been reported by G. W. Dooley (see PGNL 53:85; 54:36; 55:15; 56:23). He dealt principally with “outer-middle-toe” web from Homers, German Trumpeters, Modenas, etc. In general, simple recessive inheritance was confirmed but variability was considerable. Another type of web, between the rear and inner toes, was also studied and named “Davis syndrome”. Recessive inheritance with much variation was indicated. The symbol *ds* was proposed.

Webbing between the inner and the middle toes has often been reported in Birmingham Rollers (see Fig. 619 in Levi’s The Pigeon). Recessive inheritance is indicated (see PGNL 72:23) but the relation if any to the “outer-middle” type has not been analyzed.

E. M. Blaine reported a combined web-foot and polydactyl condition (variable) in Giant Homers (PGNL 5:30).

In addition to the “Davis syndrome” studied by Dooley, three other cases of rear-inner toe webs have been reported: a Roller hen (PS & GN 7:35) and two Racing Homers, one sex not stated (PGNL 70:23), and one female (PS & GN 2:31). The Homers also had web between the middle and outer toes. The female was tested and the mutant proved to be sex-linked, usually lethal at about hatching age but some surviving. It has been named “web-lethal” with symbol *wl* (Amer. Racing Pigeon News, Oct. 1982 p. 50).

XIII. PEARL EYE

About 1947 the Racing Homer world was sold on a new fad—"eye-sign". Thousands of breeders bought magnifying glasses and peered expectantly into the mysteries of bird vision, usually without insight.

The eye-sign enthusiasts make much of small variations in color and patterns, but are ignorant of the major genetic differences, the most significant of which are orange, pearl, and bull.

Orange is the wild-type iris color of *Columba livia*, and most feral street pigeons and those in farm flocks have this color. Pearl is strictly a domestic type, some breeds such as Tumblers and Barbs never having orange eyes. Microscopic study has shown that the only difference is in the fine pigment granules on the outer surface of the iris: they are yellow in the wild type, and white in the pearl eye.

In addition to the granular pigment, the iris is covered in varying degree with a spaghetti-like mass of tiny blood vessels. These give the iris a reddening effect. Anemia will cause paleness. And some breeds have been selected for minimal blood vessel coverage. For example, the American Domestic Flight has a staring white "fish" eye, but basically it is pearl type.

Bull eye is absence of granular pigment on the outer side of the iris; since the iris tissue is very thin, one can see the black pigment on the inner side. Bull eye is commonly associated with white plumage and may be asymmetrical or patchy.

The genetic relations of these eye-color types were studied casually by a number of European students before 1930. The most pertinent was that of S. J. Bessmertnaja in Russia, who showed that in 10 crosses of orange x pearl, only orange F_1 resulted. Backcrosses of F_1 to pearl produced both types. The conclusion was that pearl is a simple recessive, symbolized *tr*. In 1930 R. D. Owen and I reported much more extensive data, confirming Bessmertnaja. We also discovered that a sort of imitation pearl effect is produced by the sex-linked brown gene. More recently I have found that imitation pearl is also produced by the rare albino and pink-eyed-dilute genes.

The origin of pearl probably was very ancient. My guess is that it was picked up by fanciers before the tumbling trait, since all Tumblers, Rollers, and Highfliers so far as I know are homozygous for *tr*. (Some exceptions are known in Birmingham Rollers, but can readily be explained by crossing.) Related breeds having only pearl eye are the Nun, Helmet, Jacobin, and Magpie. The Barb possibly had Tumbler far back in its ancestry.

Pearl is also common in breeds not closely related to Tumblers. Show Homers and Exhibition Homers are all pearl-eyed; other Homers often have pearl, but Carriers and Dragoons do not. Runts, Fantails, and some Continental varieties of Pouters, Trumpeters, and Archangels often have pearl iris.

Breeds never showing pearl, so far as I know, are English Carriers, Dragoons, English Pouters, Modenas, Maltese, Florentines, Hungarians, Strassers, Carneaux (except some Whites), Dewlaps, Damascenes, Swifts, Owls, Blondinettes, Frillbacks, German Toys, Lynx, and the Kings. I know little of the eye color of Chinese breeds.

From this breed distribution it seems unlikely that pearl originated in Europe, or even in the Mediterranean region. Persia seems a good bet—the place we seem to trace many things back to. Back in those ancient times fanciers must have been peering into the mysteries of the eye too, without benefit of magnifying glasses, but they found a pearl.

—NPA News, March 1964, page 7

P.S. 1982: Albino and pink-eyed-dilute pigeons (see Origins XVI) also show pearl iris color as an intrinsic effect—not involving the *tr* gene.

XIV. FOOT FEATHERING

Foot feathering is common among domestic breeds of pigeons and chickens, often almost equaling the wing feathers in length. Darwin called attention to other similarities of such feet to wings. Such a condition is never seen in wild birds, though a few species of owls and grouse have short downy covering. Why should the vast majority of Aves be conservative, retaining reptilian scaly skin on the feet? Presumably any advantage of warmth or beauty from the feathers is far out-weighed by the handicap of inconvenience—there is danger of tangling, water-logging, injury of growing feathers, and loss of agility. Much as we may admire the immense muffs of Trumpeters or Swallows, to a wild pigeon they must seem a monstrosity.

Despite the existence of practically all degrees of foot feathering among domestic pigeons, it is generally recognized that only a few categories are found in pure breeds: grouse, muff, and slipper. Sometimes other names are used, but the first type has feathering more or less equally on all toes, and the shank feathers are usually not more than two or three inches long. Muffed birds have feathering on all toes but much more extensively on middle and outer toe; these and the shank feathers are typically over three inches long, and a lengthening of upper leg feathers also appears, the “vulture hock.” Slipper on the other hand has moderate feathering of shanks and middle toes only.

Intermediate and overlapping conditions are readily obtained in crosses, and this “quantitative” type of inheritance has tended to obscure the Mendelian units. However, Wriedt and Christie (1925) presented good evidence that grouse (called “Hosen” = stockings in German) is a unitary difference from wild type (clean leg). They used Danish Tumblers for their tests. All the 91 F_1 birds they obtained showed some feathers on the shank (tarsus) but

not on the toes, and might be termed “half-grouse.” Backcrosses to both pure types gave 1:1 ratios. Wriedt and Christie proposed the gene symbol *H*, since they considered it partially dominant. My own tests of grouse agreed with Wriedt and Christie’s, but the homozygous grouse seemed so much more clearly recognizable than the heterozygote that I considered grouse more recessive. I therefore have used the symbol *gr*.

The genetic basis for muff (also called boots) has not been so clearly decipherable. Doncaster (1912), Ghigi (1914), and Wexelsen (1934) reported a few crosses of muff x clean. The F_1 were intermediate, somewhat resembling grouse, and without vulture hock. The F_2 and backcross data are not adequate but show that probably two different genes are concerned in muff, one being the grouse factor.

Slipper was studied in a few matings by Wexelsen, who used Pigmy Pouter x Maltese. He obtained 19 F_1 birds, all except two of which showed variable feathering on tarsus and toes. A backcross to Maltese (clean leg) gave 4 with sparse foot feathering and 14 clean-legged. My own experience with Pigmy Pouter crosses indicates that some misclassification is likely: a bird may look superficially clean-leg but have rudimentary feather follicles on the middle toe. More careful and extensive study is therefore needed. My own preference now is to assume a single factor in slipper, with variable expression.

The origin of these leg-feathering or foot-feathering genes must be ancient, and speculation is obviously hazardous. However, there is some value in proposing a hypothesis. It looks to me as if grouse may be the oldest type; it is apparently the most widespread, especially if we assume that it is one component also in muff. Muff seems more limited in geographic origin since it occurs mostly in European rather than Asiatic or North African breeds. Slipper is the most rare type, apparently limited to the English and Pigmy Pouters. My interpretation is that slipper was derived from crosses of muffed x clean-leg pouters, and that muff is actually a combination of grouse and slipper factors. No one has attempted to test this idea by producing muff out of crosses between grouse and slipper, and it needs to be tried. If my notion is correct, muff originated as a modification of grouse, possibly a couple of thousand years ago.

A point that needs more attention is the presence of very small feathers on the sides of the shanks and toes of birds which are generally classed as “clean-leg.” Generally these tiny feathers, which I call “miniplumes,” are inconspicuous, but many a King breeder, for example, spends hours before the show pulling out these nuisances with tweezers. I wonder if any breed is truly devoid of them. Even wild *Columba livia* may have a few. Variation in this feature has never been studied, so far as I know, and may be of considerable significance in connection with variation of the more obvious types of foot feathering.

Some readers no doubt will be justifiably perturbed by my over-simplifications. May they be sufficiently activated to do more than merely complain! It is pathetic how little experimental data we have to operate with. I wish wings to the heels of him who helps advance our knowledge!

—NPA News, June 1965, pages 8-9.

P.S. 1982: Fair muffs have been produced in some F_2 derivatives of Pigmy Pouter (slipper) X Lahore (grouse) by Robert Mangile (PS & GN 1:16).

XV. SEX-LINKED DILUTION

Studies of inheritance in pigeons and doves by Darwin and by Whitman previous to the excitement of Mendelism were suggestive enough to start a number of young investigators analyzing these birds. Color and pattern were of course the most obvious as well as the most perplexing problems to attack. There was rivalry for results, and controversy over interpretation, in French, English, Italian, and soon German reports.

In 1911 Bonhote and Smalley of England gave some results of crossing silver with blue in Dragoons. Their silver was "a very pale blue with black bars and 'dun' flights." They concluded that "silver is in reality a dilute blue", and recessive. However, they thought "those blues which are impure dominants (i.e., containing the factor *d*) are of a poorer colour than the pure blues."

In 1912 Staples-Browne, also of England, gave further breeding results with silver and with dun, the dilute effect on black. He demonstrated sex-linked inheritance (he called it sex-limited) and reported segregation of dilute squabs in purebred wild *Columba livia* stock. In the same year L. J. Cole of the U. S. also reported that dilution is sex-linked, and added yellow to the list of dilute colors. Cole however emphasized "intensity" and used the symbol *i* instead of *d* for dilution. And also in 1912, R. M. Strong reported sex-linkage of white color in ring-doves (Biological Bulletin vol. 23, pages 293-320). Actually the white dove has some pigment and would better fit the name "extreme dilute". Like dilute pigeon squabs, baby white doves have very short nestling down.

In 1925 Wriedt and Christie of Norway showed that the dilute factor (which they symbolized *d* again) is not the only one which is sex-linked and causing shortness of squab down: the almond factor, quite unrelated to *d*, is another. When both factors are acting in the same squab, there seemed to be reduced vigor.

In 1930 Cole reported studies of dove crosses showing that the common "blond" color of ring-doves is a recessive sex-linked dilute in comparison with the dark wild-type color; thus there are three alleles—wild, blond, and white. The next year, 1931, Bjaanes of Norway reported that the Light Bronze Archangel has a less extreme dilution factor than the usual one, but allelic to it. The new factor was named "pale" and given the symbol d^P.

Crossing pigeons with ring-doves finally connected the separate bits of knowledge: blond and white of the dove are allelic to dilution of the pigeon (see Cole and Hollander, 1950).

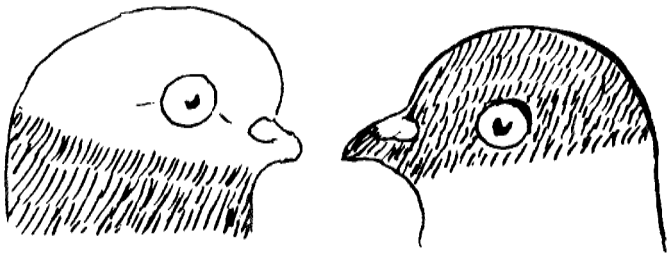
Not much else of significance has been reported, as far as I am aware, concerning the *d* alleles. From wild Iowa farm pigeons that looked just like *Columba livia* I have bred youngsters that appear to be the pale type; certainly no Archangel ancestry to pin it on. Some breeders have been introducing the pale factor from the Light Bronze Archangel into other breeds to achieve an orange rather than a yellow color.

With all that as a background, we can now perhaps make an intelligent attempt to discuss the origin of these domestic genes. Ordinary dilution is so prevalent in the most widely disparate breeds and has been so for such a long time that it would be easy to conclude it is almost if not quite as ancient as the first domestication. But the occurrence of more than one allele, even in the ring-dove, could just as well argue for repeated origins separately by mutation. Dilute types apparently are at a disadvantage in the wild, perhaps as much because of the short-down effect in nestlings as any other reason. Repeated mutation to dilution in the wild population would probably be balanced by excessive mortality of dilutes. But in domestication the dilutes are protected and even favored.

And so it seems necessary to conclude that we are totally undecided about origins here after all.

Sooner or later an extreme-dilute mutant should pop up in the pigeon, like the white of the ring-dove. Maybe it has already appeared and not been recognized as something worth following up, or maybe it just died. Well, keep your eyes peeled for it. Look for a near-albino female and test it with a blue cock. Oh yes, and don't be a miser about it—the rest of us will want some stock and the world will be all ears about the origin.

—PGNL #45 pages 6-7 (1968)



XVI. ALBINO AND PINK-EYED-DILUTE

In the previous article we discussed the near-albino "white" in ring doves, and pointed out that no counterpart of this sex-linked mutant is yet known in pigeons. In 1932 M. Tange of Japan reported a recessive true albino mutant in the ring dove (Japanese Journal of Genetics, Vol. 8, p. 1-18). He found that it was not sex-linked. Unfortunately Tange did not release any of his albinos to other breeders; Dr. W. J. Miller requested several times to obtain a specimen, without success. But finally in 1967 stock was released and Dr. Miller has imported three pairs.

In 1937 R. Lienhart of France reported on eye color inheritance in pigeons (Comptes Rendus de la Societé Biologique, Paris, Vol. 124, pp. 677-669). He stated that albino Homer squabs occurred occasionally in a big loft of Racing Homers in northern France, but always died, probably because of poor vision.

Joseph N. Koehler of Chicago in 1937-1944 found six albino squabs produced by his L. F. C. L. Tumblers. All died off after the parents stopped feeding them, except one female that he sent to me for study. She had very poor vision, with dizzy movements of the head, and her flight was very erratic. Al Westling bred a similar albino cock from his L. F. C. L. Tumblers in 1949, and also gave it to me. My breeding tests showed these to be a simple recessive type, not sex-linked. The inside of the eye is completely pink, but the iris' outer surface is pearl. Albino squabs have even shorter down than that of dilutes.

Again in 1949, at the Palmetto Pigeon Plant a pair of white Carneaux produced two albino squabs, a male and a female. These also were given to me. My tests showed the albinism was the same as the type found in Tumblers. The Carneaux stock was eventually discarded.

In 1951 Walter Gomolka, a Racing Homer breeder of Islip, New York, bred an albino cock out of blue parents and sent it to me. I crossed it with the Tumbler albino type, and got only albino squabs. However, these as well as the Homer parent had a dark ring around the iris. Therefore, I suspected that the Homer albinism might be a bit different from the Tumbler type. I have kept them separate since then, but use the gene symbol *al* for both stocks of albinism.

Albino Racing Homers were also reported to me in 1958 by Bernard E. Nolan of Saugerties, N.Y. Further cases were found by Mr. Ho Yan Ning of Hong Kong. Color photos by Mr. Ho of a young and a mature specimen are shown in W. M. Levi's 1965 "Encyclopedia of Pigeon Breeds", page 758. These have the same dark ring around the iris as in Gomolka's, and probably are genetically identical. I wouldn't be surprised if many albino Homers have been bred around the world and quietly killed off and forgotten. Certainly they are worthless for racing.

Carl Naether in his "Book of the Pigeon", 4th edition, page 183, Shows a photo of an albino mourning dove. I have been informed that no breeding test was made, and the stock seems to be extinct.

Now let's go back in our chronology to 1946. Mr. and Mrs. C. J. Joslin of Seattle, Washington, wrote to Wendell M. Levi that they had a couple of albino squabs in their Utility White Kings. He put me in correspondence with the Joslins, and they sent me the two albinos. When I crossed one of these with a Tumbler-stock albino, I was surprised to get a black squab, no albinos. Other tests soon showed that Joslin albinos in reality were a combination of a pink-eyed factor with ordinary white. When I got the pink-eyed factor by itself, I found that it also caused a dilution effect in the plumage, and short down in the squabs, but no sex-linkage is involved. These birds also have pearl iris and poor vision. Still another peculiarity that goes with this factor is a relatively short neck. I have used the gene symbol *pd* for this pink-eyed-dilute type.

Two other occurrences of similar pink-eyed dilution in pigeons have been reported to me. One was in Show Racing Homers by Earl Klotz of Ohio; his specimens failed to breed. Another was in squabbing cross-breeds recently, by Robert Clark of Livermore, California. These remain to be tested. And finally, Dr. Oscar W. Haffke of Fort Worth, Texas, has a pink-eyed-dilute mutant type in captive white-winged doves (native in S. W. United States and Mexico).

Since all these mutants have poor vision with dizzy movements of the head, they are very unlikely to become popular with fanciers. However, they have some novelty value, and they are quite useful in genetical studies. Except for their poor vision they are mostly healthy and breed well.

Similar mutants have been found in turkeys, chickens, ducks, and parakeets. Evidently some heterozygotes are scattered around in particular populations, and occasionally a mating will bring two heterozygotes together. For example, if we assume that about one Racing Homer or L. F. C. L. Tumbler out of a hundred is heterozygous, and that matings are random, we might expect about one albino squab in 40,000. (Try that on your abacus.)

The actual origin of such a recessive mutation was probably many years before the appearance of the unusual squab, but it would be impossible to say exactly when. Maybe 20, 50, even a hundred years ago. And new ones may take equally long to show up. Once they are revealed, we can grab them and breed as many as we like.

—PGNL #46 pages 4-5 (1968)

P.S. 1982: Dr. Miller has crossed albino ringneck dove X albino pigeon and obtained only albino hybrids, showing that the mutants in the parent species are identical or allelic (PGNL 59:2).

Albino Racing Homers continue to be reported to me (see Amer. Racing Pigeon News, Sept. 1982 p. 57).

Robert Clark's pink-eyed-dilute is apparently the same as that from the Joslin stock (PGNL 37:4; 39:3; 43:11; 45:27; 46:44; 52:89) and it is still available. Other reports of pink-eyed-dilutes have also come in: PGNL 58:33; PS & GN 2:40; 3:35, 45 (in Indian Fantail); Racing Pigeon Pictorial #155, Nov. 1982, p. 335.

XVII. CHECKER

Everybody knows checker (chequer, check, etc.). In French it is écaillé (scaled); in German it is *gehämmert* (hammered). By whatever name, it is extremely common. Among our feral street and farm pigeons it is generally more common than the barred pattern which Darwin considered the original type.

Charles O. Whitman, from before 1900 till his death, argued that Darwin was wrong. Whitman's strongest argument was that in his breeding cages he could get barred squabs from checkered parents, but never the reverse. This and much other information about pigeons and doves, wild and domestic, were published in 1919, and his observations are generally valid. His argument convinced some people; for example, Metzelaar in 1926 said "Since C. O. Whitman published his classic treatise we know that a chequered pattern preceded the blue black barred pattern in evolution". If we really knew that, checker could not be considered a "domestic gene". Hmm.

Whitman also found that the wild African species, *Columba guinea*, often called the triangular-spotted pigeon, when crossed with barred domestic pigeons gives checkered hybrids, and these have some fertility. So here is another possible origin for our checkered domestics. Possible, but I doubt that it is important. Mutation must be given more consideration in this matter than Whitman was willing to.

The first attempt to analyze the inheritance of checker was about 1905, by a Frenchman, Loisel, using Racing Homers. Unfortunately he botched the job—not surprising at that early date and considering the fact that he got tangled up by color combinations of red and grizzle. His ratios did not look like Mendel's so he concluded that Mendel's laws were inapplicable. Loisel was not heard from on the subject thereafter, nor were any other Frenchmen!

In England several investigators were also checking on checker. Bonhote and Smalley in 1911 gave clear evidence that checker is a simple dominant to barred, and the letter *C* was used. Nuttall in 1918 like Loisel confused the issue with colors and crude analysis, and the ball was passed to the U.S.A.

Breeding data accumulated at the University of Wisconsin laboratory were reported in 1922 by Sarah van Hoosen Jones. She agreed that checker is dominant over barred, and used the letter *C*. However, she found that checker could be hidden by darker patterns. She proposed that the various patterns comprised an epistatic series, each being able to conceal

lighter patterns: full black > black with blue tail > checker > sooty > barred > barless. (We have already discussed barless in “Origins” article IV.)

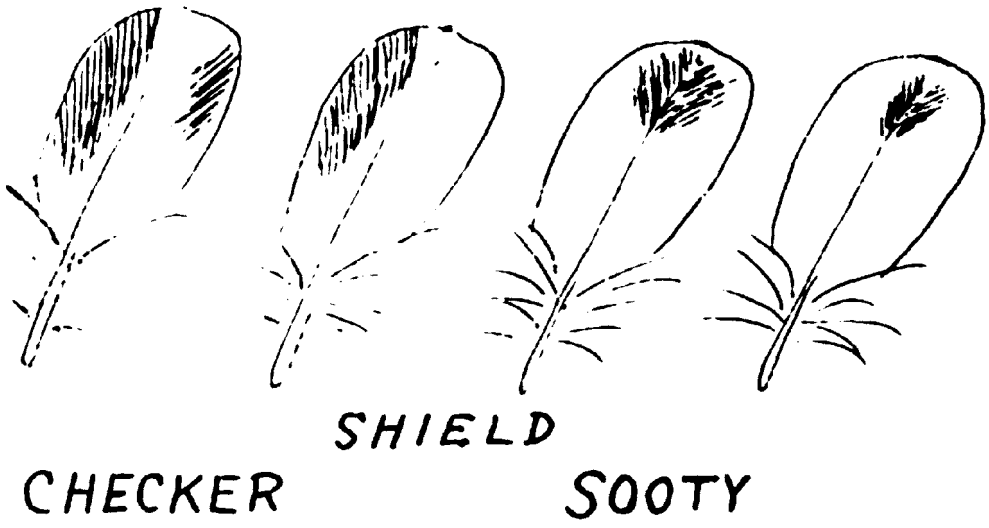
That was where matters stood when I began my studies at the University of Wisconsin. My test matings revealed that there was not simply one kind of checker, but at least three, each able to vary somewhat in appearance. I called them simply dark, medium, and light. Furthermore, the “black with blue tail” pattern was simply a still-darker form of checker. All these behaved as alleles, together with barred and barless. Full black and sooty were unrelated, though a chromosome linkage between full black (*S*) and the *C* series was discovered, together with opal. These findings were reported in 1938.

To summarize, we have at least 6 alleles in the so-called *C* series: black with blue tail, often called black check, with gene symbol C^{T}; dark checker, C^{D}; medium or ordinary checker, *C*; light checker, C^{L};barred, + or c^{+}; and barless, *c*. The dominance relations are in descending order. However, it seems that dominance is not perfect; for example, homozygotes (*CC*) are darker than heterozygotes (Cc^{+}), on the average. This fact may justify the common practice of crossing dark checkers to bar “to lighten the checker”. However, the effects of other factors, especially sooty, in darkening the patterns, should not be forgotten.

The *C*-series of alleles has no effect on the tail pattern. For this and other reasons, I have distinguished two types of black: that of the tail band and wing tips, which I call “smooth spread”, and that of the wing bars and neck, which I call “coarse spread”. The *C*-alleles affect the extent of coarse-spread pigment, apparently, but not that of smooth spreading.

These alleles are so widely dispersed among domestic breeds that speculations concerning origins may be fruitless. And the absence of an allele such as light checker in many breeds may merely signify that it is not desired in them and would be eliminated if it ever appeared as a mutation. However, something may come of a more thorough breed survey. The checkered story of the checker series is probably not finished yet.

—P. G. N. L. #50 pages 32 - 34 (1969)



XVIII. RED

Adult Blue Rock Pigeons, *Columba livia*, are ordinarily not thought of as showing any red color, except for the feet. The African species *Columba guinea* by contrast has a rusty infusion in the neck and wing shield. And our feral blue pigeons of the cities and farm barns commonly have traces of red ("kitiness") in the inner vanes of the remiges. Perhaps closer inspection of true wild *C. livia* will reveal that red is not totally lacking.

Domestic red is available in a great array of patterns and shades, but it never has the brilliance of that in such birds as tanagers or parrots. Our vocabulary of pigeon terms does not include crimson, scarlet, vermilion, cinnabar, carmine, or even blood or rose. Our reds are more subdued, described by words such as chestnut, rusty, plum, vinaceous (wine-red), and bronze with lighter shades tending toward buff or yellow rather than pink.

If you want brilliance, it can be found in some wild species of the fruit-pigeon group (Treroninae), for example in the South Sea islands. Also in the Philippine Islands there is the Bleeding-Heart pigeon, *Gallicolumba*, which has a blood-red patch on its breast. Apparently, brilliant red, yellow, etc., are dependent on lipochrome (carotenoid or fat-soluble) pigments. Our domestic birds have such pigments in the yellow baby fuzz and the adult red feet, but have not learned yet how to put them into contour feathers. Until we obtain genes to arrange distribution more to our fancy, we will have to get along with red and yellow forms of melanin—or else use dyes.

The inheritance of red took some time to decipher. Darwin in 1868 reported that a red Tumbler hen x black and white Nun cock produced four out of five squabs more or less red with light-colored tails. But when he crossed a red Spot hen with a black Barb cock, none of the young were red. Loisel in France soon after the turn of the century gave data on Racing Homers, showing that red checker birds paired together often produced blues, while blues mated together very rarely produced reds. Other European studies did not make much headway. Staples-Browne in 1908 obtained some reds in F_2 from black Barb x white Fantail. These reds bred true, and when he crossed one with a blue he got eleven young, none of which was red. However, when he crossed white Fantail x white Tumbler he got reddish-white in F_1, and some "tricolors" in F_2. Bonhote and Smalley in 1911 mixed up grizzle and mealy (reddish), with the conclusion that mealy is dominant to grizzle. Doncaster in 1912 crossed a red Tumbler with a white Fantail and got 10 F_1, none red.

The breakthrough came in 1914. Cole in the United States presented a lot of data which demonstrated the recessive nature of ordinary red in Tumblers, while the ordinary red in Homers "is dependent upon another factor, sex-linked in its inheritance." Having made this revolutionary advance, Cole next proceeded to bollix up some symbols, in this circumlocutory fashion: "Red is the fundamental color in pigeons. It appears to be potentially always present, and if we let the factor for its production be represented by the letter *R* we may say that apparently the factor *R* is never lacking from the gametic formula of pigeons. Therefore in the absence of other modifying or inhibiting factors a pigeon will be red." The inhibiting factor postulated in blacks he designated *B*; a recessive red then had the formula *RR bb*. Ah, logic! Cole also showed that yellow is the dilute form of red.

In 1918 Nuttall in England reported the results of a lot of Racing Homer matings, very much like Loisel's. Unaware of Cole's work, he concluded that a dominant red factor *R* causes the red in mealy and red checker. He did not notice the sex linkage.

Meanwhile, back in the U.S.A., Cole and Kelley were working out this factor's inheritance. In 1919 they reported their results. They called this type "dominant red" but pointed out that it is not a uniform red, having more or less "washed-out" areas, especially the tail. Some birds which they called "gray" were practically devoid of red. Commonly black or blue flecks occurred in the plumage. Cole and Kelley found the dominant red in several breeds, and demonstrated it to be sex-linked. The symbol *A* was given to it. Why *A*? They don't say. At any rate, they showed not only that dominant red is distinct from recessive red, but also that a bird could have both types together. "Red and yellow birds carrying *A* but lacking *B* are indistinguishable in appearance from ordinary recessive reds and yellows." Perhaps the red Tumbler Darwin used was such a compound.

The next study came from (of all imaginable places) Norway. Christie and Wriedt in 1923 accepted *A* from Cole and Kelley, but tossed out the rest of their symbolism. They used *r* for recessive red, and introduced the novel Drosophila system of designating wild-type alleles simply with the + symbol.

If you think the alphabet soup is adequately stirred by now, you ain't seen nothing yet. Metzelaar at the University of Michigan published a pamphlet in 1926 which introduced a new color to the scene, brown. Not knowing of Christie and Wriedt's work, and coveting the letter b to symbolize brown, Metzelaar casually stole it from Cole. In its place he put *ee* (together with Cole's *RR*), for recessive red.

Metzelaar also shook the whole red concept, pointing out that the Brander, the Archangel, and the Modena did not fit into the recessive red category or the *A* types. He introduced the idea that red is caused by a chemical reduction process which goes from black —> red —> white. In 1928 he expanded his notion, generously designating a *G* factor for washing out color in *A* birds, several *M* factors for "mahogany" of Modenas, and some *Q* and *S* factors for other types of bronzing or kitiness.

Horlacher in 1930 tried to simplify the understanding of kitiness and bronze in relation to recessive red and *A*. He tossed out Metzelaar's *S*, replacing it with *K* for kitiness, and added a *P* to Metzelaar's *Q* for Archangel bronze. Horlacher followed Metzelaar in using *ee* for recessive red, and went a step further by dropping out *R*, without comment. Steele in 1931 also did this, and from then on recessive red has only been *ee*.

Also in 1931 Hawkins reported the important discovery that brown is allelic to dominant red. Since alleles are always given the same base letter in Genetics, something had to give. Hawkins decided to change *A* to B^A. He discarded Metzelaar's *G* since he considered the washed-out effect an integral part of the inhibiting action of B^A. Flecking seemed to be local failure of such inhibition; he demonstrated that homozygous ($B^A B^A$) males had no flecks, while $B^A b$ males had only brown flecks.

In my writings the name dominant red has been changed to ash-red, to emphasize the duality of this factor's action. Other factors such as reduced, opal, and indigo show similar duality of effect. I have interpreted the duality as a reaction of two different types of underlying pattern: "smooth" spreading giving an ash reaction, and "coarse" spreading giving red. Recessive red lacks this duality of action.

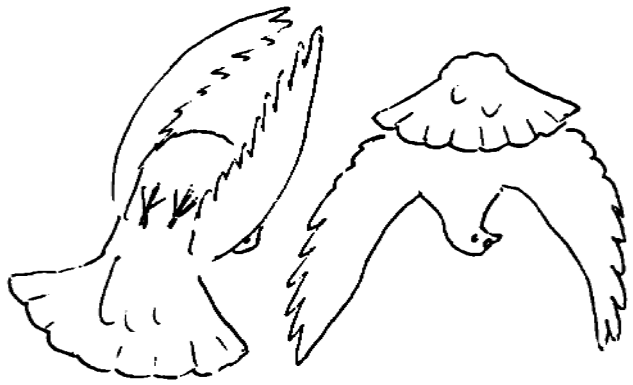
B^A and *e* occur in probably a great majority of the breeds of pigeons. Whether this reflects ancient origin or prevalence of crossing is hard to decide. It is also possible that the same mutants have recurred—we have no evidence on this question.

Recessive red when isolated (no other mutants present) is a rather weak red, and the bar pattern may even be faintly evident. It seems likely that fanciers have long striven to "improve" it, both by crossing and by stringent culling. Our lustrous show-reds are the pinnacle of success for those efforts. Crossing them with wild-type blue bar reveals the complexity of their make-up. Perhaps the various bronze types which we now recognize as distinct entities in Modenas, Archangels, Branders, etc., were originally derivatives of red crosses. We can only speculate. One way or another, it seems indubitable that red has come to stay.

—P.G.N.L. #51 pages 5-7 (1969)

P.S. 1982: In Quinn's "Pigeon Breeder's Notebook" a grand series of *K* alleles is hypothesized (*K* was the symbol proposed by Horlacher for Kite). Evidence for allelism is lacking, however, and it is more likely that Archangel bronze (Quinn's K^A) and Modena bronze (mahogany, Quinn's K^M) are unrelated. Until more test data become available it is best to use words rather than symbols. See also Origins XXIX for more on mahogany.

Much speculation has centered on the genetic basis for the red Shikli Lebanon or Miroité de Damas (red with "ribbontail" or "startail" marking). Breeding tests by WFH and others indicate that it is a combination effect of B^A , Kite-bronze, sooty, and checker, and <u>not</u> a modification of recessive red.



XIX. CREST

Of the Jacobin, Charles Darwin wrote this in Chapter 6 of his famous "Variation of Animals and Plants under Domestication" (1868): "The hood seems to be merely an exaggeration of the crest of reversed feathers on the back of the head, which is common to many sub-varieties, and which in the Latztaube is in a nearly intermediate state." The origin of the crest he regarded as a "sudden variation or sport" which early fanciers seized upon for breeding; in support of this idea he said just consider "what we now see taking place in our aviaries."

And that's all the great man had to say about crest, though he studied almost everything else one can think of in minute detail, and he even crossed a number of breeds, some of which were crested. How could he have failed to note that crest disappeared in the hybrids?? Fail he did, and thereby muffed a chance to get the drop on Mendel. But at least his sharp eye discerned the basic nature of crest—reversal of feather direction.

Wendell Levi has checked through the more important English pigeon books published before 1900 in an attempt to find comments on the inheritance of crest, and tells me that not even Tegetmeier or Lyell had anything about it. Possibly some other books are worth combing (Boitard & Corbié; de Roo?); the reader is encouraged to try!

J. C. Ewart in "The Penycuik Experiments" (1899) seems to have been the first to report that when Archangel or Turbit are crossed with ordinary pigeons, the peak crest "vanished" in the hybrids. Unfortunately he did not carry on with this family. In 1902 (Scientific Transactions of the Royal Dublin Society, vol. 7: 353) he recorded that Jacobin X Barb produced a single hybrid daughter, which had an intermediate hood. This hen with a Turbit cock produced 9 young of which two "were absolutely devoid of any vestige of hood"—but he doesn't say whether any other birds were in the same loft to compete with that Turbit.

The stage now having been set for Mendelian studies, crest began to get more attention. Staples-Browne (1905) obtained 6 young from a Nun hen and a Homer cock. The shell crest behaved as a recessive; of 29 F_2 birds, 6 were crested. However, the original Nun hen mated with a Barb cock gave both crested and plain progeny. Since crest is apparently unheard-of in Barbs, Staples-Browne suggested that sometimes there might be "failure of dominance." He said not a thing about other cocks in the loft.

T. H. Morgan in 1911 added to the confusion. From a cross of a shell-crested Swallow cock with a Fantail hen he got 7 hybrids, all crested, and in the F_2 "some have a crest and others lack it." Also, from a cross of crested Starling x Turbit, he said that two of 8 F_2 had no crest. So he concluded that crest is dominant. Can hanky panky explain any of this?

Ghigi in Italy apparently used only individual breeding cages. He reported (1911, 1914) that Archangel x Modena and Bokhara Trumpeter x Chinese Owl showed recessive inheritance of crest. But from a Barb x Chinese Owl he got a peak-crested hybrid. (What

gives with those Barbs?) And from Jacobin x Fantail, of 9 F_1 there were 4 with broad shell crest and others had some parting of feathers on the sides of the neck. Well, maybe Darwin wasn't so dumb to keep mum!

World War I halted such foolish fumbling with feathers, but after the fighting finished further fiddling followed. Christie and Wriedt in Norway reported (1923) on crosses of Petent (old-style Turbit with "Rundkappe" = shell crest) x Danish Tumbler. There were 80 F_1 none of which had crest. In F_2 and backcrosses to Petent more crests were obtained than expected on simple Mendelian scheme, and some were peak crests. The authors therefore decided that two types of crest, genetically unrelated but both recessive, are involved. In 1927 they added data on crosses of Jacobin x Danish Tumbler. As in Ghigi's experience (which Christie and Wriedt seem to have been unaware of) some of the F_1 had broad shell crest, others irregular parting of feathers on the sides of the neck. A cross of Jacobin x Rundkappe (Petent origin) gave 5 hybrids all with a broad shell crest. Along with some not too clear backcross tests, these results led the authors to believe that hood is a combination effect of Rundkappe, symbolized *rr*, with a modifier *Pe* which is dominant but only acting when at least one *r* is present.

The next voice we hear is from Sweden. Söderberg (1927) presented some data in agreement with the idea that peak crest (Archangel) and Rundkappe are recessive to plain. Then he crossed Archangel x Saxon Swallow (shell crest) and got 6 shell-crested F_1. That was enough to persuade Söderberg that Morgan was right—that there is also a dominant shell crest. Exit Söderberg.

In 1928 the voice of Moscow comes in. Unfortunately my ability to translate Russian is unable to do justice to Bessmertnaja's work, but strict recessive inheritance was indicated for peak crest and for shell again. Moreover, Jacobin cocks on plain hens gave 10 F_1 all plain. Exit Russian.

Back in U.S.A. studies resumed. Horlacher at the University of Wisconsin (1930) reported on Archangel crosses (peak), again showing simple recessive inheritance. Instead of the symbol *r* he used *c* for crest (and *C* for non-crest). Unfortunately checker had previously been given that symbol. And at the University of Michigan, after the death of Metzelaar, Feldman obtained a lot of data on crest from various breeds (unpublished; I got the information from him directly, after 1934). Archangel x Oriental Frill (both peak) gave only crested F_1 and F_2. Outcrosses gave only plain F_1 and in F_2 there were 200 plain : 69 crested. Backcrosses of F_1 to crest gave 55 plain : 53 crested. In short, simple recessive.

At Wisconsin I also briefly dipped into the problem. A Jacobin cock on a plain mongrel hen (untested! but from a family segregating for crest) gave 18 young of which 13 had a broad shell crest and the others none or minor parting. I reasoned that if Christie and Wriedt were correct, crossing the F_1 having broad shell crest with unrelated homozygous normals should give more crests and partings in the progeny; such matings gave 55 young, all plain. What happened to *Pe*? In my thesis (1937) I proposed that the symbol *cr* be used for all types of crest.

But the matter was not and is not closed. The trouble as usual is lack of coordinated attack. We get little bits and pieces of breeding data, rather than analysis. Vecchi (1935) in Italy showed simple recessive inheritance of peak in tests of the Mookee. Goessler (1938) in Switzerland crossed a Jacobin with a "Feldtaube" (plain) and got a single F_1 and this had a shell crest. Mated back to Feldtaube hen he produced 3 squabs with small shell and one plain, so Goessler suggested that maybe hood depends on two dominant factors! And Harms (1938) in Germany reported 4 F_1 from Jacobin hen x Fantail cock. None of the F_1 were plain, though they varied.

I thought I'd start the ball rolling again with a cross that would be clear, about 1964: a Jacobin cock on an English Carrier hen. Some of the F_1 were plain, but others had minor parting of side neck feathers, and one male had a small shell crest. Such reliable results are not very encouraging, and I have not pursued this elusive entity further.

It looks to me as if most breeds that are supposed to be strictly plainhead have been contaminated, if you will pardon the expression, with this gene—deliberately or not. Therefore any serious future test must be with proven homozygous normals. If these crazy results are still obtained, then maybe we will have to accept Staples-Browne's suggestion that "failure of dominance" sometimes occurs. And who knows, perhaps more than one kind of crest mutant will be verified.

We must also realize that crest is really not a feather abnormality—the feathers are perfectly ordinary. The real difference is in the skin. Possibly some of the crazy results relate to the looseness of the skin? And skin development is also related to activity of the thyroid gland. And to confuse the picture a bit more, possibly bipaternity is commoner than we think, and that would require reciprocal crosses to evaluate.

So the origin of crest is enigmatic. But even if it is lost in prehistory, there is still much we can learn about it.

—P.G.N.L. # 54 pages 8-10 (1970)

P.S. 1982: The possibility that a dominant crest factor exists in some Swallows still needs pursuit: Dan Moreno reported a mating of a crested Swallow hen X Ice Pigeon cock giving numerous F_1 all with crest (PGNL 56:72).

The seemingly erratic and asymmetric results in Jacobin crosses remain puzzling (see PS & GN 5:32).

"Eye crest" or "eyebrows" has so far appeared to be expressed only with shell crest (PS & GN 4:50, 51; 6:5; 7:30).

XX. AMPUTATED TOES

Most of the "genes" we have taken up so far have been "desirable"—at least to a fair number of fanciers. But there are others that hardly anyone is likely to love, outside of dedicated Genetics fanatics. Some are even horrors—but to me, fascinating.

"Amputated toes" is one of these. It was originally discovered by Wilbert H. Bernshouse in the strain of auto-sexing Kings developed at Palmetto Pigeon Plant, about 1945. By 1948 he worked out a pedigree chart showing that the anomaly, which he called "mutilated toes", had appeared in five matings, all more or less related. Since the parents seemed quite normal, he figured the anomaly to be recessive, and proceeded to eliminate it. He gave me a cock and a hen with the condition in 1948.

Typically the affected birds lacked the tips of the inner and rear toes; therefore I have preferred the term amputated. However, the name may be misleading, as I will show.

I outcrossed each of my original birds, and they bred fairly well. A total of 30 progeny resulted, all normal. Next I backcrossed two of the young with the originals, and got 44 young (from 60 eggs). Of the 44, there were 6 with amputated toes and 38 normal. If the abnormality were a simple recessive, we would expect a 1:1 ratio from this type of mating. What I got looked more like 1:7, certainly not simple. I don't think any escaped my notice, because I opened all unhatched eggs to see what was going on.

Also I mated F_1 birds together and got 17 F_2 squabs out of 26 eggs; none were abnormal.

Well, I wasn't willing to drop it at that, so many more matings were made. As before, outcrosses always gave only normals, 52 in addition to the first 30. Backcross matings gave me 10 more amputated: 18 normals—much closer to a 1:1 ratio. And F_2-type matings produced 5 amputated : 43 more normals. Finally I mated amputated birds together and got 17 squabs out of 24 eggs. All these squabs were amputated except one that looked normal.

Something not apparent from these raw numbers was the great variability of the amputated condition. In some cases only one toe tip of one foot was missing; others had up to all toes affected, and also missing wing tips. And in addition, several that failed to hatch had extremely short lower beak. "Hook beak" was also evident in some of the survivors, and needed periodic trimming.

My guess is that all these variations are dependent on a single recessive mutant, for which I propose the symbol *am*. Perhaps modifying factors play a part, or conditions of incubation may be decisive. Probably a fair percentage of homozygous birds pass for normal.

I still have this "gene", thanks to help from Wilmer Miller and Gerald Dooley, who carried on some of the stock. What is its future? I hope not too gloomy—it should be an

interesting tool for more embryological investigation. And “amputated” birds are well adapted to a wire-floor cage—their claws don’t catch and trip them!

—P.G.N.L. #58 page 7 (1971)

P.S. 1982: See formal report in Iowa State Journal of Research 53:109 (1978).

Harry Alexander has a family of Jacobins with frequent occurrence of rear-toe abnormalities, especially absence (letters to WFH 1979).

XXI. GRIZZLE

Webster says grizzle means gray, like gray hair. As everyone should know, that is not uniform, but an intermixture of white and colored hairs. Similarly, the classic grizzle pigeon is different from wild type by an intermixture of white, some barbs being white, some colored, in the same feather, in a seemingly random distribution. The German word for grizzle is “Schimmel”; in French it is “argenté”, meaning silvered, but not like the “Argent” variety of Modena.

It was in France that the first attempt was made to analyze the inheritance of grizzle. Loisel reported in 1905 that matings of grizzle with blue Racing Homers gave a total of 97 grizzle young out of 229. This seemed a queer ratio to him, so he concluded that Mendel’s laws don’t work. Finis for Mendel!

Bonhote and Smalley of England followed with a study of Dragoons, reported in 1911. Their ratios were fairly satisfactory, so they proposed a factor *G*. They noted complications, however, because the phenotype was variable—some birds having very little white, others very much. Also, these authors erroneously thought that “mealy” (red bar) was a grizzle combination.

Cole, in the U.S.A., tangled with the grizzle problem without even realizing it. Pictures in his 1914 report show grizzled crosses from White Tumbler by red. He called them “white splashed with red,” and thought he was dealing with quantitative inheritance, multiple factors. He noted that such birds often changed color markedly at the molt, getting more or less white.

In 1926 Bol, working with Racing Homers in Holland, confirmed the factor *G* and proved that it is not sex-linked. He reported the combination effects with sex-linked red, with checker, and with *S*-black. He suggested that the action of *G* inhibits formation of melanin, but that it is most effective in areas already having low concentrations, that is, blue or mealy. Therefore it is expressed poorly with T-pattern or *S*. Bol also considered “stork” coloration to be extreme grizzling, probably in the barless pattern, though he also suggested that it might be homozygous, *G G*.

At the same time as Bol, two Americans were also studying grizzle. One of these, Steele, included his conclusions in an unpublished thesis (University of Wisconsin). The other was Metzelaar, at the University of Michigan. Both thought like Bol that the grizzle factor is more effective on blue than on black areas. However, in his second (1928) report, Metzelaar confused matters by using the symbol *G* for sex-linked ash coloration, and did not consider grizzle. Sad.

Since then, a good deal more has been learned but not reported formally. The reader is referred to Levi's books for pictures, and to the Pigeon Genetics News Letter for scraps of information, mostly from fanciers' experiments.

It became clear that the grizzle factor is in plenty of pigeons that don't show it, or at least not in anything like the classic description. These birds—black, white, or other color—need to be crossed to blue to unmask the *G*. By contrast, some color varieties such as "smoky" may have some grizzle-like whitening of the feather bases yet not have the *G* factor at all. Also, names may be confusing; fanciers may speak of "light prints," "mottles," "tortoiseshells," or even "almonds" which are really often grizzle effects. The Brander, according to tests by Earl Klotz, may actually be homozygous grizzle, yet show only some white ventrally.

White varieties with orange or pearl rather than bull eye color seem typically to carry a grizzle factor, often homozygous. I have been following one of these, out of White Carneau originally, that looks classic grizzle in squab plumage, but then molts in much pure white plumage. Homozygotes look "stork" first, then molt to be practically pure white. This factor behaves as an allele of classic grizzle, and I am tentatively calling it "tiger", with symbol G^{T}.

Further studies are needed to clarify some of the weird combination effects, as well as the problem of change with the molt. Also, I wonder whether possibly "ice" coloration might be another allele of G, and whether the colorations called (in German) "eulig" and "Halbschnäbler" may be related to grizzling.

Where and when did *G* originate? As usual, we can only speculate. Certainly it is so widespread that ancient origin is likely. However, until recently it apparently did not exist in Fantails, German Toy varieties (except possibly the Brüster), Modenas, Dewlaps, Carriers, and most breeds of Pouters. It is so easy to cross and introduce *G* that these breeds may have it now.

Old breeds commonly having *G* are White Tumblers, Cumulets, Frillbacks, and French Mondains. The Indian Gola pigeons also seem often to be grizzled or tigered.

I'll make a wild suggestion that perhaps the "tiger" was the original mutant, leading to formation of all-white birds, and that the classic grizzle may have been a later partial

reversion (mutant) toward wild type. But whatever really happened we'll never know, as it probably occurred in hoary antiquity.

—P. G. N. L. #59 pages 37-38 (1971)

P.S. 1982: In the Frillback the common type of grizzling may be due to another allele, which Tom Barnhart calls "slight grizzle" and symbolizes G^s (PGNL 67:18).

The somewhat grizzle-like colorations of the Brüster (Breast Pigeon), Halbschnäbler, Czech Bagdad, and a few other breeds now seems to be unrelated to *G*. Mme Francqueville's tests show that it is a recessive unit. She has proposed the name "pencilled" and gene symbol *pc* (APJ March 1981, p. 16). Tests by WFH and others suggest interaction in crosses with piebald types.

XXII. POLYDACTYLY

Some 130 million years ago, according to geologists' reckoning, a pigeon-sized creature existed which had feathers, teeth, and a long bony tail. Discovery of a fossil of this link between birds and reptiles was in 1877, in a piece of lithographic slate mined in Bavaria (Germany). This primordial bird was named *Archaeopteryx* (or *Archaeornis*).

Even at that ancient time, the bones of the feet and the wings were essentially like those of a pigeon. The main difference was the presence of claws on the three digits of the wing. Birds seem therefore to have had an exceedingly stable architecture for their appendages.

But certain breeds of chickens (e.g., the Dorking) have for centuries deviated from the plan—they have an extra hind toe on each foot. This toe is functionless, but fanciers consider it a harmless trademark for the breeds. Early Mendelian studies showed the condition to be dominant over normal, though a bit irregular—occasionally a bird having the "polydactyly factor" would have one or even both feet normal.

In pigeons, polydactyly seems to have been unknown or at least unrecorded before about 1915. Even Bateson, the chronicler of freaks, never heard of a case. But in 1916 a Racing Homer having double hind toes was reported in the Journal of Heredity. Mated with its normal sister, the bird produced an offspring with an extra toe on only one foot. The fate of this family is unknown.

In 1922 Robert Fontaine in France published a small book about breeds of pigeons. He mentions that the Syrian Spot (huerté syrien) has extra toes. Unfortunately, no one else seems to have seen or commented on this variety, if it exists at all.

In 1939 a polydactyl squab was found in squabbing Silver King stock at the Palmetto Pigeon Plant. Additional cases appeared, and in 1942 Wendell Levi and I reported on 25 of them. None lived to maturity, in spite of our efforts—they not only had extra toes (sometimes more than one) but also extra wing digits, defective plumage structure, undershot beak, and over-fatness. They were moreover blind, though the eyes showed no obvious abnormality. We named this syndrome of defects "sub-lethal polydactyly," and found that it behaved as a Mendelian recessive. The symbol *py* was chosen for it. Naturally the people at Palmetto considered it a bad thing and have tried to get rid of it. Inquiries to the source of the Silver King stock, in Pennsylvania, elicited information that the condition had occurred there in the past.

We also found a somewhat similar but less abnormal type of polydactyly in a stock of Show White Carneau-Show-King mixtures. This proved to be genetically different from *py*—crosses of the two families gave only normal progeny.

Now that the dam had been broken, I began to learn of more cases. Sub-lethal polydactyly showed up in a stock of squabbing White Kings; they were given to me by Dr. D. S. Jaquette (Maryland). Then in 1948 J was given a Blue Show King hen with double hind toes by a breeder in Connecticut. In 1952 H. E. Thyen (Indiana) gave me several such birds of both sexes from his Show White King stock. This type of polydactyly seemed not too rare in Show Kings; if the extra toes were small and loose, some breeders simply cut them off and showed or sold the birds. My breeding tests of Show King polydactyly again showed recessive inheritance, but evidently the gene is not always harmless. Extreme variants fail to hatch, and may have several extra digits, as well as flared nostrils. The gene has been tentatively symbolized *skpy*.

By 1958, according to Del James, a lot of similar specimens were occurring in French Gros Mondains, probably a sign that Kings had been used in "improving" the type. And in 1961 (Amer. Pigeon Journal, November, page 409) a Modena with double hind toes was recorded—more King crossing?

Now let's go back to a different turn in the story. L. F. Tharp imported some Schautauben (German Beauty Homers) from Germany, and lo, in 1950 a brother-sister mating produced two young with an extra toe on the <u>outside</u> of each foot. They were male and female, perfect specimens of Schautauben, but he didn't want extra toes so he gave the birds to me for breeding tests. I found this type of polydactyly recessive to normal, and crosses with Show King polydactyls gave only normal young, so the two types were genetically distinct. I symbolized Tharp's kind *t*. Again, some variation was evident; some birds also had extra digits on the wings, and the feet were often more or less abnormal than the original birds.

In 1951 Gerhard Hasz opened an egg that failed to hatch in his Giant Homer loft. He found that the squab in the egg had a total of 15 toes. I was interested, so he gave me the parents. More polydactyls were produced, all dead-in-shell.

Crossing the Hasz stock with the Tharp polydactyls produced healthy young, often with several extra toes and wing digits. Evidently the two types are allelic. So far I have never got a Hasz polydactyl to hatch, so I don't consider the two identical. Therefore I am using the tentative symbol t^{H} for the Hasz type.

Are there still more polydactyly genes wandering around? Fred Schwaderer tells me he had a case of extra toes in the Syrian Reehani breed. Other breeders of Reehani seem not to have had any. Well, back to Syria—who will investigate Fontaine's huerté?

It is interesting that none of the several types of polydactyly in pigeons is dominant, in contrast to the common type in chickens. Maybe we have something to look forward to. Meanwhile the types we have are frowned upon by breeders, or barely tolerated. If eggs are not opened, the worst cases won't be seen, of course. Anyway, I get the culls.

Why have polydactyls seemed to proliferate in this century? Partly I think it is simply better observation and reporting. But the fact that all the types were found in rather large breeds, some with unique conformations, suggests that possibly these genes were connected somehow with the peculiarities being sought in those breeds. If there is a linkage or a direct involvement, these genes may not so easily be eliminated.

One thing sure—our polydactyls are not throwbacks to *Archaeopteryx*.

—P. G. N. L. #61 pages 33-34 (1972)

P.S. 1982: An extensive report on polydactyly was presented in 1968 by Gerald W. Dooley (Ph.D. thesis, Iowa State University, Ames, Iowa). This was reprinted in PGNL 53:85; 54:36; 55:15; 56:23. Independent inheritance was indicated for *t* and *skpy* but the great variability of individual expression hindered classifications.

Additional reports of new (?) types of polydactyly:

Blaine, E. M. 1968 polydactyly with web foot in Giant Homers. PGNL 45:30.

Schütte, J. 1970 Geflügel-Börse #14
1971 Handbuch der Taubenrassen p. 151, 175. (see PGNL 65:15). Syrian Spot, Chinese Tumbler.

Roche, R. 1978 Parlor Rollers. PS & GN 7:16.

Alexander, H. 1979 lethal type in Jacobins (letters to WFH).

XXIII. THE *S* FACTOR

Richard Staples-Browne of England in 1908 deduced from his crosses involving Barbs with other breeds that there is a "factor for black self-colour," which is dominant over blue. His numbers were not impressive, however, and he observed that some of the blacks had "slight indications of wing bars." He speculated "It is most probable that, if these birds were bred from, [they] would be shown to contain blue, whilst the deep black with no traces of wing bars would prove to be homozygous." In his 1912 report, Staples-Browne provided further data: from crossing Black Fantail X Silver Owl, the F_1 were all blacks and duns, showing faint wing bars; and from crossing a blue Dragoon cock with a dun Carrier, 9 blacks resulted, all showing faint wing bars. He concluded that dun is dilute black. The black factor he gave the symbol *B*.

Cole in 1914 was apparently unaware of Staples-Browne's 1912 report, but he also used *B* as a symbol for black, in the sense that recessive red is *bb* (not black). From that standpoint, a blue is also *B*. To study the difference between black and blue, Cole crossed a wild Blue Rock Pigeon cock with a Black self Tumbler hen. These "produced 10 offspring, all black." F_2 were 12 blacks and 2 blues. Other tests confirmed the dominance of black to blue. Cole stated "In blues the pigment is aggregated into clumps, while in blacks it is spread rather uniformly throughout the barbule..... We have assumed that this extension is due to a spreading factor, which we have accordingly designated the factor *S*."

Cole had no clear idea as to why some blacks are "good" (i.e., deep, rich), while others are "hard" or leaden. He recognized "black with blue tail" as a problem, and suggested that such birds have *S* and also a factor *t*, while self blacks have *S* and *T*.

Some recessive reds by breeding tests had *S*, others did not. Cole concluded ".... we have not as yet been able to identify any of the variations in red as correlated with the presence or absence of *S*."

Cole's study eclipsed Staples-Browne's so that everybody since then has used *S* for the spreading factor.

In 1922, Sarah van Hoosen Jones, a student of Cole's at the University of Wisconsin, reported extensive breeding tests of the various patterns. The *S* factor was clearly identified, and shown not to be present in black-blue-tail or "T" pattern. *S* was considered the top pattern in an "epistatic series"—that is, it could conceal any other pattern factor. Jones devoted some effort to analyzing differences between "dull" and "deep" blacks, and decided that deep blacks have a special dominant modifier, rather than being homozygous for black as Staples-Browne had earlier suggested. In other words, according to Jones, two poor blacks mated together cannot produce good blacks.

In 1926 another big study was reported, by Bol in Holland. He confirmed that *S* is epistatic to other patterns where black pigment is involved. Unfortunately he guessed that the combination of *S* with sex-linked red would be solid red; this idea was wrong.

Metzelaar at the University of Michigan (1928) made an interesting revelation, that the *S* factor inhibits the effects of "bronzing" factors, although it does not inhibit recessive red.

I think that my own studies (reported in 1938) at the University of Wisconsin were the next significant advance. First, I recognized two different sorts of spreading of pigment, one being in the wing bars of the wild type and the other in the flight tips and tail band. These two—"coarse" and "smooth," respectively—look alike in the wild type but react quite differently with different mutants. Thus the checker and T-pattern factors extend the coarse spreading areas but have no effect on the wing tips or tail band. The *S* factor, conversely, extends the smooth type of spreading over the plumage. Since the sex-linked ash-red factor makes smooth-spread areas ashy, and *S* extends these areas, a bird having both B^A and *S* will not be solid red, but more nearly solid ash.

Another relation which I worked out was that *S* and the *C* patterns are not independent, but loosely linked.

At this point progress stopped. Breeders still inquire how to make good blacks out of poor ones, and I suggest introduction of T-pattern to reinforce the spreading. Also smoky is a big help, unless a black beak is desired. The less-well understood sooty, dirty, and grease-quill factors may also be useful.

Many fanciers view the Dark Bronze Archangel as a bronzed black. Crossing with blue quickly demonstrates that it is not—it produces only blue checkers. Adding the *S* factor to the Dark Bronze Archangel results in a very glossy deep black, without bronze showing at all.

It is strange that in spite of centuries of breeding black pigeons all over the world, no mimics or mutant alleles of *S* have been demonstrated. It seems to stand alone in its glory.

Cole in 1939 suggested that the *S* factor might have been introduced originally from *Columba janthina*, a blackish wild species found in Japan. This was a wild guess, because nobody has even crossed it to test for *S*. More likely the *S* factor originated as a mutation thousands of years ago, and spread.

—P.G.N.L. #61 pages 34-36 (1972)

XXIV. SIDEBURNS

Twenty years ago (in September 1952) I raised a squab that had peculiar face feathering—the feathers on the lower beak pointed forward instead of back. The parents were of mixed ancestry, part King and part Homer. Both were quite old, the dam 9 years and the sire 7. Also, the sire was ill and dying at the time, apparently of something like canker.

Well, the funny squab lived and became a vigorous cock (580H in my records). I mated him with various hens, and some of his progeny in each mating were more or less like him in face feathering. These in turn produced further generations of funny-faces. The peculiarity is obviously hereditary, a dominant mutant. I have named it sideburns, with symbol *Sb*.

So what else has been learned in the 20 years? Well, some rather interesting and maybe surprising things. First, the expression of this mutant is variable: it may affect only the jaw feathers, or the reversing may also include the ear feathers, the frontal (producing a tuft or rose-like twist), and sometimes even the lower neck on each side above the shoulders ("epaulettes"), The feather reversal or whorling can be quite picturesque and jaunty. Contrariwise, sometimes only one side of the face may be affected, and occasionally the effect is so slight that the bird may pass for normal. Such imitation of normal was common in Modena crosses that I tried. In general, however, the variation has seemed erratic.

A fair percentage of sideburns birds have somewhat bulging cornea of the eye. This may be a sort of buphthalmia or glaucoma. In some cases the eyes look "owlish". The affected birds seem not to be bothered, and they can see OK to pick up grain etc.

Another casual observation has been that sideburns birds are more subject to respiratory trouble than are normals. In spite of apparent health and vigor otherwise, some birds have a perpetual rattly breathing. A real respiratory infection also seems harder to control in sideburns birds.

What about homozygous (*Sb Sb*) birds? Not much is known yet. Wilmer Miller and Gerald Dooley have attempted to produce them by mating 2 sideburns together. Several squabs from those matings had a head tremor—a rapid palsy-like sideways shaking-trembling. Otherwise these birds were not unusual in degree of sideburns effect. Progeny tests of such birds have not yet been decisive as to whether they are the homozygotes.

So far no attempt has been made to investigate interactions of *Sb* with any other feather-whorling type such as crest, frill, rose, etc. Perhaps some exciting new developments are awaiting. (Watch out, you Chinese Owls, Bokharas, and Jacobins!)

The sideburns mutant invites more thought about origins. So far as known, this mutant has not been observed previously anywhere, in any breed. The fact that the parents were aged and the sire ill may have been more than a coincidence in the occurrence of the mutation. In humans, at least, aging of the mother has been blamed for increased frequency of chromosome aberrations, especially non-disjunction, as a result of reduced chiasma

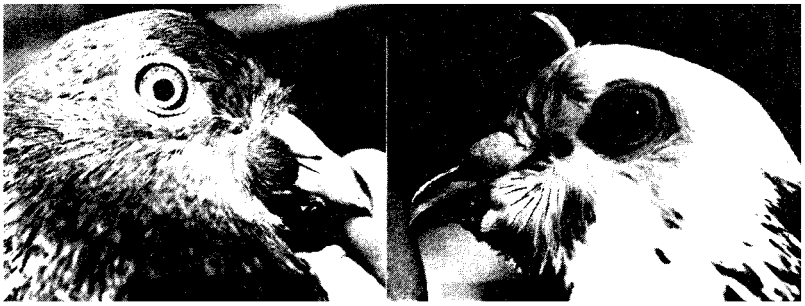
formation. Possibly *Sb* is not just a mutation but rather a whole chromosome extra? It will probably be difficult to tell, even by expert cytologists.

The future of *Sb* is problematical. Few breeders have even seen it, much less tried it. If you care to see what it looks like, on a Tumbler background, there is an illustration on page 766 in Levi's "Encyclopedia of Pigeon Breeds." Possibly some breed group will admit the mutant for showing some day. Meanwhile much remains to be learned of new combinations, and they may be decisive. Let me know if you are interested and I can give you a bird for your origin.

—P. G. N. L. #62 pages 36-37 (1972)

P.S. 1982: See formal report in Iowa State Journal of Research 53:109 (1978).

Introduction of *Sb* into Racing Homers has not interfered with good homing speed (William Pennington. Minnesota 1982).



XXV. ROSE, BEAK CREST, OR NASAL TUFT

"Rose is a rose is a rose is a rose", proclaimed Gertrude Stein, who also had some comments of equal sagacity on pigeons. Ah, but she didn't know that a rose is really a circular beak crest!

Surprisingly little study has been devoted to this outstanding peculiarity. Darwin for example used Trumpeters in some of his experimental crosses, but he ignored the rose. Ghigi in Italy was probably the first to report on the inheritance (1914). He crossed Russian Trumpeters (Bokhara) reciprocally with Chinese Owl and with Frillback (lacking rose), producing a total of 12 F_1 birds, all normal (no evidence of rose). From two matings of the Owl hybrids together he obtained 17 F_2 of which 3 had rose. Two of the three resembled the Bokhara except that they lacked a crest on the back of the head, and the third resembled the Dresden Trumpeter. There was no evidence of sex linkage. Two of the F_2 rose birds were mated and they gave 2 young, both with rose.

Bessmertnaja (1928) in Moscow (Russia) crossed the Bokhara with plain-headed birds and raised 8 F_1, all plain. A mating of F_1 X plain gave 4 young of which 2 were plain and 2 slightly abnormal. Bessmertnaja concluded that the factor for rose was generally recessive and proposed the symbol *so* for it. This symbol is not mnemonic, and I would suggest that it be replaced by *ro*.

A little additional information from crossing was reported in 1938 by Harms, in agreement with recessive inheritance. After that we have only brief and fragmentary comments in the Pigeon Genetics News Letter, again agreeing with recessive inheritance. (See #6: 5; #12: 3; #15: 1; #27: 3; #31: 2; #37: 3).

I happen to have some unreported data in my own records which are useful. In 1949 I crossed a Bokhara hen with a Modena cock. They produced 9 F_1, all plainheaded. A backcross of a son with the mother gave 10 young. Of these, 4 had rose or beak crest and one had "eyebrows" as in the Pomeranian Show Crest or Schaukappe—a few feathers sticking out over the eyes, but no definite rose or beak crest.

Later I crossed German Trumpeters with plainheaded birds (mainly Racing Homers). The F_1 without exception were quite normal, and secondary outcrosses of these F_1 with normals gave only normals (in contrast with Bessmertnaja's experience). Matings of F_1 x F_1 gave some young with beak crest but the variation of expression was surprising, indicative of modifying factors. Some of the birds had a small whorl of the feathers <u>on each side</u> just behind the nostril cere. Others were lopsided or twisted. I used some of these birds for further outcrossing as well as backcrosses to F_1. If we classify all the variations of beak crest, eyebrows, etc., together, my results can be summarized thus:

Outcrosses produced 96 young, all normal.

F_2-type matings had 95 normals and 30 beak-crested (fair 3:1 ratio)

beak-crested X F_1 gave 52 normals and 31 beak-crested. (This last is not a good 1:1 ratio but might well be from chance.)

Ghigi's F_2 data showed that beak crest (rose) and crest on the back of the head could be readily separated. My more extensive data agree: the two conditions are quite independent genetically. Therefore the beak crest might well have originated in a plain-headed stock and later combined with shell crest by crossing.

The nasal tufts of the priests and Rumanian Tumblers are probably closer to the original mutant condition than is the perfected rose of some of the Trumpeters. The similarity between some Rumanian Tumblers and the Chinese Ring Breast for example is suggestive to me of common ancestry; my guess is that the Chinese got their stock in trade from the West, perhaps several hundred years ago. Of course this is pure speculation, because no breeding tests have been made. Similarly we could speculate that the Pomeranian Show Crest (Schaukappe) may have been derived from Trumpeter crosses. But it should be recalled that a beak-crest-like effect sometimes is also produced by the dominant "sideburns" factor, of quite separate origin.

So far then it seems most likely that the basic rose factor appeared anciently and prior to the development of the Trumpeters, probably in Eastern Europe or the vicinity of Persia. But at first it probably was not a rose.

—P. G. N. L. #63 pages 16-17 (1972)

P.S. 1982: Further data showing simple recessive inheritance of beak crest are reported by Christian Reichenbach (PGNL 71:7).

The symbol *ro* was used already in Entrikin's study of rolling. Therefore the rose-beak-crest mutant would better have the symbol *ros*.

XXVI. PLUMAGE PERDITION

We have already considered several abnormalities of plumage structure, in Origins articles IX, XI, and XXII. Now let's go on to more extreme conditions. (Did I hear someone say "Ugh"?)

What would Darwin have thought about "porcupine" pigeons, I wonder. He never heard of any. The first mention of such a type that I know of was in "The Fanciers Journal and Poultry Exchange" vol. 2, page 349. This was published in Hartford, Connecticut, 1875, and is available in Wendell Levi's library. The person reporting the porcupine asked what is the remedy for this disease.

The first technical report on porcupines was that of Cole and Hawkins (University of Wisconsin) in 1930, concerning two quite separate occurrences. One of these had appeared in white Fantails before 1913; a normal-feathered pair had produced 7 porcupine young along with 4 normals. None of the porcupines was able to breed, probably because they were a bit "unsteady on their legs." The old birds were outcrossed to a Tumbler and a Homer and gave only normal progeny. These were intermated, but the porcupine abnormality did not show up again. Then quite independently porcupines appeared in a family of Racing Homers in 1927, and these were studied more successfully, although none of the porcupine males was able to breed. Outcrossing porcupine females gave only normal progeny, while F_2 and backcrosses produced more porcupines in Mendelian proportions. Cole and Hawkins proposed the symbol *p* for this recessive mutant. They also showed that the feather defect microscopically is a sticking together of the barbs and barbules.

In 1932 another case was reported in the German journal "Der Züchter", by Krallinger and Chodziesner (vol. 4, pages 53-55). And still another occurrence was found by Wendell M. Levi about this same time, a Logan Racing Homer hen. She was mated to a normal cock and produced (along with some double-yolked eggs) a number of normal progeny. In 1936 Levi gave her to me at the University of Wisconsin. I mated her with a porcupine cock of Cole's Homer stock, and surprisingly they produced 5 young, all normal. Since the mating was in an individual coop I was sure of no error, and I had to conclude that the two porcupines were genetically different. Levi's bird was less severely affected than Cole's, though quite unable to fly (see photo in Levi, The Pigeon).

At that point I left the University of Wisconsin, and the porcupines eventually died out there. However, some of the crossbreds were carried on, and after several years an occasional porcupine reappeared. One of these, a cock #G307C, was given to me by Dr. M. R. Irwin and Wilmer J. Miller in 1947. Fortunately this bird was able to breed, and all my present porcupine stock traces to him. Losses from bad weather are the biggest problem. So far I have not found any difficulty in combining porcupine with other mutants, though with silky only the porcupine effect is visible.

Other occurrences have been reported also. (Undoubtedly I have missed some.) Wendell Levi and Wilbert Bernshouse sent me a photo in 1960 of a young White Carneau porcupine, which was not bred from. Leon Whitney obtained a porcupine Racing Homer in

1961 in Connecticut (PGNL #19 page 4). And Paul G. Miller of Stillwater, Oklahoma, says (pers. com. 1972) that porcupine-like squabs have been produced in a family of pure Lahores there, and may be studied further. But breeders usually don't appreciate the fine points of porcupines, and keeping them going is a prickly problem.

Dr. Oscar Riddle at the Carnegie Institution laboratory on Long Island, N.Y., found a mutant in Homer stock about 1914, and named it "scraggly". It was first reported and figured in 1929, by Benedict and Riddle, and more photos were published in Levi's The Pigeon in 1941. Then I went to work in Riddle's laboratory, and in 1943 we published a more complete account, showing that the abnormality is a simple recessive, and we proposed the symbol *sc*. Unlike silky or porcupine, scraggly feathers lack hooks on the barbules. Also the skin is abnormal, being rather thick and unpliable. Often it looks crusty or flaky. Scraggly birds require at least twice as much drinking water as do normals, and may die of thirst if deprived for a couple of days.

After Riddle's retirement I have carried scraggly also, with considerable difficulty. I have found that it is genetically unrelated to procupine or silky. It can be produced in any color or pattern.

A naked mutant type appeared in Spokane, Washington, about 1931, again from normal Racing Homers, and two pairs were acquired by Cole in 1938. The birds were quite incapable of natural copulation, but artificial insemination was successfully worked out. Cole and Owen reported the results in 1944, showing that the naked mutant was a simple recessive for which they proposed the symbol *na*. Sad to say, this remarkable type was allowed to die out, and its possible use in producing market squabs that don't need plucking was never explored.

There have been several more recent reports of partially naked pigeons (PGNL #16: 2, #20: 3, #21: 3, #35: 2, #36: 4), but none of these was carefully pursued. Feather-eating may have been involved in some cases instead of mutation. Likewise, the naked-neck variety of Tumblers has not been well investigated, and I suspect that more than heredity may be involved (mites?). Who knows?

We have probably only begun to uncover the lode of mutants which can wreck feather development, and we can confidently expect more reports of new and possibly more bizarre types. The question is whether it is possible to maintain stocks, to make them available for scientific studies or simply for educational gawking. I think the answer is yes, but it won't be done by fanciers or commercial squabbers intent on efficient production. Anyway, let me know if you have a contribution to Hollander's Horrors.

—P.G.N.L. #66 pages 14-15 (1973)

P.S. 1982: In spite of efforts to maintain the original porcupine and scraggly stocks, disasters have caused extinction. Another porcupine mutant has appeared in Robert Mangile's stocks (letters to WFH 1981).

A somewhat scraggly-like simple-recessive mutant in the Saxon white-tail has been studied by Christian Reichenbach (PGNL 71:7) and by David Rinehart (PS & GN 6:19-25), who calls it “Deutsch scraggly”. We are using the tentative symbol *dsc*.

Absence or severe deformation of flight feathers (and also often the rectrices) has been reported in Fantails, Oriental Frills, Rollers, and others (PS & GN 1:38; 2:44; 3:35; 6:17; 6:29; 6:33; 6:47; 9:6). Breeding studies are difficult because copulation generally fails.

XXVII. VISUAL DEFECTS

My first experience with visual defects in pigeons was when I was a high-school kid. I had a pair of beautiful black Racing Homers (strain totally unknown, but the birds had a sort of Dragoon look) which surprised me by producing several pure white squabs, each completely blind. I couldn’t see anything the matter, but those squabs couldn’t see anything. Finally I got fed up and sold the stock. Later I realized that I had lost a scientifically valuable condition, and I’ve never heard of it since.

Then while I was in college another freak type showed up that I called “clumsy”—the squabs couldn’t learn to pick up a grain on the floor, and they were always bumbling around. In a small coop with feed in a cup these birds got along pretty well, so I was able to get a fair amount of breeding data, which I reported in 1938. A simple recessive, non-sex-linked factor seemed to be the explanation, and I proposed the symbol *cl* for it. I still maintain this mutant, but nobody else has shown interest. The defect here seems to be in the retina of the eye, but the birds often look as if the eye is a bit too large. On a couple of occasions in recent years pairs of clumsy birds have produced a squab with normal vision—a very unexpected result, and I haven’t explained it.

Racing Homer breeders meanwhile talked about occasional youngsters being “food-blind” or “feed-blind”, and I assumed that these were just reappearances of clumsy. But the feed-blind birds were reported to be able to race, something no clumsy bird could possibly do. Eventually I was able to obtain such a feed-blind cock from Robert Essex of Indianapolis, and made breeding tests. Again a simple recessive non-sex-linked gene seemed responsible, but it was definitely not the same as clumsy. In fact, a cross of a feed-blind cock with a clumsy hen produced only normal progeny. I am using the symbol *fb* for the feed-blindness gene (See PGNL #57: 77).

In his book “Animal Breeding”, A. L. Hagedoorn states (3rd edition, 1948, page 317): “We found one recessive lethal, complete blindness, in homing pigeons being inherited as a monofactorial recessive, the heterozygotes being good flyers and quite normal.” I have not found any details of Hagedoorn’s study in print, and it seems likely that his “lethal” was exterminated.

Still another report of an apparently simple recessive non-sex-linked abnormality in Racing Homers is given in PGNL #52, pages 7-11, by Harold Boos and David Rinehart. The defect is a bloating of the eye, usually, with total blindness, but some squabs are less severely affected, and may have slight vision.

Bloated or "bladder"-eye has also been reported in other breeds occasionally (e.g., Bokhara Trumpeter, PGNL #36:2), and is best known in homozygous almond squabs. I dissected the eye of one such squab and found that it had no lens. Some homozygous almonds however show little or no eye defect, often merely an off-center pupil or coloboma of the iris. Why there is such a variation is quite unknown, and it deserves more study.

Association of two or more sorts of abnormalities caused by a single mutant is termed "pleiotropy" in Genetics, and is not uncommon. Another example was found by Wendell Levi and me (reported in 1942), recessive lethal polydactyly in a stock of squabbing Silver Kings. Such squabs are totally blind, but a preliminary study of the eyes has not revealed any structural defects.

Carl Graefe back in the 1940's discovered a small-eyed blind condition occurring in his stock of Giant Homers. He gave me the parent birds and I made fairly extensive breeding tests. The eyes of the blind squabs were about a quarter-normal in size, with a very thick chorioid layer. Inheritance proved to be simple recessive and non-sex-linked. I proposed the symbol *mi* (for microphthalmia) when I reported the results in 1948. A similar blind condition was reported to occur occasionally in Trumpeters by Dr. Schafer (PGNL #43: 12-13).

More extreme microphthalmia, almost eyelessness, has also been found here and there. The famous example in Levi's "The Pigeon" (1963 edition, pages 333 and 375), the so-called eyeless White Carneau, was tested pretty well and no evidence of hereditary basis could be found. Perhaps something went wrong during incubation, so that the embryonic eyes degenerated. Certain toxic substances may exert such damaging effects. Of course, it is possible that similar microphthalmia could have a genetic basis.

Still another source of blindness is cataract, a clouding or degeneration of the lens. Carl Graefe found examples of this in Show Racers and gave them to me for testing. I reported the breeding results in 1958 (A. P. J. vol. 47 page 248). Again a simple recessive is involved for which I propose the symbol *ca*. The cataract develops gradually, becoming obvious by the time the bird is sexually mature, and increasing to complete inability to see more than darkness vs. light. A less severe type of cataract has been noted by Al Westling and others to occur in LFCL Tumblers occasionally.

Well, no doubt this survey is far from complete. There seems little doubt however that quite a lot of recessive mutants can be found scattered here and there, in spite of the usually fatal effects in the homozygotes. And this is not surprising; mutation is a fact of life and we can expect such random occurrences. It takes a bit of inbreeding usually to expose such hidden damage in the heredity. Ordinarily the breeder, like Mother Nature, can't tolerate

the sight of sightless birds, and they are soon weeded out; but I, fool that I am, deliberately try to keep such bad genes. New or old, I find them intensely interesting.

—P.G.N.L. #69 pages 25-26 (1974)

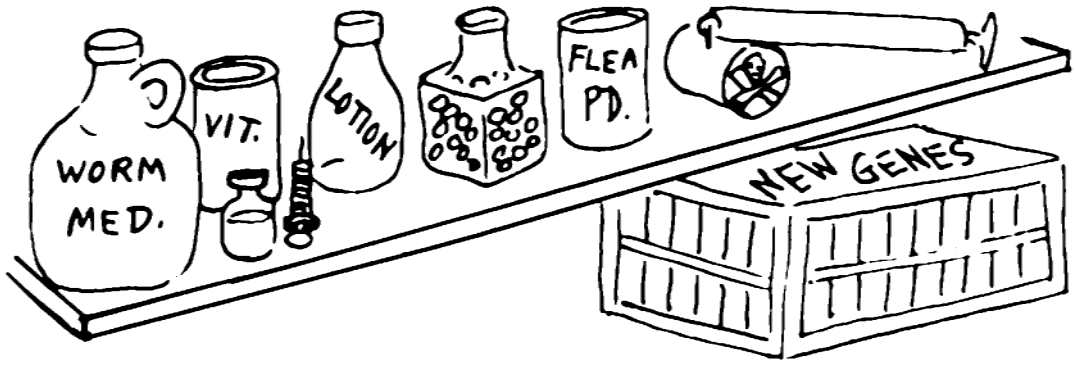
P.S. 1982: see formal review in Iowa State Journal of Research 55: 323 (1981).

Bulging cornea is fairly typical in eyes of sideburns pigeons (see Origins XXIV).

The peculiar visual defect (resembling clumsy or feed-blind) which is often associated with the barless color-pattern is still being studied. The name “foggy vision” is suggested for it.

Coloboma (fissure) of the iris has often been reported, generally in only one eye. Symmetrical irregularity of the iris is characteristic in the sex-linked web-lethal (American Racing Pigeon News, Oct. 1982, p. 50).

In old age, albino and clumsy pigeons seem prone to develop cataract.



XXVIII. FRILLNECK, CRAVAT, BREAST FRILL

(This article was written by W. F. H. and David A. Rinehart)

Everybody knows frillneck but it is a rather elusive oddity. Like crest, it is constituted by feather reversal, i.e., feathers pointing in the opposite (or at least different) direction from normal. And like crest, the extent of the frill—the area of reversal—shows extreme variation. But frillneck obviously is unrelated to crest genetically; the two may coexist in the same bird, such as a Satinette, without the least evidence of interaction.

We shall take up the ordinary cravat or vertical type of frill first, and later the "Chinese". Genetical studies of the usual frillneck have been numerous but still quite inadequate. Darwin (1868) put his finger on part of the difficulty—he noted that a Turbit cross looked normal until its third molt, when some reversed feathers finally appeared. Do we have to wait years to properly classify a bird? And if there is only one reversed feather, should we call it a frill or "nearly normal"? Later studies did not answer these quibbles.

The earliest report that I have found is by J. C. Ewart, 1899: a book, "The Penycuik Experiments," published in London by A. & C. Black, mostly on zebra-horse hybrids. He crossed an English Owl with an Archangel and found that the hybrid lacked frill. In 1902, Ewart reported additional crosses (Scientific Transactions Royal Dublin Soc., vol. 7: 353-378). English Owl X Black Barb produced some normal and some frilled young. However, crossing a Turbit with an ordinary pigeon, and a Turbit with a hybrid Jacobin-Barb gave only normal young. (The Turbit in this last cross was the sire.)

Whitman (1919, chapter VIII) reported studies mostly carried out about 1900. He had a male frillneck Homer from normal parents. He commented, "It may be that all pigeons are 'liable' to this. It corresponds to the dividing-line that is often seen in young pigeons; but in adults this fold is usually smoothed out, either by the feathers of the two sides coming together or by new feathers coming in." This Homer did not show the frill until it was a month old. Later it sired a similar youngster. Whitman also noted that the young African Owl showed "a very wide median unfeathered tract". This bare area gradually filled in by the age of 5 weeks, but a "crease" persisted, with reversed feathers. Such a "breast-crease" was also noted in certain species hybrids (e.g., mourning dove x ringdove).

T. H. Morgan in 1911 reported a cross between a Turbit and a Starling. He said the Turbit was "not very high-bred" but it did have "reversed feathers" on the midline of the breast. The 2 F_1 birds were normal; mated together, they produced 8 F_2—none showing frill.

Christie and Wriedt (1923) reported a more thorough study. They used the Norwegian "Petent", very similar to the Turbit. From 8 matings of Petent X Danish Tumblers, they obtained 68 F_1, none of which showed the "Krause" (frill). Moreover, all these were kept until after the first molt. Next were 8 backcrosses of F_1 to Petent; these gave 65 young, of which 25 showed frill of varied degree. Backcrosses of F_1 to normals gave 63 young, all normal. And 8 matings of F_1 X F_1 gave 62 young, of which 3 showed frill. Christie and Wriedt concluded that frill is recessive, and not sex-linked; they recognized that the ratios in

F_2 and backcross to Petent were deficient in frills but still favored the single-gene interpretation with possible modifiers. No symbol was used.

Bessmertnaja (1928) crossed Owl (apparently African) cocks with non-frilled hens and obtained 14 F_1, none with frill. Four backcross matings of F_1 to Owls gave 15 young, of which 8 showed frill. Bessmertnaja concluded that a single recessive frill factor is involved, and proposed the symbol *su*.

Feldman (unpublished, about 1933) used African Owl, Blondinette, and Satinette in crosses with various normal breeds, producing 40 F_1, all normal. These were mated together, usually brother X sister; where the frilled ancestor had been a male, the F_2 were 128 normal : 31 frilled, but where the frilled ancestor had been a female, the F_2 were 156 normal : only 6 frilled. This result led Feldman to hypothesize a 2-factor basis for frill, with one of the factors sex-linked.

More recent studies have been fragmentary and not in formal publications. A partial review was prepared by one of us (D.A.R.) in Pigeon Genetics News Letter #54: 86. Some more puzzling results have been obtained. Arvil Stone (personal communication to D. A. R., Jan. 1970) stated that from Oriental Frill X Roller he got "a few breast frills on F_2's". Since the frill is unknown in Rollers, it is hard to consider it as a simple recessive. Also, some crosses by one of us (W.F.H.) tend to cast doubt on the recessiveness: a Blondinette hen mated with a Homer produced 7 young of which 5 showed frill; a Turbit hen mated with a Syrian Bagdadi cock gave 4 young, all frilled; five matings of African Owl cock to normal hens having no known frill ancestry gave 15 young, of which 5 had definite frill, and some others had wide bare neck front strips as squabs.

Turning next to the "Chinese" Owl, we think Ghigi made the first attempt at analysis. In 1911 he reported that a cross of a Chinese Owl with a Barb gave one F_1, which had no frill. In 1914 he reported 2 crosses (reciprocals) of white Chinese X Bokhara Trumpeters, producing a total of 8 young, all normal. Mated together, these gave a total of 17 F_2, of which 4 were frilled but only one approached the Chinese and 2 had apparently ordinary-type cravat.

Bessmertnaja (1928) outcrossed a Chinese cock and got 4 F_1, all normal. She apparently considered the Chinese frill due to the same basic factor as that of other Owls.

Goessler (1938) gave a review of literature on the Chinese Owl, but missed Ghigi and Bessmertnaja. She made one cross of Chinese X normal Feldtaube (common pigeon) and got two F_1 females, both showing a small vertical frill. These were in turn mated with Feldtauben, and produced 8 young, of which 2 again showed frill.

Levi (1941 etc.) shows a cross of Chinese cock (poor quality) X Nun hen, giving 6 squabs showing no trace of frill.

In Pigeon Genetics News Letter #14 page 4, John Stevens reported an outcross of Chinese hen, giving 9 young of which only one showed frill, "fragmentary" about 1/2 inch

long on the front of the neck. In PGNL #16 page 4, Bertil Harrison comments that in Scandinavia Jacobins have been crossed into Chinese Owls to improve the frill. In PGNL #21 page 2, John Stombaugh noted a cross of a Chinese hen with a C. L. Tumbler cock giving two F_1, male and female, both with no sign of frill. The F_1 hen backcrossed to a Chinese cock gave 4 young, one resembling thé Chinese. And one of us (W.F.H.) reported in PGNL #41, page 3, a cross of Chinese hen with Magpie cock. The F_1 were without frill. The F_2 had some frills, quite variable but suggestive of Chinese. Later the F_2 from this experiment were totaled, showing 10 frilled out of 43, and 3 of the frills were vertical like the African. Therefore this result is in agreement with Ghigi's.

Crosses (made by D.A.R.) of a Roller cock and a Chinese hen have produced 2 young with a single reversed feather in the center of the breast and 12 normals. Other such matings have produced only normals. Matings of Chinese Owl cocks to Roller hens have produced only normals. An F_1 mating has produced 6 normal F_2's and 2 F_2's with horizontal breast frill, neck frill and pants.

A cross between an African Owl cock and a Chinese hen (made by W.F.H.) produced 4 F_1, all with vertical frill like the African. A cross between an Old Dutch Turbit cock and a Chinese Owl hen (made by D.A.R.) produced 7 F_1, all showing an intermediate or blended breast frill (no neck-frill or pants) suggesting breast frill and cravat are allelic.

What can we deduce from all these data? Perhaps that a lot more study is needed; however, more study will very likely yield similarly conflicting answers. It will be necessary to choose highly reliable normal breeds and stocks for such tests, and to examine the feather tract development carefully in the crosses. The width of the bare median strip is important, even if no feathers become reversed.

We have seen no supporting evidence for Feldman's idea of a sex-linked factor here; however, more tests would be welcome, especially in conjunction with sex-linked color factors.

At any rate, it seems we may tentatively think of each type of frill as an incomplete recessive unit characteristic with irregular-recessive behavior, allelic, and with cravat somewhat dominant to Chinese (possibly co-dominants).

In Levi's The Pigeon, 1957 edition, Brage is quoted on the Chorrera or Spanish Frill. He believes the "Chinese" really originated from the Chorrera, which is relatively ancient in Spain. Certainly all the frilled varieties seem to trace to the Mediterranean area. Goessler even states that figures of frilled pigeons are found in records of the 5th Dynasty of Egypt, 3000 B.C., but no reference for this was given. If that can be verified, the frill gene must be one of the oldest.

—P.G.N.L. #71 pages 13-15 (1974)

P.S. 1982: additional reports on Chinese Owl outcrosses (PS & GN 4:31; 9:16) and a few tests by Wilmer Miller and WFH agree with the foregoing except that no clear evidence of a sex-linked component was found. We are not using Bessmertnaja's symbol because it is not mnemonic; for the main factor in the Frill types we propose the symbol *fr*.

XXIX. STENCILLING

Metzelaar was the first person as far as I know who tried to analyze the mysteries called spangled, laced, white-barred, argent, tricolor, porcelain, acajou, spot-tail, and so forth. In his 1926 and 1928 reports, he pointed out that these various colorations affected only spread-pigment areas, not clumped. Further, he considered the basis to be a reduction, chemically speaking, of the black first to red ("mahogany") and finally to white. From the arrangements he observed, it seemed that the process was in those steps, and he proposed the term "centrifugal" reduction. For example, a feather in the bar region might have black edges, a white center, and red ("mahogany") surrounding the white area. The bronze ("mahogany") bars of a Modena in his view are simply a less complete reduction than the white bars of a Lynx, etc.

Metzelaar's ideas unfortunately concluded with a weird series of factor symbols all relating to the pattern series, which at that time were not well worked out. His breeding data were remarkably scarce, but of some value: (1) female Polish Lynx (white bar?) X male normal blue common gave "F_1 birds with imperfectly reduced wing bars and out of 6 F_2 young one showed complete centrifugal reduction of these bars and the rest incomplete or vestigial reduction." He suggested that the imperfect reduction resulted from being heterozygous. (2) Hyacinths and Suabians were used in 12 matings with black Homers and Tumblers. These produced 46 F_1 of which 21 were blacks, some showing more or less mahogany in the wing shields, and 25 checkers, all except one showing more or less reduction effect. Six of the latter had complete spangling. Metzelaar did not comment on how the matings were housed, so that I suspect possible errors of parentage. At any rate, Metzelaar was impressed by the much greater "reduction" in the checkers than in the blacks, and concluded that the *S* factor tends to inhibit reduction. (3) He crossed mahogany-spangled Modenas with black Modenas and got both types among the progeny, but nothing else. The black progeny were in turn mated with mahogany-spangled, and gave the same result. The total was 26 blacks : 25 mahogany-spangled. Here again he concluded that the *S* factor powerfully inhibits reduction.

Metzelaar's death came soon after those reports, but Feldman continued the breeding for several years, and I was able to examine his unpublished data in 1938. He outcrossed black-laced Blondinettes to bronze Modena and to Brander, and obtained solid black F_1. Crosses of blue Blondinettes and Satinettes with Suabians, Ice Pigeons, and bronze Modenas gave F_1 similar in coloration to the non-Oriental parents. Other outcrosses gave many more F_1, none showing the Oriental-type markings, but most blues showed some mahogany in the wing pattern. Backcrossing F_1 to Orientals gave 66 classifiable progeny, of which 20 showed

Oriental-type markings, 10 slight or poor Oriental, and 36 non-Oriental. Two of these backcross matings involved Oriental male X F_1 female, and their 5 Oriental young were all females.

Feldman's F_2 data from Orientals totaled 309 young, excluding ash-reds, recessive reds, almonds, and other unclassifiables. Of the 309, 28 were well marked and 11 poorly. Dividing the data on the basis of sex of grandparents, we have from Oriental grandsire 155 non-Oriental : 23 well-marked : 8 poor. From Oriental grand dam there are 115 non-Oriental : 5 well-marked : 3 poor. Unfortunately sexes of these F_1 were not recorded. However, Feldman thought that a dominant sex-linked masking factor might be involved, from the non-Oriental ancestors.

From such limited background information I tried to draw some conclusions for the monograph which Dr. Cole and I were preparing about 1939 (unpublished). It seemed to me that "reduction" was probably a misleading term because the real process in these colorations is probably an inhibition or failure of pigment development. Therefore I proposed the less compromising term "stencilling". Further I saw no evidence which proved all the types to be genetically related. It seemed safest to consider at least three types distinct:

(1) Bronze stencilling, as in Modenas, Cauchois, etc. Affects only coarse-spread areas.

(2) Toy stencilling, as in Suabians, Starlings, Priests, Monks, Ice Pigeons, some Swallows, Polish Lynx, Argent Modenas, etc. Affects only coarse-spread areas.

(3) Oriental Frill stencilling (also in some Dewlaps). Affects both coarse and smooth spread areas.

These are all discussed in Levi, The Pigeon, second edition.

At present I still consider these groups valid, but the genetic analyses remain sketchy. What progress has been made came largely from breeders' notes. I shall attempt to cover these here, but may overlook some unintentionally.

George Neuerburg noted in PGNL #3 page 4 that some Argent Modenas were produced in England from crosses with Lynx. P. J. Bihm (PGNL #11 page 2) crossed a female white bar Lynx with a blue bar Show Homer. The F_1 had bronze bars that later "turned pink". Also he crossed a female white-barred black Lynx with a blue check Show Homer and got some black F_1 with bronze checks that later lightened; also a plain black. A possible sex effect on the Lynx markings was suggested in PGNL #37 page 3, the males tending to be lighter than the females. Crossing female Lynx with male blue Mondain, Hebeler reported that the sons showed some lacing while the daughters did not. Jack Woolridge (PGNL # 39 page 1) however got no sex-linkage; he crossed a female Lynx with a blue Racing Homer and all of 4 F_1 showed bronzy bars and at least one was proved female.

Frank Dallas (PGNL #17 page 2) introduced white bars from Swallows into blue Modenas. This is comparable to the usually stated origin of Argent in Modenas from Suabian

crosses. Bob Smith (PGNL #19 page 3, #28 page 2) studied Argent variation, and also crossed with wild-type common pigeons. In one loft he crossed Argent cocks with blue hens and got 19 F_1, of which "4 males and 3 females medium to dark checks with bronze in the wings; 2 males and 2 females had laced wings with tan ground color; 2 females were blue bars, and one cock recessive red." Also 5 dark checked squabs not sexed. In another loft he crossed Argent hens with blue bar cocks. Here he got "4 males and 5 females; 7 of these were medium to very dark checkers (T-pattern) and all with bronze in the bar region which tended to molt out later (i.e., birds molted darker). One C^T cock had no sign of bronze and one hen was not checkered but a very heavy lace on a tan ground which molted lighter." He suggested that Argent lace of exhibition quality may be heterozygous.

Joe Quinn (pers. com. 9/22/74) made reciprocal crosses of porcelain Ice Pigeons X blue bars. "All progeny were intermediate....F_2 matings have produced 2 white stencils, 53 bronzes, and 1 wild type so far. I would feel more sure of myself if one bronze hen didn't molt in white this Fall. She's been a typical bronze three years." He thinks probably Toy stencil may not be a single-gene effect.

In my own tests of Toy stencilling I used Starlings, white-barred blacks (bronzy when young). Outcrosses to non-stencil, non-*S* birds gave a total of 62 well-feathered F_1. Of these, 25 did not have *S*, and all 25 showed more or less bronzing in the wing pattern. There is no indication of sex linkage. The F_1 birds showing *S* were about evenly divided as to showing some bronze or not. My data therefore agree pretty well with Metzelaar's on Suabians. It should be noted however that most of my F_1 birds were not kept beyond the first plumage, and it is possible they might have changed somewhat in the molt. I had only a little further data: second outcrosses of F_1 to non-stencil gave only a few classifiable young, some of which showed some bronzy effects; and one mating of F_1 X F_1 gave 4 squabs, of which one showed fair whitish stencil.

To summarize the results with Toy stencilling, it seems fair to say that partial dominance is typical, except to some extent when *S* is present. Perhaps we can explain the inhibiting effect of S on the basis of its similar tendency to mask underlying patterns (checker, etc.) on which the stencilling factor is dependent. However, the inhibiting effect does not always occur, and certainly the homozygous stencil may "unmask" the underlying pattern. More study of Toy stencilling seems needed before we can be reasonably sure of single-gene basis. I would suggest special attention to F_2 and molting.

The problem of bronze stencilling in Modenas has also not been adequately explored. Many outcrosses have been made, and in general the F_1, show little if any bronze stencilling. However, other bronzing factors may complicate the tests, and even recessive red (heterozygous) may have an effect. More clear-cut tests are needed before we can be assured of single-factor basis. And the problem of whether Toy stencilling and bronze stencilling are genetically related (alleles?) remains unsolved.

Oriental-Frill stencilling varies so much in supposedly pure stock, and in different molts, that it has never been adequately analyzed. Again, F_1 from outcrosses show only a slight bronzing effect in the wing pattern at most, so that we may consider the main factor recessive. Careful study in the future must also record sex to test Feldman's evidence for sex linkage.

Before winding up this discussion I want to emphasize the pitfalls in this area. "Mimics" are not uncommon: for example, the "ribbontail" reds, such as the miroite red Lebanon, are found to be merely reddened (bronzed?) B^A, and not related to Oriental Frill stencilling. Similarly, dominant opals are often called white-bar etc., and should be carefully distinguished from Toy stencilling. And homozygous indigo *S* birds may show a lacing effect resembling that of a Blondinette. Bronze stencilling is imitated or enhanced by opals, indigo, reduced, and even the grizzle factor. It is easy to be fooled by phenotypes.

Regarding origins, as usual we can only speculate. The only wild species having a stencilling effect, as far as I know, is the Diamond dove, which obviously could not be ancestral to our domestics. My guess is that the Toy-stencil mutation occurred in Central Europe, at least a thousand years ago. Probably Spanish breeds showing it were from crossing with Suabians. Also it seems likely that the Lynx and some Brünner Pouters came from such crossing.

The Oriental-Frill type of stencilling probably originated in Turkey or Syria, also probably at least a thousand years ago. Its transfer to other breeds was undoubtedly slowed by its recessive behavior.

Bronze stencilling may have originated in Europe; again, all is vague.

The future of these stencilling types seems bright, and they are being transferred to a number of other breeds. I hope their genetic bases will be clarified soon.

—P. G. N. L. #72 pages 10-12 (1974)

P.S. 1982: Oriental Frill X stencilled Dewlap produced F_1 similarly stencilled (PS & GN 4:41; 5:32, 36).

In spite of the incompleteness of analyses so far, tentative symbols for the main mutants seem justifiable:

Ts for "Toy stencil" as in Starling, Lynx, etc.
fs for "Frill stencil" as in Blondinette, etc.

The reader is herewith reminded that these mutants tend to have more definite expression in mature plumage.

XXX. WHITE AND PIED

What is whiteness? Take snow for example. Pure snow under a red light looks red, under a green light looks green. Under a white light snow looks white—unless we view it through a color filter, such as red cellophane. If we add water to snow, what happens? It becomes transparent. We can also consider impure snow: made from water containing a dye, or dirty. The foreign matter is called a pigment: the pigment absorbs light, so that reflection to our eye is prevented. Whiteness then is reflection of all light from the surface. Unlike pure water, the surface of snow is not flat but microscopically complex, crystalline and prismatic, thus giving a diffuse reflection.

All that introduction to white feathers! But the analogy is very close. Given white light, no filter, no wetting (oiling), and no pigment, the feather looks white. Its material is a clear protein, keratin, with a very complex surface.

Wild-type *Columba livia* of course has a very durable pigment, melanin, in the form of extremely small granules. However, the pigment is not uniformly distributed, being very dense in the bars and microscopically spotty ("clumped") in the blue areas. And in some areas (on the rump, outer vanes of outer rectrix, and under the wing) the pigmentation is so slight that they look white. I have used the term "albescent" for those areas to distinguish from whiteness due to complete absence of melanin such as in white flights.

The next question then is what controls the presence or absence of melanin pigment. Many studies have shown that a special type of cell produces the pigment. Such cells, called melanocytes, are migratory at first, coming from the embryonic neural tube and eventually populating all the skin and even the eyes. When a feather begins to grow, melanocytes invade the structure and settle down, looking like dark spiders, full of pigment granules. As the feather dries, the cells die but the pigment remains. Therefore, to get white feathers, either the melanocytes would have to be prevented from migrating in, or their pigment synthesis would have to be interfered with.

Fanciers have learned that repeated plucking of feathers (especially in recessive red birds) will eventually result in the growth of white ones. Maybe the melanocytes get used up, or weak, we don't know. Injury to the skin, with resulting scar tissue, also may produce white feathers, perhaps because the dense scar tissue prevents migration of the melanocytes. And there are still other possible conditions that may lead to whiteness—certain nutritional deficiencies and hormonal upsets, for examples. The general term for such whitening is "achromatosis".

Finally we get to the domestic genes. A majority of the "color genes" already discussed produce a lightening compared with wild type, as indicated by their names (dilute, grizzle, milky, etc.). They seem to interfere with pigment production in various ways. Combining two or more such mutants in the same bird generally gives still less pigmentation, so that the bird may look nearly white. For example, a dilute ash-red grizzle may be indistinguishable from a faded indigo dominant opal, and homozygous faded brown *S* looks

like a true albino. Pedigree and progeny-test information are the only keys to understanding such problems.

But the commonest types of white are not true albinos or imitation whites, but pied (piebald)—completely white in some areas and normally pigmented in others. The ordinary bull-eyed self white can be regarded as an extreme pied: pigmentation limited to the inside of the eyes.

The multiplicity of pied patterns that breed reasonably true certainly suggests a complex genetic situation. And we must keep in mind that many pied birds are mismarked just enough so that they can't win in a show. If they are kept for breeding, the fancier is likely to mate them with birds mismarked in the opposite way, "to get a balance". If possible, the fancier will pluck any dark feathers in an area that "should" be white, so the judge or buyer will not see them. But in spite of such complications, many brave investigators have tried to analyze the genetic basis for the pied varieties. So many that I shall leave comprehensive review for a future endeavor. Suffice it to say that little is conclusive.

Modena breeders have long known that the gazzi pattern (which means "gay" in Italian) can segregate pretty cleanly out of crosses with schietti (self). Ghigi in 1914 reported fairly good data showing that gazzi is a mendelian unit, mostly recessive. I have suggested the symbol *z* for it (see Levi 1957, page 345). But trying to introduce gazzi into other breeds can give some very varied results, suggestive of modifying factors.

The ordinary bull-eyed white typically breeds true, and often segregates cleanly from crosses with self. However, the evidence for simple recessiveness is incomplete at best and clouded by the frequent splashes produced. Crossing gazzi with bull-eyed white commonly gives F_1 intermediate, suggesting allelism of the two. In fact, F_1 from crossing almost any two pied types tend to be intermediate, so that the possibility of multiple allelism is impressive. And hard to test.

The baldhead pattern seems to be a probable unit that shows incomplete dominance to self. Even hybrids of baldhead with ringneck dove show fair piebaldness. My guess is that baldhead and gazzi are not allelic, and that by combining the two it should be possible to produce another bull-eyed white.

But genetic analysis of the pied varieties is likely to require an extraordinary amount of time, patience and effort. And we will want to know what is the developmental basis, in terms of the melanocytes. Are they just few in numbers at the start of their embryonic migration, so that some areas are not invaded? Or is this or that area not favorable for melanocytes to live in? Can embryonic conditions such as high or low temperatures or egg yolk quality or air pollution perhaps favor or inhibit melanocyte activity? Interesting experiments await.

What can be said about origins in the face of all this ignorance? Well, one thing that has long impressed me is the infatuation among beginning fanciers with gay-splashed birds, whatever the breed. Probably early in the domestication process it was just such birds that caught the eye, and the complexity of pied varieties has been millennia in growing.

—P. S. & G. N. #1 pages 12-13 (1976)

P.S. 1982: for references on the wanderings of pigment cells, see Journal of Experimental Zoology 172: 181 (1969).

Allelism of bull-eyed recessive white and gazzi has been fairly well established in F_2 and backcrosses—no self birds have appeared (data from Robert Mangile, Tanner Chrisler, WFH, and others). Therefore, the gene symbol z^{wh} is proposed for recessive white.

The “pied” mutant in ringneck doves is a recessive; it shows considerable change from juvenile to adult (APJ July 1971, p. 348).

XXXI. THE TAIL COMPLEX

Charles Darwin appears to have been the first to call attention to a relation between extra tail feathers (more than 12), extra tail bones (more than 7), and absence of the uropygial or oil gland. He gave much data in “The Variation of Animals and Plants under Domestication” together with historical accounts of Fantails and other breeds, in 1868. He notes that a couple of wild species (crowned pigeons) have 16 tail feathers and no gland: “It can hardly be an accidental occurrence.”

Darwin further commented on inheritance: “In making reciprocal crosses between pouter and fantail pigeons, the pouter race seemed to be prepotent through both sexes over the fantails. But this is probably due to weak power in the fantail rather than to any unusual strong power in the pouter, for I have observed that barbs also preponderate over fantails. This weakness of transmission in the fantail, though the breed is an ancient one, is said (Boitard and Corbié p. 224) to be general; but I have observed one exception to the rule, namely, in a cross between a fantail and a laugher.”

In the early years of this century further study of the problem was taken up independently by Morgan in the U.S.A., Doncaster in England, and Ghigi in Italy.

Doncaster crossed a white Fan male (23 tail feathers) with a red Tumbler and got 10 F_1: “the tail feathers varied from 13 to 16 in number. Two pairings were made between these F_1 .... (of 27 F_2) the tail feathers varied from 12 to 17; none of the F_2 young showed anything that could be called a fantail. The oil gland ... was present in all the F_1 birds which were examined. In F_2 it was recorded as absent in 4, present in 10; of the latter one had an

extremely small oil gland and another had a double one ..... suggests that it behaves as a dominant Mendelian character."

Ghigi made reciprocal matings of Fantail (about 30 rectrices) X Jacobin, and obtained ten young as follows:

	from Fantail sire					from Fantail dam				
identification & sex	♂	♀	♀	♀	♀	?	♂	♀	♂	♀
no. of rectrices	17	22	16	18	12	20	17	14	16	15
no. of vertebrae	8	9	9	8	7	?	7	7	8	8
oil gland	0	0	0	1/2	+	?	0	+	0	0

Two matings of F_1 male lacking gland X F_1 female with gland produced F_2 as follows:

	sire 17 rect., dam 14						sire 17, dam 18		
identification & sex	?	?	?	?		?		?	?
no. of rectrices	14	14	18	15	14	17	24	16	21
no. of vertebrae	8	?	?	8	8	?	?	?	?
oil gland	0	0	0	+	0	0	0	0	+

Also Ghigi mated two F_1 birds together that had 16 rectrices and no gland and obtained only one F_2 from them. It had 12 tail feathers and normal gland!

Ghigi was naturally not very sure of any rules here, and simply commented on the great variability and irregularity. I would also say that that third mating for F_2 gave a result making me suspicious of infidelity. In any case, Ghigi's results do not agree well with Doncaster's or Darwin's.

Morgan (of Columbia University, N.Y.) published preliminary cross results in 1911 —a female white Fantail having 32 rectrices X male Swallow. He got 7 F_1 having 12, 13, 13, 13, 14, 15, and 17 rectrices. Only four F_2 young were produced, all with only 12 rectrices, surprisingly. Oil gland was not recorded. In 1918, Morgan reported another cross, this time with Homers and with impressive numbers of progeny. Three pairs of parents (involving two male and one female white Fantails having 30 to 32 rectrices) produced 41 F_1 which had from 12 to 20 rectrices (average 15). Only seven of the F_1 birds were examined for oil gland; it was present in all, but described as "double" in all cases except the one bird with 12 rectrices (gland "single" = normal).

Morgan says "no marked difference appeared amongst the F_1 progeny when the fantail parent was female or male" so that sex linkage seemed unlikely.

Mating F_1 birds together, Morgan obtained 278 F_2 ranging from 12 to 26 rectrices, mostly in the intermediate to low classes. There were 46 birds having normal tails. Only 12 birds had fairly high counts (22 or more). Oil gland condition was examined in 208 of the F_2, and relation to number of rectrices established: 126 “double”-glanded had 12-26 rectrices; 36 “single”-glanded ranged from 12-22 rectrices; and 46 having no gland varied from 14-25 rectrices.

Morgan suggests that the Fantail differs from normal in several sets of factors for increased rectrix number. As for the tail gland, he thinks absence is dependent on one recessive factor because about 1/4 of the F_2 are in this class. He does not suggest a symbol. For the “double” class he proposes another non-allelic factor, from the Fantail.

The fact that birds lacking the oil gland never had less than 14 rectrices seemed significant to Morgan. He says “The curves suggest .... linkage between a gene for extra feathers and a gene for absence of oil glands,” rather than some sort of suppression of gland formation by more tail feathers.

Morgan also gives data on split middle tail feathers, which were common among his Fantail crosses. He concludes that “There are no indications that the split feather is due to the union of two separate rudiments.”

The next reported study was by Johansson (1927) from the University of Wisconsin. F_1 from Fantails X normals varied from 14 to 24 rectrices, and all except from one mating had the gland. A mating between two F_1 both having 22 rectrices and gland present gave this distribution in F_2 (v = very small gland, a = gland absent): 14, 15v, 16a, 17, 17a, 18, 19, 20a, 21v, 21a, 22, 23a, 24, 24a. Johansson also presents miscellaneous other data on absence or smallness of gland and on number of rectrices in other stocks. He is cautious in interpretation, but suggests that non-genetic variability should be considered as of some importance.

In 1935 another report came from Italy, by Vecchi. This was started by mating 3 Mookees with 3 Fantails (32 rectrices). They produced 7 F_1, all with glands, and rectrices as follows: 13, 14, 15, 16, 16, 16, 20. This last one was not used for breeding. Two matings were made for F_2, and gave the following distribution: 12, 13, 14, 14, 14, 14, 14, 15, 15, 15, 15, 16, 17, 17, 17a, 18, 18a, 18, 18a, 19, 20, 20a, 21a, 21a, 21, 24, 27a. F_3 and F_4 data were also given but tell little. Vecchi concludes that presence of gland is dominant, and that absence is not correlated with number of rectrices. (The second conclusion does not agree well with Vecchi’s own data.)

In 1938, Harms (of Germany) presented further data, concerning 5 different crossing experiments with Fantails, worth our attention. First was a male Fantail with 30 rectrices X female Maltese lacking oil gland and having only 12 rectrices. (All F_1, F_2, and backcross young lacked gland.) The tail feather counts were as follows: F_1 males 16, 17, 17, 18, 19, females 14, 16; F_2 16, 16, 16, 17, 18, 19, 20, 21, 22, 22, 23, 25. Backcross of F_1 male with 18 X female Fantail with 34 produced 28, 23, 31, 31. Backcross of F_1 female with 16 X male

Fantail with 30 produced 23, 29. Backcross of F_1 male with 16 X female Maltese with 12 produced one progeny: 18.

Harms' second cross was a female Fantail with 40 rectrices X male Barb. The F_1 birds all had glands, and rectrices as follows: males 16, 18, 20, females 14, 16; F_1: 15a, 16a, 16, 16, 16, 16a, 16v, 17, 17, 17, 18, 19, 22, 24a. Backcross of female F_1 14 X male Fantail 30a produced 22a, 23a, 30. Backcross of female F_1 16 X male Fantail 28a produced 19, 20a.

The third cross was male Fantail 32a X female Jacobin. The F_1 were males 18, 19, 21a, and female 18v. F_2 (no comment which F_1 male was sire): males 14a, 21a, 25a, and female 16v. Backcross of F_1 male X Jacobin produced 14, 14a, 18. Backcross of F_1 male 21a x Fantail produced 22a, 27a. Backcross of F_1 female 18v X male Fantail 32a produced 28a, 32a.

The fourth cross was female Fantail 26a X male German Turbit. The F_1 birds all had the gland but one female's was small. The rectrix counts: females 12, 12, 15, 15, 16v, male 14. F_2: females 12, 17a, 20, male 15.

Fifth cross: female Fantail 34a X male German Trumpeter: F_1 all with normal gland, males 16, 19, females 15, 16. F_2: 16a, 18. Backcross of F_1 male 16 X female Trumpeter: 12.

Harms' long discussion favors a non-Mendelian explanation for inheritance, probably cytoplasmic. Unfortunately Harms did not realize that the reciprocal crosses would be the test of this, and they destroy it.

Well, one more big 1938 report needs our attention: from the University of Wisconsin, by Pennebaker, whose chief interest was the uropygial gland. He demonstrated that the first indication of normal gland formation is in the 8-day embryo, and that glandless breeds fail to initiate gland formation.

Pennebaker had several types of genetic tests. First was a miscellaneous group of matings (mongrels) glandless X glandless. These produced 31 young, all glandless. Next, Fantails mated with Homers, Strassers, and Archangels produced 49 F_1 all with gland though some were small. Comparison of the reciprocal crosses showed no evidence for sex linkage. The next type of mating was glandless Pigmy Pouter X Homers, Strassers, etc. Typically the F_1 had normal gland. Where the Pigmy Pouter was sire, 15 daughters were obtained, all with gland, again indicating no sex linkage. Backcrosses of normal F_1 X glandless (including Fantail tests) gave 148 young of which 79 lacked the gland, but those having the gland varied in its size. Also other miscellaneous data were presented in support of Pennebaker's interpretation that a single gene *N* is necessary for nipple and reservoir formation, and another gene *G* (Pennebaker forgot that the symbol *G* was reserved for grizzle) is necessary for formation of glandular tissue inside the reservoir. With *nn*, no gland forms at all; with *Nngg* the gland may be very small.

Pennebaker also gave some data on relation between gland and rectrix number, especially in backcrosses of F_1 X Fantails. Here he got 39 birds of which 18 had glands and

14-26 rectrices, mean 19; 21 were glandless with 17-31 rectrices, mean 23. Also other data agreeing in showing a significant correlation. He concluded “Probably one or more recessive genes responsible for the larger number of tail feathers are linked with the factors responsible for the absence of the gland in the Fantail breed.” But, “Since the strain of Pigmy Pouters lacking the gland used in these experiments had the normal number of tail feathers, it is evident that the genes for absence of gland are not dependent upon the genes for extra tail feathers for their action.” (I saw these birds and my memory says that at least some had extra tail feathers.)

Well, at this writing, nearly 40 years after the last significant research, we haven’t learned much more. However, I think the suggestion of linkage between the *n* factor and some factor for extra rectrices is not logical. My argument is on probability: if these factors are assumed to be fairly closely linked, how did they get together originally? One is driven to assume that both mutants originated together in one original bird, perhaps thousands of years ago. This is the height of improbability, but let’s proceed. Over such a long period, evidence for the linkage would have tended to dissipate, but I do not know of any breed or variety having no gland which consistently has only 12 rectrices. Pennebaker did not note extra rectrices in his Pigmy Pouters, and Harms did not note them in his Maltese, but I suspect that they occur. (If fanciers can demonstrate conclusively a stock that breeds true for no gland and only 12 rectrices, my idea will be dynamited.) Anyway, the whole idea of linkage seems much less likely to me than a developmental interrelation of parts, and that a single mutant is the most adequate explanation. Let us hypothesize that the homozygous mutant affects not only the development of the gland but also, irregularly, rectrix formation and very likely also vertebral differentiation (extra tail bone formation).

In middle Europe and eastward the “Oriental Roller” (or Tumbler or Highflier) type is very popular, under various names. The somewhat elevated tail with extra rectrices and lack of gland resembles a Fantail mixture. It seems more likely that the Roller type is the ancestor of the Fantail, instead of vice versa. My guess is that the Oriental Roller was the main origin of the glandless condition, probably at least a couple of thousand years ago and “contaminated” many other breeds. It seems more likely that way than for the origin to have been perhaps in Maltese, or Lebanons.

The Fantail or “Broad-tailed Shaker” seems not to have been recognized before about 1600. I wonder whether perhaps the great Mogul emperor pigeon fancier, Akbar Khan, created it about that period.

Can a pure-breeding Fantail stock or Oriental Roller be developed which has the gland? I doubt it, but hope some enterprising fanciers will try. Who knows, they might even be ambitious enough to count the tail vertebrae.

On the other hand, absence of the gland in other breeds which ordinarily have normal tails may prove to be a valuable genetic variant, useful in linkage tests. Those "split-tails" that are usually culled might be the start of a new breed? The old tail complex may have an exciting future.

—P. S. & G. N. #4 pages 65-68 (1977)

P.S. 1982: McKee and Mangile have each reported Fantail-cross derivative birds having 30 rectrices and gland present (PS & GN 4:46; 7:18).

According to Goodwin (Pigeons and Doves of the World), *Goura* has 16 rectrices and no uropygial gland.

XXXII. BEHAVIOR DIFFERENCES

Domestic: what does it mean? The word is Latin, signifying house or home. Domestic animals are those living in or around people's dwellings as opposed to those tending to shun human association. Usually domestic animals are less fearful of man than are wild kinds in spite of his dominating ways. The common pigeon seems early to have gravitated to civilized areas, where buildings provided nesting sites and spilled grain might be easy picking. The house sparrow is about at that stage of domestication.

There must have been a second step, which sparrows have not taken: intimacy. Perhaps this step was simply to become a pet, to live in the house and depend almost entirely on whimsical humans. The birds were often used as religious sacrifices, probably in the early temples, and were likely kept in some sort of cage. They had to be fed and watered or they would be useless. Then I think human selection began—perhaps a white or a red bird was found in the flock, and attracted priestly attention. Darwin believed that altered "conditions of life"? were responsible for inducing variation; once oddities showed up under man's supervision they would certainly have had a better chance of being propagated than in the wild. Here was a new world for the birds—where they could evolve in all sorts of directions. Tameness was probably selected for almost unconsciously, but not with uniform success—some of our domestic varieties are still aloof and flighty. But the owner is likely to tolerate other faults if the bird is "pretty."

How did message-carrying start? My guess is that escape and return of purchased birds suggested the idea. And then it must have been soon obvious that some pigeons were better at homing than others. Elite families of Carriers were the natural development.

Clowning has always had an appeal, and a pigeon that tumbles in flight must have been an early treasure. For best entertainment the clowns should not quit flying too soon;

therefore they were automatically selected for light weight and endurance, and also for high flying. Extreme clowning might have been the start of selection for tumbling in the coop and on the ground.

We can go on with such reasonable speculation about similar origination and exaggeration of other behavior deviations: neck-shaking, elevation of the tail, wing drooping, pouting, ring-beating, diving in flight, laughing, trumpeting (drumming), etc. As for intelligence, man's protections seem to have encouraged no improvement except in navigating ability; some breeds seem rather stupid in comparison with wild pigeons, though less likely to panic.

Genetic analysis of these eminently domestic variations is difficult and it is not surprising that results have been rather disappointing. There is no question that genetic bases for the conditions exist, but evaluation of effect of age, sex, training, nutrition, illness, etc., is also essential and not simple. We must recognize that we are only at the threshold of understanding. Even scraps of data may be valuable, and fanciers should collect their scraps for future use.

We should keep in mind that some mutations may be simple yet have multiple effects. The 'sideburns' mutant (*Sb*) seems to be such an example, with the tendency to tremor in the homozygotes. However, other examples in pigeons have not yet been demonstrated—most of the behavior peculiarities seem to be rather specific. (Note: "clumsy" and "feed-blind" behavior are considered to be the obvious consequence of visual defects rather than brain disorders.)

Ataxia, a staggering behavior somewhat like drunkenness, was a mutant discovered by Riddle. It proved to be highly variable but a fairly reliable Mendelian recessive and was given the symbol *at*. I maintained this mutant for many years, but eventually failed to get it propagated. Needless to say, it was difficult to manage, especially in a flock pen, and even a fairly well-coordinated bird would occasionally go into convulsions for no obvious reason. The cerebellum of the brain is small in ataxic birds.

Tumbling and rolling seem not to have any relation to ataxia, although "loss of control" in extreme examples does resemble a convulsion. Entrikin's study (Journal of Heredity 63 pages 351-354, 1972; PGNL # 59, 1971) is the most extensive to date. The data indicated multiple-factor inheritance, but a main factor *ro* was hypothesized; environmental effects were also shown to be important. A report not noted by Entrikin was printed in APJ 56 page 293, 1967, by A. H. Kopp, who crossed a "mad" Roller cock with a Fantail hen. He got 3 F_1 which were "excellent high-fliers, and flew for several hours each time liberated. One hen was lost, and the other two rolled down when they were about a year old, the cock killing himself." Kopp also noted that F_1 from crosses of Parlors with Tipplers and with Birminghams were variably intermediate. No doubt much more such information could be dug out of fanciers' publications.

Regarding neck-shaking, there is disagreement. Darwin (in "Variation of Animals and Plants under Domestication", chapter 14) indicated that F_1 from Fantails X Barbs and Pouters

were not like the Fantail. Ghigi (1914) reported reciprocal crosses between Fantail and Jacobin and noted that the hybrids showed more or less trembling, especially the males when courting. T. H. Morgan (1918) used Fantail X Homer matings, and observed "The shaking of the head disappeared in F_1 and indications of it were seen occasionally in F_2 and especially in backcrosses." By contrast, J. H. W. Morgan (1925) stated that "neck tremble" is a dominant in crosses. A German experimenter, Reisinger, reported 4 F_1 from Fantail X Homer, and none showed neck-shaking (Zoologischer Anzeiger 81: 254-260, 1929). Informal comment from breeders has been indefinite.

Darwin (same reference) also commented on Trumpeter X other breeds; the hybrids did not trumpet. Ghigi (1914) said that F_1 males from Trumpeter cock X Chinese Owl hen had normal voice, but the males from the reciprocal cross sounded more like the Trumpeter. Schafer (PGNL # 6 page 5, and # 22 page 2) noted that crosses of Bokhara X Swallow did not trumpet. Informal comment from breeders is equally confusing but suggests quantitative inheritance.

The pouting characteristic is ordinarily recessive in F_1 but informal breeders' comments indicate exceptions, especially from crosses of Norwich Croppers with enormous globes. Clapping and diving behavior also ordinarily disappear in F_1.

Droop wing, as in Oriental Rollers, seems also to be recessive as a rule, but no data seem available on later generations.

Regarding homing, high-flying, tameness, and other sorts of behavior we find the same vagueness. The general impression we get is of quantitative inheritance, but no really satisfactory data have been accumulated. I have not been able to comb the fanciers' literature carefully, and suggest that interested fanciers make such a project a matter of priority instead of wasting effort on further small-scale tests. The recent revival of interest in scientific research on behavior Genetics favors the possibility of a major effort in this area with pigeons. Perhaps the superficial indications of quantitative inheritance will prove fallacious. However, it should be evident to anyone now that analysis of such characteristics requires a more elaborate attack than for example with crest or foot feathering, though the genetic bases may prove quite comparable.

So-called quantitative characteristics have led many investigators into clouds of mathematical modeling and speculations about a queer class of "polygenes" which do not have to follow the strict Mendelian rules. Maybe they exist? And maybe we will have to talk about origins of domestic polygenes?

—P. S. & G. N. #6 pages 15-17 (1977)

P.S. 1982: see formal review in Iowa State Journal of Research 55: 323 (1981). Donald Henderson reported a motor disorder in certain Racing Homers—more or less inability to Say So which he termed "back-legged" (PGNL 64:16; 66:34).

A discussion of the Stargard Zitterhals by Axel Sell (PGNL 66:34) indicates partial dominance.

Kenneth Bickler reported two birds in an inbred family of Show Racers which hop like a robin instead of running across the floor when frightened (PS & GN 6:13).

Robert Mangile has made a study of another motor disorder which he terms “erratic”. It seems to be a simple Mendelian recessive and has been given the symbol *er*. (Report 1982).

XXXII. BIGGER, SMALLER

Columba livia differs little in general size from its millions-of-years-old fossil ancestor, *Archaeopteryx*. Our interest in size inheritance concerns mainly a few unusual domestic variations. We have already discussed foot-feathering and the tail complex, which are in a sense size features, but now let’s zero in on what we usually think of as bigger or smaller.

There is a fascination for many people in weighing, measuring, and counting. Almost anyone can play (hopefully without errors), and with persistence an impressive pile of data can be accumulated. This then invites manipulation by myriad mathematical methods. Such research has been very popular in livestock Genetics. Whether the outcome is insight or obfuscation can be debated, but sometimes casual comments are as informative as careful calculations. And to identify specific mutants requires critical tests which are rarely made.

Darwin (1868, “Variation of Animals and Plants Under Domestication”) presented much information on size variation, and he commendably used the wild *C. livia* as his basis of comparison. One interesting correlation that he noted was that small feet go with short beak, large feet with long beak.

The next serious attempt in this line was reported by Ghigi in 1914. Only beak and feather length were involved. All his crosses gave intermediate F_1 (Chinese Owl X Trumpeter, Jacobin X Fantail, Scandaroon X Short-Face Tumbler for beak contrasts; Modena X Homer, Modena X Archangel, Jacobin X Fantail for feather-length contrasts). Analysis was not pursued further.

Short beak next interested Christie and Wriedt (1923). They crossed the Norwegian Petent (old-style Turbit) with Danish Tumbler (beak length about wild-type). The Petent measured 17-20 mm from tip of beak to corner of mouth, and the Danish measured 20-24 mm, with an average of about 22. There were 62 F_1 birds, not classified by sex; beak lengths were from 18-22 mm. The 33 F_1 from Petent hens averaged 21 mm, while the 29 F_1 from Petent cocks averaged 20, probably a significant difference but Christie and Wriedt did not note sexes of the F_1, and we can therefore not be more than suspicious of sex linkage. There

were 59 F_2 ranging from 18-22 mm. Segregation was obvious in backcrosses, however: with the Petent parent, there were 58 young, ranging from 17-21 mm, and with the Danish parent there were 53 young, ranging from 18-23 mm. In the backcross to Danish there is again suspicion of sex-linkage because the shortest beaks came from F_1 sires. Christie and Wriedt ignored minor questions and came to the conclusion that a single main shortness factor is involved, which they symbolized *ku* (for kurz). They made no comment on feet.

In 1926 Wriedt and Christie reported a measuring and weighing spree—they went to a pigeon show in Copenhaven and worked over 458 birds of 23 breeds. They got body weight, circumference of the body, keel length, length of leg, beak length, and neck (nape) feather length. The data were presented in the form of tables giving ranges of variation, means, standard deviations, standard errors, etc., but sexes were not separated. Various correlations were tested, and it was concluded that keel length was the single best general indicator of body size. Feather length, beak length, and leg length were largely unrelated to general body size, as mere inspection of the birds makes obvious.

The remarkable feather length of the Jacobin was investigated further Christie and Wriedt (1927). Neck (nape) feathers were considered the easiest to measure on the living birds, and representative of the plumage generally. Two Jacobin hens were used having feather length of 6 cm. They were mated with Danish Tumblers and other normal-length types, averaging about 3 cm, and gave 15 F_1, which ranged from 3.5-5 cm. Although only a few were recorded by sex, there seems no evidence for sex linkage here. Backcrosses to normals gave 75 young, ranging from 3-4.5 cm, and a backcross to Jacobin gave 4 young, which ranged from 5-6.5 cm. The authors concluded that at most only a few factors could be responsible for the long feathering.

After Christie's death, Wriedt reported (1931) a breeding experiment on leg length in crosses of Bagdette (French Bagadais?) with normals (Danish Tumbler, field pigeons). The Bagdettes measured 14-15 cm from knee joint to root of middle-toe claw, while the normals ranged from 10-12 cm. There were 34 F_1 birds (sex not given), averaging about 13 cm. Backcrossing to Bagdette gave 54 young, ranging from 13-15 cm. Backcrossing to normals gave 136 young, ranging from about 10.5-13.5 cm. Wriedt figured that two factors would be most probably responsible for the longer leg of the Bagdette. But why didn't he get measurements of beak length? Well, Wriedt died soon after, but all was not lost: Wexelsen, who had assisted Wriedt and Christie, took over the work and extended it considerably (1937). This report was reprinted in PGNL # 52 pages 14-27 (1969), but without bibliography.

Wexelsen dealt with 7 breed types: Bagadette (French), Danish Tumbler, Turbit (Petent), Pigmy Pouter (Brünner?), Frillback, Maltese, and Field. He apparently made an error in describing the measurement of leg length, as he said it was from the top of the tibia to the "proximal" end of the middle toe; Wriedt had specifically stated that the measure included the middle toe to the claw. Wexelsen's data cover leg, beak, and sternum (keel) lengths only—no feathers. That is regrettable because the Maltese is specially short-feathered. Wexelsen notes that keel length is not as good a general size indicator as Wriedt had claimed, because it takes up to 9 weeks for it to complete growth, while the leg and beak

are finished much earlier. Five crosses and corresponding backcrosses are given: Bagadette X Field, Maltese X Frillback, Maltese X Pigmy Pouter, Pigmy X Frillback, and Bagadette X Turbit. Beak length for the Bagadette X Field F_1 was intermediate, and in the backcross to Field beak length was well correlated with leg and keel lengths. I won't attempt to cover all the other findings except to say that intermediate inheritance was typical and probably few gene differences are responsible for the breed features. End of Wexelsen.

The next year (1938) another big report appeared, by a German named Harms. This was a collection of miscellaneous data, including some quantitative—even egg volumes. He did record wing and tail lengths, though just how he measured these is not clear. Also beak lengths, but not leg lengths: he pointed out that leg proportions are essentially similar in the different breeds, and tallness is mainly a matter of a non-crouching stance. Harms' crosses were Fantail X Barb, Jacobin, Maltese, Turbit, and German Trumpeter; Barb X Römer (Runt), Scandaroon; Scandaroon X Turbit; and Turbit X Stargard Zitterhals. Most of the experiments went into F_2 and backcrosses. Harms was convinced that all the quantitative differences showed blending inheritance, not ordinary Mendelian. His data from reciprocal crosses also seem to me to indicate no obvious sex-linkage. Interested readers may desire to study his results in more detail.

In 1947 another big study appeared: "Endocrines and Constitution in Doves and Pigeons," by Riddle. This contains a great amount of material on body and organ weights and egg weights, for various genetic groupings. Again one is likely to be impressed with the complexity and conclude that picking out single-gene effects will never be possible. Still, there are fascinating details, such as, for example, the marked sex differences in some types but not in others.

Well, it has been 30 years since that climax. Has anything further been discovered? Pigeon Genetics News Letter items have certainly not been earth-shaking, but a few deserve mention: in # 2 page 4, weights of Roller X Racing Homer; in # 3 page 2, a breed cross that apparently gave heterosis of size; indications pro and con for a size factor linked to St^F in #9 page 4, and # 28 page 5; # 39 page 2, a half-Turbit-half Tumbler cock X Racing Homer hen gave small daughters and larger sons; etc. Nobody seems to have achieved the identification of a single-gene difference satisfactorily. It is still a big challenge, and I don't think it is beyond our capabilities. But the reward is going to be strictly self-satisfaction.

Getting back to the problem of origins, we can only speculate. The very small breeds, such as African Owl, some Tumbler and Roller varieties, etc., might trace to wild small subspecies of *C. livia* which still exist in North Africa and Egypt. We could just as well however invoke mutations, selection, and inbreeding "depression" effects. Large size also seems ancient, having been noted by the early Romans. Mutations? Or could a cross with *C. palumbus* maybe have succeeded somehow and introduced a growth push? Similarly beak and plumage length variations seem ancient, but mutations are the most plausible origins.

Darwin thought variation is facilitated or caused somehow by "conditions of domestication." And pigeon breeders do provide interesting conditions—starvation, overfeeding, drugs (medicines), all sorts of diseases, and who knows what else. Can filthy

conditions induce mutations? We don't know. There's so much we don't know! But here is the challenge.

—P. S. & G. N. #7 pages 21-23 (1978)

A SWISS STUDY OF THE FRILLBACK

In 1938 a long study of some feather ornaments or peculiarities was published in Zurich, Switzerland, by Miss Elizabeth Goessler. Probably no pigeon breeder has examined this, but in spite of the fact that it is written very wordily and in German there are some interesting discoveries reported in it.

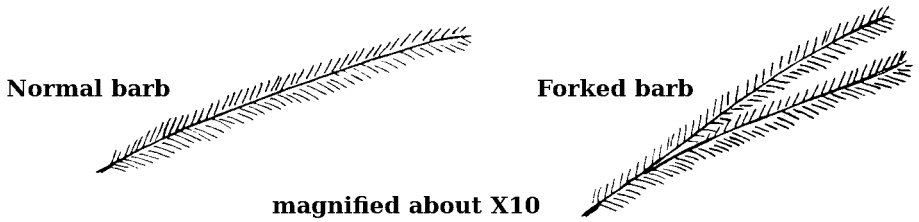
Miss Goessler's main idea was to study the frilled breeds of domestic birds, including not only pigeons but also Sebastopol geese and frilled canaries, to find out why the feathers were "curly or whirly". Most of her effort was spent on Frillback pigeons. She made all sorts of measurements and microscopic observations, and not only in adult birds but squabs even down to before hatching age. She also made a few plucking tests, and crossed a Frillback with a smooth-feathered normal pigeon for breeding tests.

Here are the more important conclusions. First, practically all the feathers of a Frillback show some degree of curling or twisting toward the tips. Second, the direction of twisting of the feather tips is not always the same after plucking. Third, the curly wing feathers are relatively longer than in normal pigeons. Fourth, there is much irregularity of spacing of the barbs (first branches) along the shaft of the feather, and very frequently the barbs are forked or even doubly forked—very abnormal conditions. Cross-sections of the shaft show that the pith center is very small, and the horny material has largely taken up the space. Dunking a curly Frillback feather in hot water will cause it to relax and lie flat; when it dries out, it curls up again. From such findings, it seems clear that the Frillback has a peculiarity of horn-material growth—more than and probably earlier than normal.

The yellow nestling down of Frillback squabs also showed a few peculiarities: the strands were generally more delicate than normal, and occasionally forked. Similarly, the tips or first-grown parts of the adult feathers showed very delicate, long, and often forked barbs.

Eight first-cross offspring of Frillback X normal were obtained. Miss G. doesn't say whether the Frillback was the mother or the father, but anyway, all the young were perfectly intermediate in all respects. These birds were mated up with one another for a second generation, which consisted of 21 squabs. Three were quite normal, but the remaining 18 had various degrees of curling: five were intermediate like their parents, four were nearly as curly as pure Frillbacks, and nine were only slightly curly. From this skimpy information she decides that the Frillback has two pairs of genes for curliness.

—Pigeon Loft, March 1945, page 20

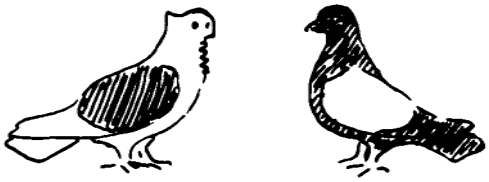


P.S. (1982): I should have commented in the above review that Miss G. gave a lot of information on the history of the curly-feathered peculiarity (fairly ancient?). Also she did cite a previous study, by Wexelsen in 1936, who mated Frillbacks with Maltese and with Pigmy Pouter (Brünner?). Wexelsen stated that the F_1 birds were variably intermediate. Ten backcross matings of F_1 X Frillback gave 46 young of which 11 were completely like Frillback. Fourteen matings of F_1 X normals gave 35 young of which 13 were completely normal. Wexelsen suggested that two pairs of factors were necessary for Frillback curl.

More study of the Frillback is being pursued by Gary Young (see American Frillback Club Bulletin No. 2, 1977, or P. S. & G. N. No. 7, pages 5-11, 1978).

THE POLAR PIGEON

—Amer. Pigeon Journal, June 1946, p. 100



POOLED ODDS AND ENDS

In case the reader has not noticed, I must state that I haven't covered all the genetic puzzles that can be found in pigeons. Many have been reported, and even in print, without catching my attention, and there is no telling how many have just been culled by fanciers without further thought, or how many were never even noticed. Foot abnormalities would seem far less "common" if we didn't have to put bands on.

But even the interesting peculiarities that have been reported and brought to my attention may nevertheless not be included here. Just not enough space, time, etc.? We need an "odds and ends" page in APJ etc.? Anyway, in time we could be swamped by accumulated abnormalities, especially if separate stocks were promoted for each. Pooling is a way of staving off the flood for a while, but it needs to be intelligent. The pooled items should be compatible and controllable. Dominant types should be pooled together if possible, but recessive types may easiest be carried "randomly" in a large population (several hundred?). If careful records can be kept over long periods, analysis of inheritance may be possible from the data, even though not planned. What we think not worth the trouble now may seem more important in the future, especially to someone else (and vice versa).

Just to mention a few peculiarities not included in the above discourses:

(1) extensive iridescence - adult plumage.

(2) hook beak - sporadic in various breeds.

(3) crossed beak - Hanebrink reported 10 cases occurring in one stock (Schautaube) PGNL 70:14.

(4) "grease quills".

(5) whitesides - adult plumage. Discussions especially in PGNL 65:26; 66:32; PS & GN 4:45; and APJ March 1982 pages 17-18.

(6) extra flight feathers - see PGNL 69:28; PS & GN 7:37; 9: 8, 9.

But the vagaries of mutation and population dynamics are likely to carry us off on unexpected, even unimagined, courses.

Who will be keeper of the archives??

THE COLOR KALEIDOSCOPE
OR
HOW TO DIAGNOSE THE BIRD IN THE HAND

(This article was prepared by WFH and Wilmer J. Miller.)

At a show or looking over a dealer's flock or checking some birds in our own loft, we continually get the question "What color is THAT?" And if we have been exposed to a bit of Genetics, we are not satisfied with just a name, no matter how fancy. We have browsed in Levi's great books, and maybe waded into Joe Quinn's Notebook, and we have had some breeding tests on the back burner. But right now we want a functional answer about THAT color. In other words, what are the controlling genes there? This essay is an attempt to smooth the way toward the answer, but we must caution against over-optimism. Identifying genes is like identifying diseases—tricky.

Shall we equip ourselves with an arsenal of glassware, a microscope, and a pocket calculator? NO! The naked eye and a judicious frame of mind seem quite adequate for most purposes here. We would like to have the history of the bird in question if possible: its breed origin, its parents' appearance and relationship, the age and sex of the bird, how it had been treated—its environment, and so on. Of course such information may not be available, but we'd sure like to have it. Sometimes answers come a lot easier with a full case history.

The next step is to refine the question. Instead of "What color is that?" let's phrase it "What mutant genes are involved here?" Ah! if the bird is a wild-caught European Rock Pigeon, "blue bar," the answer is easy: None. Or at least none showing. Now, see how simple or simple-minded it is? Anyway, the wild-type blue bar is our reference base, something like "health" to a physician who asks "What disease is THAT?" It is a standard of comparison, and in this business, comparisons are the front-line operation.

If the bird in hand is not wild-type blue bar, the next question is "What differences are here?" And that means we need to have the wild-type blue bar (adult and also young) available for comparison. If we can't get hold of the real wild-type, a blue bar of domestic stock such as Racing Homer may do. Even photos, sketches, descriptions, and mental images are helpful.

That wild-type blue bar is not really a simple thing. Examine it carefully: its wing "bar" is a row of black spots with a rather rough looking outer edge, so we have named it a "coarse-spread" area. By contrast, look at the tail band: here the black area intergrades almost imperceptibly with the adjacent blue, so we have named it "smooth-spread." The ends of the flights also appear smooth-spread. Note also the whitened areas on the bird: the rump, the underwings, and the outer vane of the outer tail feathers. This whitening is not a piebald effect, but more of a tipping, and we call it "albescence." Skin color is another aspect of our comparisons: the wild type is "more or less dark"—depending a good deal on whether it has been exposed to sunlight or not. Foot skin loses its dark pigmentation in the adult, and is simply red.

Still another consideration is the nestling. The newly hatched wild-type squab has a blackish bill-ring. The nestling down of the babies is luxuriant and yellow. However, unless

we have a record, we can only guess what the baby-down was like for a fully-feathered bird. Eye color (uvea as well as iris) is also worth noting.

We could go on and on about the wild type: how the juvenile plumage differs from the adult, how the sexes differ (the female tends to be a trifle duller), how different diets may affect it, how weathering may bleach it, how oil and powder alter the appearance, etc. It boils down to the fact that most such slight differences get to be a statistical problem, often not too important. And genes (mutants) which could only govern such minor differences will be equally difficult to diagnose. Therefore, in general we are going to be asking about more conspicuous differences, just as a physician is more concerned with obvious deviations from health—a rash rather than dandruff.

So now we compare our non-wild-type subject with wild type. Quick! what's different? And please don't give a sloppy answer such as "it's gray." Phrase your statement of the difference as a difference. For example, "the tail band is twice as broad as in the wild-type," or "the wing shows lack of pigment in the middle of the coarse-spread areas." (Sloppiness is a common human tendency, and we have been guilty of it too; so shape up!)

OK, having quickly (?) discovered and described the difference(s) of our subject from wild type, we now can try to attribute these differences to one or more appropriate mutants. To do that, we need to have a catalogue of the known mutants, including their mode of operation—how each differs from the wild type and how they may affect one another's action. To a considerable extent such information is available in Levi's books and in Joe Quinn's Notebook, but for convenience we present a listing here—as complete as we can make it. (Some information is still lacking.) For convenience we will start with the sex-linked mutants, but in discussing interaction effects others will be brought in too, and you may want to jump around in the listing. At the end we will include some presumably single mutants that have not been well studied yet.

Dilute (*d*)

The quantity of pigmentation of plumage, skin, and retina seems about half or less, and baby down about half normal length. Breeders' names for dilute black = dun, dilute red = yellow, dilute bronze = sulfur. Common term for dilute alone (no other mutants) = silver, dun-barred.

Pale (d^P)

The effects of this allele of dilute are similar but less extreme. That is, the phenotype is nearer normal. Heterozygous $d//d^P$ males seem about the same as dilutes. Pale reds are often called orange; pale bronze in the Archangel is called light bronze, or gold.

Ash-red (B^A)

Coarse-spread areas (including neck) are red-pigmented instead of black; smooth-spread areas are light ashy instead of black. "Reversionary flecking" is common in the plumage of heterozygous males. Breeders' name for dilute ash-red = cream; for ash-red alone = mealy or silver, red-barred; with *S* factor, = spread ash or lavender. B^A is hidden (no effect) when with recessive red ; bronze effects show up well with B^A except in the coarse-spread areas where they are not recognizable. B^A with dominant opal gives orange coloration of coarse-spread areas.

Brown (*b*)

Pigmentation brown or chocolate instead of black, and iris pigment "false pearl" instead of yellow. Heterozygous B^A//*b* males have brown flecking. Dilute brown is often termed khaki or drab. Brown with recessive red looks same as recessive red except less tendency to "smutty" effects. Bronzing effects show well with brown. Indigo with brown gives a sort of mimic ash-red appearance. Brown plumage bleaches readily from weathering.

Almond (*St*)

Pigmentation of plumage and skin greatly lessened (almost white), with considerable tendency to reversionary flecking, especially in heterozygous males. Baby down usually less than half normal length. *St* with recessive red is often called "De Roy", a salmon color usually with red flecking. Bronze with *St* shows yellowish. *St//St* is usually all-white, with dark iris.

Faded (St^F)

Some lessening of pigmentation of plumage and skin, and slight tendency to reversionary flecking. This mutant has little effect on red except double-homozygous males look salmon. St^F//St^F (only possible in males) alone looks very much like *St*.

Reduced (*r*)

Coarse-spread pigment areas reddish black edging, and smooth-spread areas ashy instead of black, effects generally not as pronounced as those of B^A, and the red is weak in juvenile plumage. The iris is often dark. Reduced ash-red is "pinkish" ash-red; reduced recessive red is pinkish red; reduced with *S* is light ashy with tendency to darker edging (lacing).

Autosomal Mutants:

Recessive Red (*e*)

Pigmentation chestnut-red instead of black except in retina, and skin, beak, and claw pigmentation lightened. With *S* and/or brown the reddening may tend to be enhanced. The recessive red squab ordinarily has a reddish bill-ring. Recessive red tends to hide pattern mutants (*C*, *S*) and also ash-red or brown.

Spread (*S*)

Smooth spreading of pigment throughout the plumage, but coarse-spread areas may remain faintly evident. *S* generally prevents bronze effects. *S* with indigo is called "Andalusian blue", and *S* with dilute is called dun. "Lavender" is typically *S* with B^A, and the most delicate lavender shade also has the milky factor. *S* with Toy-stencil homozygous does not inhibit the latter, the combination being black with white coarse-spread areas such as bars. *S* tends to enhance recessive red.

Checker (*C*)

Coarse-spread areas are extended somewhat. Several slightly differing alleles exist: light, medium, and dark.

T-pattern (C^T)

This is an extreme allele of checker; coarse-spread areas much extended, even into body plumage but not the tail. Breeders often call the effect black check, "velvet", or even simply black, or with B^A simply red. With Toy stencil the wing shield is typically "laced." T-pattern is an enhancer for black with *S*, and an enhancer for red with recessive red.

Barless (*c*)

Coarse-spread areas practically lessened to absence. However, it is possible for the "sooty" (dapple) effect to be produced on the barless background.

Opal (*o*)

This recessive mutant has been found so far in Homers, not yet other breeds. Coarse-spread areas more or less reddish, instead of black except edges; smooth-spread areas more or less ashy instead of black. There is great variability of shade, from near wild-type to near ash-red. Males tend to be lighter than females, and shade change may come with molt. Transverse faultbarring and rippling patterns in feathers indicate metabolic sensitivity, probably to thyroid hormone levels. Opal with B^A tends to give a "bright" ash-red; with recessive red it gives "weak" red. With dilute or with brown, opal is usually inhibited. With *S*, the bird is similar to an *S*-reduced: more or less ash with tendency to edging (lacing).

Dominant opal (*Od*)

Coarse-spread areas generally are whitish-yellowish to reddish instead of black; smooth-spread areas more or less ashy instead of black. As with recessive opal, there is much variation in shade, some birds being almost indistinguishable from wild type, and others even approaching ash-red phenotype. With B^A the coarse-spread areas look orange. With *S* some ash effect is seen, but often more of a washy dun. Homozygous *Od*//*Od* squabs seem usually shaky and too weak to survive, very light-colored, with ragged plumage.

Indigo (*In*)

Coarse-spread areas weaker black, some tendency to red; smooth-spread areas dull-ashy or slaty. Homozygous *In*//*In* birds resemble B^A but with experience one can detect differences—slight tendency to lacing in coarse-spread areas, and dark head and upper tail covers. With *S*, indigo gives dark ashy effect with tendency to lacing, "Andalusian blue." The homozygotes are light ashy with tendency to lacing and darker head. Indigo with B^A appears little different from B^A alone. With recessive red, indigo seems to have no effect.

Milky (*my*)

Plumage pigmentation lessened to grayish, little tendency to bronzing in coarse-spread areas. Breeders call the effect "powdered silver." No effect on baby down or skin. With *S* a dull "lavender" results; with B^A a very light ash-red results. With recessive red a pinkish effect is produced, pearly on the neck.

Smoky (*sy*)

Coarse-spread areas less dense than in wild type; outer tail vanes blue, not albescent, and other albescent areas more or less blue. Tendency to grizzly-whitening of feather bases, and skin pigmentation light. Smooth-spread areas may be richer than in wild type; terminal blue edge of tail generally more distinct or enhanced. With *S* the plumage is rich black. With

B^A a dull ash-red effect results, with tendency for flecks to be very small—peppery. With recessive red there seems to be little effect except for tendency of feather bases to be whitish.

Grizzle (*G*)

There are probably several allelic forms of this mutant. Ordinary grizzle seems to be failure of some pigment cells, especially in the otherwise blue (clumped pigment) areas, and least in smooth-spread areas. Homozygous (*G//G*) birds typically are "storked" in juvenile plumage—all-white except smooth-spread areas—but they tend to molt whiter. The "tiger" grizzle type, which we may symbolize G^T, when heterozygous usually shows rather little grizzling of juvenile plumage, but molts in many white feathers.

Breeders have confused the grizzle types with almond, piebald-splashing, and even with auto-sexing (faded) effects, and various names are used, including "tortoise," "mottle," "print," "tiger," etc.

With *S* the grizzle factor is more or less inhibited, and a completely black bird may have it. The tigering is less inhibited by *S*. Bronzing effects seem to be augmented somehow by *G*.

Gazzi (*z*)

This mutant seems to involve absence of pigment primarily in the breast region. In stabilized breeds the effect may be fairly constant and symmetrical, but irregularity is very common—uneven borders, pigment spots in white areas, whitening in the wings, etc. It seems likely that a number of modifying genes are available, and other named patterns such as "Nun," "Helmet," and "Hungarian" may be just modifications of gazzi.

Self White (z^{wh})

In spite of the ubiquity of self-white pigeons, their genetics is still cloudy, but evidence indicates that gazzi is allelic. Self-white birds lack all pigment in plumage, skin, and iris, but the retinal pigment seems unaffected. F_1 from gazzi X self-white tend to be intermediate.

Baldhead (*Bh*)

Here again the genetics has not been well studied, and the gene symbol is tentative. Pigment absence effects are involved, mainly involving the head, flights, feet, and tail. In stabilized breeds the pattern may be fairly constant and symmetrical, but irregularity is common. Modifying genes probably are important, and named patterns such as "snip," "bavette," "Magpie," and "saddle" may be modifications. We speculate that combination of gazzi with baldhead has probably been responsible for other white pattern effects and perhaps also a self-white effect genetically different from the one discussed above.

Albino (*al*)

Albinism is so rare in pigeons that it is unlikely to be a problem. Three sources have been distinguished: C. L. Tumblers, Carneaux, and Racing Homers. They show almost total failure of melanin-pigment production (but, unlike the self-white, pigment cells are not absent). The iris is not pigment-free, but is pearly instead of orange. The baby down is very short.

Pink-eyed-dilute (*pd*)

This rare mutant looks almost identical with sex-linked dilute except that the retinal pigment is practically undeveloped. The baby down is very short, and body growth during the first two or three weeks tends to be rather retarded.

Sooty (*so*)

Coarse-spread pigment seems to be added to blue areas especially in the wing shield around the distal rachis of the coverts. This is distinct from checker effects, and may even appear in barless birds. It probably is a major enhancing factor for red and black colorations. Sooty is usually less evident in juvenile than in adult plumage. In Racing Homers the sooty effect has also been called “dapple”. Though widespread in other breeds, it ordinarily gets no name, or perhaps “smut.”

Ice (*ic*)

The principal effect of this mutant is lessening of pigmentation in blue (clumped) regions. It has not been well analyzed, but seems partially dominant to normal?

Toy-stencil (*Ts*)

Coarse-spread areas are more or less whitened, the edges being least affected. Heterozygotes may only show bronzy effects. *S* does not greatly inhibit the action of *Ts*, so that in homozygotes white-barred etc. black can result. *Ts//Ts* with T-pattern is commonly termed “laced.”

Oriental Frill Stencil (*fs*)

Both coarse- and smooth-spread areas are more or less whitened, the edges being least affected. The possible relationship of this type of stencil to Toy-stencil is unknown at present. With *S* the Frill stencil can produce lacing throughout the plumage.

Mahogany (*ma*)

This is also termed Modena bronzing. The coarse-spread areas show more or less reddening, the edges being least affected. With T-pattern the effect is termed simply “bronze.” With dilute the effect is termed “sulfur.” With *S* the mahogany is inhibited. The possible relation of mahogany to Toy-stencil is unknown at present, but probably they are independent, not allelic.

Kite Bronzing (*K*)

Also termed Archangel bronzing, this condition has not been well analyzed. It seems primarily to add red pigment to otherwise blue (clumped pigment) areas of the body and tail, but coarse-spread areas may also be somewhat affected. With B^A (and other factors?) “ribbon-tail” or “star-tail” effects may result. With *S*, kite bronzing is suppressed.

Dirty (*V*)

This factor may be the predominant type in *Columba livia intermedia*, the wild subspecies living in India. The blue areas of the plumage are rather dark, and the albescence of underwings and rump darkened bluish. The feet of squabs are blacker than normal, and the bill ring is indistinct at hatching because the whole bill is dark.

Pencilled (*pc*)

This recently identified mutant causes whitening of most plumage except head and neck, leaving dark edges and often some sandy sprinkling. It is found in the French breed "Tête noir de Brive" and probably also in Saxon Breast Pigeon and Hana Pouter.

Well, we have listed some 30 mutants and no doubt the list is not complete. How do we use the information? With all those mutants a vast number of combinations can be imagined.

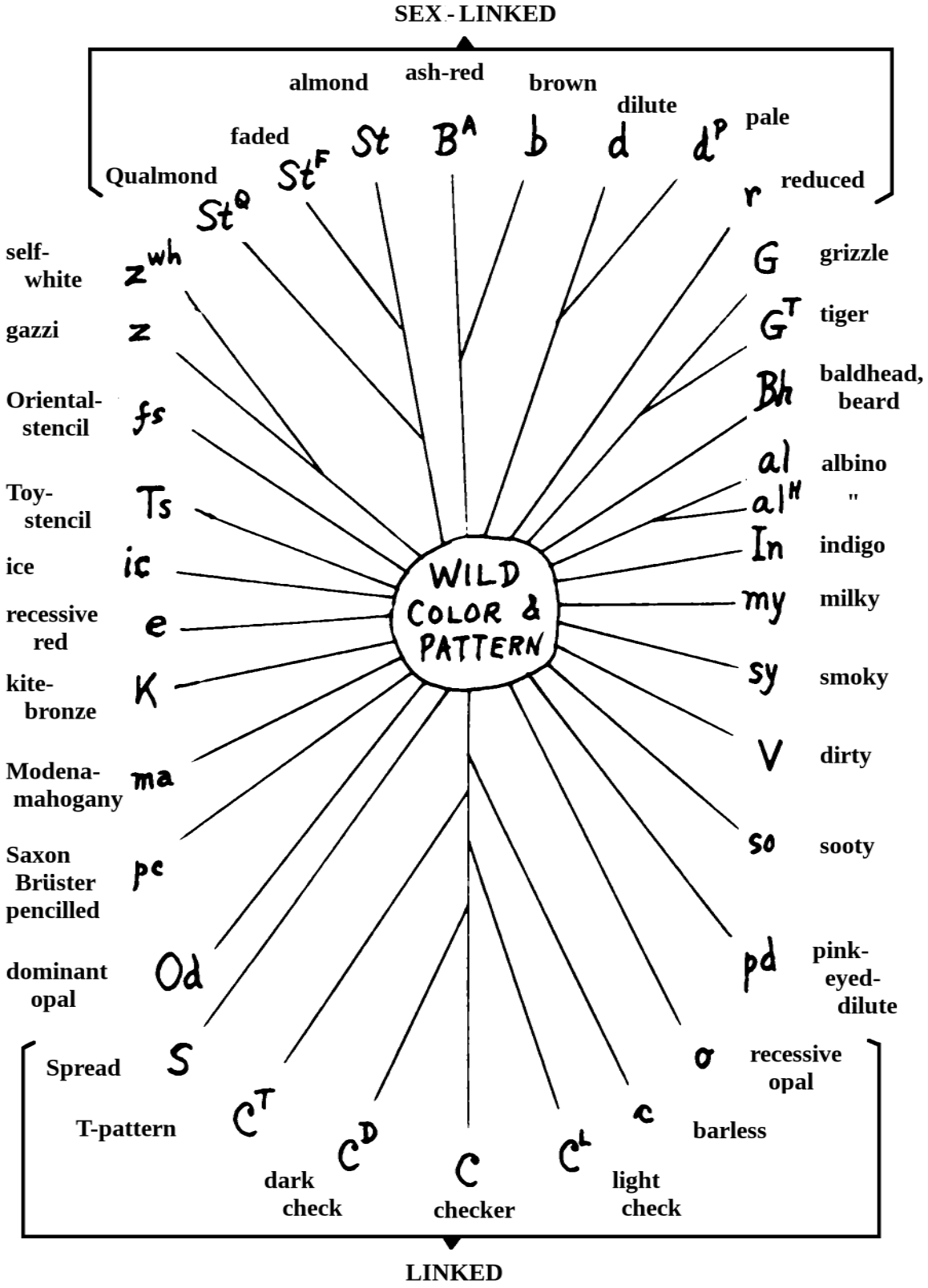
The essential principle we can see about combinations is that each mutant seems to try to do its "own thing", and if two mutants do not affect the same thing, the result is simply "additive." If the two mutants do affect the same thing, the effect of one may hog the stage—conceal or prevent the other's—or some other sort of interaction may result. Perhaps they will cancel each other, or they may synergize. It is not always easy to predict, but some examples will be instructive.

(1) Barless and dilution: these mutants have unrelated domains of action, so we could predict the combination to be barless dilute.
(2) Barless and mahogany: since barless prevents formation of coarse-spread areas, we could predict that it would leave nothing for mahogany to work on.
(3) Ash-red and *S*: the extension of smooth-spreading throughout the plumage by *S*, and the ash-effect of B^A on smooth-spread areas should let us predict that the combination will be generalized ash ("lavender").
(4) Albino and *S*: the combination should still be albino (no pigment).
(5) Indigo and grizzle: these mutants seem to have unrelated sorts of action, and we could predict that the combination should be additive.
(6) Milky and ash-red: we might predict synergism here—a lighter ash-red.
(7) Toy-stencil and sooty: predict a dappled stencil?
(8) Brown and mahogany: additive?

And so on. Turning the argument around, if we have a barless gazzi bird, we can surmise that it is the combination of those two mutants. If we have a yellow bird, it is probably the combination of recessive red with dilute or maybe some other lightening factor (almond?). If we have a white-checkered black, it probably is the combination of *Ts* (Toy stencil), *C*, and spread (*S*). If we have a light soft lavender, maybe it is milky ash-red and *S*. Anyway, these maybes are useful preliminary approaches. Maybe we can get other supporting or contradictory information from other sources, or maybe the decision cannot be definite. If a progeny test can be made, maybe that will clear up the puzzling cases. And some can be very puzzling. And sometimes our preliminary guesses are simply wrong; two birds may look a lot alike and have quite different make-up. Maybe you and we will diagnose the same bird quite differently. Well, it can be fun!

Ah, here's a good one to try our skill on: a hen with red checker left side and right wing mostly black. If you said "Mosaic!" we agree. Two birds fused into one. Heaven knows how she will breed, but we can make some interesting bets, and test her out.

SINGLE MUTANT COLOR AND PATTERN INFO (1982)



Capital (initial) letter symbols mean at least partial dominance of the mutant over wild-type. Lower case indicates recessives. Branched lines show that the connected mutants are allelic.

SKIN COLOR

What strictly American kind of pigeon has yellow feet and is not foot-feathered? Answer: the Bandtail (*Columba fasciata*). Except for that, as almost everybody knows, the skin of the feet of most kinds of adult pigeons and doves is rich red. Is it blood vessels showing through? No—a study by Piepho (1957 but published 1976) showed that the red pigment is not hemoglobin but a class of fat-soluble compounds including carotene. Very little such material is present in squabs' feet, however. Instead, the wild-type contains brownish-black melanin. As the bird matures, the melanin is eliminated and carotenoid pigments accumulate.

Skin of other areas of the body and head may show a similar pigmentation tendency, especially if the plumage cover is removed so that "sunburn" can occur. Even adult wild-type skin may become blackened if thus exposed, with some reddening also, as is commonly seen in the eye ceres. In some breeds the skin seems unable to develop reddening (except in the feet). This condition is easiest to see in birds having little or no obscuring melanin. The genetic basis has not been analyzed.

Skin color is important to producers of "New York-dressed" squabs because of strong market prejudice against any darkness. This ridiculous pressure ensures selection of breeds with naturally light skin color, including the feet. Several of the mutants affecting plumage pigmentation tend to reduce the skin's melanin content. The commonest is of course "recessive white". Almond, homozygous faded, and albino squabs also have clear skin, but the near-white "storked" (homozygous grizzle) squabs usually do not.

Squab skin color is also generally light from the effects of the color genes brown (*b*), dilution (*d*), recessive red (*e*), and smoky (*sy*). Even squabs doubly heterozygous for recessive red and smoky tend to be light, but most other crosses do not. The only mutant which seems to increase skin melanin pigmentation (more than wild type) is the dirty factor (*V*).

GENES & JUICE

A toast to genes! Hic jacet Gregor.

Times have changed; maybe you thought you knew about genes, but they are slippery little rascals. Mendel never heard about them—he was satisfied to talk about “determining elements”. But now even junior high-school kids are taught about the double-helix structure of DNA and that triplets of nucleotide bases code for the assembly of specific amino-acids into polypeptide chains (proteins). OK—still with me?!

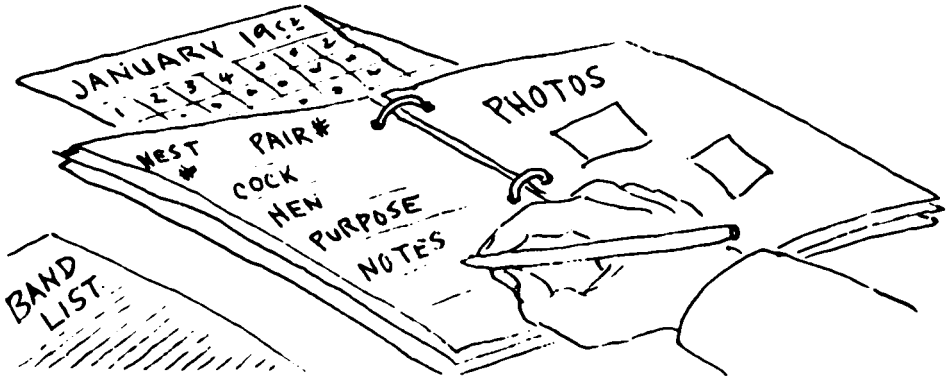
Well, the assembly-line requires lubrication. The genes can’t operate when dry. (No, this is not a liquor commercial.)

For people who find the relation between genes and feathered feet or homing ability a hopeless enigma, it is comforting to find that gene products— proteins—are available fresh from the assembly line. All we have to do is get some juice. For example, blood plasma or serum. They are full of proteins. Various kinds all sloshing around together—albumens, globulins, enzymes, etc.

Splendid, but it would be nice to separate them. Can do. By putting the juice in a high-voltage direct electric current, we can “drive” the proteins in a particular direction. Each kind moves at its own speed, so pretty soon we have a series of them. In a starch gel or comparable medium we can hold the series and stain the bands of proteins with a dye to make them visible.

Now compare the series of bands from the plasma of one pigeon with that of another. Usually there is no great difference. Sometimes a particular band is missing or doubled or faster or slower than usual. Aha! we next reason backward to the alleles! And voluminous speculations and calculations can be derived. And this is where I shall leave the subject to the experts, such as Wilmer Miller, Russell Brown, Ed Blaine, Irwin et al., and Zinkham & Co. Prosit!

—P. G. N. L. No. 52 page 32 (1969)



A BROWN PIGEON THAT TURNED WHITE

In January 1953 the Palmetto Pigeon Plant in Sumter, South Carolina, shipped me a peculiar specimen. This was a male Silver King pigeon, not quite two years old, which had molted out most of its brown-colored plumage and replaced it with white. Nothing like this had ever been heard of in pigeons before, so far as I can find out.

The history of this bird was short and simple. He had been raised as replacement stock, but after breeding for about a year got sick. He was put in a hospital pen to recover, but seemed partly blind, and began to molt white. So instead of going to pigeon heaven, he went to my haven.

His right eye was cloudy and completely blind, and the left was also somewhat affected. But he had a good appetite and was soon mated with a bluish hen, in a small breeding coop. He was fertile, and I got three squabs from the mating. Like any ordinary Silver King, he transmitted the brown color factor. None of the squabs showed any white.

After keeping the bird over a year and a half without further change, I finally decided to kill him, to see whether a clue could be found inside why he turned white. But nothing definitely abnormal was revealed at all. He seemed in good condition, head and all, except for the eyes.

My theory is that this bird had had a brain infection, in the region of the optic nerves. This damaged vision and also destroyed a pigment-control center in that region. But this is only speculation. Only experimental study could prove or disprove it.

A good many cases of chickens turning from black to white have been reported (for example see F. B. Hutt's 1949 book "Genetics of the Fowl"). No one has yet found for sure the cause of the mystery. Any breeder finding such a bird, pigeon or chicken, should notify zoologists or other University specialists so that it can be studied further.

—N. P. A. News, July 1958, page 8.

PRETZEL BREEDING

Experts in the peristeronic world disagree about the best way to breed pigeons. Some say you should line-breed, but just how straight or crooked the line should be, and whether it should go backward or not, seem totally arbitrary. Some say inbreeding is good; same say it is bad; some say a dash of it is okay but don't overdo it. And some say cross-breeding or at least strain crossing is fine, some say it is criminal, and some say Ssh, don't tell about it or your stock will get a bad rep.

For some inexplicable reason, breeders have repeatedly asked me how do I breed. These fellows of course have never seen my birds; that may have something to do with their faith in Science. My specialty is pretzel breeding. It's very simple, not only to explain it but also to practice it. First in, then out, then follow the line around, then back-cross, and then start over again, anywhere. To do the job up brown, expose briefly to a hot argument and add a grain of salt. In my experience the squabs produced by this system are nicely variable and go well with sage and celery dressing.

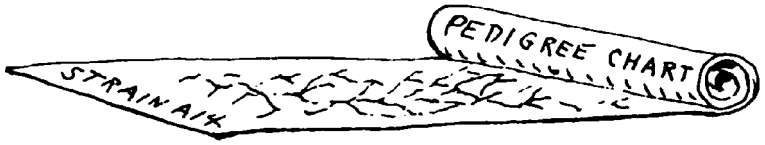
The Bible says quite a lot about breeding, but unfortunately in a lot of the series of "begats" the females got omitted completely, so the exact system isn't clear. It is too bad that Moses didn't get an eleventh commandment such as "Thou shalt not pretzel breed", or something.

Apparently the first pigeon man to go all out for inbreeding was Noah. In view of his success perhaps we should consider it seriously, although it has been argued that he was all wet. A French experimenter named Lienhart put the matter to the test (1930). By the eighth generation of consecutive brother-sister matings, his birds became extinct from sterility and weakness. On the other hand, crossing pigeons with ringneck doves at the University of Wisconsin also wound up with extinction from sterility (Cole and Hollander 1950).

If you consult the textbooks on scientific breeding, for example "Animal Breeding Plans", by J. L. Lush, you get into all sorts of complications, such as the use of arithmetic in figuring out homozygosity and the relative significance of heterosis. It is questionable how much advanced the new textbooks are over the Old Testament when it comes to advice.

So you see, obviously we are between the devil and the deep blue yonder. The only way out is to do like the music—go round and round. Try pretzel breeding. You may not like the results, but you can eat 'em.

—American Pigeon Journal, August 1953, page 254



GENETICS FOR COMMERCIAL SQUAB PRODUCTION

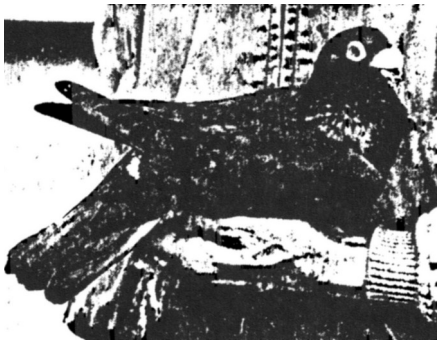
Being monogamous altricial birds, pigeons are not adapted to intensive methods of rapid multiplication so successful for chickens, turkeys, and ducks. Also pigeons are difficult to gear for seasonal market fluctuations. Therefore the squab business has been relatively unprofitable and unprogressive.

From the genetical viewpoint, the market has controlled chiefly size, and color of skin (and pin feathers). The breeder has responded ordinarily by pure-breeding—it generally gives the desired size and color without much technical difficulty. But pure-breeding also generally gives problems of vitality: compared with crossing there may be more infertility, mortality, poor growth, etc.

Auto-sexing colors have not achieved much acceptance in squabbing yet. In part the reason may be a tendency for the males to be a bit lower in vigor, at least in the nest. Crosses among auto-sexing breeds may overcome this problem.

The so-called Hubbell type (broad-breasted) has become favored in recent years. The genetic basis is not yet worked out.

In view of the commercial difficulties in squabbing, I think revolutionary ideas may be in order, and that means more research. Perhaps the multitude of fascinating genetical problems and mysteries can be studied in conjunction with market development—a collaboration of research and commercial objectives.



WHAT STRAIN?—This old cock has perfect No. 10 eyesign. His father was a blue Syrian Bagdadi, and his mother a black and white Turbit. These breeds were chosen for a simple cross essentially like that which is reputed to be back of the Belgian Racing Homers in the early part of the previous century. There are probably other breed crosses which also could produce excellent flying birds. The potentialities for such hybrid vigor have been little explored.

—American Racing Pigeon News, September 1972, page 42

REFERENCES

Most of the citations are available in the bibliography of Wendell M. Levi's book "The Pigeon" (1957 edition). His 1965 book "Encyclopedia of Pigeon Breeds" is also a basic reference, especially for illustration in color.

Beginners may also find the "NPA Information Booklet—Project on Genetics" (1951; reprinted with slight revision 1980 by the Ink Spot Printing Co., Burrton, Kansas) a helpful introduction.

The following list is selective rather than complete.

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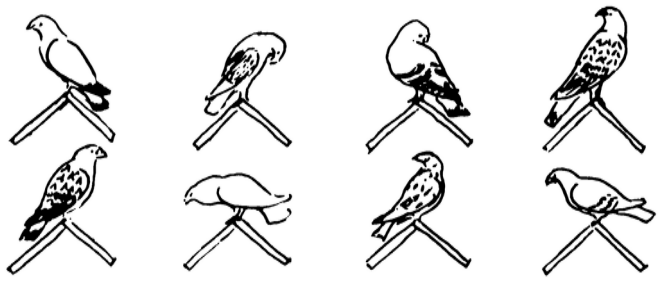

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Alphabetical list of symbols for fairly well demonstrated mutants
1982

Symbol	Name	Page
ac	lethal	PS&GN 8:17
al	albino	83
am	amputated	93
at	ataxic	125
b	brown	55
B^{A}	ash-red	87
Bh	baldhead pied	118
c	barless	59
C^{L}	light checker	86
C	checker	85
C^{D}	dark checker	86
C^{T}	T-pattern	86
ca	cataract	108
cl	clumsy	107
cr	crest	90
d	dilute	81
d^{P}	pale	82
ds	Davis syndrome	77
dsc	deutsch scraggly	107
e	recessive red	87
er	erratic	127
F	frayed	71
fb	feed-blind	107
fr	frillneck	110
fs	Frill stencil	114
fz	frizzy	71
G	grizzle	94
G^{T}	tiger-grizzle	95
gr	grouse	79
ic	ice	138
In	indigo	56
K	kite-bronze	88
L	silky	69
ma	mahogany	89, 113
mi	microphthalmia	108
my	milky	61
n	no oil gland	123
o	recessive opal	71
Od	dominant opal	73
p	porcupine	105
pc	pencilled	96, 139
pd	pink-eyed-dilute	84
py	polydactyly	96
r	reduced	58
ro	rolling, tumbling	125
ros	rose, beak crest	103
S	spread	99
Sb	sideburns	38, 101
sc	scraggly	106
skpy	Show-King poly.	97
Sl	slipper	80
so	sooty	86, 138
St	Almond, magnani	63
St^{F}	faded	66
St^{Q}	qualmond	65
sy	smoky	68
t	extra outer toes	97
t^{H}	Hasz' lethal	98
tr	pearl iris	78
Ts	Toy stencil	113
V	dirty	138
w	outer-toe web	74
wl	web-lethal	77
z	gazzi	118
z^{wh}	self white	119

Notes:

GENETICS

ANOTHER ASPECT OF OUR WIDE

PIGEON HOBBY

SUPPORTING PROJECT
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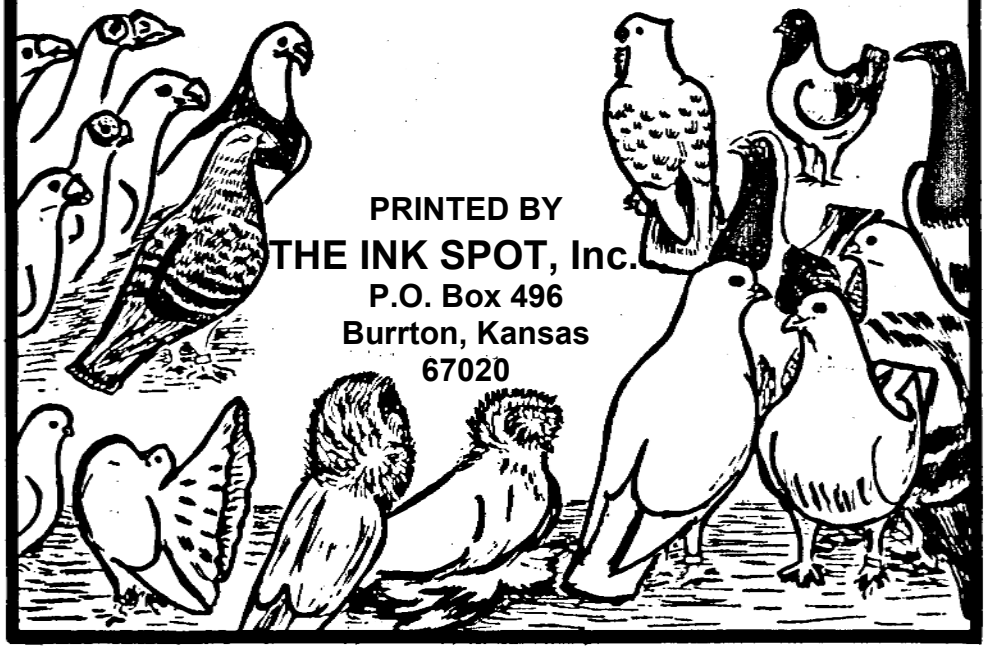
A REVIEW IN PROGRESS



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