THE PIGEON BREEDER'S NOTEBOOK

AN INTRODUCTION TO PIGEON SCIENCE

by J.W. Quinn

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DEDICATED TO

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FORWARD

The breeding of pigeons and the scientific study of birds are complementary activities. For some reason it has never been possible for me to separate the study of pigeons, from the breeding of pigeons. Each new discovery or insight adds enjoyment of a personal kind to my hobby of raising pigeons. Chance favored my education. In my youth I met Carl Graefe of Cuyahoga Falls, Ohio, whose dedication to the scientific study of pigeons is well known. The hours spanning thirty years of time, that I have spent listening to this great teacher, cannot be measured as to their importance in my personal life and chosen hobby.

I mention these things because the science and the breeding of pigeons have been separated into two worlds for a long time. There has been much confusion and conflict over this unnatural division. It is not unusual to hear at a meeting of breed authorities such things as: "From the cock, color; from the hen, type", an idea which became scientifically meaningless with the discovery and testing of sex linkage by Cole and Staples-Browne in 1912. It was not always this way---the union of science and breeding practice to form the breeding art occurred once---possibly a reunion is in order.

The scientific study of pigeons once had a "Golden Age". It began in the last century with Darwin, Tegetmeier,and Lyell in England and spread all across Europe. Publications concerning pigeons were written and carefully illustrated in great number. The Illustrated Book of Pigeons by Robert Fulton, a magnificent work, was published by Lewis Wright in 1875 (?) and later revised by Lumley in 1895 with many color plates of exquisite quality. The larger libraries at the turn of the century had collections which included the works of Neumeister, Eaton, and John Moore and were also widely read among pigeon breeders. Boitard and Corbie had ended the first quarter of that century with breed descriptions, and by the three-quarter century mark Bonizzi was describing a single breed, Modenas. Monographs on special breeds from this period are truly classics in clarity of description. The changing of centuries was most difficult. Charles Darwin, the pigeon breeder, had shaken the world with The Origin of Species and The Descent of Man. Gregor Mendel's papers were rediscovered and intense biological study was to dominate science for the next fifty years.

In a brief period, the world's students had "Evolution" and "Genetics" to explore. At this point our "Golden Age" flourished. Darwin had chosen the Rock pigeon to anchor his theory of the origin of species. The writings of pigeon breeders represented a solid informational base to encourage the use of pigeons in experimentation to study these new unifying biological ideas of evolution and genetics. In the following thirty years most of our scientific knowledge concerning pigeons was collected and analyzed. The names Loisel, Ghigi, Staples-Browne and Bonhote began to show up in scientific journals reporting on the heredity of pigeons. These in turn were followed by a host of researchers in many countries. Hundreds of papers were presented dealing with the inheritance of those factors and characteristics that had been established in breeds of pigeons over the course of hundreds of years. Scientists began studying the breeder arts. For the most part, a cooperative relationship existed between the scientists and the breeder---there was a mutual interest in understanding the mechanisms involved in pigeon heredity.

As we look back on this "Golden Age", it is difficult to grasp the factors which brought the period to an end. Possibly, the geneticists' need for a more rapidly producing subject led to a change from pigeons to fruit flies or mice.

Very possibly, the scientific advancement was so great that the gap between breeder and researcher widened to a point that informational exchange stopped, leaving the scientist without the much needed breeding evidence and perspective. Only actual breeders can provide this aspect to the study of inheritance. It is also noted that the stream of books and monographs on pigeons, which collectively made the pigeon an ideal choice for study, had for some reason slowed to a trickle. Rising publication costs and a reduced market demand might account for this decline in pigeon literature. The Turbit Handbook by George Kleinpell is only the second breed specialty book, I know of, that has been published on a special breed in this country in fifty years.

If we were to recite the names of the scholars who made major contributions to pigeon science to today's breeders---only a rare few would recognize them. Even names such as C.C. Whitman and Oscar Riddle, would be unknown to most. Whitman was possibly the most learned and dedicated student of pigeon science in history. His three dust covered monuments have been read by less than fifty breeders, perhaps as few as a "living" dozen. Riddle's failure to receive a Nobel prize by one vote for pigeon research is more likely to be known by a medical student than a pigeon breeder. The "Father of Enzymes" that isolated prolactin from pigeon milk and also edited Whitman's works, has been hardly noticed by the pigeon fancy.

The list could be extended to include hundreds of truly great pigeon breeders, or pigeon scientists, whichever title you prefer. In any period of darkness there is always a few with a torch or a light. In pigeon science, there are only three names that bridge the gap from the "Golden Age" to the present. It would not be enough for these three men to just be students of pigeon science or to just continue the projects begun so long ago, to warrant such distinction. The research and books of the past are for the most part buried in the past. To keep knowledge alive we must have teachers. A teacher of rank, teaches teachers. A cycle of regeneration may start with a single person.

Wendell Levi dedicated his life to the collection, synthesis, and publication of information about pigeons. One can only speculate on the hours devoted to the writing of The Pigeon. The printing of this monumental work in 1941, provided the scientific world the base of information so necessary to renewed research.

Rising from this base of reliable information the pigeon is slowly regaining its position of a laboratory animal deserving of further study. The breeders of pigeons are Levi's prime concern, as evidenced by every line of his books. The high place the American breeding art is held world wide, certainly stems from that dedication so clear in the pages of The Pigeon written by our foremost teacher, Wendell Levi.

Dr. Willard F. Hollander, by a different road has held the trust of research, for future pigeon breeders. Almost every mutation mentioned in this notebook has been studied and analyzed by our scientific mentor. A list of his publications alone would fill many pages. As a student of Cole and colleague of Riddle, Dr. Hollander used personal ways to clear the path forward. His articles, letters, and personal discussions have quietly rolled back the dusk of confusion. He has almost single handedly preserved the rare mutation stock in domestic pigeons.

Carl Graefe taught well---while claiming to be only a breeder and student. His correspondence carried pigeon science information to all parts of this country. The presence of rare colorations in any breed is likely to have been initiated by a letter, followed by a crate of pigeons, from Carl Graefe, Cuyahoga Falls, Ohio.

Three men..., forty years..., and pigeon science still lives. The finest text on pigeon genetics is of course chapter V in The Pigeon by Wendell Levi. The best separate monographs on mutant genes are the "Origin of Domestic Genes" series by W.F. Hollander. There are many insights to be gained from the clarity of expression of Carl Graefe's writings on various mutations. I hope one day, with their permission, to publish these classics separately or in some blended fashion. That of course, is for another day. I have made every effort to be creative and not extract from these gentlemens' previous works,but I realize that is impossible. Every line of what I write indirectly belongs to one or the other of these men. Teachers have that problem with their students. The only original credit I can claim is the responsibility for the errors I might have included.

I have taken some time to review the scientific study of pigeons from the "Golden Age" to the present, so that the reader will realize the gap he has to bridge to develop the breeding art. "From the cock, color; from the hen, type", has prolonged the darkness. Three teachers have kept pigeon science alive and their students are many. There is evidence on all sides that practical breeding procedures based on solid scientific research and study may have a new flourish in our lifetime. In any case, it is more fun to know than to wonder, and I sincerely hope this notebook will contribute in some small way to your enjoyment of breeding beautiful pigeons.

J.W. Quinn

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Introduction

Each pigeon breeder deals with complexity in his daily life. A mechanic or telephone repairman faces the problems of our technical society as if it were routine. To an outsider, the diagrams, charts, and vocabulary of any specialized field will all seem strange. In any technical skill or complex art, there is a required amount of practice and study before any proficiency is gained.

Something about human nature dictates that the complexities and challenges of the tasks to be done determine both the status and the feeling of accomplishment associated with the activity.

Other hobbyists seem to relish in the technical conversations in their hobby field. "Hot-rodder" groups talk mechanical technology; "ham radio" operators can discuss the latest wave theories; and even the local bee keepers will amaze the outsider with their scientific education in their chosen pastime.

The historical twist that separated the breeders of small animals and birds from the mainstream of technical growth has been effective. The pigeon fancy, by avoiding all scientific complexity in the breeding of pigeons, has denied to youth that modern attraction to a hobby. Boys of the 1970's are lost in space, computers, microscopes, and all that belongs to their age. A visit to any science fair or grade school science class will affirm youth's interest in this scientific age. Our unwillingness to breach the gap between science and the breeding of pigeons has prevented the growth of this most interesting hobby.

The first step is to break the mental barrier. We must begin and stay with it till we succeed or fail in mastering the breeder art. There is just no way to keep a fourteen year old interested in, "From the cock, color; from the hen type", when his school biology text and even his science fiction reading are in conflict with such information.

The complexities are few because we simply don't know as much about pigeon breeding as we do about radios or automobiles. With just a little background, our breeding pairs will encourage us on the way. If you master even an area of fundamentals, you might explain it to an interested youth. It is my sincere opinion that the future of the pigeon fancy will prosper only when the bridge from the past carries us forward to mastering the art of breeding pigeons scientifically.

Notebook Organization

The design of this notebook is repetition. Repeating the fundamentals in a wide variety of words and diagrams is the basic organization format. As has been found in most art forms, it takes wide variation of presentations for a person to develop the sense of order so necessary to understanding. It is said, "One must play a thousand hands of poker to understand the game." The same may be true in a sense for tennis, golf, or just driving a car. Looking at a wide variety of breeding situations appears necessary before we begin to grasp the simplicity of the breeding art.

Insight---that moment when you look back and say, "That was easy---I wonder why I had so much trouble with it", comes to everybody if he sticks to the study and practices the art. Once we have "arrived" and understand the basics, we tend

also to forget the confusion and difficulty we ourselves experienced in learning. In preparing this notebook, after each section I mentally said; "But, I still don't understand", and then proceeded to try again with the next section to say it more simply.

Some readers may be bothered by this constant repetition, but it is my sincere opinion that all of us are a bit slow in some matters. It is nature's way of protecting us from the easily learned - easily forgotten types of information. We care about breeding pigeons---it is important to understand, and our minds move cautiously. Might I cite a personal example. I have listened to others talk scientifically about recessive red since my youth. I have studied genetics and pigeons intensively, but only I know how long it took me to understand. I would never admit that I wrote e//e symbols for years concerning a matter I only vaguely grasped. It has only been through repetition and practice with red self pigeons and discussions with their breeders that I can now, with some assurrance, say I understand the breeding aspects of the mutation called recessive red. There is not a single nest of reds or yellows produced in my loft that doesn't add to this knowledge and feeling of assurrance. We can begin with studying the inheritance of recessive red and then spend an enjoyable lifetime learning to perfect the richest expression possible of the gene. Genetically, e//e birds all have identical genes for recessive red---but what a difference in expression. Development of beauty in the pigeons is always the product of someone that understands, (however vague), the nature of the art he's applying, even if the change from normal being developed is an accident of nature. I would hope this notebook will represent a beginning point for a breeder who cares enough to endure the repetition and practice necessary to learn the art of breeding pigeons.

It is my opinion that these breeders can contribute much to the future of their chosen breed in a technical age.

Our study of pigeons includes many topics about which little is presently known. I have included in these sections some clues as to the nature of the subject and a few suggestions concerning related breeding practices. Hopefully, the breeder will later contribute necessary facts relating to these topics. Sensible application of basic research and recording procedures to loft management will do much to solve these problems for all of us.

Essentially the notebook attempts to combine a minimum of biological knowledge with logical breeding practices. To this goal the sections have been arranged to provide growth rather than a logical classification order of topics. Topics that the breeders have found easier to understand are presented first, with repetitive follow up in later sections adding greater detail.

Classification of Pigeons

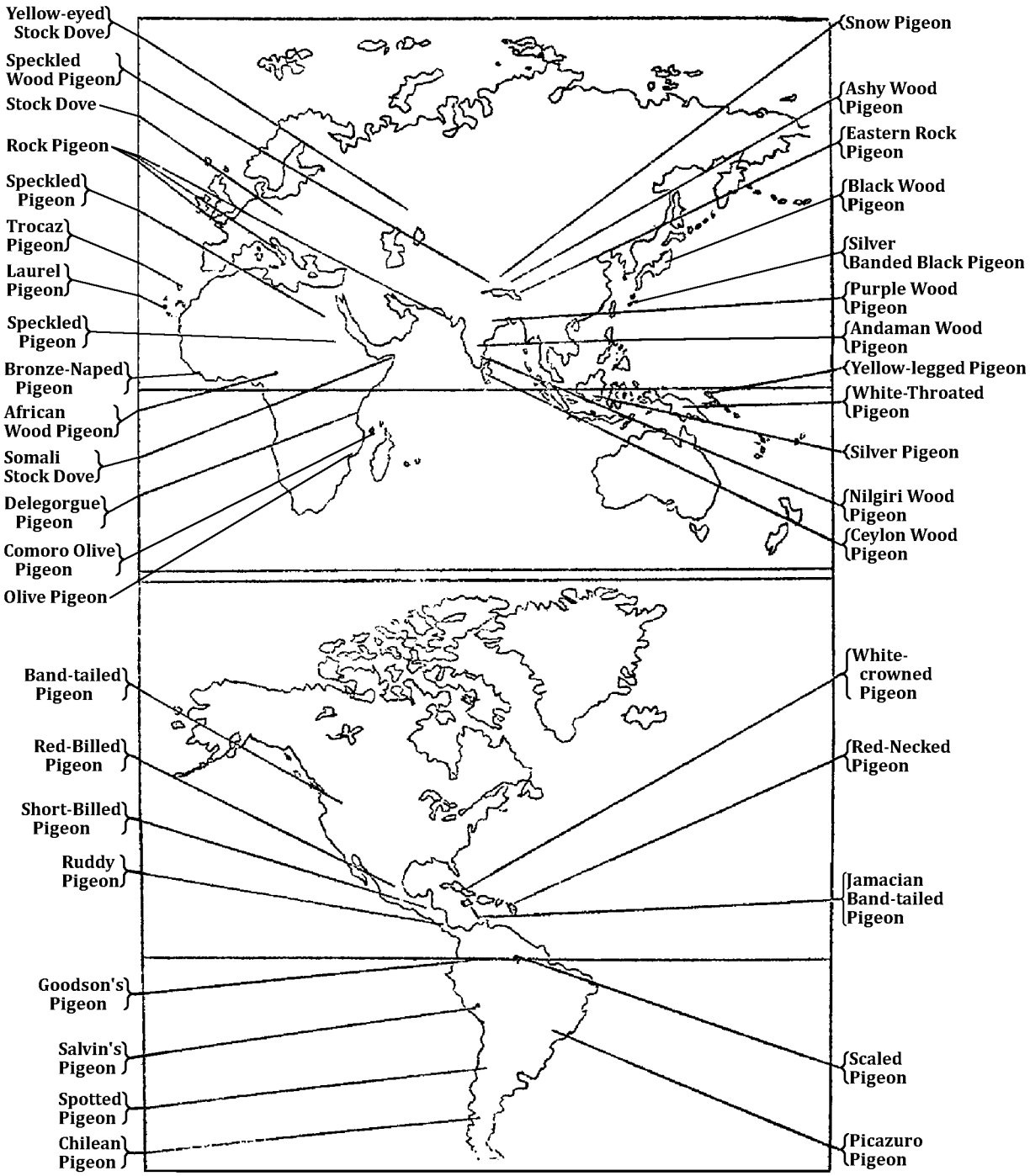
Pigeons are classified in taxonomy as:

Phylum	Vertebrate (back-boned)
Class	Aves (birds)
Order	Columbiformes (pigeon-like birds)
Suborder	Columbae (pigeons, doves, dodos and solitaires)
Family	Columbidae (pigeons and doves)
Genus	Columba
Species	livia

Pigeons and doves represent numerous species with world-wide distribution. Columba livia domestica, the domestic pigeon, is classified as one group including all breeds of domestic pigeons. The words, pigeon and dove, are interchangeable; merely French and English name derivations for the same bird. We might just as

well use Due (Danish) or Doo (Scottish) for names but common usage has dictated otherwise. Pigeon breeders would find most of the wild species that will withstand confinement a delightful addition to their hobby. The delicate Diamond Dove or the partridge-like Nicobar can help develop an understanding of genus, species and classification.

The following maps indicate the distribution of some of these beautiful related species



Vocabulary - The First Challenge

The following words are used throughout the text. The student is asked to read through the definitions, without any attempt to memorize them. At each place where the words are used in explanation, a guide to its definition is contained in parentheses ( ) after the word. The list includes general terms of biological or genetical importance to the breeding art. It has been found that re-reading the list of terms from time to time will make them naturally part of the breeder's vocabulary with very little effort.

Vocabulary and Definitions

Allele
Any of a series of possible genes which occur at the same locus on the same chromosome.

Auto-sexing
A method of distinguishing the sex of young by the introduction of mutant genes into the breeding stock which produce a particular phenotype in the male or the female. The value of auto-sexing is in providing an accurate aid to sex determinatio prior to any sexual development.

Autosome
All chromosomes within the nucleus excluding the sex-determining chromosomes.

Backcross
The cross of a hybrid (F_1) with a parent individual or genotype identical to one of the two parent types.

Carrier
An individual heterozygous for a recessive gene; the phenotype of which is obscured by the presence of a dominant allele.

Cell
The smallest, self-sufficient unit of life capable of independent reproduction.

Cere
Fleshy skin about the eye, beak wattle.

Chiasma
The points of crossover between two of four chromatids observed during the first meiotic prophase; Part of the mechanism of crossing-over.

Chromosome
Structure located within the nucleus composed of a DNA thread. They regulate processes within the cell as well as carry the genes responsible for genetic transfer, in a definite linear order. The number of chromosomes present is a species characteristic.

Classification
The grouping of organisms into an evolutionary hierarchy of groups. The formal hierarchy proceeding from the largest to the smallest group is: Kingdom, Phylum, Class, Order, Family, Genus, and Species.

Clutch
A nest of eggs.

Columba livia
The wild Rock Dove, ancestor to the domestic pigeon, Columba livia domestica.

Complete Penetrance
The case in which a dominant gene always produces a particular phenotypic effect or a recessive gene in the homozygous state always producing a consistent observable effect.

Control
A basis for comparison; A check of an experiment; Part of an experiment performed under identical conditions except for one varied factor. The results of the varied factor can then be measured against those of the control.

Crossing-over
The breaking and rejoining of non-sister chromatids during meiosis. The results being a exchange of genes which in turn produce combinations different from those of either parent.

Crossover unit
The distance between genes which results in a crossover rate of 1%; A distance of one unit on the chromosome map.

Cull
To pick out and discard inferior animals from a breeding stock.

Dam
The female parent in animal breeding.

Diploid Number
A cell in which each chromosome has a homologous chromosome, thus (2N) chromosomes are present.

DNA
(Deoxyribonucleic acid) The chemical which composes the information carrying material within the gene.

Dominant
An allele is dominant when it is phenotypically expressed in the heterozygous as well as in homozygous condition.

Embryo
An organism in early stages of development. In birds the period prior to hatching when the organism is dependent upon the egg yolk supply for nutrition.

Enzyme
A molecule that produces a specific chemical reaction, while not becoming involved in the final chemical result.

Epistasis
The masking or supression of the action of one gene by another gene at a different locus.

Expressivity
The degree to which a given gene is expressed; measured in % of expression of the expected phenotype.

Evolution
The cumulative change in the characteristics of populations of organisms related by descent, occurring during the course of successive generations; descent with change.

Feather Tracts
(pterylae) - Restricted lines of feather growth which are usually named for the area in which they occur. Wing tract (alar pteryla), tail tract (caudal pteryla), etc.

Fertility
The ability to reproduce.

Fertilization
The union of two gametes, or sex cells, to produce a zygote (new individual).

Frill
A condition in which the feathers are reversed, usually on chest or neck areas.

Gamete
A mature male or female sex cell which contains one half the number of chromosomes typical of the species.

Gametic Number
The number of chromosomes found in a mature gamete. This number is half the number found in somatic (body) cells.

Gametogenesis
The process involving meiotic division by which mature sex cells are formed.

Gene
A particular hereditary determiner which occupies a fixed chromosomal locus. The genes are arranged linearly on the chromosome and they are transmitted from parents to progeny.

Gene Pool
The sum of all genetic units from which the next generation will arise.

Genetic Map
The arrangement of gene loci in a linear order as derived from observed crossover rates.

Genetics
The branch of biology concerned with the inheritance of similarities and differences among organisms.

Genotype
The gene make-up of an individual, composed of expressed and repressed genes, as distinguished from its appearance (phenotype).

Genus
A classification of plants or animals above species and below family level.

Haploid Number
The number of chromosomes (N) present in a sex-cell (gamete) half the number of chromosomes as found in a normal cell (2N).

Hemizygous Gene
The condition where only one of a pair of alleles is present as a result of the sex determination arrangement. The pigeon hen can be hemizygous for any sex-linke gene.

Heredity
The transmission of traits from parent (P_1) to offspring (F_1).

Heterogametic Sex
That sex which produces two different kinds of gametes both in a 1:1 ratio; The female pigeon.

Heterosis
The noted increase of vigor in the hybrid of two inbred lines; can be in part associated with an increase in the number of heterozygous genes.

Heterozygosity
The extent to which an individual has pairs of alleles at the gene loci, resulting in unlike gametes.

Heterozygote
A diploid individual that has inherited two different alleles at one or more loci and therefore will produce two different gametes each carrying a different allele.

Homologous Chromosomes
In a somatic cell, homologous chromosomes are one maternal chromosome and one paternal chromosome. These chromosomes pair during meiotic division and contain the same linear sequence of gene loci.

Homozygosity
The situation arising when identical alleles occur at one or more loci.

Homozygous
The occurrance of identical alleles at a gene locus. The individual will produce only one kind of gamete with respect to that locus.

Hybrid
A plant or animal resulting from a cross between parents that are genetically unlike

Hypostasis
A gene whose phenotypic effect is suppressed by another gene which is not an allele.

Inbreeding
The breeding of individuals very closely related within the population.

Independent Assortment
A gene pair which segregates in a random fashion with respect to any other gene pair. The assortment implies each independently assorting gene pair is on a different chromosome.

Lethal Mutation
A mutation resulting in the death of the organism. Dominant lethals kill in either the heterozygous or homozygous cases. Recessive lethals destroy only homozygous individuals.

Linkage
The genes located on the same chromosome. This linkage tends to keep these specific genes together as the chromosome moves during meiosis.

Locus
(Plural, loci) The position that a gene occupies on a chromosome. The only place at which a particular gene or one of its alleles can be found along the chromosome.

Meiosis
The process by which germ cells containing a diploid number of chromosomes are transformed into gametes containing a haploid number of chromosomes by the process of reduction division.

Melanin
The black pigment responsible for the coloration of skin, hair, feathers, etc., in most animals and birds.

Mendel's Laws
Law of Segregation---from each parent only one of the allelic forms is transmitted in a gamete.
Law of Independent Assortment---for non-homologous chromosomes the assortment of alleles into a particular gamete occurs independent of all other chromosomes.

Metabolism
The sum of all chemical processes by which the cell is maintained and by which energy is made available for the uses of the cell.

Mitosis
The construction of identical cells initiated by nuclear division. This process, when extended to the cytoplasm, results in two identical daughter cells. Mitosis is the means of reproduction for the simplest life forms and all growth.

Monohybrid
An offspring from homozygous parents differing from each other at only one locus. This individual will be heterozygous at this locus for both parents' genes.

Mosaic
An individual with irregular patches of an unexpected phenotype against a background of normal phenotype.

Mutant
An individual whose genotype contains a changed gene which expresses itself as a difference in the phenotype of the individual.

Mutation
An unexpected change in the genotype which results in a difference from the normal or wild type.

Nucleus
The structure present in most cells which contains the chromosomes and acts as the growth and reproduction control center of the cell.

Partial Dominance
The condition where a heterozygous gene in the F_1 generation produces an expression of phenotype intermediate between either parental phenotypes.

Pathogen
An organism orvirus which produces toxin or disease.

Pedigree
A listing of an individual's ancestry, found usually in chart or table form.

Penetrance
The degree to which a gene produces a phenotypic effect. A dominant gene which always produces a given phenotype is said to have complete penetrance.

Phenotype
The appearance---any measurable and observable property of an organism which results from the genotype and the environment.

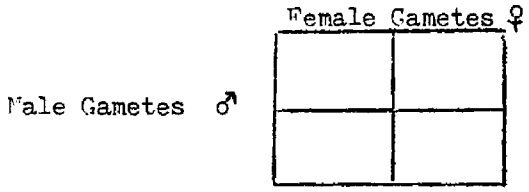
Pleiotropy
The condition where one gene has an influence over a number of different traits.

Polygenic character
A characteristic which is dependent upon the interaction of a series of genes.

Probability
The ratio of a specific event occurring to the total number of events possible; The chance of occurrence, odds favoring.

Progeny Test
A method of determining the value for breeding purposes of an individual by examining the performance of its offspring.

Punnett Square
A checkerboard method of computating all possible genotypes and phenotypes of a given mating.



Recessive
One of an allelic pair which produces a phenotypic effect only in the homozygous genotype.

Recombination
An effect, where progeny have genes in different combination than found in the parental genotypes. Recombination is a result of crossing-over. The percent of progeny having recombinations is directly proportional to the percent of cross-over.

Rectrices
The major tail feathers, usually twelve in number.

Remiges
Main wing feathers, flights or secondaries.

Replication
The process during both mitosis and meiosis when the DNA molecules within the chromosome "reprint" themselves for the purpose of effective division.

Reversion
The appearance of an ancestral trait; a throwback.

RNA
Ribonucleic Acid; The acid associated with DNA in the transcription of genetic information.

Selection
Any process, natural or otherwise, which favors the propagation of individuals possessing certain desired characteristics.

Semilethal Mutation
A recessive lethal gene which lacks complete penetrance, which kills less than 100% of those individuals homozygous for the gene. Such genes are also classified as subvital genes.

Sex Chromosomes
Chromosomes involved in sex determination. In pigeons, the male has two sex chromosomes, the female one.

Sex Determination
The mechanism in a given species by which sex is determined. The determination is a characteristic of the species.

Sex Linkage
A special case of gene linkage in which the gene involved resides on a sex chromosome. Genes located on the X-chromosome of man or the Z-chromosomes of birds are sex-linked genes.

Siblings
Brothers and/or sisters; the offspring of a mating of members of the same species; Individuals, regardless of time, having the same parents.

Sire
The male parent in animal breeding.

Species
A classification below the genus level but above the variety level. Individuals of the same species may interbreed with themselves but not with members of other species.

Sport
A common usage word describing an unusual change i.e., a mutation.

Sterile
Incapable of producing offspring.

Tarsus
The shank of the leg.

Testcross
A cross between a genetically unknown genotype and an individual which is homozygous recessive for the gene or genes being tested.

Variation
The extent of non-circumstantial differences among existing individuals of the same species.

Viability
The degree to which one genotype is capable of reaching maturity relative to the normal. Mutants affecting viability are sub-vitals or semi-lethals.

Wild Type
The most frequently observed phenotype; The phenotype which is much more common in the population. This type is used as the standard for comparison.

Wild-Type Gene
Those genes most prevelant in the general population. Those genes possessed by the wild type.

W,Z Chromosomes
Those chromosomes involved in sex determination when it is the female which is the heterogametic sex. In such a system the W-Chromosome is the female determinator.

X
Mated with, or bred to.

Yolk
A storage of cytoplasm within the egg which is to be used as food by the embryo.

Z Chromosomes
The heterogametic female system of pigeons and other birds. The sex determination method in which the sex chromosomes are found once in the female and twice in the male.

Biological Background

Introduction:

The question may be asked ..."of what value is a detailed biological understanding to the breeder?" The answer ..."it will be of little value." An attempt at genetic understanding beyond the essentials can be confusing and tends to discourage the breeder from attempting to learn practical genetics at all.

The attitude, one of "I can't grasp it all, so I won't try" ... is too prevalent, and is related to details, rather than basics of biological understanding.

The value of learning the basics is obvious; it adds a new dimension to the breeders option. He is now capable of better directing his breeding program toward his desired goal.

Basic genetic concepts are simple and logical; they enable the breeder to place less emphasis on memorization of previous breeding results, and gives new importance to a well kept set of loft records.

A Note on the Approach to This Section:

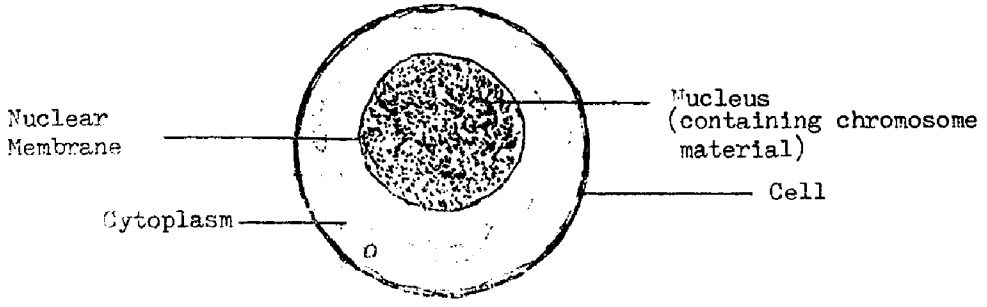
Genetics is a highly technical field and, as in any science related field, be it engineering or particle physics, a vocabulary evolves around the science, which is unique to the science, understood by the professionals, and by few others.

In the course of this section, the technical vocabulary will be kept to a minimum. The goal of this section is to give essentials. The principles will be presented generally, applicable to man or beast. Whenever warranted, the genetic information related to birds will be given.

Our first look at heredity will be a study of changes within the nucleus during cellular reproduction. It is within the nucleus of the cell that the mechanism of heredity is to be encountered.

The Cell:

The cell is the basic unit of life. It is the building component of all living things, in either the plant or animal Kingdom.



Nucleus:

The nucleus regulates growth and development of the cell. So it is within the cell that we first examine the life process. The center of genetic potential within the cell is the nucleus. Within the nucleus are the chromosomes. Genes, located on the chromosomes, determine the hereditary instructions.

Chromosome:

The chromosomes are thread-like fibers in the nucleus.

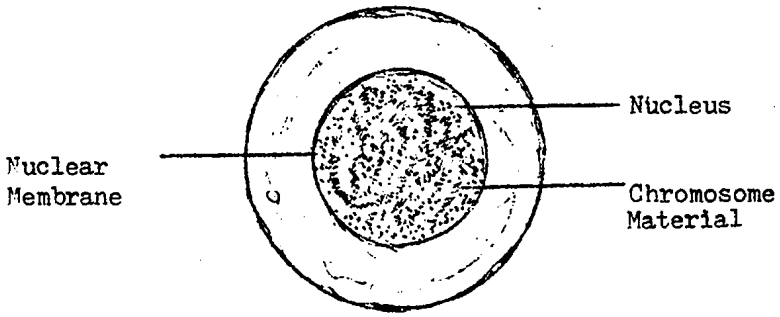
Having seen the cell and located the structures involved in the genetic process we will now look at the mechanics of the cell.

Cell Division:

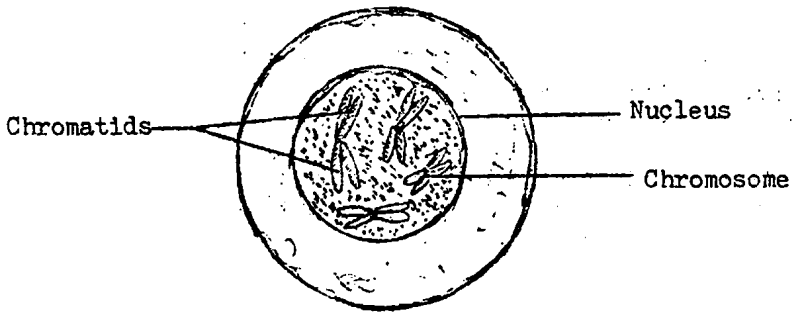
Cell division is the means by which a cell reproduces itself, and the process by which many celled organisms grow. Cell division (mitosis) can therefore be described as a system of duplication.

The process of cell division takes place in five steps.

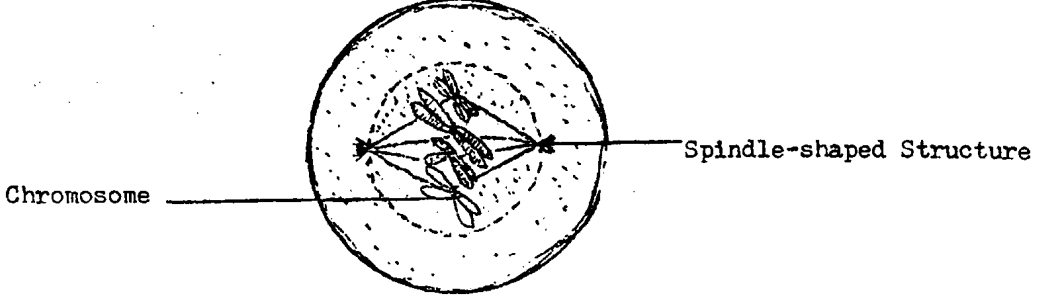
Interphase ---the static state prior to the beginning of cell division.



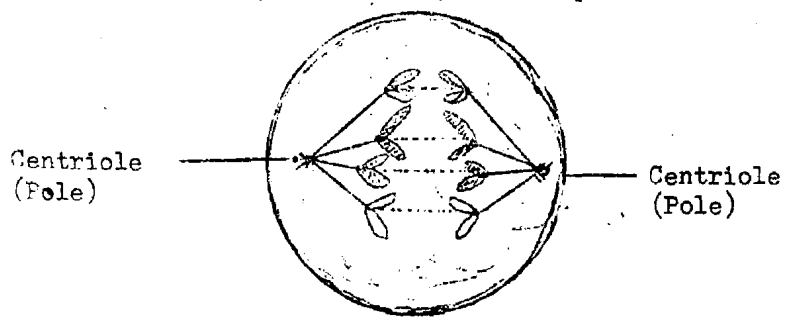
Prophase ---in this stage the chromsomes of the nucleus begin to grow shorter and thicker. During this period two strands (chromatids) become visible in each chromosome.



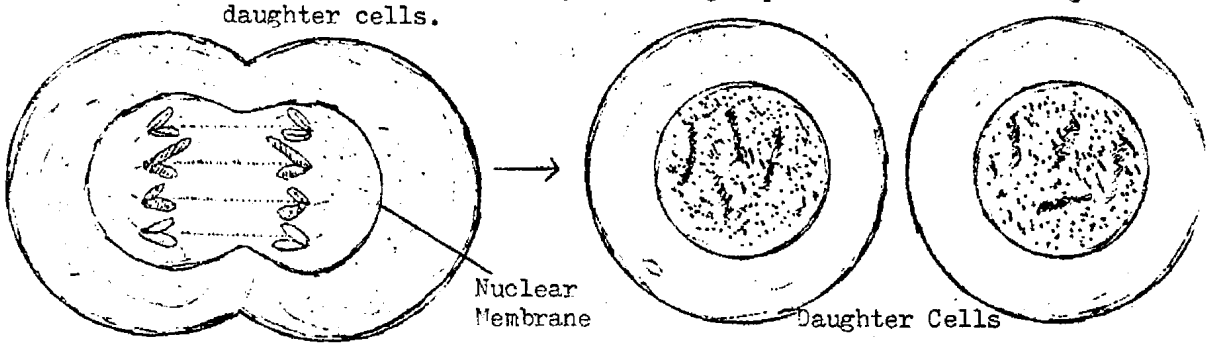
Metaphase ---separate chromosomes are now visible, the nuclear membrane fades, and a spindle-shaped structure is formed.



Anaphase ---chromatids, having replicated, each move toward a separate pole (centriole) at the ends of the spindle.



Telophase ---the nuclear membrane begins to regroup around the resulting daughter cells.



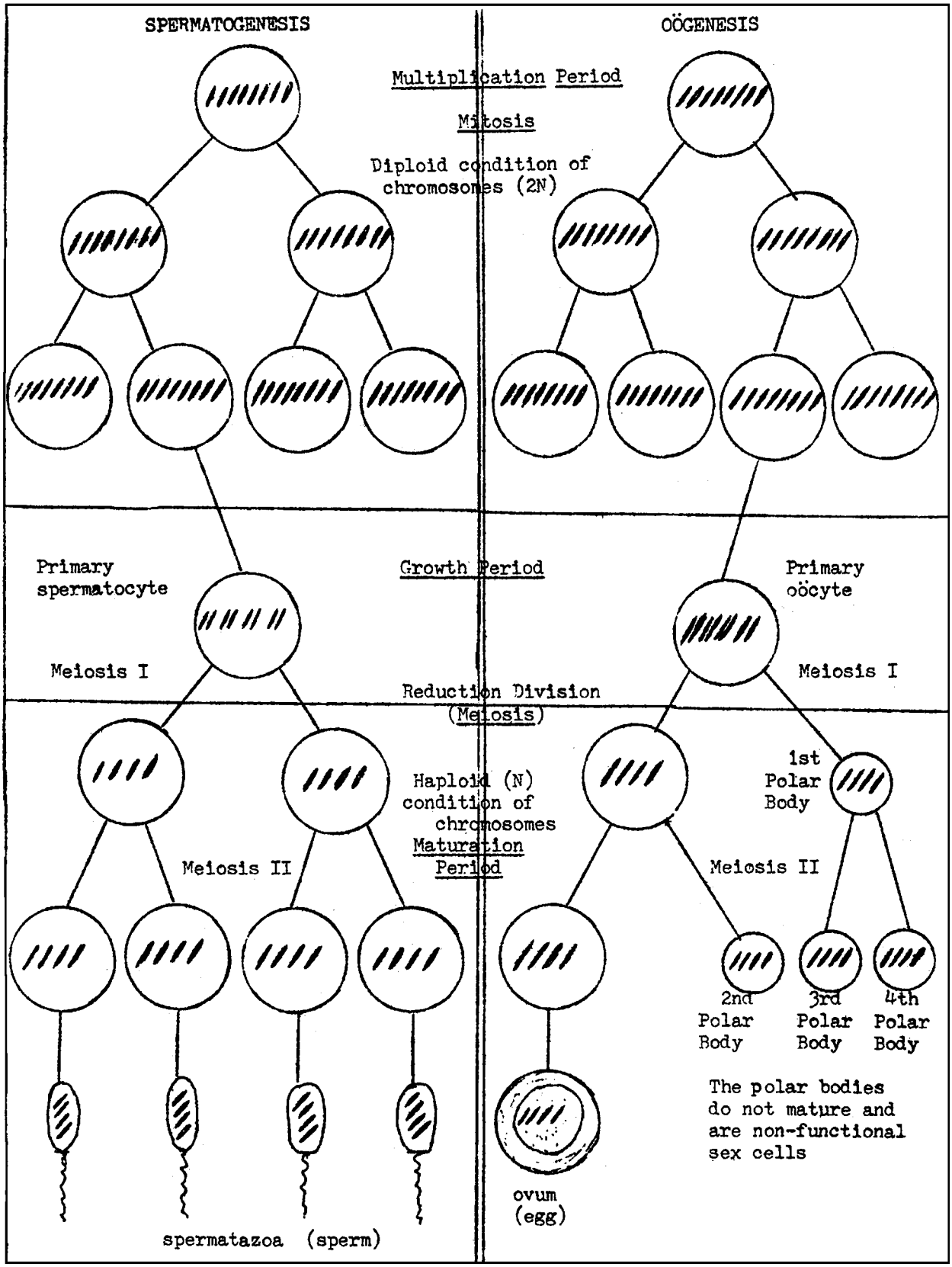
And finally the cytoplasm of the cell separates, and two new identical daughter cells begin carrying out their cellular functions until the process occurs again .

Mitotic cell division is found in all life forms, and it is mitosis which is responsible for growth. This type of cell division in simple animals is the means of reproduction. Such simple animals are said to reproduce asexually.

In the higher, more complex animals, man being an example, we find a different type of cell division occurring in certain cells within the sexual organs.

Meiosis occurs in all higher sexually reproducing plants and animals. It is the mechanism by which certain cells in the sexual organs, containing a normal compliment of chromosomes (commonly disignated as the (2N) diploid number), are transformed by reduction division into two sex cells which contain only half the normal (2N) number of chromosomes (written as the haploid number (N). This process, occurring in the male as spermatogenesis , and in the female as oogenesis, produce gametes, sperm in the male, and eggs in the female, which when united in fertilization, are capable of producing a normal (2N) cell, zygote, which in turn by means of mitotic division, is capable of growing into a mature individual member of the species.

Mitosis is irreplaceable. It is essential for growth. Meiosis is important only in providing for greater individual variation. In mitosis, both daughter cells are identical, as will be every cell in successive divisions. In mitosis, there is little possibility for variation. However, in meiosis, we find an enormous potential for change and variation, due to the re-shuffling of genes which occurs in the process.


SPERMATOGENESIS
OÖGENESIS
Multiplication Period
Mitosis
Diploid condition of chromosomes (2N)
Primary spermatocyte
Growth Period
Primary oöcyte
Meiosis I
Meiosis I
Reduction Division (Meiosis)
Haploid (N) condition of chromosomes
Maturation Period
1st Polar Body
Meiosis II
Meiosis II
2nd Polar Body
3rd Polar Body
4th Polar Body
The polar bodies do not mature and are non-functional sex cells
ovum (egg)
spermatazoa (sperm)

We have to this point noted only the cellular mechanics. We will now examine the rules which govern the possibility for individual variation. In each cell we find (2N) chromosomes grouped as (N) homologous pairs. One member of each pair is maternal, the other paternal. Along each of these chromosomes, arranged linearly, are the genes. Therefore, for each gene, there are two locations for it (loci) in a homologous pair, one location on each of the two chromosomes. According to Mendel, only one gene of the pair is usually expressed.

At this point the concept of an allele comes forward. An allele is an alternate form of a gene, occurring as a mutation from wild type. Alleles usually only affect one characteristic.

It should be understood that regardless of the total number of mutation-produced alleles, only one can occupy the given locus on a particular chromosome. We may then conclude that at most, an individual may be homozygous for any one of these allelic genes, or heterozygous for any two of the set of alternatives at that point (locus) on the two chromosomes.

Generally, the alleles can be arranged in an order of dominance from the least dominant (the gene phenotypically expressed when homozygous), up to the most dominant (that gene which is always expressed phenotypically, even when only heterozygous). At the pattern locus in pigeons, for example, we consider T-pattern is dominant to checker, is dominant to bar, is dominant to barless.

Written symbolically: $C^T > C > + > c$

Since most mutations which occur are recessive, wild type will usually be the dominant allele in a series, but there are numerous exceptions. Finally, one can expect to find at least as many different phenotypes as there are alleles involved at any loci.

There are many genes in the population which are classified as modifiers. A modifier is any gene which alters the visible phenotypic effects of other genes. Modifiers have the effect of enhancing or suppressing some genes.

Epistasis (masking):

Epistasis is a condition in which one gene suppresses the expression of another gene. This differs from dominance, in that the genes involved are non-allelic. One type of epistatic effect is when a gene responsible for pigment production is absent. The result being that there is an absence of color. Another common type of suppression, masking, occurs when an intense pigmenation covers over the true phenotype of the individual. Spread is a masking gene for pattern, as recessive red is a masking gene for both color and pattern.

Reversion

Reversion is the occurrence of "throwbacks", that occasional chance genetic combination, which overrides any masking qualities involved; the result being the expression of long suppressed characteristics. Reversion is often noted in the breeding of two highly inbred varieties of the same species. This type of inter-variety mating will occasionally result in an offspring unlike either parent, but resembling a common ancestor.

Reversion is quite often noted in pigeons. Due to the large number of highly ornamented and colored breeds, an inter-variety mating will occasionally produce a somewhat "wild type" offspring.

Lethality

There exists in the total gene population, certain genes which influence viability to such an extent, that they have been labeled as "lethal genes". Dominant lethal genes have the immeadiate effect of destroying all individuals carrying the gene. Recessive lethals can be carried in the heterozygous condition, and often pass unnoticed until the mating of carriers occurs,---very often by chance. Lethal genes can be considered to be independent of time. Death, due to lethal genes, may occur at any point during the life span of the individual, from fertilization onward.

We will now examine the phenomenon known as linkage.

Linkage is the tendency of genes on a particular chromosome to remain together. Genes are said to be linked when they occur on the same chromosome. When linked genes occur on the sex determining chromosome, the genes are said to be sex-linked.

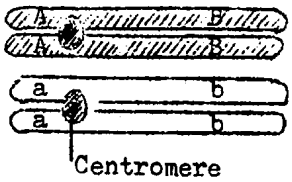
Most sex-linked genes are found on the X-chromosome in mammals, and the Z-chromosome in pigeons. In pigeons, the males possess two Z-chromosomes, and the females only one. For this reason, the expression of sex-linked genes follows a "criss-cross pattern of inheritance. This pattern in pigeons takes the form of

father ——→ daughter ——→ grandson

This unusual set of results is due to the fact that the Y-chromosome in mammals, and the analogous W-chromosome in pigeons, contains practically no genes allelic to those found on either the X or Z chromosomes.

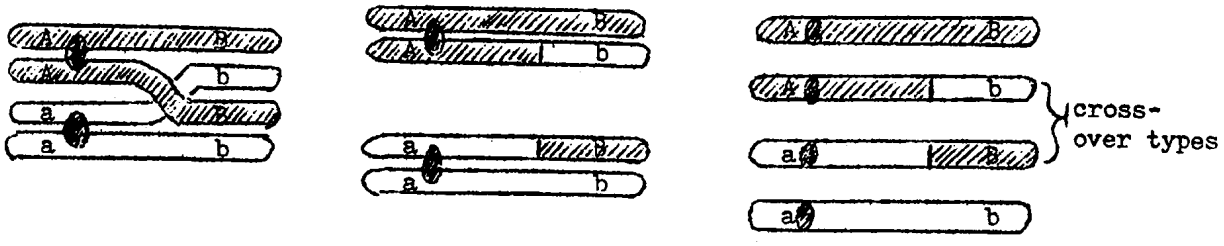
Linkage , however, will not always be able to keep the genes together. Linkage is often interrupted by a process known as crossing-over.

Crossovers occur during the first meiotic division. It occurs when both homologous chromosomes, having replicated (reprinted), lie in close proximity to each other.



The centromeres depicted are devices that aid in aligning the chromosomes.

At this time, if a crossover is to occur, one of the homologous strands will lie across the other in such a manner, that a breakage results at that point (chiasma). A subsequent fusion of opposite broken ends (chromatids) results:



It should be noted that ½ the resulting gametes produced will be like the paternal gametes, and ½ will be a recombination.

The frequency of crossover is a measure of the linkage which exists between genes. The more closely linked genes are, the less likely to be separated. Genes widely separated on the chromosome are most often involved in crossing-over.

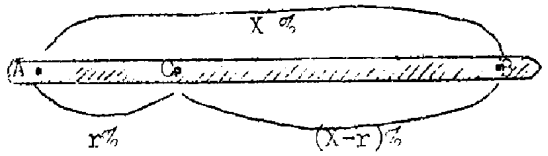
Crossing-over has been observed in almost all higher orders of plants and animals. The significance is that it provides an opportunity for an increase in genetic variation.

The data obtained from observing crossovers can be used to establish gene location along the chromosome, and leads to the development of a chromosome map.

The basic idea behind the chromosome map is that the greater the separation between two linked genes, the greater the possibility for there being a crossover between these two gene positions (loci).

Therefore, no crossover is possible between alleles, this being due to the fact that alleles occupy the same locus. In drawing up a chromosome map, we use a system where a crossover rate of 1% is used as the unit on the chromosome map.

The next condition which must be satisfied is that of crossover addition. What this states is that the crossover rate between two widely separated loci must be equal to the sum of the crossover rates with a locus located between the widely separated loci.



$X\% = (X - r)\% + r\%$

What this means is that the crossover rate between A and B must equal the sum of the crossover rate between A and C, and B and C.

Once this addition has been confirmed as correct, the loci can be mapped relative to each other.

To this point, we have examined the basic rules governing genetics. In this next short section, we will make some brief observations on three areas often associated with breeding; hybrid vigor, inbreeding, and progeny testing.

Hybrid Vigor (Heterosis)

Hybrid vigor is that condition where the performance of the progeny exceeds that of the parents. A theory behind hybrid vigor is that heterozygosity tends to improve vigor by producing a greater number of loci where an individual is heterozygous. This results in fewer loci where homozygous recessive deleterious genes can occur to depress vigor. In a cross between unrelated highly inbred individuals, there will be fewer homozygous recessive deleterious genes to depress vigor. These genes may still be present, but only in the heterozygous state, where because of the presence of a dominant allele at the other locus, vigor is not impaired. The general pattern of hybrid vigor is that it seldom persists for more than one or two generations, before performance falls back within the normal range of performance, and must be bred for again.

Inbreeding

The most obvious effect of inbreeding, for example father X daughter matings, is the increase in the number of homozygous gene pairs. This is often done when the breeder is striving to improve a particular characteristic. Inbreeding, when extended beyond a point, has potentially damaging effects, in that it increases the possibility that recessive lethals, carried by closely related individuals, will be "matched up" in the mating. The initial sign of inbreeding reaching a depressive level, is a lowering of reproductive efficiency.

Progeny testing

The value of progeny testing is that it determines the worth of a breeding individual by means of genotype, rather than phenotype.

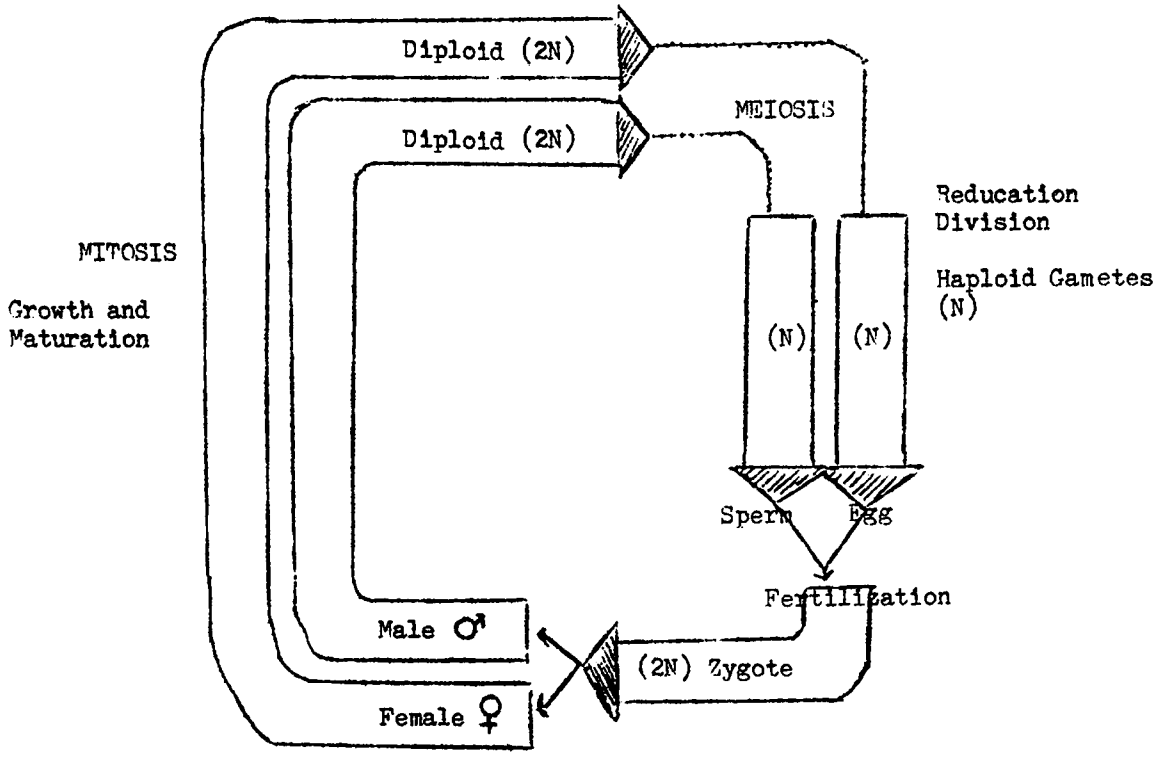
In the era of artificial insemination, it is absolutely essential, especially for example, in cattle, that the breeding males be tested by means of a progeny test, rather than pedigree.

In general, all that progeny testing involves is an establishing of the breeding value of an individual before it is too widely used in stock development. It should allow the individual being tested an opportunity to produce several progeny from different matings (with its own offspring),and these offspring should be judged in reference to the qualities desired.

This ends the section on biological background. It has been an attempt to lay the groundwork for what is to follow. This effort will have succeeded or failed only in reference to your understanding of the material that is to come. If parts of this section appeared unclear or disjointed, it is because in striving for basics, much connecting material has been omitted. The reader is therefore asked to continue, regardless of his mastery of this section.

The biological background obtained from this section, especially those parts devoted to meiosis and chromosome mechanics, are vital to a basic understanding of pigeon inheritance.

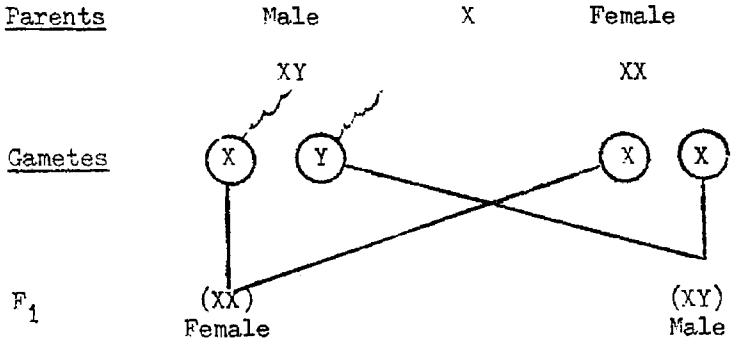
Life Cycle of Sexually Reproducing Species



Sex Determination In The Pigeon

The mechanism for the determination of sex in the pigeon plays a most important part in the breeding art. A basic understanding of this mechanism will help in the understanding of the related sex-linkage.

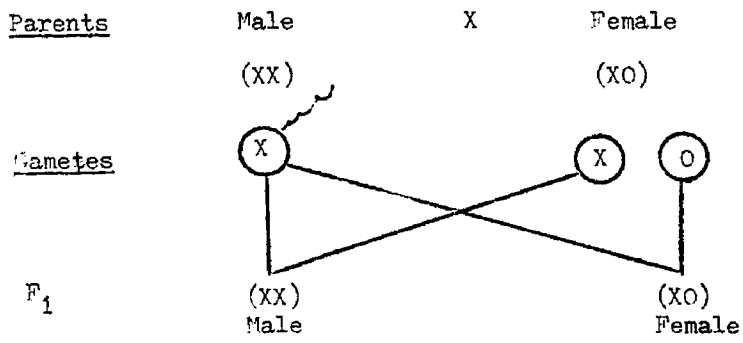
We might begin academically with the arrangement in humans. The female human (all mammals) has two identical sex chromosomes (XX), while the male has two different types of sex chromosomes (XY). In the formation of any zygote, (fertilized sex cell), the female will contribute one X chromosome. Since she has only one type of sex chromosome to provide the sex cell, we refer to the female (mammal) as the homogametic sex, meaning one type of gametes. We then refer to the male as the heterogametic sex, because he produces equal numbers of different gametes, one half carrying an (X) chromosome and one-half carrying a (Y). Obviously when he contributes an (X) to go with the female contribution of an (X), the result is (XX) or a female. When the male contributes a (Y) chromosome to the gamete uniting with the (X) of the female, the resulting zygote is (XY), or a male offspring. The male determining chromosome, (Y), thereby determines the male sex. It carries few known genes and, other than determination of sex, is rather useless as a genetic carrier.



By this arrangement approximately equal numbers of males and females are produced.

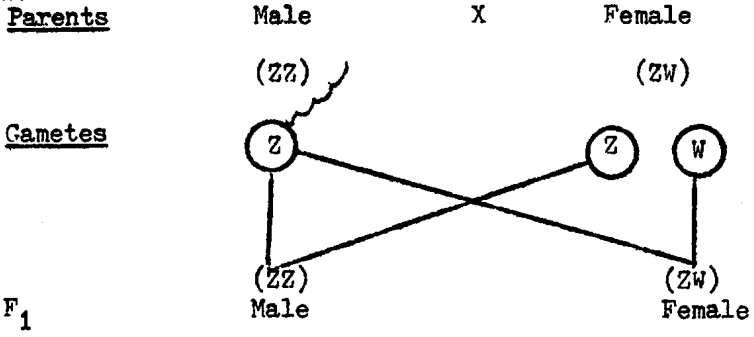
In species where the female is the heterogametic sex, often the arrangement has the male with two chromosomes and the female but one. In this case the female determines sex by either contributing or not contributing her sex chromosome to the gamete and therefore to the resulting zygote.

This is often shown:



The O representing the missing Y

This diagram has long been associated with the sex determination of many bird species. It works well as a tool for understanding the sex-linkage of the pigeon. I use it frequently, even though a chromosome somewhat similar to the (Y) of the mammal males has been found in pigeons. For scientific clarity, pigeons are represented as (ZZ) male and (ZW) female to separate them from the group where the X chromosome is unpaired. Like the Y in male mammals, the W chromosome in female pigeons carries apparently few important genes. The correct arrangement in pigeons is shown:



It is a little simpler to understand and study pigeons if we think of the male having two sex chromosomes (XX) and the female having one (XO). A silver cock would be shown d//d, while a silver hen would be shown d/•; with the dot representing the W chromosome just to remind us we really know it's there, even if we choose for study and explanation to ignore it.

Wild Type

The origin of domestic pigeons plays a major role in supporting the evolutionary theory proposed by Charles Darwin. Since Darwin assumed the Rock Dove, Columba livia, to be the progenitor of all domestic pigeons and gave considerable evidence for this assumption, common usage has directed that the blue bar Columba livia be accepted as the wild type. As such, it is the standard of reference for comparison of all mutant genes. For us, a mutation is a gene oriented non-Rock Dove characteristic. Crest, (cr), is a difference from the plain-headed Rock Dove, and therefore a difference from wild type. The $(+)^{cr}$ wild type gene at the now defined crest locus is a plain headed or non-crested pigeon.

The big plus (+), as the base referent for all genetic change, leaves the impression that we are rather sure of the meaning of "wild type". Descriptions of the "Blue Rock Pigeon", Rock Dove, or Rock Pigeon vary somewhat in detail. Columba livia is a well recognized species of near worldwide distribution. Levi depicts it as a blue bar pigeon of medium size with general dove characteristics, especially the finenesss about the head and neck. The Rock Pigeon will consort, co-habitate, and interbreed with the domestic breeds of pigeons and it is generally believed that all domestic forms are derived from it. Because of the strong potential for hybridization during the long history of the pigeons' cultivation, it is doubtful that present Rock Pigeons are not without the taint of the pigeon breeders selective practices.

In reviewing a 1913 edition of Indian Pigeons and Doves by E.C. Stuart Baker, it became apparent that the description of the eastern form of the species might possibly be closer to the original than that which we are able to observe. (All American feral (common) pigeons are descended from escaped domestic pigeons, and not directly from Columba livia, which does not occur on this continent in the wild state.)

Columba livia Description, Adult Male: Head dark purple-gray; nape, neck all around, upper-breast and the extreme upper part of the interscapulary region dark gray glossed with brilliant metallic purple and green, according to the light in which it it held; upper-back ashy-gray grading gradually into white on the lower back...; rump and upper tail coverts dark gray, generally a little darker than the upper-back; tail dark gray like the rump with a broad black band across the end leaving only a narrow final tip of gray. The outermost rectrices with a broad border of white on the outer web between the base and the black band. Wing coverts and the innermost secondaries gray, of the same shade as the back, with two broad bars of black, the first formed by the black bases of the greater coverts and the second by the innermost secondaries which are mostly black or blackish-brown, though with the concealed bases and the tips gray; primaries brownish-gray, paler on the inner webs except at the tips. Lower parts slatey-gray, darkest on the breast; under-wing coverts and axillaries white, the former more or less suffused with very pale gray. Color of soft parts, Iris orange-red; bill vinous slate colour, inclining to white on the cere; legs red (Salvadori).

Columba livia Description, Adult Female: Same as male in most aspects, though slightly smaller, darker and less iridescent.

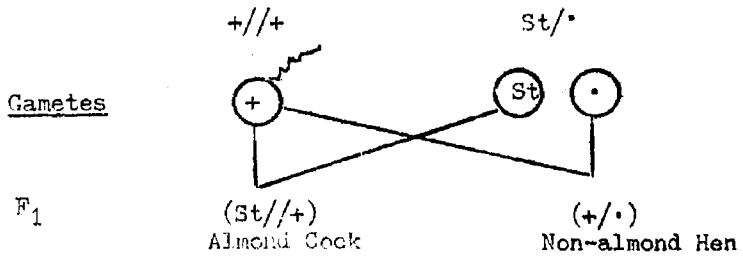
In our usage, wild type is the phenotype resembling Columba livia. The blue barred domestic pigeon within the breed serves as wild type at times. This would indicate that a mating to wild type has several meanings. If we are comparing a color mutant within a breed, a mating to a blue barred representative of that breed is considered correct within this definition. If the characteristic to be tested is more involved, such as with a structure gene, a mating to wild type would imply mating to a reasonable substitute for the Rock Dove. It is generally accepted that the blue barred Racing Homer is as close as present breeding practice permits us to approach the true wild type---Columba livia.

Sex-linked Matings

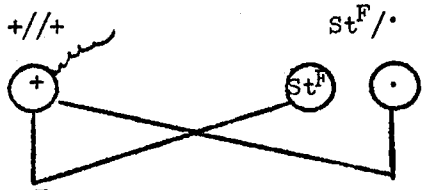
Any mating which utilizes the pigeon sex chromosome arrangement to determine the sex of the offspring by the resulting phenotype of the progeny is a sex-linked mating. The hen has only one sex chromosome to contribute or not contribute to the genetic make-up of the squab. If her sex chromosome contains a gene dominant to either of the alternatives (alleles) present on the two sex chromosomes of the cock, a criss-cross inheritance takes place. That is, all cocks will resemble the dam (♀) and all hens will resemble the sire (♂).

Obviously any almond or faded hens (very expressive sex-linked dominants) mated to any non-almond or non-faded cocks will produce almond or faded cocks and non-almond or non-faded hens.

Example 1 Parents Non-almond Cock X Almond Hen



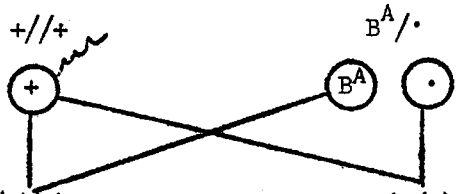
Example 2 Parents Non-faded Cock X Faded Hen



F_1 $(St^F//+)$ Faded Cock $(+/\cdot)$ Non-faded Hen

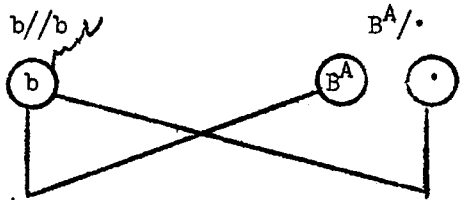
Similarly, any blue or brown cock mated to an ash-red hen produces the same situation.

Example 1 Parents Blue Cock X Ash-red Hen



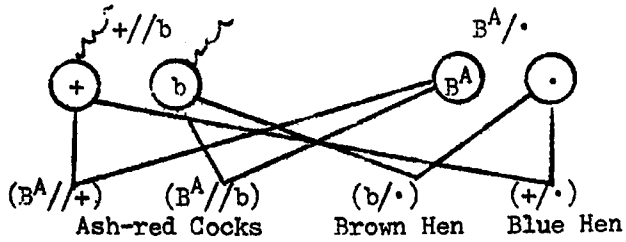
F_1 $(B^A//+)$ Ash-red Cock $(+/\cdot)$ Blue Hen

Example 2 Parents Brown Cock X Ash-red Hen



F_1 $(B^A//b)$ Ash-red Cock $(b/\cdot)$ Brown Hen

Example 3 Parents Blue Cock carrying brown X Ash-red Hen

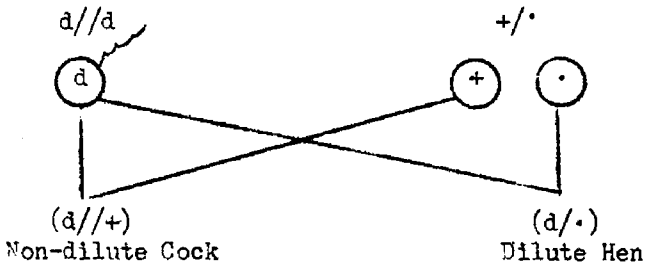


F_1 $(B^A//+)$ $(B^A//b)$ Ash-red Cocks $(b/\cdot)$ Brown Hen $(+/\cdot)$ Blue Hen

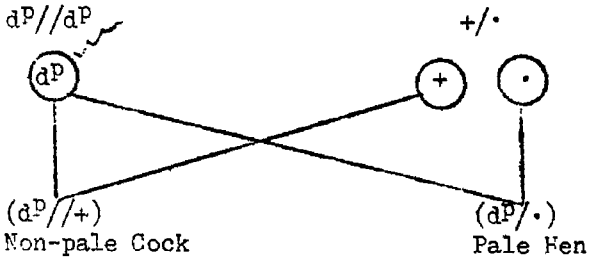
It should be noted the ash-red cocks produced carrying blue $(B^A//+)$ will have blue or black flecks, and those carrying brown $(B^A//b)$ will have brown flecks.

Following the same logic, any dilute, pale, or reduced cock mated to wild type hens will also be a sex-linked mating of this type.

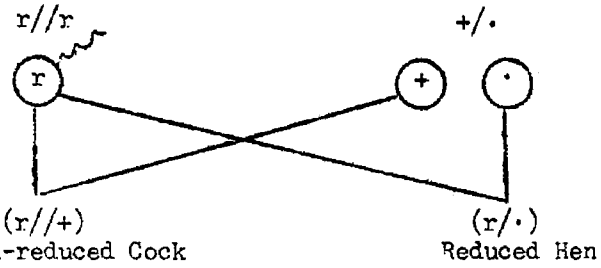
Example 1 — Parents: Dilute Cock X Non-dilute Hen (Intense)



Example 2 — Parents: Pale Cock X Non-pale Hen

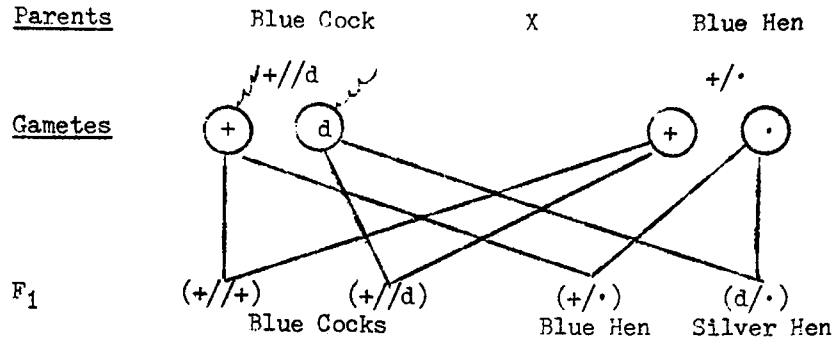


Example 3 — Parents: Reduced Cock X Non-reduced Hen

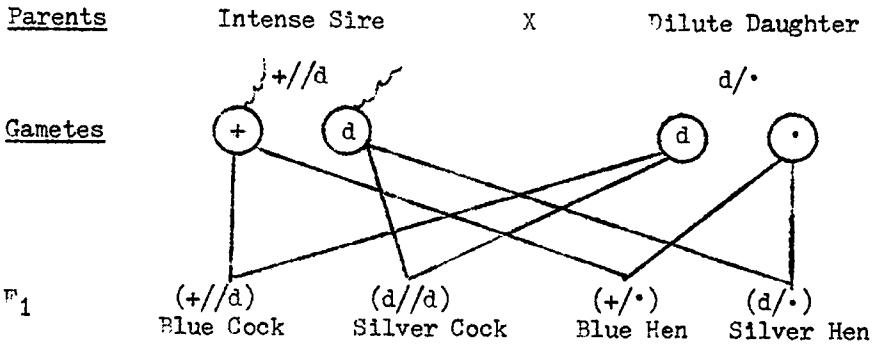


In the case of sex-linked genes, the hen will be what she is, both phenotypically and genotypically. Any yellow, silver, or khaki produced from non-dilute (intense) parents must be a hen and the sire carries the dilutant, in this case, dilution (d).

If a pair of blues produces a true dun bar silver it will be a hen, and the genotype of the cock is automatically known for the dilute locus.

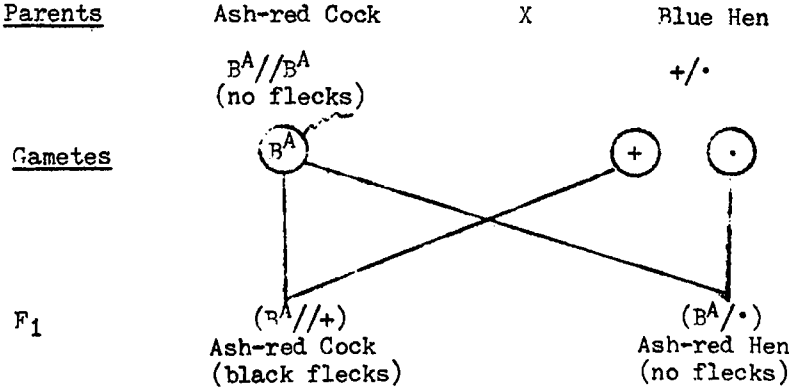


We also know that one-half of the blue sons will carry dilution, and that in future matings this cock should sire one-half dilute and one-half intense daughters A mating of a silver daughter to her sire will produce silver cocks and hens.

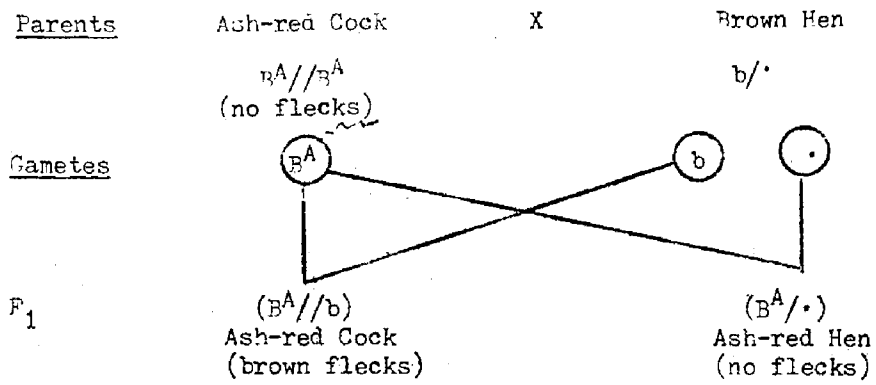


Sex determination made possible by this sex linkage phenomenon does not end with our several examples. A wide variety of sex-linked matings for combinations of sex-linked genes can be easily worked out. The flecking aspect of ash-red cocks adds another dimension to sexing the offspring of several matings. The matings of homozygous ash-red cocks $B^A//B^A$ (no flecking) to blue or brown hens will produce all ash-red offspring, but the flecking will make possible the sexing of young birds.

Example 1

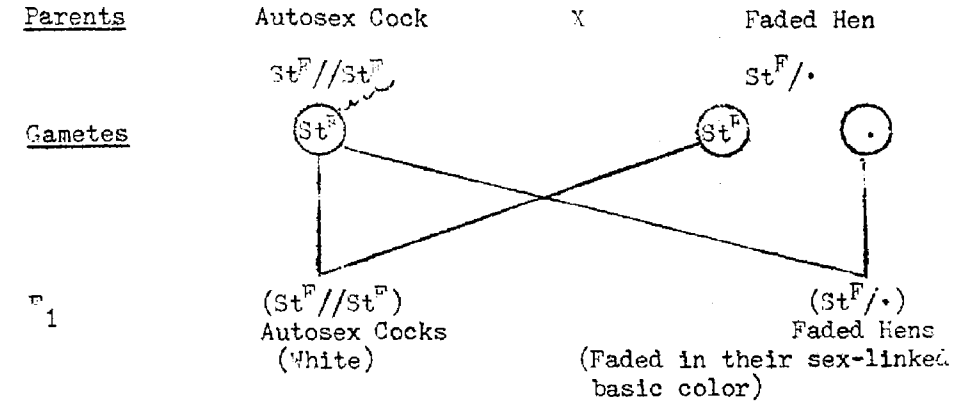


Example 2



It should be stated that this is not entirely fool-proof because a few rare racing homer hens have brown flecks in the tail. The tail is the most likely detection area for flecking, and in white tailed birds such as baldheads, there is a greater chance of mistakes in sexing squabs by this method. Flecking in such birds is little understood and varies from profuse to slight patches. There is possible error in those marginal cases in the first moult. With age the flecks will increase, but I'm sure by that time the sex will already be known by behavior.

Wherever the homozygous cock differs from the hemizygous hen for a sex-linked gene, a situation of auto-sexing results. Almond (St) and faded (St^F) produce this condition. Almond (St) and faded (St^F) are alleles and produce similar effects to the homozygous condition. Homozygous almond cocks (St//St) are pure white with occassional flecks, whereas the St/· hens are typical almond. Homozygous almond St//St cocks are nearly always bladder or pop-eyed and blind; and for that reason are hardly suitable as breeders. There is no noticeable vision or eye problems associated with the homozygous faded cocks ($St^F//St^F$) and faded has become the basis of auto-sexing breeds such as Texans. Both almond and faded are covered in special sections of this booklet, but I will note here the auto-sexing arrangement.



I have for several years used cocks of the genotype $St//St^F$ mated to kite hens to produce one-half almonds, one-half faded in both cocks and hens. The combination of these two alleles produces an effect similar to St//St or $St^F//St^F$. Such cocks are nearly white with some slight flecking.

The Shorthand of Science

We have briefly covered certain biological processes of reproduction. There is one more step necessary in order to develop a meaningful understanding of the practical applications of these ideas to the breeding of pigeons. We must simply destroy the mystery surrounding the use of formulas and symbols.

In the preceding sections, we have used gene symbols and diagrams of gametes producing a zygote. Breeders use shorthand at every show on coop tags and entry blanks, The abbreviations O.C., O.H., Y.C., Y.H. show classes for each breed. Such shorthand notations are warranted because it saves the valuable time for show secretaries and conveys exactly the necessary information needed by breeders and exhibitors.

In the scientific study of pigeons, for exactly the same reasons, we resort to the use of initials, symbols and shorthand to state exact information in the briefest possible way to simplify recording and analysis of breeding information.

The section on notation uses the following initials as symbols.

Sex-linked Genes

St	almond
St^F	faded
B^A	ash-red
(+)	blue-black (wild type)
b	brown
d	dilution
d^P	pale
r	reduced

Autosomal Pattern Genes

C^T	T-pattern checker
C	checker
(+)	bar (wild type)
c	barless

Autosomal Structural Genes

cr	crest
p	porcupine
n	glandless

Autosomal Color Affecting Genes

G	grizzle
S	spread
e	recessive red
o	opal (recessive opal)
Od	dominant opal
my	milky
sy	smokey
In	indigo
al	albino
pd	pink-eyed dilute
g	gazzi
tr	pearl eye

It should be apparent that for the most part the symbols are just initials for the gene involved. A variety of charts are shown to indicate the many ways of clearly stating the necessary information for study or instruction.

Nomenclature-Symbols-Notation

1. Names of genes are distinguished from the symbols and written in the lower case initial letter regardless of whether the mutant is dominant or recessive; ash-red, dilution, recessive red. Ash-red, the capital "A" is used only where grammar would dictate i.e., the beginning of a sentence.

2. The symbols for genes are typically abbreviations of the name, e.g., my for milky, r for reduced, G for grizzle. The initial letter of the symbol and the name should be the same unless excepted by other rules.

3. Recessive mutations are indicated by a small initial letter, cr for crest, p for porcupine, o for opal.

4. Dominant mutations are indicated by the use of a capital initial letter for its symbol, i.c., C^T for T-pattern checker, B^A for ash-red, St for Almond (Magnani).

5. Superscripts are used for identifying remaining alleles following rules one through four; therefore the alleles at the brown locus are written B^A, + and b,for ash-red (B^A), blue-black (+), and brown (b). Alleles at the pattern locus are written following the same rules; T-pattern (C^T), checker (C), bar (+) and barless (c).

6. Wild type is designated by the symbol (+).
   In a sentence, wild type + is determined by the context. If we are speaking of recessive red (e) and + occurs, we are clearly using it for non-recessive red; if the context is about dilution and + occurs, we are clearly using it for non-dilution (i.e., intense); or wild type at the dilution locus. The locus symbol is usually the gene symbol which defines the locus with a superscript $^+$, b^+ = wild type at the brown locus i.e., blue-black; c^+ = wild type at the pattern locus, i.e., bar. I usually vary this rule to include the reverse notation which I prefer, $+^b$ and $+^c$ respectively. I often, for clarity or typed copy use parentheses. This would appear $(+)^b$ for the wild type at the brown locus, $(+)^e$, wild type at the recessive red locus. In this notebook the symbols b^+, $+^b$ and $(+)^b$ all refer to the same wild type gene, but $(+)^b$ is the preferred symbol for wild type at the brown locus.

7. Mutants of similar phenotype but of a different locus are given different names and symbols. Some confusion is caused by opal (o) and dominant opal (Od), because of the similarity of both name and phenotype. When referring to opal only o (recessive opal) is indicated. Recessive opal is linked with the pattern locus and spread (S), while dominant opal (Od) is on a separate chromosome.

8. In published articles in which symbols are used, the symbols should be set in italics.

9. We use symbols for genotype formula and written shorthand. Simplicity is the rule. In shorthand usage, typed or written sentences, I usually write linked genes in sequence; Stb for brown almond; SC^T for spread T-pattern (black) or B^Ad for ash-red dilute (yellow); whereas if they are not alleles I usually show a space between the symbols, i.e., Stb G for brown almond grizzle; B^Ad Od for ash-red dilute dominant opal. Of course in typing copy this area is prone to include many errors, so I have basically reverted to the comma for clarity. Speaking of a lavender, a word which describes several genotypes, I might follow the word lavender with (B^A, S, my my) to state clearly I mean only ash-red spread homozygous milky rather than (+, S, my my) or (B^A, S). Symbols should

not be mysterious and,though in the shorthand form (B^A, S, my my) the second my isn't necessary, I always include it if the gene is homozygous. If a couple of letters makes it clearer, I use them.

10. In common usage the / represents a chromosome and therefore tr//tr would represent a homozygous pearl-eyed bird. In the absence of other notation, wild type is assumed, that is, a pearl-eyed blue bar that carries no other mutants. In my mind simplicity must yield to clarity,so I always write it tr//tr to show both chromosomes. The ink for the extra / is cheap. To show the heterogametic sex (the hen) I simply write d/· for dilute hen, and the dot represents that hard to find (W) chromosome.

11. In writing formulas I usually begin with the sex chromosome. I generally follow the notion that it is simpler to start with what you know most about and procede to that area of doubt. Dr. Hollander consistently writes formulas several ways just to keep people like me from establishing an order that will have to be revamped when more information is available. I agree fully with Dr. Hollander on this point, but in the record book, at least initially, consistency is helpful. It is easier for me to write it the way I say it. In my formulas, the sex chromosome is followed by the autosome containing the pattern series,followed by any way the rest of the formula comes out. I make sure each set has its own two chromosomes //. $B^Ad//B^Ad$ $C^T//C^T$ e//+ my//+ G//G would describe a yellow T-pattern grizzle cock carrying recessive red and milky, or a cock homozygous for ash-red (B^A), dilution (d), grizzle (G) and heterozygous for recessive red (e) and milky (my).

12. In written text the order of dominance of alleles is often symbolized T-pattern is dominant to checker which is dominant to bar (+) which is dominant to barless at the pattern locus, thus $C^T > C > + > c$ states this. I seldom use this arrangement because I am not sure the statement is true. I found that +//c has narrower bars than normal; that C//- has more open checks than C//C; that $C^T//c$ generally shows more checkering than $C^T//C^T$. In other words, I sense a blending aspect of some sort which confuses me. Since I hate to be confused, I think of C^T as dominant to wild type, C as dominant to wild type and c as recessive to wild type and open to discussion as to their relationship to each other. I will someday put the combinations in an otherwise mutant free stock of pigeons and see whether I can't classify the following distinct groups.

1.	$C^T//C^T$	Homozygous T-pattern.
2.	$C^T//-$	T-pattern heterozygous for a less expressive allele.
3.	C//C	Homozygous checker.
4.	C//-	checker heterozygous for a less expressive allele.
5.	+//+	Homozygous bar (wild type)
6.	+//c	bar heterozygous for barless

I can already with some accuracy separate out class 3,4,5,6, and to a degree 1,2. Well, classification of phenotypes requires some precise criteria and modifiers affect the pattern expression. I would require the test stock to be free of sooty, dirty and any form of bronze.

In breeding practice, it is desirable to think of T-pattern as dominant to checker which is dominant to bar which is dominant to barless at the pattern locus and $CT > C > + > c$ is a usable aid to understanding.

13. Matings are usually symbolized by X with the heterogametic sex listed first. I recommend convenience take precedence. If I raised cattle, the breed book would show the dam first because it would be more convenient to list the cow (which I own) followed by a sire (which I probably bought in a semen cartridge). I keep my records in such a way that I find it more convenient to list cocks first:

Cock X Hen

or more appropriately : Cock, Hen } or Cock, Hen → F_1

Very often in illustration we show the pedigree using □ for male and ○ for female;

□—○ represents mating

In a pedigree we can shade the figures to show a variety of things, but for simplicity, usually just blacken symbols to show the occurrence of the gene being studied.

Example A. A homozygous(S) spread (black) cock mated to a wild type (blue) hen (obviously (S) masks bar or else pattern would be noted

S//S X +//+

F_1 S//+ S//+ S//+ S//+ → all black

F_2 S//S S//+ S//+ +//+ → 3 black, 1 blue (non-spread)

Phenotypic ratio 3:1

or

1 homozygous spread (black)
2 heterozygous spread (black) Genotypic ratio 1:2:1
1 homozygous wild type (blue)

Example B.

colored figures.....black
white figures.....blue

P - Parental Generation

F_1 - 1st Filial Generation

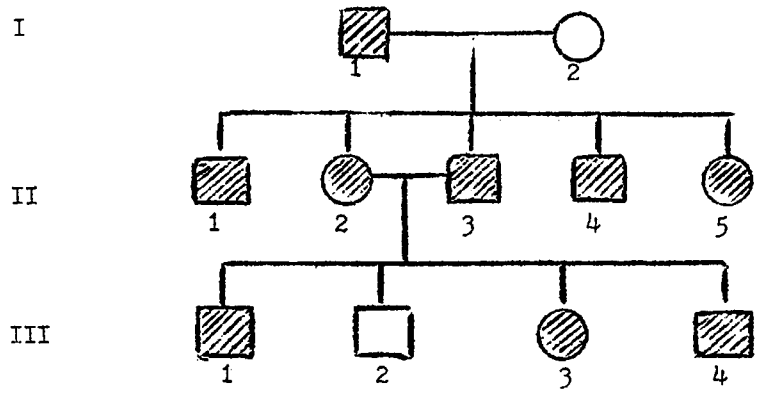
all black

F_2 - 2nd Filial Generation

3 black, 1 blue

I raised the progeny to eight to show both the blue cock and blue hen produced. An actual pedigree would show what occurred, not the ideal. Using such diagrams are purely instructional.

Example C. While being educational we sometimes prefer to show what's going on in the cross and revert to this type of graphic illustration:



Roman numerals are used for the generations.

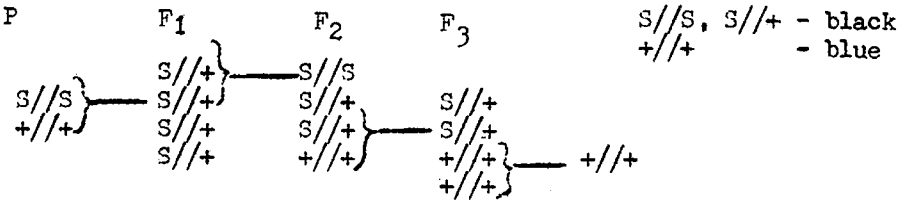
I	-	Parental	Individuals in the pedigree
II	-	F_1	all receive Arabic numerals
III	-	F_2	within their generation.

I, 1 is our original black cock
II, 4 is a black cock the 4th hatched from this mating in the F_1 generation.
III, 2 is a blue cock, the second hatched from the mating of II,2 X II,3 in the F_2 generation.

We often symbolize a bird ◇ for sex unknown and occasionally place a pointing finger or arrow at some key individual in the pedigree chart.

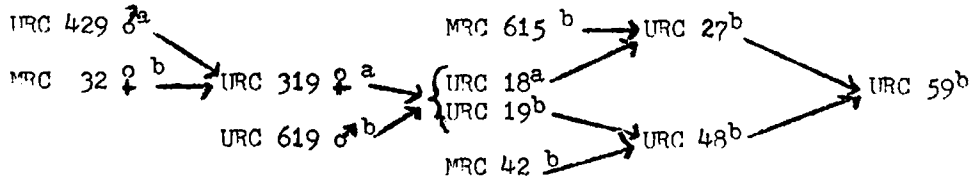
I realize this is all very wonderful, but it is a creative not a scientific art. Anything is acceptable in symbols that gets the point across. The working geneticists usually simplifies all this using an ⟶ to indicate produces, yields, results in and shows the pedigree from left to right.

Example D.



or rather precisely by listing the band number of the bird properly identified in the study using arrows to describe whatever mating complexities are involved.

Example E.



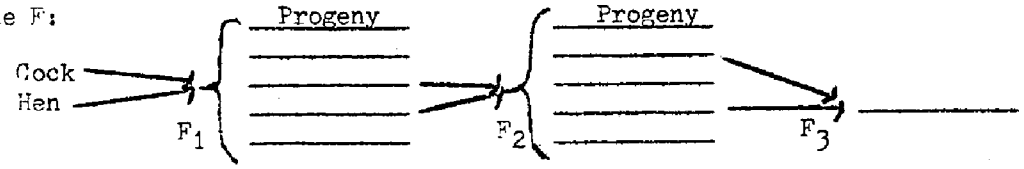
Certain mutants may be labelled (coded) a, b, c, d, etc. and added to the diagram; for example a = wild type
b = barless

In addition to the convenience of being able to show a variety of matings, back-crosses, outcrosses and filial generations on the same diagram, it becomes a working history of a family.

With a little care an entire loft pedigree can be shown on a single large sheet. The arrowed lines can be drawn any way, just as long as they indicate the proper progeny.

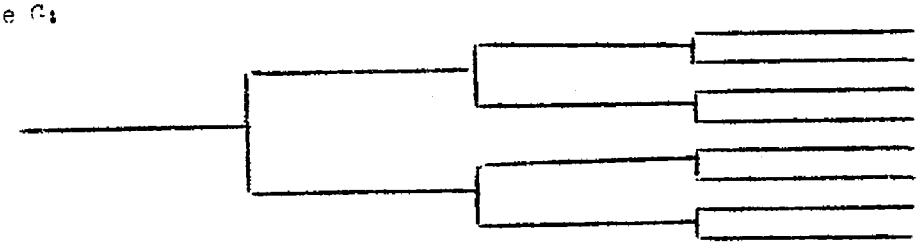
If desired ——→ may represent from the sire and - - - - → from the dam to give an even more elaborate working pedigree. I use "working" as a term because it makes analysis of many genetic aspects easier. I have found it takes some artistic (at least placement) ability to make the more complex charts readable. I suggest...

Example F:



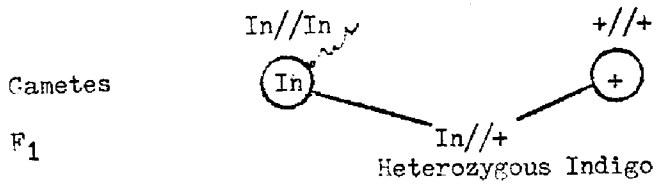
Those interested in recording illustrious ancestors have found the right to left type of chart more convenient, at least most of the printed forms are in this order. Note that in the suggested form it is possible to trace other relatives and various other progeny of a given set of parents.

Example G:



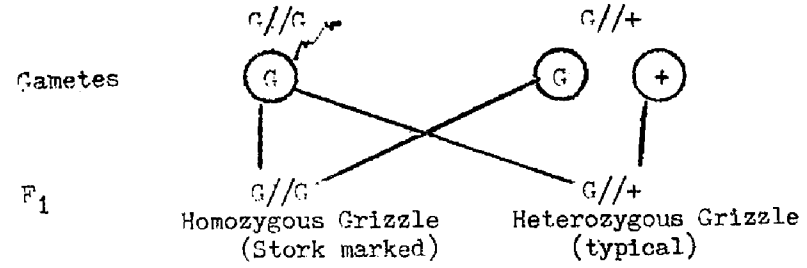
Matings may be shown to include gametes:

Example H: P Homozygous Indigo Cock X Wild Type Hen



This is a little more descriptive in the science and preferred in this notebook:

Example I: Parents Homozygous Grizzle X Heterozygous Grizzle



In Examples H and I, an autosomal dominant gene is involved and the homozygous individual is recognizable as such by the phenotype. In Punnet Squares (the checkerboard) it looks like this:

Ex. H.

Female Gametes
Homozygous Wild Type

Male Gametes Homozygous Indigo	+	+
In	In//+	In//+
In	In//+	In//+

All indigoes heterozygous for wild type at that locus.

(sex not a concern)

If we had an F_2 generation it would be:

In//+ X In//+
Female Gametes
Heterozygous Indigo

Male Gametes Heterozygous Indigo	In	+
In	In//In	In//+
+	In//+	+//+

3 indigoes
1 wild type
Phenotypic ratio 3:1 but In//In is quite a different coloration from In//+ and the result is that the phenotypic ratio becomes 1:2:1 which is the genotypic ratio.

Ex. I.

Homozygous Grizzle X Heterozygous Grizzle
G//G G//+

Male Gametes = ♂ or ♂
Female Gametes = ○ or ♀

Female Gametes
Heterozygous Grizzle

This situation is not typical for dominant genes but it illustrates modified phenotypic ratios at a base level.

Male Gametes Homozygous Grizzle	G	+
G	G//G	G//+
G	G//G	G//+

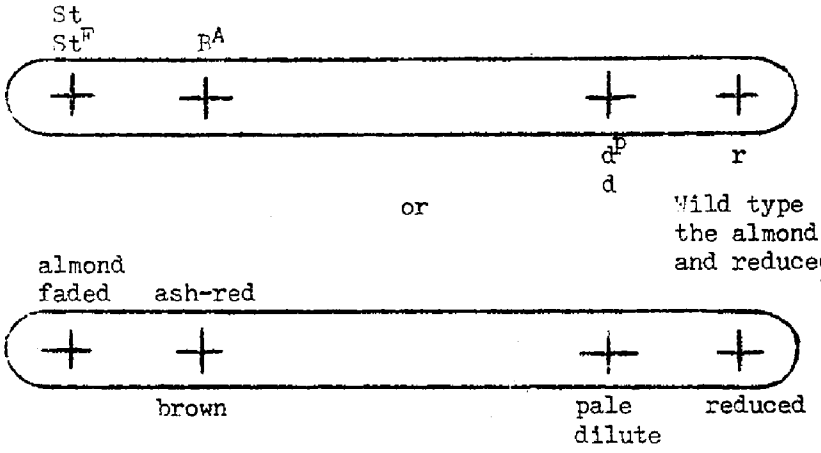
All grizzles but it should be noted that the phenotypes will be 1:1 because grizzle, like indigo, can usually be classified phenotypically on the basis of genotype.

G//+ is typical grizzle, G//G is nearly white with smooth spread areas (ends of flights and tail feathers) showing little depigmentation, and the stork marking

The following chart for the segregation of two genes on different chromosomes segregating independently might help. In this case a barless milky is mated to wild type. Milky and barless are simple autosomal recessives and not on the same chromosome.

Phenotypes	
9 blue bar	
3 barless blue	Phenotypic ratio : 9:3:3:1
3 milky bar	
1 milky barless	(Chart on next page)

We have postulated, the sex chromosome arrangement as:

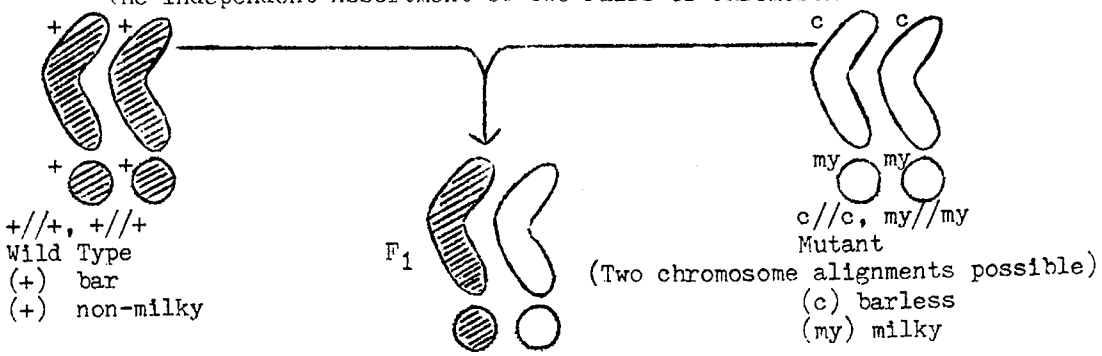


Of course we have not established the order; almond and brown are closely linked (possibly 2% crossovers) and dilute and reduced are similarly close to each other. (possibly 7% crossovers). We have established that these points on the sex chromosome are quite distant from each other and a rather consistent crossover rate of 38 to 40% has been established between the brown and dilute locus. It should be obvious that in order to clarify order (to map) this chromosome we need a sex-linked gene somewhere between these two sets of genes.

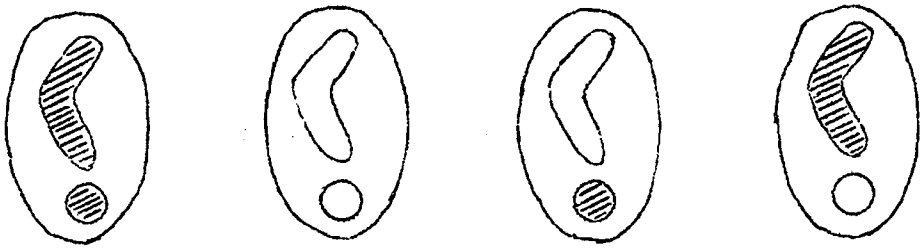
If we were to write the possible genotypes possible for a single sex chromosome, we could begin with the almond locus. The almond mutation first occurred in a blue-black pigeon, and it can be assumed that 99+% of the existing almonds are blue-black almonds (Magnani). Of the genes on the sex chromosome, I would list wild type (+), ash-red (B^A) as very common and widely distributed in the domestic pigeon world. Dilution (d), brown (b), almond (St), and faded (St^F) are relatively common mutants, while pale (d^p) and reduced (r) are extremely rare. I have indicated with * the combinations I have not observed. An identical set can be made for faded (St^F) as was done in a color booklet by Bob Clark. Faded and almond are allelomorphs (alleles) and by definition are alternative forms of a gene at the same locus. By merely substituting this alternative (St^F) for (St) in the genotype the set of possibilities for faded is complete.

(Note Page 35)

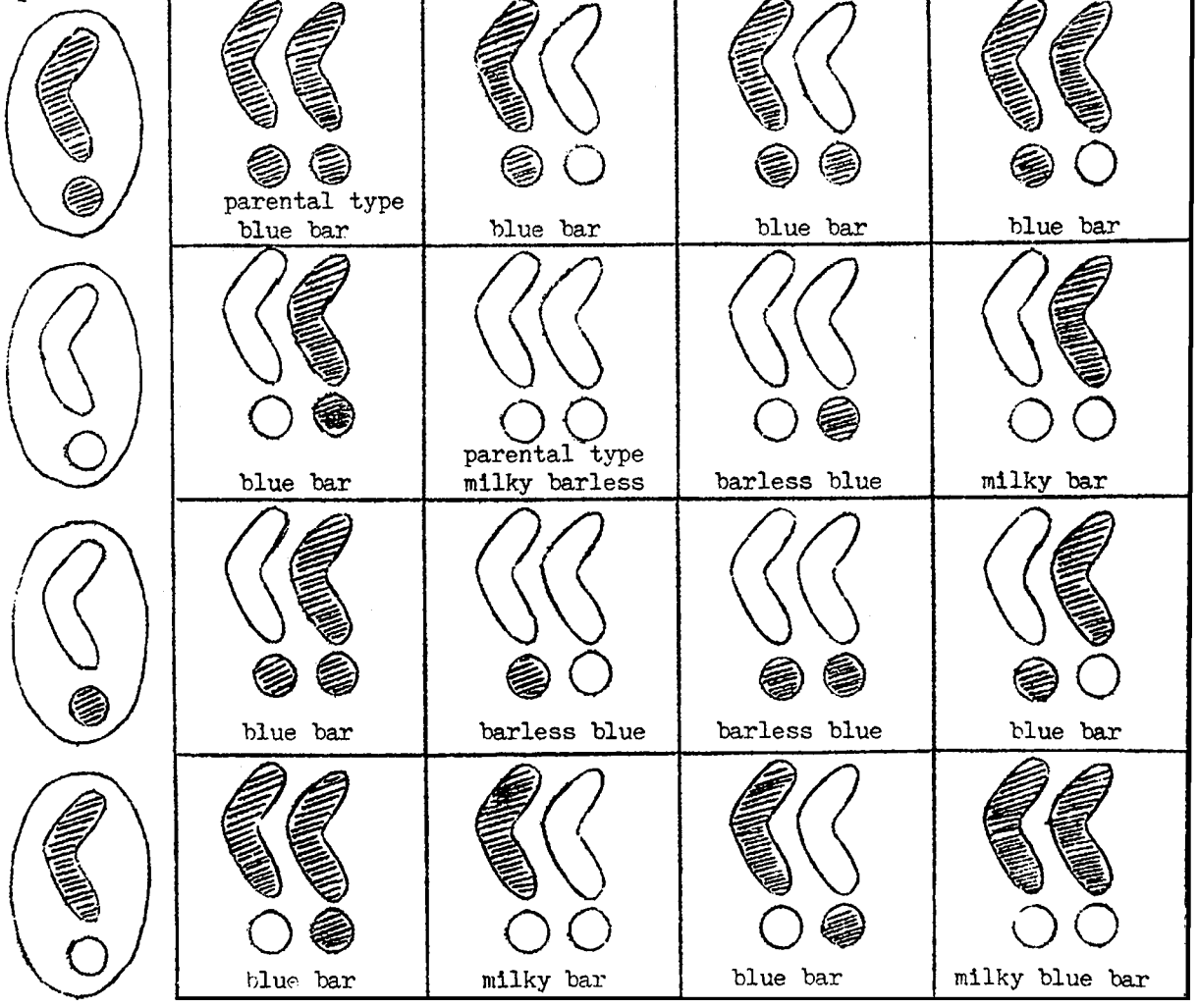
The Independent Assortment of Two Pairs of Chromosomes



F_1 Gametes



F_1 Gametes



Possible gene arrangement on a single sex chromosome of the pigeon:

St	almond	
Std^p	pale almond *	almost all almonds are
Std	dilute almond	(+) wild type at the
Str	reduced almond	brown locus (blue-black
Std^pr	pale reduced almond *	almonds)
Stdr	dilute reduced almond *	
St^{B^A}	ash-red almond	(because of the tight
$St^{B^A}d^p$	pale ash-red almond *	linkage between (St) and
$St^{B^A}d$	dilute ash-red almond	(b) only a few ash-red
$St^{B^A}r$	reduced ash-red almond *	almonds exist)
$St^{B^A}d^pr$	pale reduced ash-red almond *	
$St^{B^A}dr$	dilute reduced ash-red almond *	
Stb	brown almond	(because of the tight
$Stbd^p$	pale brown almond *	linkage between (St) and
Stbd	dilute brown almond	(b) cnly a few brown
Stbr	reduced brown almond *	almonds exist.)
$Stbd^pr$	pale reduced brown almond *	
Stbdr	dilute reduced brown almond *	

* phenotypes that I have not observed

At the brown locus $(+)^b$ there are three alternatives; ash-red (B^A), wild type (+) and brown (b). The possible genotypes for a single sex chromosome are:

B^A	ash-red
B^Ad^p	pale ash-red
B^Ad	dilute ash-red (ash-yellow)
B^Ar	reduced ash-red
B^Ad^pr	pale reduced ash-red *
B^Adr	dilute reduced ash-red
+	blue-black, wild type
d^p	pale
d	dilute (silver, dun)
r	reduced
d^pr	pale reduced *
dr	dilute reduced
b	brown (chocolate)
bd^p	pale brown
bd	dilute brown (khaki)
br	reduced brown
bd^pr	pale reduced brown *
bdr	dilute reduced brown

Symbolically and notation wise this is the extent of complexity for sex-linked genes at present. The hemizygous hen could be described by any of the listed genotypes and cocks could be described by any two of the listed genotypes. All domestic pigeons have a gene for ash-red, blue-black or brown in hens and a combination of any two in all cocks. These three colors can be altered by reduction of pigment granules in both number and size by (d) dilution, (d^p) pale, and (r) reduced---- or altered by the "overprinting", "flecking-oriented" mutations of (St) almond and (St^F) faded.

Sex-linked Pigeon Colorations

Basic pigeon colors are usually limited to the consideration of three color producing sex-linked genes. Ash-red, blue-black, and brown are probably very ancient mutations. Our present information describes four mutational points on the pigeon sex chromosome:

"Known Mutations on the Sex Chromosome"

Locus 1	Locus 2	Locus 3	Locus 4
(St) almond	(B^A) ash-red	(d) dilution	(r) reduced
(St^P) faded	(b) brown	(d^D) pale	

At the known mutation positions, alternatives to wild type at that point are extablished by the gene change.

The vast array of colors found in domestic pigeons would indicate that we are studying a very complex topic. Actually the changes (mutations) from wild type are rather rare and several dozen mutants would represent a rather complete study of known differences from wild type.

Pigeon Colors Determined By Genes on the Sex Chromosome

Blue-black Colorations (+)

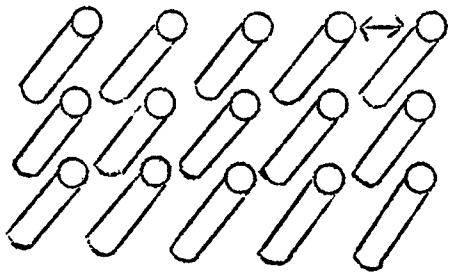
The wild type Columba livia is slate gray and shades to metallic blue-black in the head, neck and smooth spread areas (ends of flights and tail). It is the base for all comparisons, the standard against which changes are measured and therefore the basic test mating for unknown colorations. Blue-black is generally used in place of blue in an attempt to clarify the problem of pigment arrangement.

Pigment Arrangements

Melanin is black and the rod-shaped granules are arranged very precisely. If the microscopic granules are arranged in spread fashion, the color will appear black. The granules are usually rod-shaped in blue-blacks and are placed parallel to the long axis of the barbule of the feather.

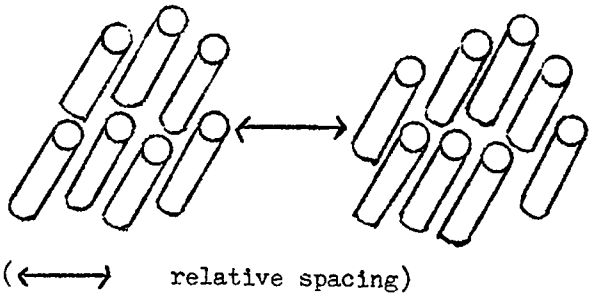
Spread Arrangement

Black



Clumped Arrangement

Blue



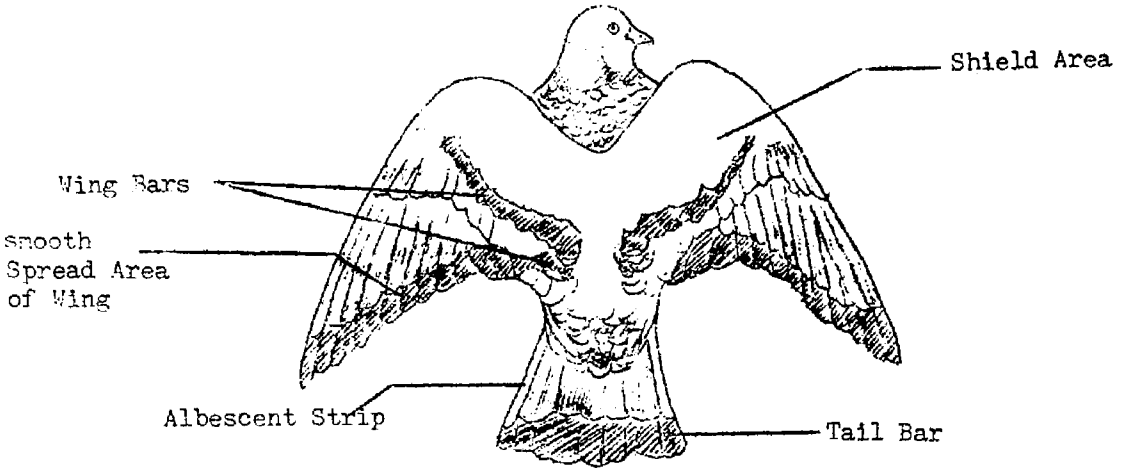
(⟷ relative spacing)

If the granules are arranged in clumped fashion the light is reflected differently and what we see appears blue-gray.

The pigment arrangement is the same for ash-red, blue-black and brown pigeons, but the shape of the granule is altered in red and brown.

Blue Bar

Blue barred pigeons have a gray shield with two clear black bars originating in the secondaries and extending across the wing.



Blue pigeons have a broad black bar extending across the end of the tail. It can be stated since many color mutants do not affect the smooth spread areas (ends of flights and tail), that the tail is a good guide to the basic genotype of a bird, regardless of the other mutants present. The bronze Modena, Hyacinth or Spangled Ice Pigeon are very highly colored, but exhibit a rather normal blue tail, and are genetically wild type.

Blue pigeons typically:

1. Are dark-skinned and heavy-downed in the nest.
2. Are orange-red eyed.
3. Have horn-colored beak and toenails.
4. Are noticeably lighter in color in adult plumage, with cocks being detectably lighter than hens.
5. Have a white albescent strip on the outer edge of the outer-most tail feathers.

Blue pigeons come in all patterns:

1. Blue T-patterns (C^T), often called blue-tailed blacks or black velvets, when other richening modifiers like bronze or dirty are also present in the genotypes.
2. Blue Checkers ---neat "spitze" or arrowhead patches of blue outlined in black in the shield area.
3. Blue bar ---wild type.
4. Blue barless ---colored as in bar, but without any black pigment sho in shield area.

Gradation in blues with added factors is endless. Blue, like other colors, vary in intensity and hue due to modifiers. Good rich blues are as much of a challenge to produce as any other color.

Common or feral pigeons are mostly wild type blue-blacks.

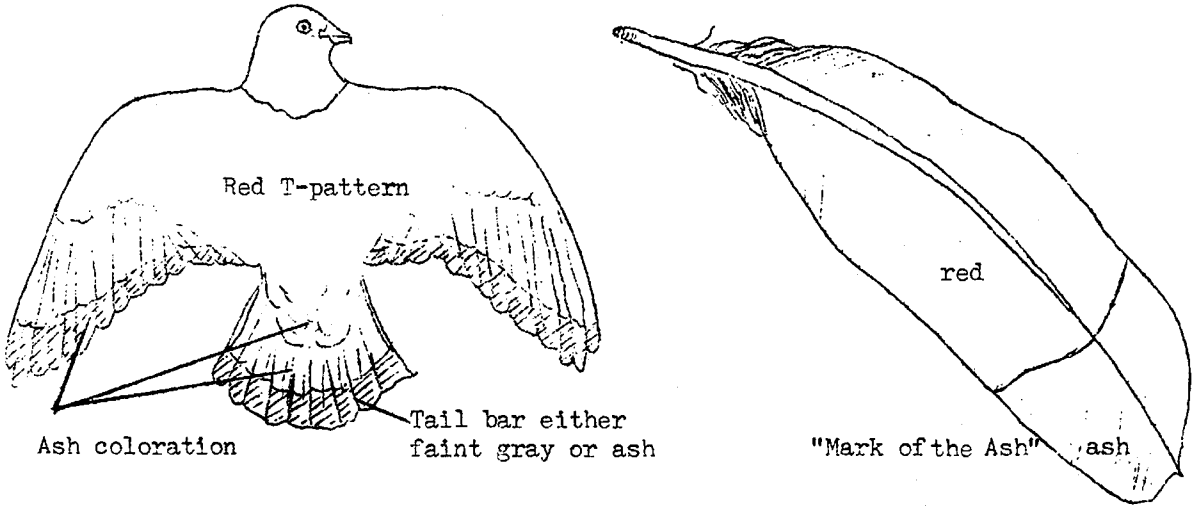
Ash-red Colorations (B^A)

Ash-red is a dominant mutation, that is, the gene producing blue-black became altered is some way to produce a new effect. Since the wild-type gene was changed, the new mutant (ash-red) occupies the same location on the chromosome, as does blue-black. Once produced, it becomes an alternative to blue-black. We call such alternative genes, alleles. In matings to blue-black, the new mutant (B^A) has been shown to be dominant to blue-black.

The pigmentation granules of red are the same basic melanin, but differ in shape. I often state, it is as if the typical granules have been compressed to form irregular balls of pigment. These larger appearing granules are called phaeomelanin, while the normal rod-shaped granules are called eumelanin. Eumelanin appears blue or black depending on arrangement,while phaeomelanin appears brown to red depending on pigment arrangement.

Initially the term dominant red was used for this facter, but W.F. Hollander wisely chose the name ash-red, because of the characteristic washing out to ashy or ashen coloration associated with the gene.

Ash-reds wash-out to gray (ash) towards the tail and ends of the flight feathers. This so-called "mark of the ash" is a reliable identification clue.



Ash-reds represent the rare condition where a mutant appears to be an improvment over wild-type. Generally mealies and red checks are very tight feathered, somewhat superior in feather quality to wild type blues.

Ash-red Bar

The mealy or misnamed "red-bar silver" is usually red-brown in head and neck, light gray in the shield with two red-brown wing bars. The tail bar is lacking due to the washing effect of the mutant.

When color is expressed in the tail it normally is from the feather quill outward. Dark tail feather shafts with ashy ---off-white webbing are typical of ash-reds of all patterns.

The bars and checkers of ash-reds are generally less distinct (smeary) than the pattern examples in blue-black or brown.

The clumped or spread arrangement of pigment is identical to that of blue-blacks.

Patterns in ash-red involving distribution of pigment are the same as in blue-black.

Ash-red: Mealies, red checkers and red T-patterns (or velvets) are common in many breeds.

Brown Colorations (b)

Brown is a recessive mutation to wild type. In this mutation the gene producing blue-black was changed in a different manner, producing a new effect. The occurrence of black and brown, as alternatives (alleles), is found in many higher animals besides pigeons. In a fashion similar to that noted with ash-red, the rod-shaped eumelanin granules are altered in shape to form phaeomelanin, the brown-red producing granules. It should be understood that in both eumelanin (blue-black) and phaeomelanin (red-brown), the basic pigment is still melanin (black); the change in appearance is an optical effect rather than a change of the basic pigment.

The brown pigeons are often confused with dun-colored pigeons. Dun is dilute black and short downed in the nest, whereas brown is normal downed.

Browns occur in the same patterns of clumped and spread pigment as found in blues. The patterns of browns are clear and distinct as in blues.

The coloration of brown varies but approaches chocolate in most phenotypes, whereas dun approaches gun metal (bluish-brown) in most phenotypes. In general, brown pigeons fade markedly if allowed access to open sunlight. This is a matter of degree because the bleaching effect of the sun is noted for most colorations in pigeons.

Brown pigeons seldom have orange eyes (wild type) because the mutant affects certain aspects of iris pigmentation producing a creamy white "pearl-like" eye coloration. This so-called "false pearl" eye is a good identification clue for brown.

Review of Basic Colorations

The wild type gene producing blue-black has mutated twice. Once to produce the dominant alternative to blue-black we call ash-red, and once to produce a recessive alternative to blue-black we call brown. Since these alternatives can only fit in one place (locus) on the sex chromosome, then only one of them can be present on any single sex chromosome. In pigeons, the female has only one sex chromosome, and it will carry one of these alternatives producing only three types of female pigeons. All female pigeons are either ash-red, blue-black or brown. They can not carry another basic color gene hidden because they have no other sex chromosome to carry it on. Cocks, of course, have two sex chromosomes and therefore can have two of the alternative basic sex-linked color genes just because they have two sex chromosomes. There are only three basic color genotypes for hens: ash-red ($B^A/\cdot$), blue-black ($+/\cdot$) and brown ($b/\cdot$). The cocks can only be

Formula	Genotype	Phenotype (Appearance)
$B^A//B^A$	Homozygous ash-red	Ash-red (no flecks)
$B^A//+$	Ash-red carrying blue-black	Ash-red (black flecks)
$B^A//b$	Ash-red carrying brown	Ash-red (brown flecks)
+//+	Homozygous blue-black (wild type)	Blue-black
+//b	Blue-black carrying brown	Identical to +//+
b//b	Homozygous brown	Brown, chocolate

Sex-linked Dilutants

Dilution (d)

At some distance from the brown locus $(+)^b$, another gene mutated producing a reduction in both the size and number of the pigment granules to about 1/3 normal (intense) coloration. We call this new change (mutant) dilution, and symbolize it (d). This recessive sex-linked gene, dilution (d), in the presence of the normal (intense) gene, is completely hidden. Cocks have two chromosomes and a blue cock carrying dilution on one chromosome appears normal blue (+//d). In order for a cock to show dilution, it must be homozygous for this recessive gene (d//d). In the hemizygous hen, with one chromosome, if (d) is present there can be no other alternative also present, therefore (d/·) represents a dilute hen. Because the hen can not carry another alternative of any sex-linked gene, "she is what she is", and this accounts for the great number of dilute hens compared to a fewer number of dilute cocks.

The dilution effect is to make a "half-tone" copy of the original coloration. A typical blue bar becomes a true silver. Dilution on an ash-red checker produces an ash-yellow checker, and in combination with brown produces khaki or drab. Dilution is very appropriately named ---imagine a black velvet ---dilute the pigment to 1/3 and imagine a dun velvet. Dilution is a real alternative to normal coloration (intense), and adds greatly to the varied beauty of domestic pigeons.

Pale (d^p)

At the same point (locus) at which the normal gene (intense) mutated producing dilution, at another time, mutated again to produce another alternative to fit in this one space on the sex chromosome. This new change was also recessive to wild type (intense) and produced an intermediate effect between wild type and dilution. Pale is a very rare gene, with few examples in the pigeon world. The difference between Dark Bronze, and Light Bronze Archangels is simply a difference in replacing wild type with pale at this dilute $(+)^d$ location. Light Bronze Archangels are homozygous pale ($d^p//d^p$) in cocks and hemizygous pale ($d^p/·$) in hens.

Pale is quite beautiful in combination with ash-red and produces "orange". In the various patterns, pale and ash-red make a striking combination. In combination with brown (b) and wild type $(+)^b$, the effect is rather ordinary. Pale is a good name choice; pale blues and pale browns are just that, somewhat lightened blues and browns.

Review

The series of alternatives at the dilution locus includes wild type $(+)^d$, pale (d^p) and dilution (d). All hens will have one of the alternatives on her one sex chromosome, and all cocks will have any combination of two dilutant genes. All hens are either intense $(+)^d$, pale (d^p) or dilute (d). There are only three types of hens with respect to this locus: (+/·), (d^p/·), (d/·).

The cocks can only be:

Formula	Genotype	Phenotype (Appearance)
+//+	Homozygous wild type (intense)	Normal
+//d	Intense carrying dilution	Same as +//+
+//d^p	Intense carrying pale	Same as +//+
d//d	Homozygous dilute	Ash-yellow, silver, khaki
d//d^p	Dilute carrying pale	Similar to d^p//d^p
d^p//d^p	Homozygous pale	Orange, pale blue or brown

Reduced (r)

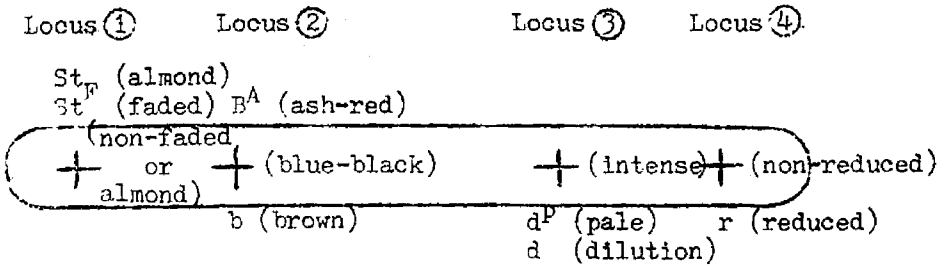
Reduced (r) is a sex-linked recessive mutation discovered by Carl Graefe. It represents a change from normal at a place close to the location of the dilution series. As only one mutation is known at this point, we have reduced and non-reduced as alternatives to fit this location on the sex chromosome. Because reduced has a variable dilutant effect which produces a host of striking pastel pink and buff colorations, it will be discussed in a separate section.

All female pigeons are either reduced or non-reduced at this locus on their one sex chromosome. With respect to this locus, there are only two kinds of hens; wild type (+/·) and reduced (r/·).

The cocks can only be:

Formula	Genotype	Phenotype (Appearance)
+//+	Homozygous non-reduced (wild type)	Normal
+//r	Wild type carrying reduced	Same as +//+
r//r	Homozygous reduced	A variety of beautiful phenotypes

In this major section we have put together a tentative map of the pigeon sex chromosome. On the basis of evidence, we know that from the thousands of genes along its length, four genes have mutated producing alternatives (alleles) to fit that location (locus). These four sets of alleles have been tentatively mapped as follows:



Locus 1	almond (St), faded (St^F), non-faded or non-almond (+) wild type.
Locus 2	ash-red (B^A), blue-black (+) wild-type, brown (b).
Locus 3	intense (+) wild type, pale (d^p), dilution (d).
Locus 4	non-reduced (+) wild type, reduced (r).

Throughout the course of the notebook we will refer to this suggested map of the sex chromosome of the pigeon.

For simplicity, we have three basic sex-linked colors for pigeons. These three colors can be affected by two mutations called faded and almond. These two factors have an "overprinting", "flecking oriented" effect on the basic colors. The basic colors can be affected by two dilution factors (dilution and pale) which reduce the size and amount of pigment producing "half-tone" copies and lastly, reduced produces a variable dilutant effect to produce pastels of these basic colors.

Every pigeon has a gene at each of these places, sites of mutation, called loci. We have named these places:

1. The almond locus $(+)^{St}$
2. The brown locus $(+)^{b}$
3. The dilute locus $(+)^{d}$
4. The reduced locus $(+)^{r}$

Through the mechanism of crossing-over, possible for sex-linked factors in cocks which have two sex chromosomes, a pigeon may be created to carry any combination of alternatives at these four locations (loci). A dilute reduced brown almond is possible, but has not yet been produced. There are thousands of challenges left to be worked out using natures' mechanism for change and variation.

All basic colors can be combined with other mutant genes on the same (sex) chromosome. Three other sets of alleles are known to exist on this chromosome. The first set, located very close to the basic color gene set is the almond, faded and non-almond set. At another location very distant from these two sets is another two sets of alleles. Reduced and non-reduced form one set and intense (wild type), dilute and pale make up the other.

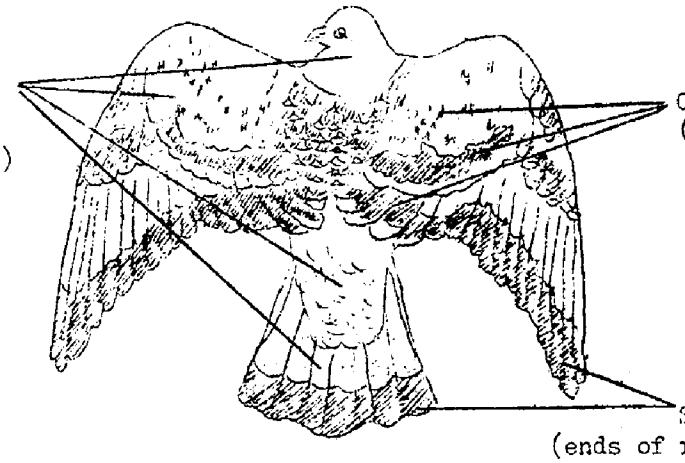
The almond, faded set are taken up in separate sections. These "overprinting" or "flecking" mutations can occur in combination with ash-red, blue-black and brown.

Having taken a brief look at the sex-linked genes, it is now necessary to explore more thoroughly the other 40 pairs of chromosomes and the known genes they contain.

Pigmentation Areas

We have been using the term smooth spread to describe the heavily pigmented ends of the flight feathers (remiges) and the tail bar. It was Dr. W.F. Hollander that first described the peculiar way in which some mutations affect the blue, smooth spread and coarse spread areas. Under the microscope there is little difference in these areas, other than the clumping-spread arrangement previously described. The selectivity of mutations to affect these areas in different ways is an observable fact. Dr. Hollander's description represents a valuable and easily learned guide to identifying many mutant genes.

Pigmentation Areas



Example 1:

Modena bronze ($\underline{K^M}$) affects primarily coarse spread pigment. The rich bronze of T-pattern, tri-color (checker) and bronze bar (wild type) all show this color variation in the wing shield. With the exception of a slight grizzling near the shafts of flight feathers, the remaining areas of blue and smooth spread are little affected and appear normal for the basic coloration of the bird.

Example 2:

Grizzle (G) affects coarse spread pigment, with a strong tendency to also affect blue areas, producing irregular white flecking in the head and neck and shield feathers. Acting as a partial dominant, G//+ is the typical grizzle of the Dragoon. In homozygous grizzles G//G, the blue and coarse spread areas are depigmented toward white, but the smooth spread areas remain near normal to produce a near white with black edges on flight feathers, and a black band on the tail; i.e., the "stork marked" grizzle.

Example 3:

Archangel bronze ($\underline{K^A}$) affects primarily the blue (clumped areas) of pigmentation. The rich lustrous bronze of the head, neck, breast and underparts has a metallic sheen. The coppery coloration in the same areas of the Light Bronze Archangel is produced by the sex-linked factor pale, but the ($\underline{K^A}$) mutant shows little affect on either coarse or smooth spread areas.

Example 4:

Shikli Ahmar (the red of Lebanons) ($\underline{k^1}$) genetically appears ash-red (B^A), T-pattern (C^T) and modifiers that produce the saturated T-pattern or red velvet. This mutation of Lebanons bleaches the smooth spread areas from ash to white and produces a rich red pigeon with wings and tail edged in white.

Review:

Pigmentation areas are affected differently by some mutations. Some mutants, such as dilution (d), affect all areas in similar fashion producing the "halftone" copy. Example 1, Modena bronze, affects primarily coarse spread pigment. Example 2, Grizzle (G), affects coarse spread pigment, but also affects to a marked degree the blue areas. Example 3, Archangel bronze affects primarily blue areas. Example 4, the Shikli Ahmar red mutation, affects primarily smooth spread pigment. This curious situation of differing mutational effect, provides for easier identification of mutants, and also a more accurate means of their description.

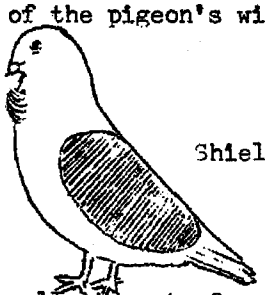
Note:

The (_) in the symbols ($\underline{K^M}$), ($\underline{K^A}$), and ($\underline{k^1}$) indicate that the exact genetic nature of these mutational bronzes has not been worked out.

Basic Patterns of Pigmentation

In addition to the basic sex-linked colorations, all pigeons have a specific pattern for the arrangement of the clumped and spread pigment. The genetic determination of pattern may be masked or altered by other genes, but the pattern genotype remains unchanged in such birds. A recessive red self which shows no pattern, because recessive red is epistatic to pattern (masks pattern), is just as truly a T-pattern, checker, bar or barless, as when these patterns are expressed in the phenotype.

In this section we will use the Punnett Square (checkerboard) method for explanation of matings, to give the reader practice in the use of this valuable tool of the breeding art. The pattern locus has four alternatives (alleles) for pigment arrangement in the coarse spread area. Coarse spread pigment is the black areas of bars and checkers, which occurs in the shield portion of the pigeon's wing.



Shield Area

I use the term shield, to include secondaries and wing coverts; the area of pigmentation on shield pigeons and turbits, or the area of white on a Whiteside tumbler.

The allelic set of pattern genes as generally stated; $C^{T} > C > +^{c} > c$, or T-pattern is dominant to checker, which is dominant to bar, which is dominant to barless. We will begin with the recessive gene producing barless (c), and proceed up the scale of dominance for pattern genes. In the absence of other notation, wild type is assumed in all formula. Therefore, all diagrams in this section refer to blue-black.

Barless (c)

Barless is a recessive autosomal (not sex-linked) mutation which eliminates any coarse spread pigment in the wing shield area. As the name implies, barless is a typical blue without the two distinctive black bars on the wings. As an allele of bar $(+)^{c}$, it is an alternative to bar at that point (locus) on this chromosome.

All barless pigeons have the genotype c//c.

Matings of barless to barless:

		Female Gametes c	Female Gametes c
Male Gametes	c	c//c	c//c
	c	c//c	c//c

All progeny barless

A pair of barless can produce nothing but barless offspring, except in that extremely rare case of a mutation. Any progeny of another pattern from such a mating can be considered illegitimate.

Bar $(+)^c$

$(+)^c > c$, Bar is wild type at this locus. It has been shown to be dominant to barless, and recessive to checker and T-pattern.

Matings of bar to barless:

This is often called a test cross, to determine if the barred bird carries barless. The barred bird has two possible genotypes +//+, +//c, and the barless can have only one genotype c//c.

If homozygous bar +//+, then +//+ X c//c will yield:

Homozygous bar Gametes \ Homozygous barless Gametes	c	c
+	+//c	+//c
+	+//c	+//c

All bars heterozygous for barless +//c

All progeny produced by a mating of any pattern to barless will carry barless.

If +//c, then +//c X c//c will produce:

Bar carrying barless Gametes \ Barless Gametes	c	c
+	+//c	+//c
c	c//c	c//c

2 bars
2 barless

1:1 Phenotypic Ratio

As expected, from a test cross to a homozygous recessive bird, when the bird being tested carries the hidden recessive, the result is a 1:1 ratio of progeny of the dominant and recessive types.

A pair of barred birds can on rare occassions produce a barless offspring in a mating of two carriers; +//c X +//c.

Matings of bar to bar:

A barred bird may have two genotypes; homozygous bar +//+, and bar carrying barless +//c. Any offspring, not barred, from such a mating, will be barless and the complete genotype of the parents is then known for this locus.

Bar Gametes - 2 possible genotypes

Homozygous bar

Homozygous bar \ (A)	+	+
+	+//+	+//+
+	+//+	+//+

Bar carrying barless

(B)	+	c
+	+//+	+//c
+	+//+	+//c

Bar Gametes - 2 possible genotypes

Homozygous bar

Bar carrying barless		+	+
	+	+//+	+//+
	c	c//+	c//+

Bar carrying barless

		+	c
	+	+//+	+//c
	c	c//+	c//c

Section A ---both parents +//+, can only produce +//+, all homozygous bars.
Section B ---all barred offspring; c is recessive to $(+)^c$.
Section C ---the same arrangement as B ---all barred progeny; c is recessive to $(+)^c$.
Section D ---The one single barless produced out of four offspring clearly indicates both parents must be c//+, and we can expect this mating to continue to produce 3 bars to 1 barless. The 3:1 ratio is expected for the segregation of a simple recessive factor, in this case barless (c).

All checkered or T-pattern offspring of a barred pair can be considered illegitimate.

Checker (C)

Checker is a dominant mutation at the pattern locus. It is an alternative to bar, therefore an allele. A checker can have three genotypes; homozygous checker C//C, checker carrying bar C//+, and checker carrying barless C//c. In a mating of checkers, it should be apparent that unless the complete genotype is known, C//? will have to suffice, until breeding tests yield the necessary information.

Matings of checkers to barless:

We will combine the charts of the three possible checker genotypes with one barless genotype.

Parental Gametes
Barless c//c

Parental Gametes
Checker C//C

	c	c
C	C//c	C//c
C	C//c	C//c

All checkers C//c

(All carrying barless)

	c	c
C	C//c	C//c
+	+//c	+//c

Checker carrying bar C//+

$\frac{1}{2}$ checkers, $\frac{1}{2}$ bars

(All carrying barless)

Checker carrying barless C//c	Barless c//c (C) c	c
C	C//c	C//c
c	c//c	c//c

½ checkers, ½ barless

(All progeny either barless or carrying barless)

Section A ---indicates checker is homozygous C//C, as no barless or bars are produced.
Section B ---indicates checker is heterozygous for bar C//+.
Section C ---indicates checker is carrying barless C//c.

Barless represents the test cross,i.e., the homozygous recessive and the 1:1 ratio in B and C are as expected, and identify the pattern gene in the formula C//? for a random checker.

Matings of checkers to bars:

We will combine the charts for the three possible checker genotypes with the two possible bar genotypes. In this case, C//? X +//?, indicates we don't know the other allele in each pair. In C//?, the (?) can be C, +, c, but in +//?, the (?) can only be + or c.

Parental Gametes Bar

Parental Gametes Checker

Homozygous Checker C//C	Homozygous bar +//+ (A) +	+	Bar carrying barless +//c (B) +	c
C	C//+	C//+	C//+	C//c
C	C//+	C//+	C//+	C//c

Checker carrying bar C//+	(C) +	+	(D) +	c
C	C//+	C//+	C//+	C//c
+	+//+	+//+	+//+	+//c

Checker carrying barless C//c	(E) +	+	(F) +	c
C	C//+	C//+	C//+	C//c
c	c//+	c//+	c//+	c//c

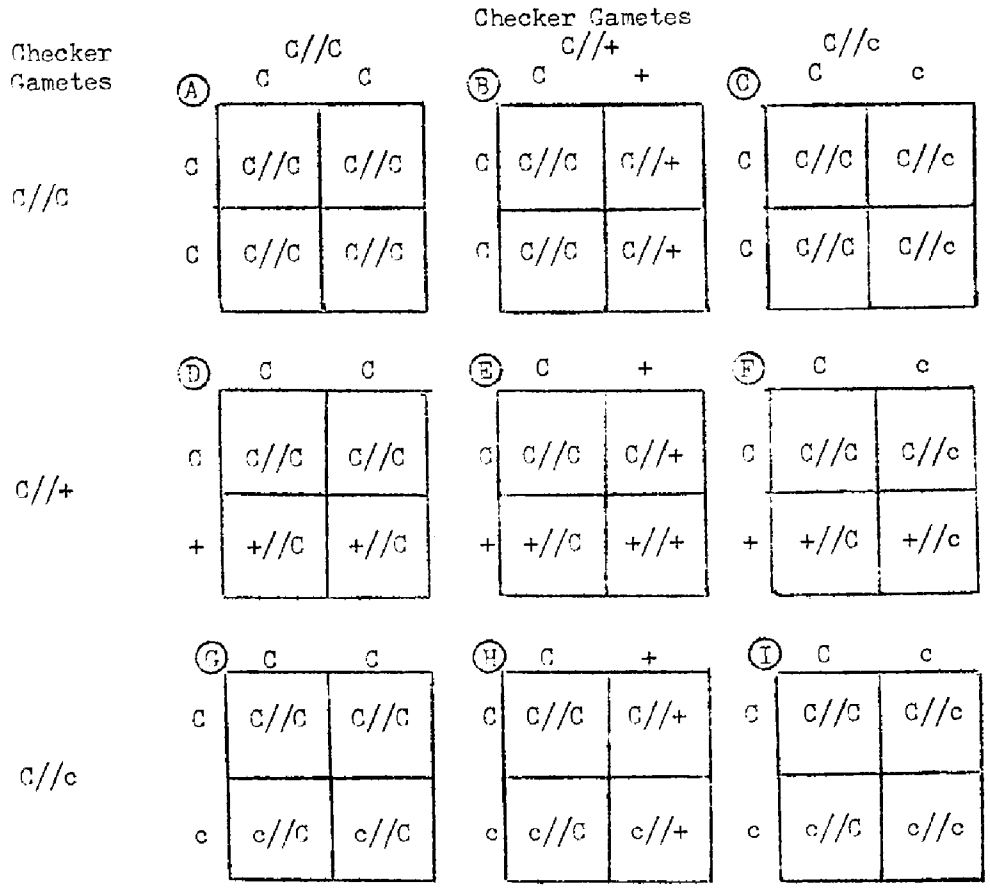
Section A and B ---indicate the checker is homozygous C//C, as no bars or barless are produced.

Sections C,D and E ---indicate the checker is heterozygous, but do not tell whether the (?) in C//? is + or c. All three sections produce $\frac{1}{2}$ checkers and $\frac{1}{2}$ bars.

Section F ---producing $\frac{1}{2}$ checkers, $\frac{1}{2}$ non-checkers, indicates that the checker must be genotype C//c, because a barless offspring was produced and therefore, the barred parent must be genotype +//c for the same reason. Any barless progeny indicate both parents carry the recessive alternative (c). This mating of C//? X +//? becomes C//c X +//c as evidenced by the single barless offspring, c//c.

Matings of checkers to checkers:

We will combine the charts of the three possible genotypes for each parent. The checkerboard gets larger, but is basically the same four-celled arrangement for each mating of possible genotypes, C//? X C//?.



Sections A,B,C,D,G ---indicate one or both of the parents are homozygous checker, because no non-checkers were produced.

Sections E and F ---produced 3 checkers and 1 bar, and we know that both are heterozygotes, and at least one is of C//+ genotype.

Section I --- we are sure of the genotypes of the parents, C//c X C//c.

In any mating of two checkers, we expect a predominance of checkers in the offspring. Any cases of non-checkers being produced from such a mating, indicates both checker parents are heterozygous, but leaves us uncertain as to whether C//+ or C//c is the genotype, except in the case of the barless c//c produced in section I.

T-pattern Checker (C^T)

T-pattern checker is a dominant alternative to wild type (bar) at the pattern locus. In order of dominance, (C^T) is the highest of this series of alleles. The coarse spread pigment nearly covers the shield producing a near black condition. The T-pattern is so named for the ⌒ lacing of blue in the feathers of the shield. This blue T-marking is frequently filled in and the blue-tailed black is produced. We often refer to such birds as saturated T-patterns or velvets.

There are four possible genotypes for T-patterns:

1. $C^T//C^T$ Homozygous T-patterns ---all offspring of this genotype will be T-patterns.
2. $C^T//C$ T-pattern carrying checker.
3. $C^T//+$ T-pattern carrying bar.
4. $C^T//c$ T-pattern carrying barless

There are 16 possible matings of any given T-patterns with different genotypes. Each sex cell (gamete) will carry only one of the set in equal numbers; thus one-half the gametes from number four will have the gene for T-pattern, and the other one-half will have the gene for barless.

In matings of T-patterns, we expect a predominance of T-patterns in the offspring.

Matings of T-patterns to barless:

The test cross will clearly identify the genotype of T-patterns. A mating of $C^T//?$ X c//c will quickly identify the (?) in the formula. Since barless is the most recessive of this series of alternative forms of pattern genes, a barless pigeon can have only one genotype c//c for the one barless phenotype.

T-pattern Gametes

Homozygous T-pattern $C^T//C^T$

Barless Gametes

Ⓐ

	c	c
C^T	$C^T//c$	$C^T//c$
C^T	$C^T//c$	$C^T//c$

T-pattern carrying checker $C^T//C$

Ⓑ

	c	c
C^T	$C^T//c$	$C^T//c$
C	C//c	C//c

T-pattern carrying bar $C^T//+$

Ⓒ

	c	c
C^T	$C^T//c$	$C^T//c$
+	+//c	+//c

Barless Gametes

T-pattern Gametes	(D)	c	c
T-pattern carrying barless $C^T//c$	C^T	$C^T//c$	$C^T//c$
	c	c//c	c//c

Section A ---identifies all T-patterns; homozygous T-pattern parent.
Section B ---identifies $\frac{1}{2}$ T-patterns, $\frac{1}{2}$ checkers. (The T-pattern carrying checker)
Section C ---identifies $\frac{1}{2}$ T-patterns, $\frac{1}{2}$ bars. (The T-pattern carrying bar)
Section D ---identifies $\frac{1}{2}$ T-patterns, $\frac{1}{2}$ barless. (The T-pattern carrying barless)

All offspring of a mating to barless will carry barless. All offspring receives one of the set of alleles from each parent and the barless has only (c) to give to the resulting zygote. The test cross to barless quickly identifies the hidden pattern gene of its mate by the patterns observed in the progeny produced.

T-patterns mated to bars:

The four possible genotypes for T-pattern, combined with the two possible genotypes for bar, make eight possible mating arrangements.

Bar Gametes

T-pattern Gametes

$C^T//C^T$

	+//+		+//c	
(A)	+	+	(B) +	c
C^T	$C^T//+$	$C^T//+$	C^T $C^T//+$	$C^T//c$
C^T	$C^T//+$	$C^T//+$	C^T $C^T//+$	$C^T//c$

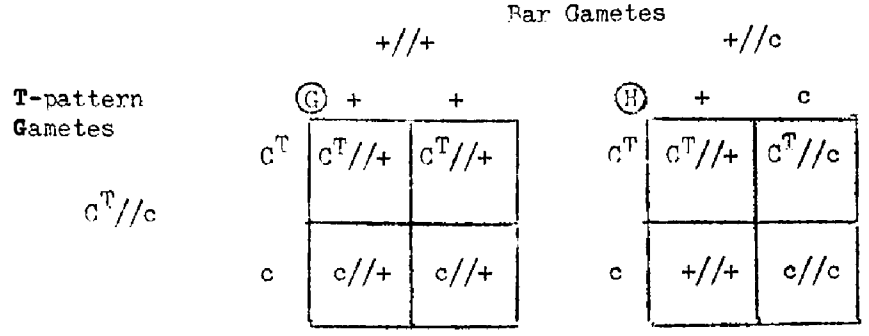
$C^T//C$

(C)	+	+	(D) +	c
C^T	$C^T//+$	$C^T//+$	C^T $C^T//+$	$C^T//c$
C	C//+	C//+	C C//+	C//c

$C^T//+$

(E)	+	+	(F) +	c
C^T	$C^T//+$	$C^T//+$	C^T $C^T//+$	$C^T//c$
+	+//+	+//+	+ +//+	+//c

Bar Gametes



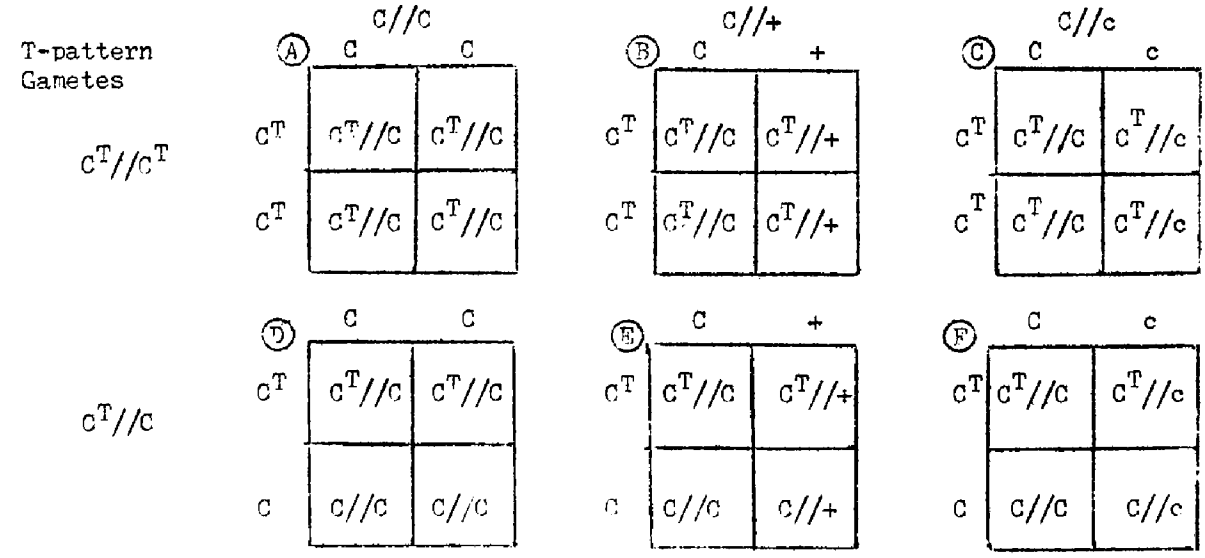
Sections A & B ---indicate homozygous T-pattern; in that no other patterns are produced.
Sections C,D,E,F,G,---produce 1 T-pattern to 1 non-T-pattern, indicating that the T-pattern is heterozygous for a less expressive pattern gene.
Section H ---indicates clearly the genotypes of both parents as $C^T//c$ X +//c.

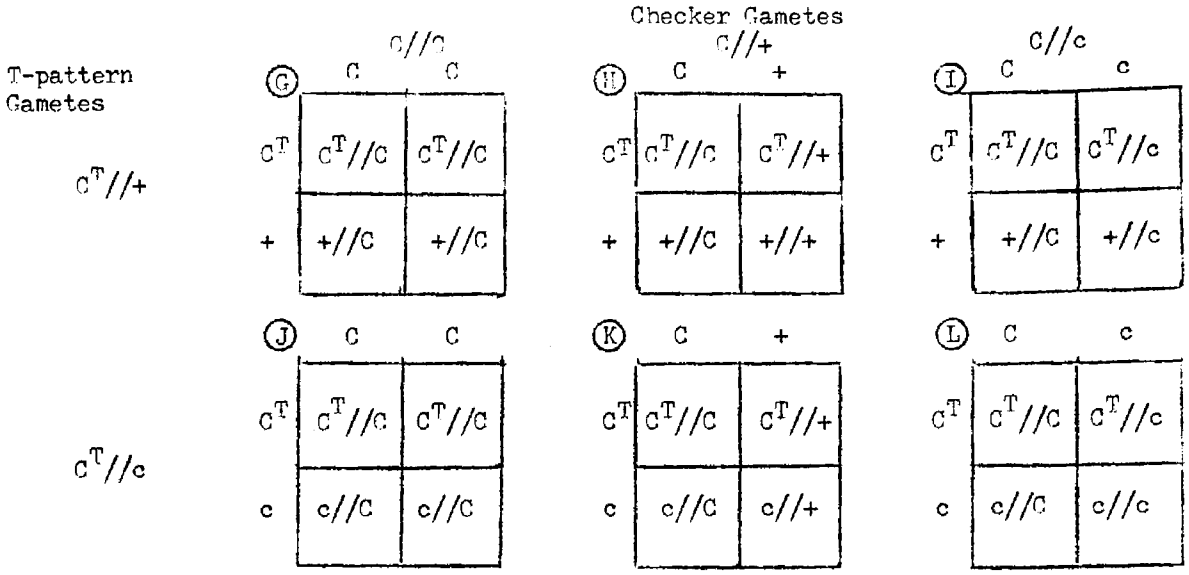
If we were absolutely sure that the bar parent was +//+, we would only need Sections (A,C,E,G,) of our chart to show possible matings. In many breeds where barless is unknown, matings to wild type +//+ is also considered the test cross and will identify all pattern genes present in the parents by the patterns of the resulting progeny.

T-patterns mated to checkers:

There are four possible genotypes for the one phenotype T-pattern (C^T), but only three genotypes for the one phenotype checker (C). This will bring the cells of our combined charts to include the twelve possible mating arrangements for a mating of a given T-pattern $C^T//?$ to a given checker C//?.

Checker Gametes





Sections A,B,C ---indicate a homozygous T-pattern parent, because no non-T-pattern progeny are produced.

Sections D,E,F,G,H,I,J,K ---indicate the typical 1:1 ratio. (One T-pattern to one non-T-pattern) which tells us that only one T-pattern gene is involved.

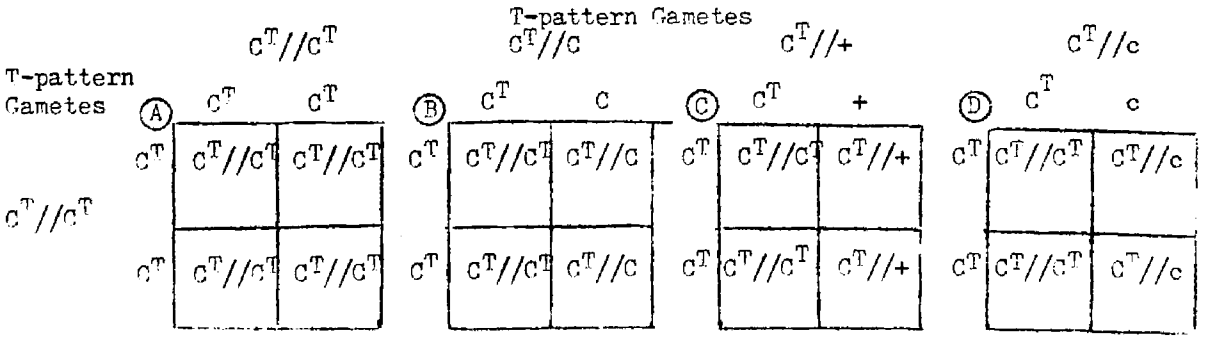
Sections H,I,K,L ---indicate that both the T-pattern and the checker parent are heterozygous.

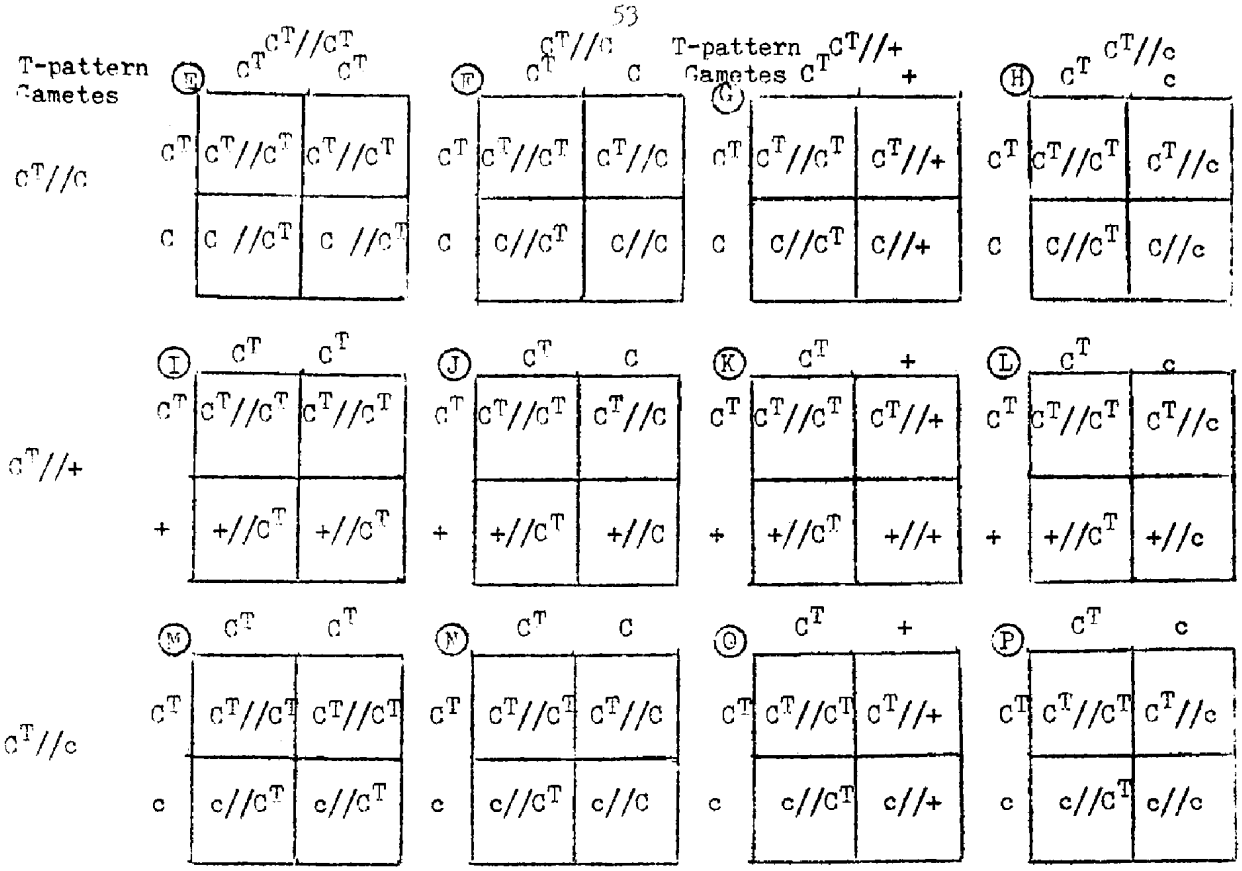
Sections H,I,K ---show a segregation of 2 T-patterns, 1 checker and 1 bar, indicating that both parents are heterozygotes with at least one of them carrying bar.

Section L ---clearly shows the genotypes of both parents. Both must carry bar-less (c) so the T-pattern can only be $C^T//c$, and the checker can only be C//c in the genotype.

T-patterns mated to T-patterns:

We should naturally expect that a mating of two T-patterns, each with four possible genotypes, will make 16 mating arrangements possible. Each mating arrangement has its own four-celled checkerboard and the combined sections will show the 64 offspring. It requires 16 matings to include all the possibilities for a given pair of T-patterns $C^T//?$.





Though we are sure of the genotypes of only one bird in the sixty-four offspring from these matings, there are several other clues as to genotype for both parents and progeny. Within the same family the variations in pattern are restricted due to the selective process, and if the stock is somewhat free of bronze or sooty, we may be able to reliably guess at the genotypes following the suggestions given on page 28.

Review of Patterns

We have considered four basic pigmentation arrangements called patterns. The most recessive genotype, barless c//c, produces little coarse spread pigment and the shield is almost entirely made up of clumped pigment (blue). The most dominant allele of the set, $C^T//^-$ produces almost entirely a spread arrangement of pigment (black) in this area. The four pattern alleles represent an order of dominance: $C^T > C > + > c$, with bar representing wild type. The genes (C^T), (C), and $(+)^c$ are very common, but (c) is very rare in pigeon populations.

All pigeons have two genes from these four alternatives; one from each parent.

Matings to barless represent that test cross and all offspring help identify the genotype of the tested parent.

Example: Checker X Barless

C//? c//c

All checkered progeny indicates a genotype of C//C for the checkered parent.
One-half checkers, one half bars indicate C//+
One-half checkers, one-half barless indicate C//c.

In the use of Punnett Squares, we seldom get more involved than the single four-celled section of our combined charts.

A mating of checkers, heterozygous for bar, would be:

C//+ X C//+

Male Gametes \ Female Gametes	C	+
C	C//C	C//+
+	+//C	+//+

3 checkers
1 bar

3:1 Phenotypic Ratio

1 Homozygous checker
2 Checkers carrying bar
1 Homozygous bar (wild type)

1:2:1 Genotypic Ratio

The expected phenotypic ratios give a good estimate of your chances of producing a particular pattern phenotype from a given mating.

Note:

I have deliberately neglected to include two pattern genes recently identified by Dr. Hollander. He has segregated out two checker patterns, (C^D) dark checker and (C^L) light checker in this series. These newly identified genes fit in order of dominance as follows: $C^T > C^D > C > C^L > +^c > c$. These two pattern genes are considered at this time to be quite rare, and are not to be confused with the breeder terms "dark checker", which refers to T-pattern (C^T) and "light checker", which the breeder uses to describe an open checker that shows much blue in the pattern. These "light checkers" are usually of C//+ or C//c genotypes. As these newly identified genes become more common, the reader should have little difficulty in including them in the pattern gene pool of his loft or breed.

The Gene Pool

Before looking at other mutant genes, it would be wise to use the pattern genes to demonstrate a very important aspect of science related to pigeon populations. Gene pool concepts help answer many questions about dominant and recessive genes. The words dominant and recessive refer only to comparison to wild type. More properly stated, a gene is not a dominant, it is dominant to wild type at a point on a specific chromosome.

The beginning student should have a minimum of experience handling certain ideas related to populations. The gene pool of the loft or breed presents both the potentials and the problems of the breeding art. I would like to include several ideas which help explain why dominant genes do not necessarily increase in frequency without some form of selection.

The present population theories are similar to the past population theories. All present studies tend to support the concepts first reported by Hardy and Weinberg in 1908. It is a unique idea that will hold for this period of scientific advancement without basic alterations. I would think the simplicity of

the mathematics involved would encourage all breeders to become more familiar with gene pool concepts. Let us begin ... a population exists through time; it's like a motor pool, with the functioning sex cells as vehicles.

Let's assume we develop a new pigeon population with 60 pure blue bars and 40 pure (homozygous) checkers. We all know that (C) is a dominant mutant, but it is error to think it will increase in frequency in the pool because of this dominance. Mating at random will produce:

Bar X Bar ⟶ Bar; Checker X Checker ⟶ Checker, but Checker X Bar ⟶

+//+ Wild type bar Gametes	C//C Gametes C	C
+	+//C	+//C
+	+//C	+//C

All checkers heterozygous for bar.

Let us look at this random mating procedure in terms of just the gametes involved. Each gamete will contain a single pattern gene.

Egg Cells ♀ Gametes		Sperm Cells ♂		Zygotes F_1	
Gene	Frequency	Gene	Frequency	Genes	Frequency
C	0.40	C	0.40	C//C	0.16 (.40 X .40)
C	0.40	+	0.60	C//+	0.24 (.40 X .60)
+	0.60	C	0.40	+//C	0.24 (.60 X .40)
+	0.60	+	0.60	+//+	0.36 (.60 X .60)

In other words, 16% of the population will be homozygous checker C//C; 48% will be checkers heterozygous for bar C//+, and 36% will be homozygous bars +//+. Now if we were to stop right here, it would appear an increase of checkers has developed. Considering our population definition, in terms of gametes, a look at the available genes for the next generation will show the real situation. Segregating the gametes of the F_1 will result in:

C gametes = .16 plus ½ (48C//+) or .24 = .40 or 40% gametes carrying C.
+ gametes = .36 plus ½ (48C//+) or .24 = .60 or 60% gametes carrying $(+)^c$.

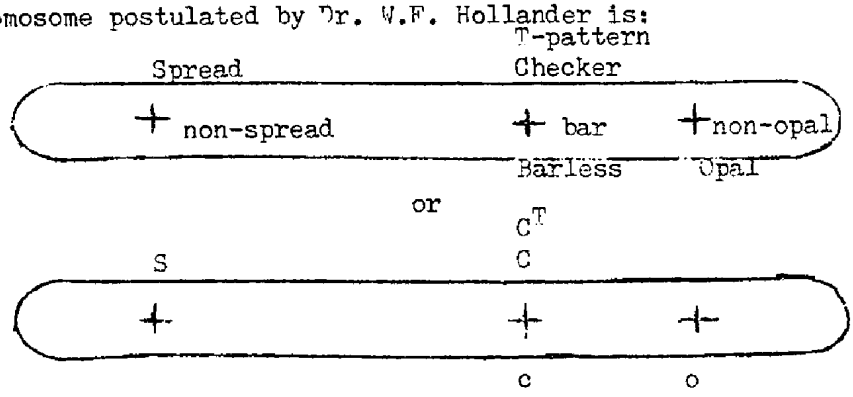
It should be obvious this is the same proportion of genes present in the original population. The fact that checker (C) is dominant to bar $(+)^c$ has no effect on the proportion of these genes in the pool. Dominant genes do not ordinarily tend to replace recessive ones in a population. Did you ever wonder why there aren't more ash-reds, almonds, etc., in feral populations? Selection, natural or breeder-directed, is the means of changing the frequency of a given gene in the pool.

Opal (Recessive) (o)

Opal, is an autosomal recessive gene which is quite common in Racing Homers. Testing has demonstrated that opal is on the same chromosome with the pattern locus $(+)^c$ and spread (S). The opal homers are often called "mosaics".

Recessive opal (o) produces a variable effect from near normal to intense colorations. Lacing in flight feathers, pastel pinks and delicate reds often are expressed in the wing shield. Generally, some washing occurs in the smooth spread areas, often producing an edging of darker pigmentation on the feathers. The mutant is seldom found in breeds other than racing homers. It has been estimated that between 1-2% of most strains of racers are homozygous opal o//o, and that between 15 to 20% of most strains carry the factor o//+ which suggests that opal must have been present very early in the development of the racing homer.

The chromosome postulated by Dr. W.F. Hollander is:



We define linkage as the tendency for genes to go together in meiosis (formation of sex cells), because they are present on the same chromosome. As the chromosomes "go", so also go the genes. The mechanism of crossing-over provides a means for reshuffling genes on the same chromosome. We have indicated that the farther the genes are separated on the chromosome, the more likely they are to become reshuffled. The first suspicion of linkage comes when we observe unexpected phenotypic ratios in the offspring. Let us just say we had an opal blue bar and mated it to a homozygous blue checker. If we assume independent assortment for opal and checker:

Wild type (non-opal) Parental Gametes

Opal Parental Gametes	+	+
o	o//+	o//+
o	o//+	o//+

F_1 All offspring are non-opal

Bar Parental Gametes

Checker Parental Gametes	+	+
C	C//+	C//+
C	C//+	C//+

All offspring are checkers

In the F_2 generation:

Parental Gametes

Parental Gametes	o	+
o	o//o	o//+
+	+//o	+//+

3 non-opals (blue)
1 opal

Parental Gametes

Parental Gametes	C	+
C	C//C	C//+
+	+//C	+//+

3 checker
1 bar

We can expect $\frac{1}{4}$ of the progeny to be opals o//o.
We can expect 3/4 of the progeny to be checkers C//C or C//+.
We should then expect 3/16 of the progeny to be opal checkers o//o, C//-.
($\frac{1}{4}$ chance X 3/4 chance = 3/16 chance)

Well, what really happens is, we get $\frac{1}{2}$ opals. We also get 3/4 checkers, but we hardly ever get opal checkers; the opals that are produced are barred birds. The opal color and bar pattern are staying together from the original mating. Opal (o) and bar $(+)^c$ are therefore on the same chromosome (i.e., linked).

Note:
The use of the word mosaic by homer breeders for opal o//o birds should not be confused with a true mosaic, which is a genetic mishap. A bird checkered on one side and barred on the other is an example of mosaicism.

Spread

Spread (S) is an autosomal mutation which produces a uniform distribution of pigment. In wild type, a solid or self black is the result. The word spread causes much confusion. We call the black areas of the wing bars and checks on a blue pigeon spread areas (by definition, coarse spread), but they microscopically differ little from other spread areas. The mutation spread (S) distributes all the granules in the manner usually found only in the bars, checks, and tail bar of a blue pigeon. This double usage of the word spread confuses many students.

Very often breeders will attempt to include (S) black in the pattern series with T-pattern, checker, bar and barless because solid seems to logically fit after the intense T-patterns (blue-tailed blacks). The scientists that first studied patterns thought so too, and prior to testing, included it in the series.

Spread is not an allele of C^T, C, +, c. The gene (S) is not located at the pattern locus, and for all practical purposes should be thought of as a completely different "horse". Spread, as a simple dominant gene, reacts as expected in matings:

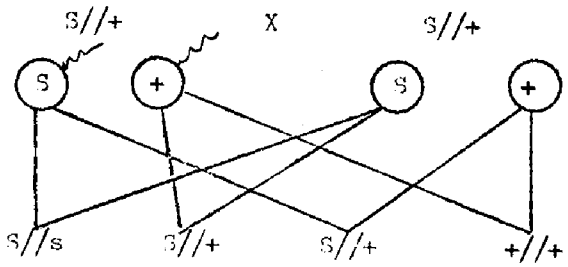
Wild type (non-spread)
Gametes

Homozygous Spread
Parental Gametes

	+	+
S	S//+	S//+
S	S//+	S//+

All black progeny

In the F_2 generation:



3 Spreads
1 non-spread

The homozygous spread, S//S, is not distinguishable from the heterozygote, S//+, and all three offspring having (S) are black. It may be more convenient in the breeding of blacks to have a genotype of S//S in stock birds, but there isn't any evidence that S//S is "blacker" than S//+. We can tentatively identify a black pigeon as S//? or S//- because without testing, there is no way of telling the full genotype. The S//? or S//- indicates our lack of knowledge. In this mating, let us look at the one non-spread produced. This non-spread will be either a blue T-pattern, checker, bar, or barless depending on the genotypes of the parents for pattern genes.

It might clarify matters to demonstrate how the evidence was developed to prove (S) is not an allele (alternative) at the pattern locus. Let us assume, for a moment, that (S) is in the pattern series and a homozygous S//S black would be pure for <u>that</u> pattern. It could then have no other pattern genes. In mating a series of such S//S blacks to homozygous bars +//+, we would produce in the F_1 generation:

S-pattern Gametes (error)

Bar pattern Gametes	S	S
+	+//S	+//S
+	+//S	+//S

All blacks carrying bar

The F_2 generation would produce:

S//+ X S//+

Female Gametes

Male Gametes	S	+
S	S//S	S//+
+	+//S	+//+

3 blacks, 1 bar should be produced.

In many matings of such birds, in individual coops, checkers and T-patterns keep cropping up in the progeny. The mating, as assumed, can produce only two kinds of offspring, bars and spreads ---when that third type of progeny, a checker, shows up we know that S <u>cannot</u> be an alternative (allele) at the pattern locus. Chromosomes are paired, only two alleles can be carried by the paired chromosomes. The checker (C) must have been hidden (masked) in the original black S//S. The mating to blue and the F_2 generation merely unmasked the gene for checker.

At this point it should be apparent that all black pigeons are <u>one</u> of the same basic patterns (T-pattern, checker,bar, or barless) as are <u>all</u> pigeons. The patterns cannot show because (S) spreads out all the pigment which would otherwise be clumped, forming the blue areas of the pigeon. I, at times, think of (S) as an <u>anti-clumping factor</u>. It just stops development of blue, and regardless of the pattern of the bird, all the feathers will be the color of the bar on the blue pigeon. We have previously stated that the amountof black pigment is

the same in the blue and the black areas, but that the blue areas have the granules in a clumped fashion producing an optical blue-gray. This mutation just unclumps these granules (or more properly, prevents their natural clumping) so the entire bird is self or solid black.

We can say then that (S) black is not a pattern, but masks all basic patterns. We call this masking effect epistasis; when a gene which is not an allele covers or hides the expression of other genes. Pattern genes are hypostatic to spread (are masked by).

Very often, on a poor grade black, it is possible to see bars or checks showing through the mask. The richness of solid black coloration can be enhanced by using "velvets" (T-patterns), some bronzes and other darkening factors such as dirty and sooty in matings to blacks. Dirty factor birds which are spread (S) usually are darker in the underwing and tail coverts.

Smokey (sy), an autosomal recessive, in combination with black will lighten the beak and skin color to near white. Most (perhaps all) light beaked blacks are smokey factor sy//sy homozygotes.

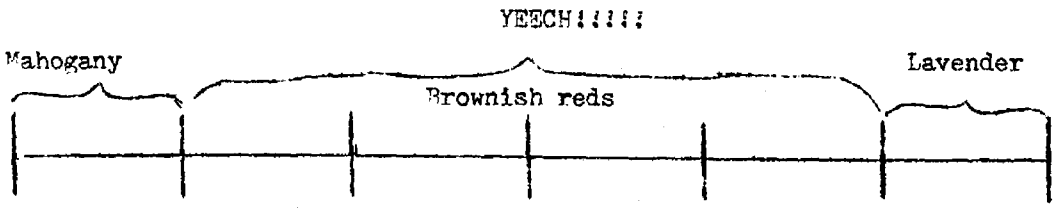
Spread in combination with brown acts as with blue. It masks all patterns, spreads out the pigment granules, and produces a solid or self brown pigeon.

For reasons not well understood, spread in combination with ash-red,creates a whole new set of complications. As with blue and browns, it masks all patterns, but the mechanism for depigmenting towards the tail and ends of flights apparently is in some sort of conflict with the mechanism for spreading out the clumped pigment.

Dr. Hollander once described a mutation as having a "sand-in-the-gears" effect on pigmentation. In this combination we have a sex-linked dominant, ash-red (B^A), and an autosomal dominant, spread (S), both operationally effecting pigment distribution. Well ---that's really a lot of "sand-in-the-gears", and the net result is an infinite series of colors from the darkest mahogany to the lightest lavenders.

As if on a continuum, with about 5% on either end of the scale of spread ash-reds (Mahogany and Lavender)being quite attractive phenotypes, the remaining 90% are probably the least beautiful of all pigeon colorations. Smutty, dirty, and off-browns of all descriptions result. Luckily, (S) segregates cleanly and these birds can produce, in non-spread progeny, ash-reds of colorations typical of the ash-red parental stock.

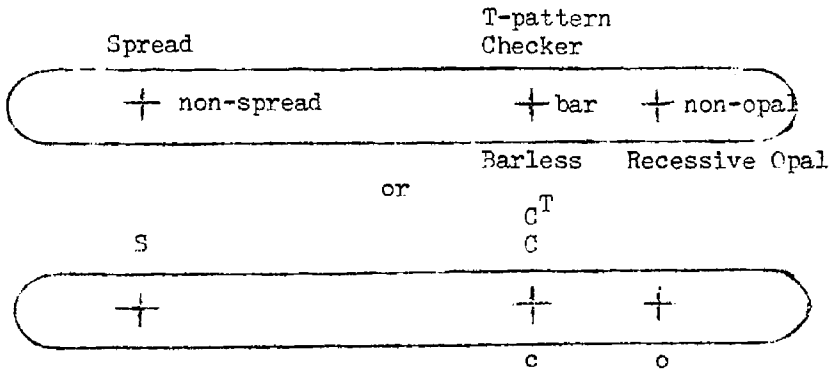
Scale of variation for combinations of ash-red (B^A) and spread (S).



Since very often the combination is made by crossing a black to an ash-red, cocks of the genotype B^A//+ are produced in combination with spread. The flecking associated with this genotype adds messy black flecks to an already very botched attempt at spread ash-red. With little supportive evidence, I have speculated

that the dark mahogany phenotypes are most likely T-patterns, with the lavenders most probably barred birds. I based these speculations on the high frequency that red velvets produce the darker variation (mahogany), and mealies produce the lighter coloration (lavender) in spread combinations.

Spread is on the same chromosome (autosome) with recessive opal (o) and the pattern locus. The chromosome is postulated:



Linkage is defined as the tendency for genes to go together as units in matings, because they are on the same chromosome. Crossovers occur proportional to the distance the genes are apart. Such crossover measures place (S) a great distance from the pattern locus $(+)^C$, which is very close to the opal locus $(+)^o$. Except for the sex chromosome, this is the only other chromosome where linkage has been demonstrated in the pigeon. Thus, in formula, a black bird with a given pattern, say homozygous checker, would be shown $\frac{S\ C}{?\ C}$ indicating this linkage, of S and C, by showing them on the same chromosome.

It is curious that (S), in combination with ash-red (B^A), produces on occassions a lavender coloration (silvery gray). Spread in combination with homozygous milky, my//my, produces a lavender coloration in both blue-black and ash-red. Thus, "lavenders" can have three genotypes; (B^A, S), (+, S, my my), $(B^A, S, my\ my)$.

Spread masks pattern, but also masks the albescent (whitish) strips on the outer tail feathers of a blue pigeon. The smokey factor birds, sy//sy, also affect distribution of pigment in this white area of the tail, only in this case, the whitish area is filled in with pigment that is clumped blue or brown. Ash-red leaves so little pigment in the tail generally, that it is more difficult to assess the presence of smokey from this identification mark in ash-reds. Spread is epistatic to most bronzes, so that the black schietti Modena shows no traces of the bronze characteristic of the breed, and such blacks are rich colored generally. It has been mentioned that most bronzes intensify pigmentation, and are a valuable asset in the breeding of rich blacks.

Bronze stencilling (toy stencil bronze) (K^S) has the effect of stamping out the underlying pattern of a black self. To a degree, reduced, (r), which affects pigment areas differentially (affects spread areas more than blue) will also show phenotypic differences in a spread pigeon due to the masked pattern. The so-called "Blue Lace" are reduced spread pigeons. The lightest birds are those which mask T-pattern, rather than checker or bar.

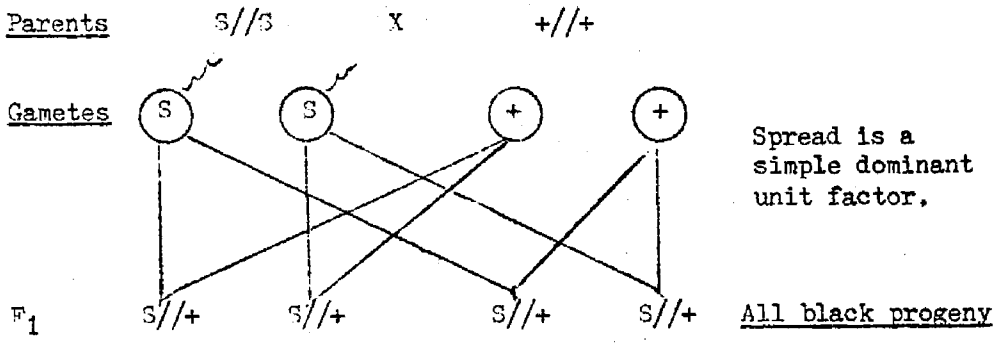
This unique aspect of toy stencil (K^S), that affects a spread pigeon in this manner, has made possible the creation of some of our most strikingly colored pigeons. The "marbled" (checkered) black Starling, the white barred black Brünner Pouter, and the Argent Modena, all are cases in point.

One of the most prevalent items of confusion among breeders relates to ash-red (^{BA}) and spread (S). In that small percentage of light silvery lavenders (^{BA}, S) produced by this combination, many examples appear as mealies without bars. The spread masks the pattern. Breeders often call such birds, "barless mealies" and thereby confuse two genetic terms, barless and mealy (barred ash-red). These birds are not barless pigeons (c//c), just merely part of the complexity known as spread ash-red.

Expectations of Phenotype Classification

We are now ready to state concisely the expectations of certain matings as to phenotype of the progeny. Expectations of phenotype classification help identify the nature of the genes involved. A mating of a dominant to a recessive produces all progeny of the dominant type.

Example 1. Black (Homozygous Spread) X Blue (Homozygous non-spread or wild type at the spread locus).



The F_1 generation mated together, producing the second filial generation (F_2) will permit the recessive gene $(+)^S$ (non-spread or wild type) to segregate (separate) out. The frequency of this happening follows a normal expectation for phenotypic ratio, assuming dominance of one member of a pair of alternatives (alleles).

F_2 Parental Gametes

Parental Gametes	S	+
S	S//S	S//+
+	+//S	+//+

Phenotypic ratio 3:1

3 blacks
1 blue (non-spread)

Genotypic ratio 1:2:1

1 homozygous spread S//S
2 heterozygous spread S//+
1 homozygous non-spread - blue +//+)

It is not complicated to figure the phenotypes to be expected when the mating involves more than one pair of alleles segregating independently at the same time. The expectation, assuming dominance, expands geometrically.

No. of Pairs of Alleles	Genetic Assortment	Phenotypic Ratio
1	(3 and 1)	3:1
2	(3 and 1) (3 and 1)	9:3:3:1
3	(3 and 1) (3 and 1) (3 and 1)	27:9:9:9:3:3:1

It appears at first rather complicated, but the chances of these genes occurring together is merely a product of their chances occurring separately. An easy way to calculate this is by multiplication.

Let's say we have a mating in which both parents were checkers heterozygous for bar C//+ and both heterozygous for milky my//+. In this mating we have 2 pairs of alleles segregating independently.

C//+ my//+ X C//+ my//+

We could set up our checkerboard as we have done in the previous sections. Each parent has four gametes possible, so our checkerboard will have 16 squares. I find it simpler to just put down the ratios and multiply:

X 3 checkers plus 1 bar X 3:1
3 non-milky plus 1 milky 3:1
9:3:3:1

9 non-milky checkers (blue checker)
3 non-milky bars (blue bar)
3 milky checkers
1 milky bar

The multiplication is performed in steps:

I	II	III	IV
3:1	3:1	3:1	3:1
3:1	3:1	3:1	3:1
9	3	3	1

A little practice will make this exercise fun. This cross of heterozygotes for 2 pairs of alleles is called the "two mixture cross", or what the geneticists call the dihybrid cross.

Example 2. A dihybrid cross involving indigo and crest.

In//+ cr//+ X In//+ cr//+

X 3 indigos plus 1 non-indigo X 3:1
3 plain-head plus 1 crest 3:1
9:3:3:1

9 plain-headed indigos
3 plain-headed non-indigos
3 indigo crests
1 non-indigo crest.

Expectation of phenotypic classification in pigeon breeding seldom get more complicated than these examples.

Review

In this major section, we have considered another chromosome about which we have some knowledge. Of the thousands of genes along its length, three genes are known to have mutated producing alternatives to wild type at that point.

Locus 1	Locus 2	Locus 3
Spread (S)	T-pattern (C^T)	Non-opal $(+)^O$
Non-Spread (wild type) $(+)^S$	Checker (C)	Opal (o)
	Bar (wild type) $(+)^c$	
	Barless (c)	

The pattern locus $(+)^c$ and the opal locus $(+)^O$ are close together (linked) and the spread locus $(+)^S$ is quite distant from these loci.

It should give the student some idea of the world of challenge remaining to be conquered, when I state that the pigeon has 40 pairs of chromosomes (give or take 2 or 3 pairs, depending on who counts). There are several other genes that are possibly linked, but the studies have not been conducted.

In this section we have introduced several ideas which are considered valuable in the breeding of pigeons. The Punnett Square and pigmentation areas are valuable aids to understanding. The concepts of "gene pool" and "expectations of phenotypic classification" are basic to further study. All mutations described in later sections can be assumed to be on a chromosome with no other known genes. They therefore can be assumed to segregate independently, i.e., according to phenotypic ratios for non-linked genes.

Grizzle (G)

Grizzle is an autosomal dominant gene which produces variable depigmentation in feather coloration. The lightening aspect caused by an uneven distribution of pigment granules related to this gene affects a typical blue feather to produce a patchy, freckling of blue-black-white blended colorations. To produce typical grizzles, the usual mating is grizzle to blue bar. The typical grizzle coloration is that of the grizzled Dragoon which shows a peppery effect of minute flecks of black, white, and blue about the head and neck, giving a "frosty" appearance. The typical show grizzle is a heterozygote, G//+, in formula.

Mating a typical grizzle to blue:

Wild type Parental Gametes

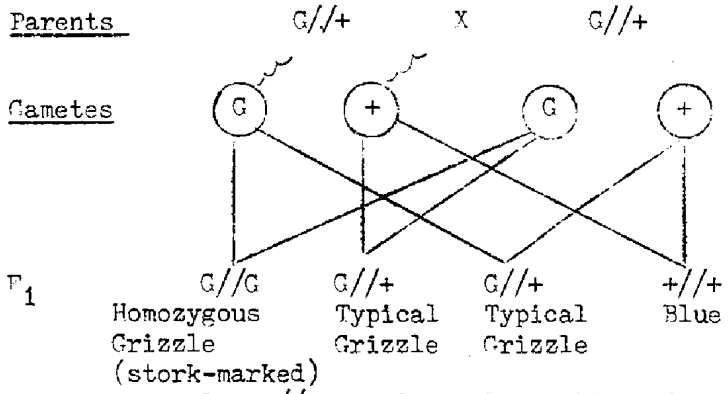
Grizzle Parental Gametes

	+	+
G	G//+	G//+
+	+//+	+//+

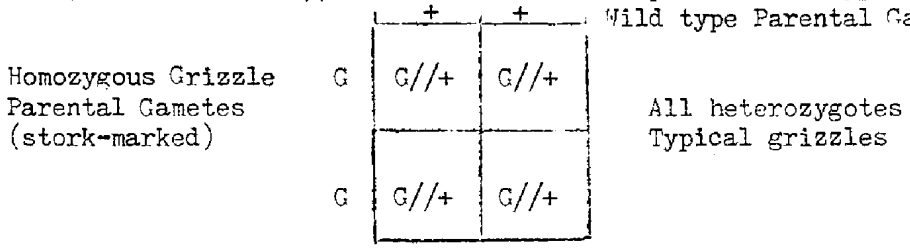
½ grizzles (both cocks and hens)

½ blues (both cocks and hens)

Mating of two typical grizzles G//+ produces three phenotypes.



The homozygous grizzle, G//G mated to blue will produce all typical grizzles.



It should be apparent that to produce grizzles, this is the most practical mating. The homozygous grizzle, G//G, is usually recognizable as a near white pigeon with color only showing about the head, neck, and the ends of the remiges and rectrices (smooth spread areas). This is expected because grizzle (G) affects primarily the coarse spread and blue areas. A typical grizzle has a near normal tail bar, and the coloration of the ends of the flights is also near normal for blue.

A single dose of grizzle depigments and rearranges pigment in the direction of white. A double dose grizzle, G//G, nearly completes this process, but the smooth spread areas are only slightly affected and the result can be a beautiful white pigeon with its wings and tail edged with black. (The stork-marked grizzle.)

Almost all white pigeons with colored eyes (pearl or orange) are ash-red (B^A) homozygous grizzles. The mutation, ash-red, depigments the smooth spread areas, washing them out to ash or white. It is logical that combinations of (B^A) and (G) would tend to produce near white phenotypes. The areas that grizzle affects least are the areas most affected by the mutant ash-red. Since this type of white is produced by grizzle, G//G, and ash-red (B^A),and not by piebald factors, which have an association with dark eyes (bull eyes), the colored-eyed white is not only possible, but quite easy to produce. In the development of such a white self within a breed, it will be noted that many young birds show some color in the neck (bellneck region) prior to the moult, and some adults will have a foul colored feather or two.

In grizzles, the clumped pigment areas, because of increased spacing, are lighter than spread pigment areas. It is easily detected that the ligtening effect of grizzle will be reduced with an increase in spread pigment. For this reason, checker and T-pattern grizzles show less expression of (G), and are not nearly as attractive as bars.

Recessive red (e) and spread (S) both suppress the effects of grizzle, as do most of the bronzes. This effect is very apparent in black and red mottles, which are genetically spread (black) and recessive red grizzles.

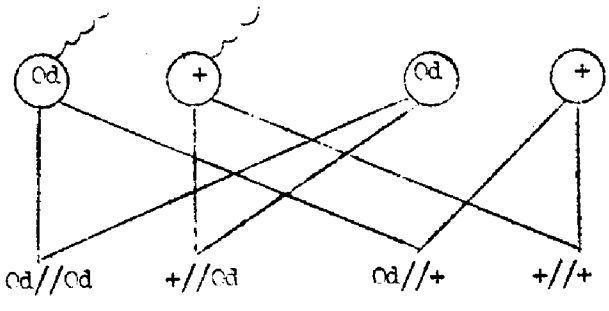
Grizzle in combination with brown (b) is similar in effect to that noted in blue, but with a "toned-down" expression. There is a strong possibility that not all grizzles are the same. The "tiger" grizzle of Tipplers, often called "Tippler light-print", acts non-typically in many ways. Possibly, the combination with Tippler bronze (tippler red) produces this variation, but the evidence at present suggests at least two forms of grizzle; "typical" as in Dragoon and the "light print" of the Tippler and show Rollers. Some grizzles darken with the first moult, others lighten, especially in combination with recessive red. Testing may show a whole series of genes which produce this effect, and it is likely that some will be alternatives at a given locus i.e., alleles. If the breeding evidence indicates this, we may have to add (G^L) to our symbols for "light print" grizzle and (G^M) for the Mäuser version of the German Toy breeds. Here again, the toy stencil bronzes of these German breeds may well be just giving a new look to our well established mutation called grizzle (G).

Dominant Opal (Od)

Dominant opal (Od) is an autosomal mutation which produces the white bars of Strassers and several other breeds. This mutation produces highly variable phenotypes and is similar to both opal (o) and reduced (r) in some combinations. White barred and white checkered Rollers have been found to be Od//+ in genotype. The bars and checkers are not clearly white ---pinkish or buff white is a more accurate description of dominant opal expression. The bronze stencil (toy stencil) (K^S) produces the clear white barring and checkering of Brünner Pouters and German color pigeons such as Swallows. In most of the German toy breeds with white barring, both genes (Od and K^S) are present, making identification of (Od) without testing difficult. Dominant opal produces depigmentation in coarse spread areas, and some washing in smooth spread areas. I have often suggested that dominant opal is possibly a lethal or sub-lethal factor. I have supported this statement with the observation that I have never tested a bird of Od//Od genotype, or produced a different phenotype from matings of two heterozygotes, Od//+ X Od//+.

A mating of white barred blue Rollers will produce:

Parents Od//+ X Od//+



We should expect: ¼ homozygous dominant opal Od//Od.
½ heterozygous dominant opal Od//+.
¼ blue bar (white bar) (+)Od//(+)Od

The actual numbers imply that there is a missing percentage of progeny i.e., that homozygous dominant opal Od//Od dies in an early phase of embryonic development. At this point, the evidence is not conclusive concerning this lethal aspect of dominant opal, but the absence of one genotype certainly suggests this possibility.

In combination with each basic color and pattern, beautiful phenotypes can be created using (Od). One of the most striking pigeons I have ever seen was dilute T-pattern dominant opal, d//d, C^T//-, Od//+. This mutation has been transferred to numerous breeds in recent years because of the beautiful phenotypes produced in combination with other mutants.

Indigo (In)

Indigo is a dominant autosomal mutation discovered by Wendell Levi, which produces an ash-red "mimic" (look-alike) phenotype on a blue pigeon. Indigo affects primarily spread pigment, changing the typical black bars of the blue pigeon to a rust-red. The homozygous indigo, In//In, produces a rust-red expression on the head, neck, and chest to enhance this "mimic" effect. With the exception of the bluish-steel gray of the rump and tail feathers, and the absence of the washed-out "mark of the ash-red", a homozygous blue indigo could pass for an ash-red pigeon. Indigo produces a metallic blue-black (gun-metal) coloration, in combination with spread (S). The so-called "andalusian blue" has attained much popularity in the pigeon fancy. Acting as an incomplete dominant, indigo (In) operates genetically similar to grizzle (G), in that the homozygous indigo, In//In, differs in phenotype from the heterozygous indigo, In//+.

A mating of homozygous indigo to wild type yields:

Parents — Homozygous Indigo X Homozygous non-indigo

In//In X +//+

Gametes: In, + (sex not a concern)

F_1: In//+ In//+ — All indigos In//+

The mating of the F_1 progeny will yield:

Parents F_1 In//+ X In//+

Gametes: In, +, In, + (sex not a concern)

F_2: In//In In//+ In//+ +//+

3 indigos
1 non-indigo

Phenotypic ratio 3:1

(The phenotypic ratio,(3:1), becomes 1:2:1 because In//In is distinguishable from In//+, making a third phenotype.)

Genotypic ratio 1:2:1

Genotype	Phenotype
1 Homozygous indigo, In//In	looks like ash-red
2 Heterozygous indigos, In//+	some reddishness, with metallic steel gray shown in flights, rump, and tail.
1 Non-indigo, $(+)^{In}//(+)^{In}$	normal for pattern and color

The "andalusian blue", produced by combining indigo (In) with black ($+^{b}$, S), was named for its resemblance to the phenotype of the andalusian chicken. In fowl, a similar incomplete dominant autosomal mutant (Bl), in matings to black, produces the heterozygous condition of "andalusian blue". In chickens and pigeons this steel-gray, blackish-blue coloration is found only in birds heterozygous for the dominant mutant. Andalusian blue pigeons are wild type $(+)^{b}$, spread (S), and heterozygous for indigo, In//+. Matings of homozygous indigos to homozygous spread (blacks) will produce all andalusian blues.

A mating of andalusians will yield:

Parents In//+, S//- X In//+, S//-

1 Homozygous indigo
2 Andalusian blues
1 Black if all progeny have (S)

We might state that half the progeny of a mating of andalusian blues will be andalusian blue. It should be noted that (S) will be segregating independently of (In), and it would require the S//S genotype in both parents for all the heterozygous indigos, In//+, to be andalusian blue.

Let us try our multiplication for a dihybrid cross, assuming both parents are of the genotype In//+, S//+. The mating should yield:

1 homozygous indigo In//In 2 heterozygous indigos In//+ 1 non-indigo $+^{In}//+^{In}$

3 spreads (S//S or S//+) 1 non-spread $+^{S}//+^{S}$

1:2:1 < 3 spread homozygous indigos In//In, S//-
6 spread heterozygous indigos In//+, S//- (andalusian blue)
3:1 3 spread non-indigos S//- (black)
3:6:3:1:2:1 < 1 non-spread homozygous indigo In//In
2 non-spread heterozygous indigos In//+
1 non-spread non-indigo $+^{S}//+^{S}$, $+^{In}//+^{In}$ (wild type)

We could also make a Punnett Square of 16 cells, and show the combinations for the four possible gametes of each parent.

Type 1 Gametes	In, S	carrying indigo and spread
Type 2 Gametes	In, $(+)^{S}$	carrying indigo and non-spread
Type 3 Gametes	$(+)^{In}$, S	carrying non-indigo and spread
Type 4 Gametes	$(+)^{In}$, $(+)^{S}$	carrying non-indigo and non-spread

The expected phenotypic ratio, 9:3:3:1, is modified by the fact that indigo produces 3 phenotypes instead of two in this mating. There are (6 + 3) = 9 spread indigos, 3 spread non-indigos, (1 + 2) = 3 non-spread indigos and 1 wild type, or the results are really the 9:3:3:1, in a modified form.

The popularity of "andalusian blue" among breeders has produced the incentive necessary to provide for the development of this coloration in many breeds. The rust-red associated with the mutant becomes a problem in spread combinations, as many andalusian blue pigeons show a rust lacing on shield feathers that is considered undesirable. The lacing tends to disappear in succeeding moults. Indigo in T-patterns appears very bronze in the shield, resembling the coloration of the bronze Modena.

Review

We have considered three autosomal dominants which affect pigeon colorations. At this point, I would like to offer a general idea that I have found helpful in understanding color mutants, with respect to reddish pigmentation. Color mutants are generally directional from blue-black to red to white.

Of the mutations we have studied, ash-red (B^A), brown (b), recessive opal (o), dominant opal (Od) and Indigo (In), seem to encourage production of phaeomelanin (red-brown pigment). When homozygous, almond St//St, Faded St^F//St^F, and grizzle G//G, produce near white phenotypes. Further combinations of depigmenting genes tend to approach white.

Directional Mutant Expression

1. Some mutations tend to affect the process of pigment development and/or pigment distribution.

2. Any disruption of the process tends to produce odd-shaped granules that appear red or reddish.

3. Any further disruption of the process tends to stop pigmentation, producing white.

The areas concerned will be the areas which the mutant normally affects. A mating of a toy stencil (white bar) to wild type (black bar) produces bronze (red bars) in the F_1 generation; mutational direction, black to red to white, with added color affecting genes.

Recessive Red (e)

Recessive red is an autosomal mutation that produces a regular distribution of phaeomelanin pigment. The term red is confusing, because in pigeons, red belongs in the group of brown-red color hues. Many mutations produce such pigmentation. The entire family of bronzes are reddish, as is the sex-linked dominant mutation ash-red (B^A). We now introduce another entirely different form of red, produced by an autosomal recessive gene (e).

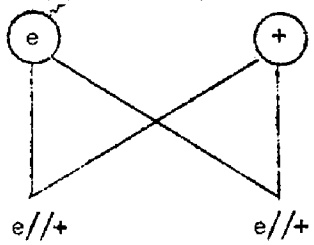
The "mark of the ash" quite clearly identifies (B^A), but there is still confusion concerning the several reds. Recessive red shows no washing out to ash in flights or tail. The feathers are red to the ends. Any pigeon with a red tail can be assumed to be recessive red, e//e. Whenever a pair of non-recessive reds produce a recessive red, the genotype of the parents is known,+//e. Such a mating will continue to produce $\frac{1}{4}$ recessive red offspring. Since recessive red has no other alleles, except non-recessive red (wild type at this locus), all progeny of a recessive red, e//e, will carry recessive red, because all gametes will carry (e) with respect to this locus.

A mating of recessive red, e//e, to wild type yields:

Parents — Recessive Red X Wild Type (non-recessive red)

e//e X $+^{e}//+^{e}$

Gametes



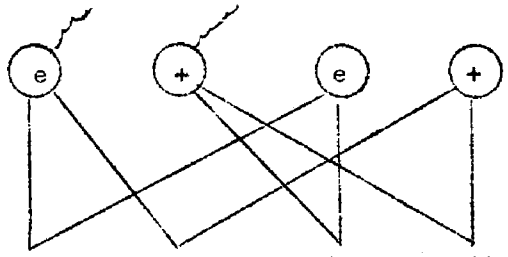
(sex not a concern)

F_1 — e//+ e//+ (all wild type carrying recessive red)

The F_2 generation yields:

F_1 Parents — e//+ X e//+

Gametes



F_2

e//e	e//+	+//e	+//+
recessive red	wild type	wild type	wild type

3 wild type
1 recessive red

Phenotypic ratio
3:1

Recessive red makes an ideal subject for studying epistasis. Recessive red, e//e, masks all basic colors. Ash-red (B^{A}), blue-black $(+)^{b}$, and brown (b) pigeons, carrying two doses of this gene, e//e, will show identical recessive red phenotypes. Recessive red is epistatic to pattern. It masks T-pattern (C^{T}), checker (C), bar $(+)^{c}$, and barless (c). As mentioned earlier, spread (S) also masks pattern, but recessive red masks spread. We can have sixty genotypes for a recessive red pigeon hen, with reference to basic color, pattern and spread; and double that number for a cock, because he has two sex chromosomes. When a breeder asks, "what will I get when I mate this recessive red to a blue bar?" The answer is, "about anything!" If we include the bronzes, which recessive red also masks, the genetic possibilities of a recessive red become astronomical.

Recessive red acts as a simple recessive, but its effects are rather complicated. Recessive red masks the powerful sex-linked overprinting mutations of faded (St^{F}) and almond (St), producing a near red, but in the case of almond, some depigmentation occurs and the recessive red almond (DeRoy), though variable, appears somewhat between recessive red and its dilute, recessive yellow. With age, the typical flecking associated with the almond mutant begins to appear, and a somewhat reddish almond phenotype develops.

Producing rich reds is a challenging task, for the breeder. Ash-red, sooty and several bronzes will enhance the color of recessive reds. I have found brown, spread and dirty also increase the intensity of reds, and the addition of "grease quills" to the make-up adds a rich sheen to the plumage.

Now that the reader has been impressed with the masking qualities of recessive red, it is time to state that recessive red usually does a rather poor job of masking basic colors. It is quite difficult to get a uniform red pigmentation

throughout the plumage. Recessive reds masking blue-black, typically show bluish (plum color) in the rump and vent areas. The tail especially is prone to be washy or bleached out. A recessive red self of uniform pigmentation throughout its plumage is an accomplishment to be proud of in the art of breeding.

As recessive red is rather a poor mask for basic colors, its wild type allele has similar problems. A bird of the genotype +//e should show no evidence of the presence of this recessive, but alas, this is not always the case. Almonds, bronzes, ash-reds, and many other phenotypes are richer in color when (e) is present in the genotype. Blacks produced from e//e matings often show a red lacing on the feathers. In Tumblers, this "frostiness of red" seriously detracts from the appearance of blacks, and is undesirable from the breeder's standpoint.

The dilute (d, e//e) recessive red is recessive yellow. The pale (pd, e//e) recessive red is a beautiful phenotype called "gold". The reduced (r, e//e) recessive red is a pale yellow,and deserving of more notice.

Recessive red has more problems masking milky, my//my, and the result is a pink phenotype. In combinations with grizzle, recessive red suppresses the expression of (G), but does not mask it, and the result is a recessive red or yellow mottle.

This mutation, which has so many expressions, apparently has a disruptive effect on phaeomelanin production or the transportation of the granules to the developing feather barbules. This pigmentation weakness makes possible natural or artificial reversion to white. The tiger Swallows, with alternating red and white flights, are produced artificially by plucking the feathers several times, which depletes the pigment reservoirs, and from then on the feathers moult in white. This will also occur in other colorations, but only with severe plucking.

What can be done by plucking, also happens naturally by the operation of the mutant(s) responsible for the whiteside red and yellow Tumblers and Trumpeters. These birds are red selfs in the nest, and with the first moult, the feathers of the shield revert to white. This natural tendency to revert to white is a characteristic associated with recessive red. Recessive red selfs are very prone to moult in white feathers, as they age, to produce rosewings or just mismarked red selfs.

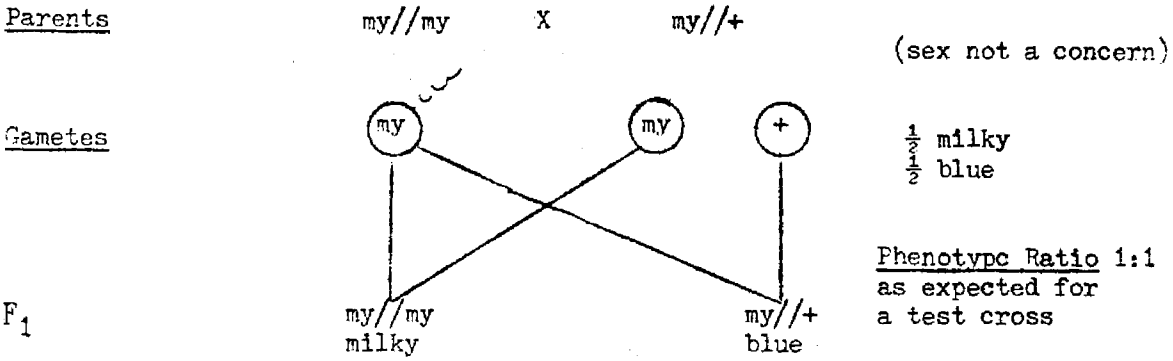
Recessive red is possibly linked with the factor that produces the baldhead (piebald) pattern. All (?) red baldheads are ash-red, not recessive red. In the breeds where baldheads are common, recessive red is also common, but though recessive red occurs in beard, badge, and magpie (piebald) patterns, it apparently never occurs in baldhead. This matter certainly deserves study. Possibly a reader will take up the challenge? It is my hope that I have conveyed to the reader the monumental accomplishment of producing a rich red e//e pigeon of uniform coloration.

Milky (my)

Milky is an autosomal recessive color modifying mutation. The gene produces a lightening effect similar to grizzle, but without the patches of white associated with (G). The silver pastel effect on blue produces the so-called "powdered silver" of Fantails.

I have always preferred "milky" to "powdered silver" as a descriptive term, because of the confusion the word silver (dilute blue) causes when it is used in this erroneous manner. Powdered silver Fantails are not dilute (d), merely homozygous milky, my//my blue pigeons. Dr. Hollander's "soaked-in-milk" description quite nicely describes this beautiful addition to basic color modifiers.

A mating of a milky my//my blue to an unknown genotype blue will test the unknown for milky (my). If all blues are produced, the unknown blue can be assumed to be $(+)^{my}//(+)^{my}$ or wild type at the milky locus. If the tested bird carries milky, the mating will yield:



A recessive gene, in order to be expressed, must be homozygous. It therefore follows that in phenotypes of recessive mutants, the recessive parent has only one type of gene for this locus to provide the gamete and resulting zygote. Logically then, all progeny of a milky, recessive red, barless, smokey or gazzi pigeon will carry the recessive factor provided by that parent.

A milky recessive red my//my, e//e, appears as a pink phenotype. In combination with spread (S), in both ash-red (B^A) and blue-black $(+)^b$ pigeons, homozygous milky, my//my, produces a lavender coloration (silvery gray). Lavender Lahores and Modenas are rather unusual milky (my) expressions.

Smokey (sy)

Smokey (sy), as an autosomal recessive gene, is well named. The appearance of smokey on wild type has a soft blurring effect. Generally there is a darkening of the blue areas, and a slight washing effect in the bars or checkers. Imagine, if you would, a normal blue as seen through a smokey mist. Smokey tends to lighten the beak, cere, and soft parts of the body. White-skinned and light-beaked blacks are almost always sy//sy in genotype. The albescent (whitish) strip on the outer tail feathers of blues disappears in smokey birds, the area being filled in with clumped pigment (blue). There is also a darkening of the rump and a lightening of the tips of the rectrices (tail feathers). It is a strange gene that darkens one area, lightens others. The coarse spread areas (wing bars, checks) are lightened or blurred. The blue tips of the tail are lightened to a more distinct blue, yet the smooth spread areas (ends of remiges and tail bar) are noticeably darkened, while the whitish areas of rump, underwings and the outer tail feathers' albescent strip are more bluish than typical wild type.

Because of these peculiarities of smokey, it is often mistaken for the sooty or dirty factor. Smokey has only one phenotypic characteristic in common with the not well understood (apparently dominant) gene(s) called dirty. Both dirty and smokey darken the underwing coverts; here the resemblance ends. Smokey in a checker pattern somewhat washes the pattern, and produces a bird similar in appearance to a sooty bar pattern blue. Sooty apparently throws a "little sand" in the clumping mechanism for pigment granules, producing some spread (black) pigment in the blue areas. In sooty birds, small flecks of spread pigment occur in the shield area in varying amounts. The slightly washed out checker produced by smokey sy//sy, and the splotching of black flecks in the shield area produced by sooty, obviously look alike to the untrained observer. The albescent strips on sooty and dirty factor birds are normal; blue in smokey birds. The emphasized blue tip of the tail feathers makes smokey identification easier. Sooty and dirty form part of the "dirty-sooty" confusion that we have not as yet, through proper testing, found a solution identifying these genes or their mode of inheritance. Both dirty and sooty have dark beaks, eye ceres, and skin. The similarities of these factors to smokey are very minor and the differences so noticeable, there should be little problem in identifying smokey.

Sooty

Sooty (no symbol) is an autosomal gene (or genes) which in our very limited studies, appears to act as a dominant. It has a variable expression, in that it adds small flecks (smears) of spread pigment in areas that would normally be blue. These small black patches have no distinctive pattern, and should not be confused with checkering. The checkers (of the pattern series) are formed by rather clear blue and black areas, while the barred sooty birds show smeary patches of spread pigment, which can at first glance, appear as checkering. Sooty in barred brown and ash-red, produces this same condition. A mealy (ash-red barred) carrying sooty will have red flecks (minute patches) and the barred brown will have brown flecks in the shield area.

Dirty

Dirty (no symbol) darkens noticeably the pigmentation of the blue pigeon. Dirty is appropriately named. Of the little we know of this factors' inheritance, you might assume it to be rare. Actually, it is widespread in the pigeon world. Evidence suggests it operates as a simple autosomal dominant. It is my considered opinion that in selection for many richening modifiers of colors in most breeds, the breeders have accidently selected for sooty and dirty factors. It is surprising that these factors which are very unattractive in themselves, in some combinations, may be responsible for the added effect we consider beautiful.

Ice (Ic)

Ice is an autosomal partial dominant factor which is presently under study. I have tentatively symbolized ice, (Ic). The ice factor or factors produces a very soft "azure" blue coloration on wild type. The mutant(s) produces a creamy blue-white coloration in the blue areas, while at the same time darkening the underplumage, (covered portion of the feathers). This coloration is found in several unrelated breeds of pigeons. I have assumed the ice blue of the Polish and Russian Highflyers, Ice Pigeons, Damacenes, Tung-Koon-Paak (Chinese), and Moos-Sulli (Syrian Coop Tumblers), have the same genetic factors, because the phenotypic

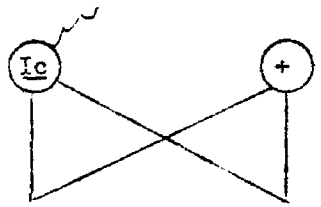
descriptions are so similar. The characteristic light blue head and neck is covered with a silvery iridescent mantle (the icing), which adds a beautiful compliment to the light blue of the shield and underparts.

Ice affects all patterns similarly, and is especially attractive in the barless pattern. The Forellen Pigeons are a beautiful checker with the frosty-ice-blue head, neck,and underparts. Ice phenotypes are found in white bars (Ice Pigeons) and black bars (Damacenes). The factor(s) involved in the alteration of bar color appears, at this time, to be another expression of toy stencil bronze ($\underline{K}^S$), so common in German toy breeds. The typical Damacene ice has ebony black bars, deep in pigmentation, which contrast beautifully with the "azure" blue of the shield.

In matings of ice to wild type, an intermediate light blue is produced. Depending somewhat on the presence of other factors (dirty of sooty), the F_1 progeny are intermediates, generally closer to ice than to wild type in coloration.

Parents Ic//Ic X +//+

Gametes



(sex not a concern)

F_1 Ic//+ Ic//+

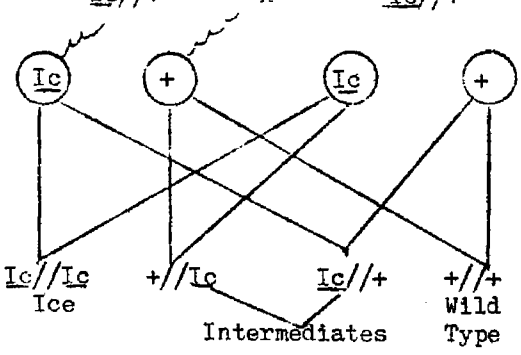
All F_1 progeny are intermediate ice, and if it were not for the Fantail usage of the word "powdered", I would call ice heterozygotes, Ic//+, "powdered blue". In crosses of Ice pigeons to wild type, the white barring with its pencilled black edge disappears, and the F_1 progeny show the variable bronze bars associated with toy stencil bronze ($\underline{K}^S$). I feel confident that the white barring factor of the Ice Pigeon is identical to that of toy stencil ($\underline{K}^S$), because crosses of Ice pigeons to toy stencil (non-ice) white barred breeds produce the typical ice intermediate, Ic//+, but the white bars remain clearly the same as in the parent breeds, suggesting identical genotypes for the factors involving white bar.

The F_2 generation produces some homozygous ices, Ic//Ic, but the numbers of progeny produced in these tests are not as yet great enough to warrant a conclusive statement about dominance or assigning a symbol. Ice, (Ic), is a working symbol, the (_) indicates its tentative status.

There is no evidence to suggest sex-linkage, and the factor or factors producing this condition are clearly autosomal in nature.

F_1 Parents Ic//+ X Ic//+

Gametes



Phenotypic Ratio
3 Ice to 1 wild type
3:1

Modified to the Genotypic Ratio 1:2:1, because Ic//Ic is recognizable, producing a third phenotype.

As with grizzle (G) and indigo (In), the presence of a third recognizable phenotype alters the phenotypic ratio, to become identical to the genotypic ratio, 1:2:1. In the results of such matings, there is conspicuous shortages of wild type offspring. The $\frac{1}{4}$ expectation is not fulfilled, because only a rare few of the progeny are not considerably lighter than the wild type parent. Wild type has to be identified by the absence of the peculiar dark underfeather associated with this factor.

At this time, there are still some problems to be worked out in relation to ice. The major difficulty is to produce the silvery ice mantle about the head and neck. This aspect responds to selection, but is quite variable, and the F_1 intermediate usually shows only a trace of this attractive iridescent compliment to ice.

In spite of these difficulties, the dominant characteristic of the light blue (Ic) has made it possible for this beautiful additon to pigeon coloration to be successfully transferred and "graded-up", to show quality in both the Roller and Tumbler breeds.

Iridescence

It would seem appropriate after considering the silvery ice iridescent mantle associated with the ice factor (Ic), and prior to discussing the family of bronzes which generally show a high metallic sheen on the feathers, to make a few comments about the nature of this metallic sheen we call iridescence.

The metallic sheen on the feathers of the pigeon glistens in light. This surface reflection tends to relate to the basic color. On wild type (blue-black) pigeons the purple or green sheen is typical. In show coloration, blacks should have the so-called "beetle-green sheen", with the off-purple version being less desirable. In the wild species, the green effect is natural to black areas, while purple predominates in blue areas.

We sould begin studying this matter with a clear understanding that iridescent color is structural. It is not related to pigmentation, except as an added dimension of it. Iridescence is produced by the slight twisting of the feather barbules, so they present a sort of $\frac{1}{4}$ side view, rather than an edge, to the light. This structural positioning of the feather barbules further separates the light, and produces the optical conflict which results in a series of colors called interference colors. The same effect can be produced by putting a drop of oil on water or flashing a light at a soap bubble. Each of these examples will display the purple to green blends typical of iridescent pigeon feathers.

This optical effect is produced by the light striking both the outer and inner reflective surfaces at the same time. The glowing colors of the clouds and "mother of pearl" ornaments in sunlight are similar optical phenomenon.

In birds, the hackle feathers about the head and neck generally show this condition more than other contour feathers. Naturally, the other major contour feathers have more critical functions to the bird, and the twisting of barbules reduces the general feather strength. It is logical that functional feathers, flights, secondaries, and tail feathers show less iridescence than other groups of feathers.

There are many factors which seem to enhance the sheen of the overall plumage of the pigeon. The entire family of bronzes described later have "rich sheen", as a typical characteristic. The Archangel bronzes are possibly the most iridescent pigeons, and seem to glow in the light. Pigeons that have "grease quills" tend

to have a rich sheen on their plumage. Many South German toy varieties, such as Franconian Satin-shields, have such a heavy sheen as to appear soft satin.

This type of structural coloration is not common in the bird world. Pigeons share with ducks, turkeys, peacocks, etc., this unusual optical phenomenon. The black of the Mallard drake's head (in breeding plumage), appears "beetle green", and the peacocks brilliant "eye-feathers" of the tail are the same phenomenon.

Soap bubbles, peacocks, and pigeons ---selection for sheen and matings that naturally enhance it, are just part of the breeders art. We try to approach with our domesticated pigeon what nature does so well in wild species. The reader is asked to experiment in a darkened loft with a flashlight to clearly demonstrate this peculiar aspect of interference coloration. As the light source changes, the color should change if the feathers remain stationary. Rotate a flashlight on a given bird and watch its appearance change rapidly as to hue and coloration. The flashlight lacks parts of the spectrum of sunlight, but the changes, though subdued as compared to sunlight, are dramatic nonetheless. Any study of pigeon coloration creates an honest scientific demand for standardized lighting for any show where color is a factor to be considered in judging.

Note :

Grease quills are unopened pin feathers found in the flank just forward of the tail. These somewhat undeveloped feathers exude an oily substance, hence the name grease quills. Frequently these feathers extend from the wing to the tail, along a median line, ending just level with the vent. The inheritance of grease quills has not been studied. The genetic factor or factors producing grease quills appears dominant, but its relation to the rich colorations and silkiness of plumage has not been worked out.

The Family of Bronzes

In our discussion of red pigment, we considered the mutational effect of changing rod-shaped eumelanin (black) granules , into irregular ball-shaped granules of phaeomelanin. These red granules appear larger under the microscope than the rod-shaped granules, viewed from the end. In the family of bronzes, both red and black pigment granules occur together in the feather barbules. This sprinkling of red in with black, produces an optical blackened-red or bronze. If more red than black occurs, the effect is reddish. Bronze phenotypes are common in pigeon breeds. The question arises, is there bronze, or are there bronzes? For purposes of study, I have classified bronze phenotypes by the breed which characterizes them. There would be no way to analyze all these conditions, if we didn't begin somewhere, and then proceed logically to test the matter.

We have two aids to understanding, which will help us in this review of bronze. Initially, we have learned that some mutants affect blue, coarse spread, and smooth spread pigment differently. The way in which the bronze of a breed affects these areas, gives us a guide for their classification. We have also learned that mutations can be affected differently by the presence of another color affecting mutant such as spread (S). The reddish effect of mutants such as indigo (In), dominant opal (Od), and ash-red (B^A), must not be considered a part of the bronze phenomenon. We must also eliminate from our consideration those effects of recessive red, which in matings to blacks, produce offspring with some kitiness or reddish tinge on the feathers. This condition usually disappears in succeeding moults.

The family of bronzes, classified for study, are assumed to be alleles and tentatively symbolized on the base of kite (K). We have no evidence to suggest this allelic relationship, but such assumptions are necessary until information clarifies the matter.

1. Kite (K) ---the color of the English Short-Faced Tumbler kite and its parallel form in Parlor and Oriental Rollers.

2. Modena bronze (K^M) ---all Modena colorations except Argent.

3. Archangel bronze (K^A) ---to include the bronze of Nuremberg Larks, Lucern Larks, and some Catalonian Tumblers.

4. Roller bronze (K^R) ---the bronze of Rollers imported into the United States from 1860-1910; not to include the bronze of all later imports, which are Tippler bronze, usually in combination with Tippler light print grizzle.

5. Brander bronze (K^B) ---the color of the Copenhagen Tumbler (Fire Pigeon).

6. Tippler bronze (K^T) ---to include the Tippler red and the color the Show Bronze Tippler. The bronzes of all late Roller imports are of this type.

7. Toy stencil bronze (K^S) ---to include the bronze of the German Toy breeds, Polish Lynx, Brünner Pouter, Hyacinth, and including the bronze involved in producing the Argent Modena.

8. Lebanon bronze stencil (k^1) ---the bronze of the Shikli Ahmar red Lebanon.

These classifications are arbitrary, and subject to change when tests indicate the necessity. It is still possible that all bronzes might be due to one factor with differing effects due to the presence of modifiers. These genes could be alleles, and therefore alternative to each other, or entirely unrelated. There is enough difference in expression to warrant their separation for purposes of study. All bronzes except Lebanon bronze stencil (k^1) have been tentatively symbolized with capital letters, indicating a dominant gene. The progeny produced from mating types 1 thru 7 to wild type; all show some degree of bronzing, suggesting at least partial dominance. Lebanon bronze stencil appears to act as a recessive.

Kite (K)

Pigmentation Areas Affected

Normally, kites are T-pattern (velvets) which show bronzing in the inner webs of flight feathers. The area showing the most red pigment is in the transitional black to blue areas of the flight feathers, not including the tip.

Matings to Wild Type

Matings to wild type produce kites of generally reduced quality for redness. Backcrosses to kite, and some F_2 progeny will approach kite parental phenotype.

Discussion

The bronze of kite shows best on the unfolded wing, which exposes the trailing edges of the feathers. The classical almond is the expression of almond on a kite base. The general appearance of kites is blackish, but a tinge of bronze is often found throughout the plumage. Kite is completely masked by spread (S).

Modena Bronze (K^M)

Pigmentation Areas Affected

Modena bronze affects primarily coarse spread areas of the shield. The smooth spread and blue areas are affected little, and appear normal for wild type.

Matings to Wild Type

Matings to wild type produce offspring showing a very slight bronzing in the coarse spread areas. Backcrosses and the F_2 generation produce some bronzes of parental type, but segregation of types is variable. It should be noted that occassionally, matings to wild type produce rich bronzes, but it is felt the toy stencil bronze (K^S) present in the Modena breed is responsible for these exceptions.

Discussion

Modena bronze differs from other bronzes by affecting primarily coarse spread areas. Spread masks (K^M), as it did kite (K), but Modena bronze is also masked by ash-red (B^A). The ash-red and black Modenas show no traces of the bronze characteristic of the breed.

Archangel Bronze (K^A)

Pigmentation Areas Affected

The brightened copper or red bronze of Archangels affects primarily blue areas. The head, neck, and underparts exhibit the coloration. It is nearly the reverse of expression of Modena bronze (K^M) . The coarse spread areas are near normal, as are the smooth spread areas.

Matings to Wild Type

Matings to wild type produce offspring with slight bronzing in blue areas. Backcrosses and F_2 progeny produce some parental type bronzes, but again, the segregation of phenotypes is variable and unclear.

Discussion

Archangel bronze is a distinct form. It is difficult to assess the effect of "grease quills" and smokey,sy//sy, on the phenotypic bronze. It may be that both factors enhance the bronze, but the effect on blue areas quite clearly distinguishes Archangel bronze from the rest of the group of bronze phenotypes.

Roller Bronze (K^R)

Pigmentation Areas Affected

Roller bronze is a weak form of bronzing in both coarse and smooth spread areas. The mutant(s) has little effect on blue areas. The tendency to show bronze in smooth spread areas increases the red of these areas on ash-red pigeons.

Matings to Wild Type

Matings to wild type produce near identical weak bronzes of parental type. Backcrosses and F_2 progeny do not seem to increase the expression of this form of bronze.

Discussion

Roller bronze is a weakly expressed mutant. It is difficult to increase or decrease the amount of red by selection. The bronze of Rollers responds very slowly to modification. It took nearly sixty years of rigorous selection to develop phenotypes that approach the bronze kite of Tumblers for use in almond Roller matings. To the extent that kite (K) can be easily "graded-up" in Rollers, I have given Roller bronze a separate classification. Spread (S) is epistatic to Roller bronze (K^R).

Brander Bronze (K^B)

Pigmentation Areas Affected

All areas show a mixture of red and black pigmentation.

Matings to Wild Type

Matings to wild type produce variable bronzes. Backcrosses and the F_2 generation produce progeny similar to the F_1 generation. "Grading-up" to parental type is difficult,and requires extensive selection.

Discussion

Brander bronze (K^B) resembles Tippler bronze (K^T) in many ways. Both show some red in the tips of the flights. Spread suppresses the Tippler version, but some evidence exists that many Branders are actually spread pigeons. Tippler bronze (K^T) has a close association with grizzle (G), which suggests possible linkage. The Brander bronze does not revert to the "gay pied" expression so common in Tippler bronze.

Tippler Bronze (K^T)

Pigmentation Areas Affected

Tippler bronze (K^T) affects coarse spread pigment, and to a degree, the blue areas.

Matings to Wild Type

Matings to wild type produce variable bronzes in all forms of grizzle and pied combinations. No rhyme or reason seems to apply to the segregation of phenotypes. You are just as likely to get near self bronzes from pied matings, as from matings of birds selected for the absence of white or grizzle.

Discussion

The bronze of Tipplers is suppressed, but not masked by spread (S). Many such black pigeons will show a high degree of bronzing. It is rather curious that the breeds of Rollers and Tipplers, which have a common starting point, should have such a different expression of bronze. The Rollers imported into this country prior to 1930 show no traces of Tippler bronze or Tippler light print grizzle, but the later imports are over ninety percent of this phenotype. The question, "What breeding practice would account for such massive infusion of Tippler associated genes into Rollers in such a short span of time?", is at present, unanswerable.

Toy Stencil Bronze (K^S)

Pigmentation Areas Affected

Toy stencil bronze (K^S) affects primarily coarse spread areas, but also has a pronounced effect on the transitional areas of the wing and tail, where a mixture of both clumped and spread pigment exists. The blue and smooth areas are little influenced.

Matings to Wild Type

A mating of white stencil, $K^S//K^S$, to wild type produces rich bronzes. The bronze is primarily in the areas affected by the homozygous condition. Backcrosses and F_2 offspring seldom show white stencilling, but also seldom show wild type. The variation of bronzes is less than that of other types, but the difficulty recombining the gene or genes necessary to produce white stencil suggests a more complicated form of inheritance. Possibly two or more genes are operating, but our information is lacking at this point.

Discussion

Toy stencil bronze (K^S) differs from all other forms, in that it will stamp out the masked pattern in a spread pigeon. The depigmentation of coarse spread areas to white in a spread pigeon is a unique problem for us. The genetic pattern factors involved are masked by spread, producing a black self. The pigment is all spread and no blue areas appear. How toy stencil ($K^S//K^S$) can bleach to white these unexpressed patterns, is a real question for pigmentation experts.

Lebanon Bronze Stencil (k^1)

Pigmentation Areas Affected

Lebanon bronze stencil affects primarily smooth spread areas.

Matings to Wild Type

Matings to wild type produce wild type offspring, showing the presence of some darkening factors and a tinge of bronze. The expression of (k^1) has only been studied in matings of Shikli Ahmar red, which is an ash-red T-pattern (velvet).

Discussion

Shikli Ahmar red is a combination of ash-red velvet, and a stencil factor that acts as a recessive. Evidence is not conclusive, but (k^1) has the strongest support for being a unit factor of the family of bronzes. The $k^1//k^1$ ash-red velvets have the smooth spread areas bleached out to white, producing a red pigeon with white edging on the wings, and a white bar on the tail.

FAMILY OF BRONZES

Bronze	Tentative Symbol	Pigmentation Areas Affected	Description of Progeny for Matings to Wild Type	Relation to ()
Kite (E.S.P. Tumblers, Parlor and Oriental Rollers)	K	transitional areas of remiges	kites	hypostatic to (S) (is masked by)
Modena Bronze	K^M	coarse spread areas	slight bronzing in shield	hypostatic to (S) and (B^A)
Archangel Bronze (Archangels, Larks, Catalonian Tumblers)	K^A	blue areas	slight bronzing in blue areas	unknown
Roller Bronze	K^R	coarse and smooth spread areas	parental type of mild bronzing	hypostatic to (S)
Brander Bronze (Copenhagen Tumblers)	K^B	all areas	variable bronzes	apparently unaffected by (S)
Tippler Bronze (Tipplers, Show Rollers)	K^T	coarse spread and to a degree blue areas	variable bronzes "gay pieds"	suppressed by (S) but not masked
Toy Stencil Bronzes (Toy pigeons)	K^S	coarse spread and transitional areas	rich bronzes	bleaches out pattern in (S) factor birds
Lebanon Bronze Stencils (Lebanon varieties)	k^1	smooth spread areas	wild type	unknown

Review

The family of bronzes are rich in pigmentation and luster of plumage. They are a valuable asset in developing rich colorations in non-related phenotypes. The goals of the breeder in producing classical almonds, deep chestnut reds, or blacks with "beetle-green" sheen, may well key on the practical use of a form of bronze in the breeding program.

Bronze is a poorly defined condition of pigmentation, where red and black granules are mixed in such a manner, that both color hues are visable. Our approach has been to attempt classification of the various bronzes for purposes of study. Arbitrary classification is a necessary beginning point. The reader should understand the difficulty of classifying these variable expressions if they were ever mixed in the genotype.

Several Roller breeders working together, sharing information and results, have made a major step forward by developing and "grading-up" all eight bronze forms, to performing Roller type. The twenty years of work required is about complete. The next step is to test all forms in matings to a pure strain of blue bar Rollers, developed for this purpose. This exciting and creative investment of breeding skill will make it possible to analyze bronze without the complexities and variations involved in testing a factor(s) in eight different breed mixtures. The problem of most scientific study is in controlling the variables that may confuse results. The rich ($\underline{K}$), ($\underline{K}^{M}$), ($\underline{K}^{A}$), ($\underline{K}^{B}$), ($\underline{K}^{T}$), ($\underline{K}^{S}$), and ($\underline{k}^{1}$) Rollers, representing pure extracted forms of the several bronzes, is a tribute to the dedication of these breeding artists. With renewed effort, we may soon be able to state clearly, without arbitrary assumptions, the nature and mode of inheritance of this complex family of colorations called bronze.

Oddities and Their Value

The breeder, in general, attaches little importance to the study of oddities. Most mutations produce an adverse, rather than a beneficial effect, and we might expect that there are many deleterious genes present in pigeons. Domestication of animals tends to increase mutations (possibly just prevents natural selection against them). Such traits are very important to the genetical study of pigeons, but to the breeder, they often only represent a nuisance and a problem.

Before describing just a sampling of the mutations that are generally considered undesirable, it is necessary to take a moment to give some of the reasons why the breeder should study them, as he would desirable mutations such as recessive red (e^{1}), dilution (d), or crest (cr). A weed can be defined as a plant out of place. Many beautiful mutations in color or structure can be considered a nuisance, if they are floating in the wrong breed stock. Head tremors are a problem in most breeds, but necessary to all champion Fantails. Crest is beautiful on Danzig High Flyers--- no self respecting Danziger would be without one, but the same recessive gene present in a strain of Giant Homers can be a real problem. Who wants crested Giant Homers? The elimination of crest from Giant Homers is essentially the same as eliminating albino, porcupine, or a genetic form of blindness.

When oddities occur, we recommend the recording and testing of such mutations. If the reason for this is to eliminate the undesirable trait from the breeding stock, then this is reason enough for a breeder to study the oddities that occur in his finely bred pigeons.

Any strange progeny, freaks, or unusuals produced from your breeders, may or may not be genetically caused. A major portion of all monstrosities are the result of environmental, chemical, or temperature variations in the growth of the embryo within the egg. Testing, when possible, such individuals to find out if the condition is inheritable is important. The time spent is rewarded by the relief in knowing this undesirable trait will not eventually waste your years of breeding by constantly reoccurring in your finest pigeons. If is just as important at times to know what you "haven't" in your loft stock, as it is to know what you"have", genetically speaking.

> I'll tell just a short tale about a dog to illustrate this point. Acetabular dysplasia is a genetic condition in dogs which distorts the hip and rear legs. It usually appears after the dog matures. The beautiful German Shepherd is most often afflicted. About fifty years ago it was estimated that about 12% of all German Shepherds carried the gene (or genes) responsible for producing this pathetic condition. In common practice, breeders used the "kill, cull and hide" methods in breeding, and little knowledge could be acquired from breeders about the matter. Nobody would ever admit the condition occurred in their dogs. Well, genes segregate and resegregate, but they seldom disappear. Ten years ago various estimates suggested, that possibly as high as 25-30% of all German Shepherds now carried the gene (or genes) producing this malady. You would think that about this time, the frequency of dysplasia in German Shepherds would frighten breeders into studying the matter, especially those that had some love for this handsome animal. In the past ten years, breeders have just killed, culled and hid more dogs. In the 1970's, our estimates from verterinarian reports of dysplasia conditions in German Shepherds brought in for treatment by owners, indicate possibly over 50% of the German Shepherds now carry the gene or genes for this genetic bone malformation.
>
> I am not a breeder of German Shepherds, and yet I think it a dog of great beauty. I also have difficulty understanding the dog breeders' attitude. I'm not really sure that this genetic problem that could have been solved easily fifty years ago, with their help, or with some difficulty ten years ago, with their help, may now be impossible to solve, with or without their help. There is a point of diminishing returns in all life. I hope I'm wrong about the German Shepherds. I sincerely wish that my estimates of the gene pool frequency of this gene(s) prove to be fantastically high. It doesn't really matter though, because in the 1970's, they, with renewed vigor, "kill, cull, and hide" the facts. It is possible to fool the buyer and the registry. It is also possible to quietly give a second dog to the tearful child to replace (not really) the dog she loved that had to be destroyed. Fifty years of history prove that dog breeders can deceive themselves into believing such things will "go away". Nature is not ever deceived, and yet, she permits us through study and related testing to control her, using a natural art form ---the art of selective breeding.

I have included a brief description of several mutations that have been studied in pigeons as examples of the variety of mutational expression. We know similar mutations will occur again and again in the breeding lofts of this country. Identification of the mutation can save much testing time, and therefore such descriptions can be valuable to the breeder.

To develop the general procedures for increasing and decreasing selectively the percentage of such genes in the pool (loft or breed), I have selected pink-eyed dilute and albino as examples to study. These genes are quite rare, but have been found in several breeds of domestic pigeons.

Albino (al)

Albino (al) is an autosomal recessive mutation which produces white plumage, without any form of pigmentation. The typical albino characteristics found in other forms of animals, such as pink-eyes and light skin are present in albino pigeons al//al. Such birds usually have neurological deficiences which produce poor vision and head tremors. Albinos usually are delicate, and because of the vision problems, have some difficulty learning to eat and drink, hence they usually die unless handled specially during the fledgling period. The gene is not sex-linked, and reacts in matings, as do other autosomal recessives. Pigment cells are present in the tissue of albino pigeons, but are without any melanin forming potential.

Pink-eyed Dilute (pd)

Pink-eyed dilute (pd) is an unusual autosomal (not sex-linked) mutation which influences eye color, and produces a dilutant effect in plumage coloration similar to sex-linked dilution (d). The vision of such birds is rather poor, but they are robust and breed well in individual coops. Most fanciers would immediately dispose of such a bird, but it is an important addition to the study of the genetics of the pigeon. In combination with white plumage, produced by other factors such as grizzle or piebald, it truly is a "pseudo-albino", that is, an albino phenotype produced by a combination of factors, rather than the gene for albinism, al. Pink-eyed dilute birds have rather jerkey head and neck movements, especially in eating and walking. This is possibly related to their vision problems. The occurrence of such a bird in your loft should first be reported and the bird saved, if possible. Since we assume it is a product of your best stock, it represents both a problem and the solution for the breeder who does not wish to have this condition occurring in his loft. The pink-eyed dilute pigeon, pd//pd, as the homozygous recessive, represents the test cross for the mutant. All pd//pd birds may be mated to other birds in the loft to test for carriers. The occurrence of one such homozygote, pd//pd, indicates the strong possibility of many more carriers, pd//+, being present in the flock. Once this or any other homozgyous recessive occurs, we may wish to increase it or eliminate it from the gene pool. The point is, that killing or culling this homozygous individual, without some study, can jeopardize you breeding stock and eventually the breed. These hidden recessives will occur with a gradually increasing frequency if linebreeding mating schemes are followed.

Pink-eyed dilute is a unit characteristic, and we can assume that both normal parents of such a bird carry (pd) and will, if left mated, produce $\frac{1}{4}$ pink-eyed dilutes of both sexes.

pd//+ X pd//+ both parents normal

Male Gametes \ Female Gametes	pd	+
pd	pd//pd	pd//+
+	+//pd	+//+

3 normal
1 pink-eyed dilute

Phenotypic Ratio 3:1

It can be easily shown that the elimination of that one pink-eyed dilute produced does little to the presence of such a mutant in the flock. The two normal heterozygotes, pd//+, produced will take care of that matter. If the stock is highly inbred, the percentage of carriers can be deceivingly high. It is a rather common practice, when such mutants occur, to break up the mating, remate to other birds and go on with the breeding program. Well, (pd), or any other genetic recessive of an undesirable nature (from the breeders point of view), will not be influenced at all by such procedures. These genes will be back in future nests, and depending on "luck" (chance selection), their numbers and frequency can be very discouraging to any breeder of domestic pigeons.

After it has been established that the phenotype is genetically produced: testing is the solution to all such problems. Mating such unusuals to their parents will usually tell the tale in several nests. If it reproduces itself, the frequency and sex of such offspring will tell us much about this unusual difference from normal (wild type). For the good of the strain, or breed, and to increase our knowledge of pigeons, all information should be recorded carefully. The breeder may ask, "why record?" "I can kill the bird and forget it in several seconds!" True! ---but the intelligent breeder should recognize that killing the homozygote is like burying your head in the sand. It is true for the moment, you won't have to look at this unwanted difference from normal, but genetically, you will see it again and again and .....

There is such a diversity of recessive mutations, that the responsible breeder really has not other choice but to proceed sensibly. The breeder will test all such mutants and then select scientifically to increase or decrease the frequency in his strain. In a few short years of interesting experimentation, the whole problem can be corrected. The breeder, in doing so, has made his contribution to his chosen breed, and the pigeon fancy in general. If pink-eyed dilute occurred in a racing homer, it would certainly be undesirable and a problem to the breeder. By testing this unusual bird in matings to one of its parents, others would be produced. In this case, if the pd//pd offspring produced by two normal birds is a cock, we have some information indicating the gene is not sex-linked. because if (pd) were sex-linked, we would expect the female parent to show some phenotypic expression of it. In the absence of the wild type (normal allele), the female pd/· would be pink-eyed dilute if the gene were sex-linked. In actual testing, it has been shown to not be related to sex. Therefore, the normal parents of a pink-eyed dilute squab must be formulated pd//+, or heterozygous for an autosomal mutation.

With this knowledge, the breeder can produce several pd//pd pink -eyed dilutes to mate to his finest stock birds. If the stock bird carries (pd) and is normal, his genotype will be pd//+; if he doesn't carry (pd), his genotype will be wild type at the pink-eyed dilute locus $(+)^{pd}//(+)^{pd}$, and all the offspring of such a test cross mating will be normal.

		Pink-eyed dilute parental Gametes: pd	pd
Normal parental Gametes	+	pd//+	pd//+
	+	+//pd	+//pd

All progeny normal

After several successive nests , in which all normals are produced without a single pd//pd squab, the chances of the normal parent carrying (pd) are reduced to the point that it can be assumed to be pure for wild type and returned to the breeding program. If it is mated to a similarly tested bird, we can go forward without the undesirable mutant or the problem occurring again.

If the stock bird being tested is heterozygous for the undesirable gene, in this case (pd) in a racing homer, the mating will yield:

Normal Parent Gametes	pd	pd
pd	pd//pd	pd//pd
+	+//pd	+//pd

Pink-eyed Dilute Parental Gametes

½ Normal
½ Pink-eyed Dilute

The 1:1 phenotypic ratio is what we have come to expect from the test cross. We should note that as in the original parents, if <u>any</u> pd//pd birds are produced (even one), we can assume the normal parent is a carrier of (pd). It is a little easier to detect the carriers, than to be <u>absolutely</u> <u>sure</u> that "chance" hasn't dealt us a strange hand, and that the bird that produces all normals isn't still heterozygous. In matters of chance, unusual things have been known to occur.

As with all phenotypic ratios, it is a matter of probability. When such a mating produces all normals, we have a <u>great</u> <u>deal</u> of assurance that the tested bird is not a carrier. The more normals produced, the more assurance we have that the bird is $(+)^{pd}//(+)^{pd}$, homozygous normal or wild type at the pink-eyed dilute locus. When the first pd//pd bird is produced, we know the tested bird is pd//+, and we can cull it if we wish. When all normals are produced, because of chance, we just get surer with each normal offspring, that the tested parent is not a carrier.

I should say that if a highly desirable bird would test heterozygous for an undesired mutation, the bird may <u>still</u> <u>be</u> used in the program. The carried mutant may segregate independently, as in this case, and by mating to a tested $(+)^{pd}//(+)^{pd}$ (wild type at this locus) bird, we may continue using such a bird, and testing the progeny for pure normals to add to the regular breeding program.

Normal bird tested heterozygous for pd//+, but which has many desirable characteristics we wish to continue	X	Normal bird tested with some assurance that it does not carry the gene in question.
pd//+	X	$(+)^{pd}//(+)^{pd}$

Tested Wild Type Gametes

Tested Heterozygote Gametes	+	+
pd	pd//+	pd//+
+	+//+	+//+

All Normal in phenotype

½ Carriers
½ Normals

By mating F_1 birds to the test cross, homozygous pink-eyed dilute pd//pd, we can isolate the carriers and pure normal progeny, and thus raise many usable offspring from a bird carrying an undesirable mutant gene.

It takes time, but an entire inbred strain may be tested gradually without interruption of the breeding program. By testing the breeding stock in several matings (test crosses) in individual coops, during the off-season, the breeder can rather quickly solve his problem. The results of this type of planned program has many advantages over the "kill, cull and hide" method in common practice:

1. Our knowledge of the genetics is increased to assist the scientific study of pigeons.

2. The problems of the occurrence of undesirable mutations in pure-bred stock can be handled in a manner that accomplishes the breeder's goal of elimination of such genes from the breed or strain by genetic testing.

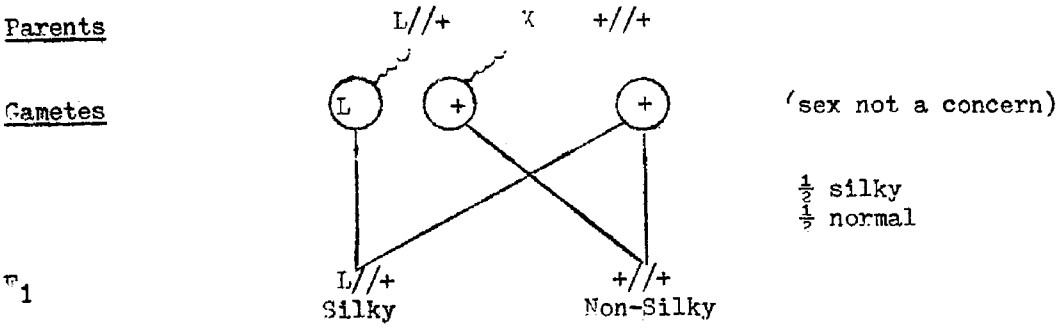
Mutations Influencing Feather Structure

In those changes (mutations) that have occurred in pigeons, several as would be expected, influence feather structure. The condition of having feathers is basic to the definition of birds. The genetic "naked" pigeons studied by Owen certainly could present problems to a breeder of pigeons. Of course, it is asking a little too much of any bird breeder to study a featherless bird. Between the naked and the normal are several variations which occur and deserve notice. Silky or laced, at least in a Fantail, presents a delicate and beautiful phenotype. It is difficult to say, just on the basis of description, what might be considered attractive by breeders in future years. Naked-necked pigeons are bred in Poland ---these specimens are not at all as divergent from wild type as the Fantail or its progenitor must have been in ages past.

Silky or Lace (L)

Silky is a structural autosomal gene, dominant to wild type and not sex-linked. The gene produces a soft, weakened feather strucutre. The silky feathers fail to web properly, due to a twisting of the feather as it grows from the follicle. All the proper barbs and barbules are present in the feather, but they fail to hook up properly due to the twist. The fragile nature of the feather makes flying difficult, and the feathers tend to become broken and frayed. silky squabs can be recognized in the nest, because the down twists in the manner of the mature feathers. Silky squabs are "fuzzy". The dominant gene (L) produces the typical silky of the Fantail, which is quite pleasing to view. Show silky types are formulated L//+, because the homozygote, L//L, expresses the condition in the extreme. By the end of the season, homozygous silkies L//L, do not have much left of their feathers except the shafts. Normally, the homozygote L//L, is not used in breeding; cocks have difficulty treading. Silky pigeons are usually mated to normals of the breed.

Breeding a silky heterozygote to normal produces:



Frayed (no symbol)

Frayed is a mutation recently reported by W.F. Hollander, which represents a less extreme version of the silky condition previously described. This "slightly silky" mutation, when homozygous, produces about the same effect as the heterozygous silky, L//+, type expression. This of course, could make possible a silky type that would breed true for the silky feather qualities, without the problems related to homozygous silky, L//L. Frayed is an autosomal dominant gene. It is not known at this time whether it is an allele of silky (L) or not.

Scraggly (sc)

Scraggly is a simple recessive which produces a similar silky condition, but with a more extreme distortion of feather structure. Scraggly pigeons are further handicapped by a thick scaly skin condition.

Porcupine (p)

Porcupine is an autosomal (not sex-linked) recessive condition which influences feather maturation. The feathers of porcupine pigeons, in addition to other structural defects, fail to unfold and generally remain in the sheath. Without the insulating effects of the unfolded feathers, porcupine pigeons cannot incubate their eggs. Flight is impossible and copulation by the male is difficult.

Note:
A similar condition of delay in "feathering-out" of young birds, possibly due to a nutritional deficiency, occurs from time to time. This delayed feather opening is usually temporary and its appearance gives a mild illustration of what porcupine looks like, but it should not be confused with it.

Eye Coloration

The first consideration of eye pigmentation should deal with the eye color in squabs. In general, squabs are dark-eyed at birth, with the pigmentation of

the adult gradually being acquired within two or three months. The major exceptions are almond and brown squabs, in both intense and dilute phases. In these exceptions, the eyes tend to be pink and the pigmentation is delayed several weeks.

Wild type coloration in pigeon eyes is orange-red, with the reddish tinge in the normal iris being due to the reflection of light from very small blood vessels.

The bull or black iris usually contains an adequate amount of pigmentation, but it is only present on the innermost layer of the iris, and the dark appearance results. Such dark eyes are usually associated with white plumage on the head.

The highly pigmented orange eye is wild type $(+)^{tr}$ and dominant to pearl eye (tr). Matings of orange to pearl usually result in orange-eyed progeny. I say usually, because where piebald or white is involved, the tendency to produce dark (bull) eyes complicates our ratios.

Pearl-eyed Parental Gametes
tr//tr

Orange-eyed Parental Gametes +//+		tr	tr
	+	+//tr	+//tr
	+	+//tr	+//tr

All orange-eyed offspring

The F_2 generation gives us a fair fit for the expected 3:1 (3 orange, 1 pearl) ratio of phenotypes involving a single recessive gene.

tr//+ X tr//+
Parental Gametes

Parental Gametes	tr	+
tr	tr//tr	tr//+
+	+//tr	+//+

3 orange-eyed (wild type)
1 pearl-eyed

We should note that in crosses involving brown (b), an unexpected increase in the number of pearl-eyed birds occurs. Actually, one of the side effects of the sex-linked mutation brown (b), is to develop a pale creamy yellow iris, which approaches and is often confused with pearl coloration. This "false pearl" is an excellent identification badge for brown. Browns hardly ever have orange eyes, because of this related coating effect of pigment in the iris. The homozygous, tr//tr, pearl-eyed browns do not show this pale creamy coloration. Only the brown pigeons that would normally have orange eyes (wild type) will express this feature.

There is much room for study in this area of eye coloration. In crosses of orange with dark (bull) eyes, each mating gives somewhat varied results: some pairs producing all orange-eyed progeny, others mixed eye phenotypes, and some pairs producing only bull eyes. In general, the tendency of bull eyes to suppress pearl or orange expression is not well understood. Where white about the head is involved, patched, cracked or odd-eyed combinations occur frequently.

Pearl-eyed or orange-eyed baldheads or white selfs can be produced in any breed. This, of course, is another challenge to the breeding artists. The ordinary breeders will have to settle for, and adjust to, what most often occurs --- the bull (dark) eye on piebald phenotypes.

Feathered Ornaments

Wild species of Columbidae show various feather ornamentation. Columba livia, our wild type, is without any of these, and it seems quite strange to see such a variety of feather reversal, enlargement, twisting, and disfigurement present in our domestic breeds. Domestication and the consequent selection of curiosity, when it occurs by mutation, possibly accounts for such an accumulation of feather structure mutations. Considering the widespread existence of such mutant types, we know surprisingly little about the inheritance of such conditions. This area is practically virgin territory for the researcher.

Head feathering and neck feathering

Crest (cr) is a simple autosomal recessive which produces a reversal in the feathers on the back of the head, and usually the adjacent neck area, to produce a kind of collar or hood of reversed feathers.

The variations, all felt to involve the same gene, are:

Shell

Peak

Hood (Jacobin)

Scientific reports on the study of crest (cr) have caused much confusion over the years. Some reports have indicated that the shell crest of the Swallow behaves as a dominant factor, and some matings of crested birds to Barbs and Homers have produced erratic reports of crested and non-crested progeny. For the most part, it has come to be accepted that the various crests are the product of a single unit factor, with the various expressions being due to modifiers.

Matings of a crested to a plain-headed bird indicate that a simple autosomal recessive gene is involved.

Crested Parental Gametes
cr//cr

Plain-headed Parental Gametes
+//+

	cr	cr
+	+//cr	+//cr
+	+//cr	+//cr

All plain-headed Progeny

The matings of F_1 individuals yield:

Parents +//cr X +//cr

Gametes + cr + cr

F_2 +//+ +//cr +//cr cr//cr

Plain-headed Crest

3 plain-headed
1 crested

Phenotypic Ratio
3:1

Matings of the shell crested form to the peak crested (pointed tuft) tend to produce shell crested birds, while the matings of hood type crests to shell types usually produce an intermediate form of hood.

In crested birds, the arrangement of the reversed neck feathers shows as much variation as do the crests. The neck feathers (mane) vary from the straight line on the back of the neck of the Turbit, which ends at the fine point of the peak crest, to the hood of the Jacobin. The Jacobin's "parka" hood covers the entire neck and shoulders. The so-called "mane" tends to fit appropriately the crest it supports.

It very frequently happens, even in breeds pure for crest, that the crest is misshaped in some manner. There appears a chance variation in the development of the ideal crest. Such "mis-crested" birds, when mated, seem to produce as nicely crested progeny as their more perfect crested close relatives. I am not suggesting that a breeder of crested pigeons shouldn't select for the ideal crest, but I am indicating that an otherwise perfect bird with a foul crest should not be excluded from the breeding program on the basis of what is very often just a chance variation, and not a genetic one.

Review

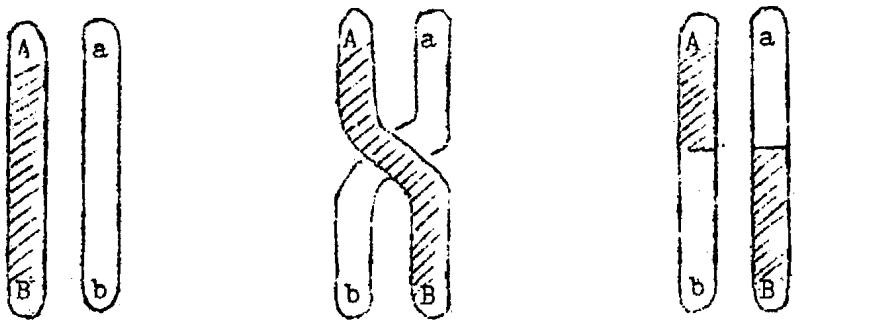
We have considered a small sampling of genetically produced conditions that may be considered undesirable from the breeder's point of view. The recording of such information about such oddities is vital to the progress in pigeon science. A program of testing for these unusual conditions that occur from time to time in every loft is an important aspect of the breeder art.

The Crossover Mechanism

The method employed by nature to provide for increased variation within species is termed crossing-over. By this mechanism, genes on the same chromosome can be reshuffled or arranged. In our studies of pigeons, there are only two chromosomes where linkage has been established. The sex chromosome contains four mutant loci: the almond locus $(+)^{St}$, the brown locus $(+)^{b}$, the dilute locus $(+)^{d}$ and the reduced locus $(+)^{r}$. The autosome containing the spread locus $(+)^{S}$, the pattern locus $(+)^{C}$ and the opal locus $(+)^{O}$, has also been studied. The first requirement in studying crossovers is to know that at least two identified mutants are linked, i.e., present on the same chromosome.

Crossovers can occur because of a break and alternate union of opposite broken ends of the chromatids (replicated chromosomes). Since only two of the four chromatids are usually involved in crossing-over, we will show the diagrams in this section by showing only the two involved chromatids. It should be remembered that crossovers occur during the first meiotic division, when the replicated homologous chromosomes are lying in close proximity to each other. If one of the homologous strands lies across another, there is potential for a crossover occurring. The reader is referred to page 16 for a review of this procedure.

In this section, crossover diagrams will appear as:

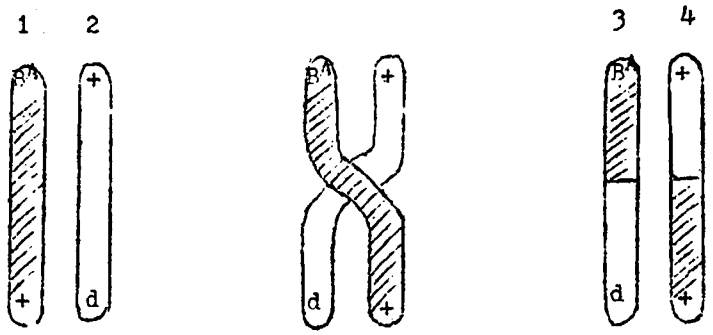


Parental Types Crossover Types

In this section on crossovers, we will only concern ourselves with the sex chromosome. Example 1: A breeder that has a dun bar silver (d/·) hen may wish to create a cream bar line of birds. The procedure is to produce a cock of the genotype $\frac{B^{A}\ +}{+\ d}$, from a mating of a mealy cock to this silver hen. All cocks produced from this mating, ($B^{A}//B^{A}$ X d/·), will be B^{A} +//+ d in genotype. Crossovers for sex-linked genes can only occur in male pigeons, where two sex chromosomes are aligned in meiosis.

These B^{A} +// + d cocks produce several types of gametes, which in turn determine the genotype for sex-linked factors in all female progeny.

Pattern genes will segregate independently of sex-linked genes, but for simplicity, all pigeons are bar pattern in this section. A B^{A} +//+ d cock will produce gametes of the following types:



	Gametes		Genotype and Phenotype of Hens Produced
1	B^A $(+)^d$	Parental Type	Ash-red $B^A/\cdot$
2	$(+)^b$ d	Parental Type	Silver d/·
3	B^A d	Crossover Type	Cream bar B^A d/·
4	$(+)^b$ $(+)^d$	Crossover Type	Blue bar +/·

It should be understood that the crossover type gametes are just as likely to combine with the gamete carrying the sex chromosome from the dam forming a male offspring. In this case, crossover type is likely to be hidden.

Matings of this B^A +//+ d cock to hens of any basic color, will produce similar results. For an example, let us look at this cock in several matings: to an ash-red, blue-black and brown hen.

Male Gametes B^A +//+ d	X ash-red hen $B^A/\cdot$ Gametes $\ominus$		X wild type hen +/· Gametes $\oplus$ $\odot$		X brown hen b/· Gametes $\ominus$ $\odot$	
	Cocks	Hens	Cocks	Hens	Cocks	Hens
$B^A(+)^d$ Parental Types	$B^A//B^A$ ash-red	$B^A/\cdot$ ash-red	$B^A//+$ ash-red	$B^A/\cdot$ ash-red	$B^A//b$ ash-red	$B^A/\cdot$ ash-red
$(+)^b$ d	+d//B^A+ ash-red	d/· silver	d//+ blue	d/· silver	+d//b+ blue	d/· silver
B^A d Crossover Types	B^Ad//B^A+ ash-red	B^Ad/· ash-yellow	B^Ad//++ ash-red	B^Ad/· ash-yellow	B^Ad//b+ ash-red	B^Ad/· ash-yellow
$(+)^b(+)^d$	+//B^A ash-red	+/· blue	+//+ blue	+/· blue	+//b blue	+/· blue

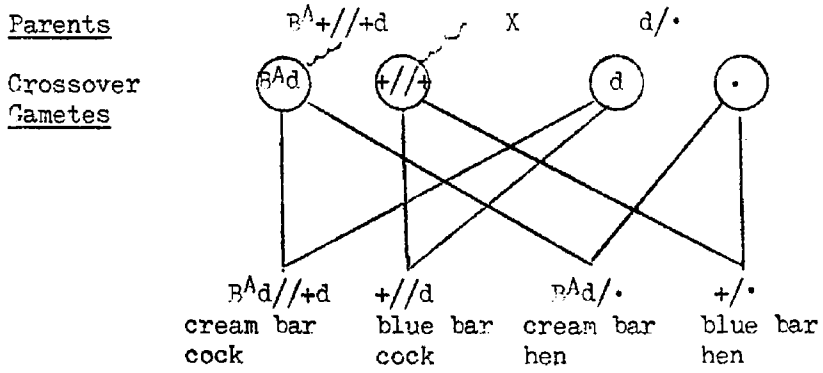
We should observe that all the hens produced from these matings are the same, regardless of the genotype of the dam. The female parent does not contribute a sex chromosome to the hens produced from the mating, and the dam's genotype relative to sex-linked genes, does not affect the female offspring. This cock mated to any hen will still produce ash-red ($B^A/\cdot$), silver (d/·), ash-yellow B^Ad/·, and blue hens (+/·), with respect to basic sex-linked color mutants. The ash-yellow B^Ad/· and blue +/· hens of the crossover type are produced in all matings in the same proportion, and are easily identified. The one-half of the crossover carrying gametes from the sire, which combined with sex chromosome carrying gametes from the hens, are in all cases undetectable in the offspring. We could very well test all male offspring and observe the female phenotypes produced to identify these hidden crossover chromosome arrangements.

Where the crossover rate is high, (as in this case 38-40% crossover between $(+)^b$ and (d), detecting crossovers in male offspring may be accomplished by further testing.

The close linkage between the almond $(+)^{St}$ locus and the brown $(+)^b$ locus would make such a practice illogical, if the crossover type is the project goal. In testing 100 cocks for the crossover type desired, we could expect only one or two such genotypes. It is far simpler to mate cocks with the proper sex chromosome gene alignment to produce the desired crossover and wait on that chance reshuffling of genes in female offspring.

In any case, we are only absolutely sure of the crossover when we produce an ash-yellow hen B^A d/· or a blue hen +/·.

If we had chosen to mate this cock, B^A+//+d, to a silver hen d/·, the crossover cocks could be easily detected, because of the dominance of ash-red to wild type

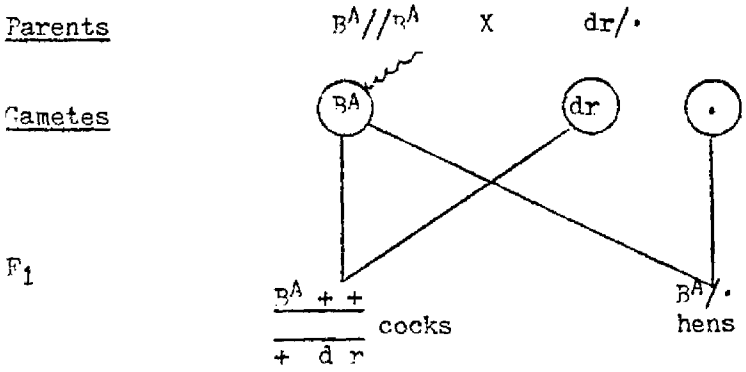


All crossover type offspring identified in both sexes.

We are sure that the cream bar (ash-yellow) cocks are examples of the crossover type, because the ash-red gene was originally associated with non-dilute $(+)^d$, and since dilution, to be expressed must be homozygous d//d in a cock, we are sure that the one sex chromosome from the sire must be B^Ad or the crossover type. Likewise the blue bar cock must also be a crossover type because of the separation of $(+)^b$ from (d) in the parental type.

Almost all crossovers are of the single break type. On rare occassions, more than one chiasma and chromatid break occurs, producing a double or multiple crossover. The nature of the chromosome determines the kind of crossovers that will result from this meiotic mechanism. We assume that the somewhat sausage dimensions of the chromosomes make such crossovers between loci closer than ten map units (10% crossover) apart, improbable. This implies that the bending of the chromatids in such a manner as to produce two or more points of contact and resulting interchange of homologous sections, is highly unlikely. In nature, the unlikely does happen. It happens with consistent "chance oriented" precision, making the occurrence of double crossovers as predictable as the single type.

To demonstrate both types of crossovers we could produce a cock of the genotype $\frac{B^A + +}{+ \ d \ r}$ by mating a homozygous ash-red cock and a dilute reduced hen.



We now have three sex-linked genes positioned to test the crossing-over mechanism. A cock of this genotype, B^A + +//+ d r, can produce eight kinds of daughters.

The parental types of hens

1. B^A/· ash-red
2. dr/· dilute reduced

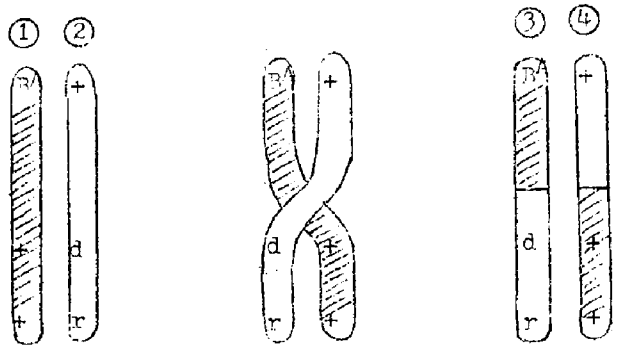
The crossover types of hens

3. B^Adr/· dilute reduced ash-red
4. +/· blue-black,(wild type)
5. B^Ar/· reduced ash-red
6. d/· dilute blue-black

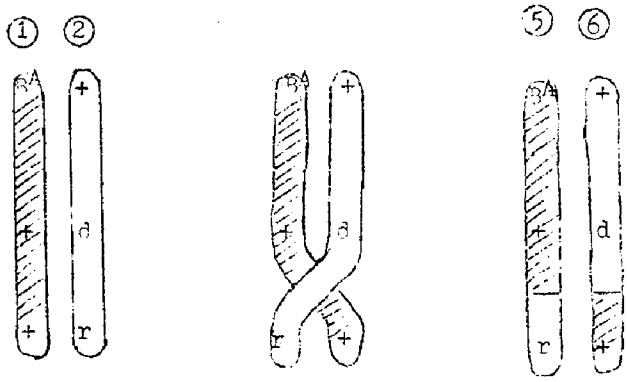
The double crossover types of hens

7. B^Ad/· dilute ash-red (yellow)
8. r/· reduced blue-black

In a diagram form, it appears as:



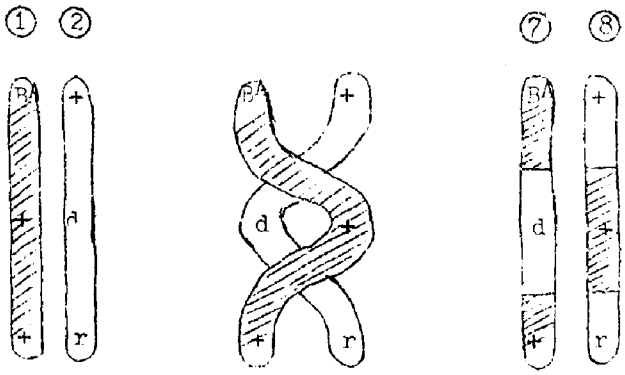
Genotypes (3) and (4) represent the most common type of crossover for such gene alignments.



It should be understood that discussion of double crossovers in pigeons is an <u>academic</u> and not a <u>scientific</u> exercise. We are not sure of the order of the genes on the sex chromosome. In our diagrams, we show dilution $(+)^d$ between the brown locus $(+)^b$ and the reduced locus $(+)^r$. It could just as well be that the reduced locus is the innermost of the three loci, and is between $(+)^b$ and $(+)^d$.

<u>If our postulated order is correct</u>, the following double crossover types are also correct, because double crossovers involve the interchange of homologous inner sections of the chromatids.

Parental Types Double Crossover Types



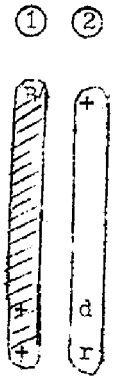
Genotypes (5) and (6) are produced when the junction (chiasma) is such that (d) and (r) are separated, or more precisely, the linkage is broken. We have suggested a crossover rate of about 7% for these two loci, $(+)^d$ and $(+)^r$.

In order to further reshuffle these genes in one step, a double crossover has to be formulated. The occurrence of the double crossover type is rather rare in comparison to the other types shown. It should be understood that the relationship of each gene to its allele remains unchanged in crossing-over. The interchange is between homologous sections containing the genes, and the linear alignment remains the same.

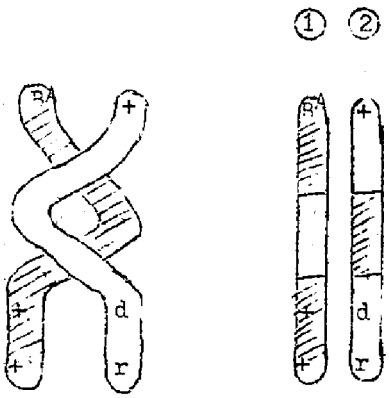
In our academic example, the dilute ash-red hen $^{B^A}d/\cdot$ and the reduced blue-black hen $r/\cdot$ are double crossover types.

Double crossovers have a predictable rate based on the distances between genes. Since we only have identified two widely separated sets of loci, the double crossovers usually will only represent an interchange of unknown genes in the middle of the chromosome, which will produce parental types for our identified genes.

Parental Types

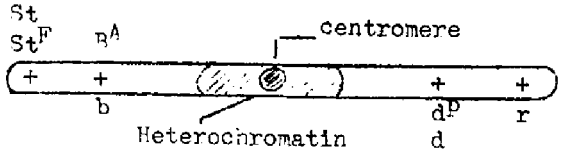


Double Crossover Parental Types



It would appear double crossover discussions have little bearing on gene order. This is not the case. We have a technical problem. We have not identified a marker gene towards the center of the chromosome so as to begin the mapping procedure as described on page 17. In the absence of such a mutant, we have to settle for what we have, and this includes the known occurrence of single and double crossovers. Accurate records of crossovers should indicate something of the gene order. If the order is $(+)^b$———$(+)^d$ $(+)^r$, the single crossover will separate reduced (r) from its position about 7% of the time, and it will require a "double crossover" to separate dilution from the chromosome $(+)^b$——(d)—(r). The double crossover should occur about 2-3% of the time. The percentage difference between crossover rates will then support either placing (d) between $(+)^b$ and $(+)^r$, or the reverse order, with respect to these closely linked genes (d) and (r).

Note: A center portion of the pigeon sex chromosome has been postulated to contain an area of neutral heterochromatic material, which carries no genes. The mutational positioning of this material may well have a phenotypic effect, but evidence is lacking on this point.



Heterochromatin is not usually resolvable into distinct genes by the usual methods we have described. Possibly these areas stabilize the centromeres or regulate the crossing-over mechanism in some way.

The double crossover, as distinguished from the single type, may well involve all four, three, or only two of the four chromatids producing recombinations, but the occurrence is still predicted on inter-gene-distance.

Almond (3t) (Sex-linked Dominant)

We have placed the sex-linked mutations of almond, sandy, and faded in separate sections, to illustrate the manner in which complex genotypes may be resolved into simpler components for study.

The breeding of almonds in classical show coloration is the highest challenge to the color breeder. The mutation from wild type to almond was a somewhat massive change in either the gene structure or the chromosome itself. I refer to an "overprinting effect" of almond to describe the tendency of this gene to produce unusual admixtures of ground color and flecks on the standard colors and patterns.

Variation in almond seems endless, and it is easily understandable that the classical almond coloration is difficult to achieve. Classical almond is usually associated with English Short-Faced Tumblers.

Description:

The classical almond should have a uniform ground color of a rich rust yellow, and be liberally flecked with black throughout. In the flights and tail three colors; almond, black and white should occur in combination, each clearly separated as to color on each feather.

There has been much confusion about the matings of almond with several related almond-bred colorations. Practically speaking, the only desirable mate for an almond is a kite K//K.

Description:

Kite coloration is a rich metallic black, infused with red forming bronze. The more bronze, the richer the coloration, and the more suitable phenotype for mating to almond.

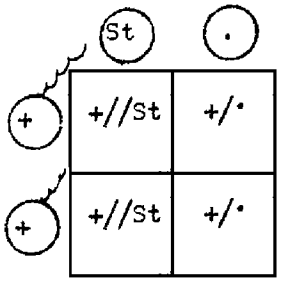
Kites are typically not blacks, that is, not spread pigeons (S). A kite is a T-pattern checker, carrying bronze (K) and presumably homozygous K//K. The richer kites usually carry a single dose of recessive red, +//e.

Almost all almonds are blue-black almonds. Kites are blue-black bronzes. It can be assumed that both the classical almond and the excellent kite are homozygous T-patterns, $C^T//C^T$, and bronzes, K//K, from the extensive selection for the modifiers involved in producing classical almonds.

With these assumptions of proper genotype for (C^T) and (K), the following almond matings can be considered.

Mating I — Kite Cock X Almond Hen

+//+ X St/·

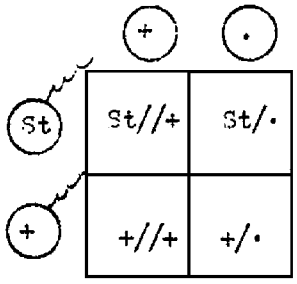


All almond cocks
All kite hens

It should be apparent that only one of the three sex chromosomes involved in this mating contains the mutant almond gene (St). The hen produces two kinds of sex cells; with and without, her sex chromosome. The cock always contributes one sex chromosome, hence when the female gamete contributes this chromcsome (with St) to the resulting zygote, it must be a male, and just as clearly must be an almond. Mating I produces almond cocks and kite hens in equal numbers.

Mating II — Almond Cock X Kite Hen

St//+ X +/·



Male Gametes

½ almond (cocks and hens)
½ kite (cocks and hens)

An almond cock of classical coloration is always heterozygous for almond, St//+. Homozygous almond cocks, St//St, are nearly white with some related eye complications.

Matings of almonds to kites produce , ½ almonds and ½ kites, but because of the sex-linkage involved, the mating of almond cocks to kite hens produce both almond and kite in both sexes. While matings of kite cocks to almond hens produce all almond cocks and all kite hens.

In the breeding of good colored almonds, the real challenge is in breeding the rich kites, to bring out the proper expression of ground color. The poor coloration of almond (Magnani) Modenas is simply an absence of the kite (K) form of bronze within the breed.

We have postulated the classical almond to have, in addition to kite (K)and T-pattern (C^T), a single dose of recessive red, e//+, and grizzle, G//+. Recessive red enriches the ground color expression, and grizzle delineates the flecks, producing neater and more contrasting stripes. The classical almond cock would then be formulated: St//+ $C^T//C^T$ e//+ G//+ K//K . It should be easily seen that a mating of a kite and an almond becomes complicated with these other necessary mutant modifiers.

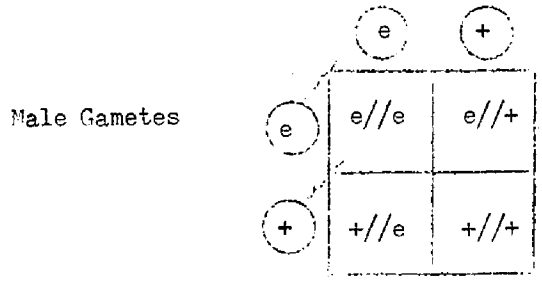
Almond cock $\quad$ OR $\quad$ Kite hen

St//+ $C^T//C^T$ e//+ G//+ K//K X $(+)^b/\cdot$ $C^T//C^T$ e//+ G//+ K//K

From this formulation, the need to use almond bred birds in your breeding program should be readily seen. To the extent that both bronze, K//K, and $C^T//C^T$ can be kept reasonably pure, much of the variation possible in expression can be controlled. Almond checkers and bars are attractive, but the blue replacing black flecks certainly detracts from the desired classical expression.

In this mating, it can be seen that one-half of the progeny will be almonds (both cocks and hens). It should also be noted that the autosomes carrying recessive red (e) and grizzle (G) will segregate independently, giving rise to several almond bred colorations not yet described. Obviously, both parents are heterozygous for (e) and (G).

Female Gametes



(sex not a concern)

1 Homozygous recessive red

2 Heterozygous, e//+

1 non-recessive red, +//+

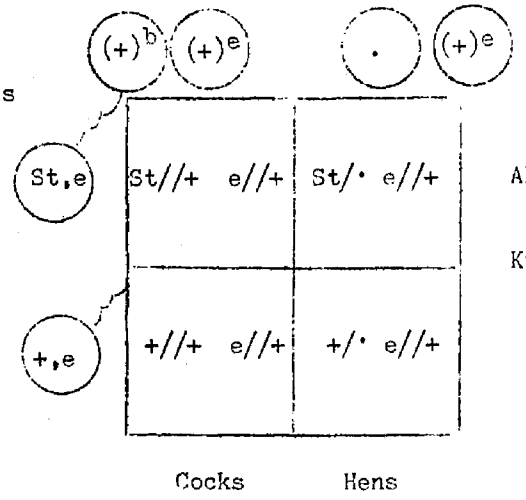
Two of the four possibilities in combination with almond, will produce the desired genotype, e//+, and coloration. The recessive red, e//e, in combination with (St), produces the DeRoy almond. DeRoy phenotype is between that of a red and yellow self (e//e). The e//e masks somewhat the almond (St), and the resulting DeRoy is often confused with yellow (d, e//e). The non-recessive red almond, $(+)^e//(+)^e$, is more whitish showing generally poor ground color. Its corresponding non-recessive red kite shows less expression of bronze. It is interesting that the two not desired phenotypes, recessive red (DeRoy) almond and the non-recessive red kite, will produce the desired combination, if mated together.

DeRoy almond Cock
St//+ e//e

X

Kite Hen
$(+)^b/\cdot$ $(+)^e//(+)^e$

Female Gametes



Almonds (cocks and hens) of desired genotype.

Kites (cocks and hens) of desired genotype.

Cocks $\quad$ Hens

I find the DeRoy mating with almond bred "slightly bronzed" kites, a very consistent producer of the desired classical phenotype.

Now, looking at the grizzle of our original mating, we can see the same general segregation occurring. The almonds and kites produced will be:

Female Gametes

Male Gametes

	G	+
G	G//G	G//+
+	+//G	+//+

(sex not a concern)

1 Homozygous grizzle G//G

2 Heterozygous grizzle G//+

1 Non-grizzle +//+

The homozygous grizzle (G//G) almond (St) is far too whitish, and the grizzling in the flights and tail detract greatly from classical expression. The bronze of kites (K) surpresses grizzle, as do several other almond modifiers, and the G//+ kite seldom shows much grizzling, except about the head and eyes. The kite pepperhead is G//+ in genotype. The homozygous G//G kite is often gaily pied, but never does it approach the stork-marked, near-white, typical of homozygous G//G wild type pigeons without bronze, or recessive red.

Recessive red, e//e, in combination with grizzle, G//+, produces red mottles. Very often, the expression of white is restricted to the same areas of head and neck, as found in kite grizzles.

Returning to our original mating;

St//+ $C^T//C^T$ e//+ G//+ K//K X $(+)^b/\cdot$ $C^T//C^T$ e//+ G//+ K//K

The almond ground color produced by this almond genotype, is the color of the inside of the shell on an almond nut. This coloration is produced by the sex-linked mutation (St) on a kite pigeon.

If both parents were homozygous T-pattern, $C^T//C^T$, and the bronze of the kite K//K, we are still dealing with two autosomal genes which will segregate independently. We can from the sex-linkage involved say, that approximately half of all progeny will be almond, and half kite (both cocks and hens); so the real question is, how will the factors necessary for classical almond expression segregate?

With two factors segregating independently, we need a PunnettSquare 4 X 4, with 16 progeny cells to show the possible combinations.

We have a preference for multiplication in these matings:

Genotypic Ratios

	X	1 e//e 1 G//G	2 e//+ 2 G//+	1 +//+ 1 +//+	recessive red grizzle
F_1	=	(1) G//G e//e	(2) G//G e//+	(1) G//G +//+	
X 0:0:0 1:2:1		Red Mottle (much white)	gay pied kite	gay pied kite (less bronzing)	kite phenotype
		Mottled DeRoy (Agate)	almond splash (some ground color)	almond splash	almond phenotype
	=	(2) G//+ e//e	(4) G//+ e//+	(2) G//+ +//+	
X 0:0:0 2:4:2		Red Mottle (less white)	excellent kite	kite grizzle (pepperhead)	kite phenotype
		DeRoy (slight grizzling)	Classical almond	almond (weak in ground color)	almond phenotype
	=	(1) $(+)^G$//$(+)^G$ e//e	(2) $(+)^G$//$(+)^G$ e//+	(1) $(+)^G$//$(+)^G$ $(+)^e$//$(+)^e$	
X 0:0:0 1:2:1		recessive red (self)	rich kite	kite (reduced bronzing)	kite phenotype
		DeRoy almond (whole colored agate)	rich almond (patchy flecking)	almond (variable expression weak ground color patchy flecking)	almond phenotype

Of the 16 progeny produced by our original pair:

St//+ C^T//C^T e//+ G//+ K//K (classical almond cock) X $(+)^b$/· C^T//C^T e//+ G//+ K//K (rich kite hen)

Only four progeny can be expected to be of the correct genotype for recessive red, e//+,and grizzle, G//+, and only two of these can be expected to be of the classical almond phenotypes. Is it any wonder that breeding classical almonds is a challenge? The reader should note the value of almond bred phenotypes. Many matings of these by-product phenotypes will produce higher frequencies of the desired expression, than does the mating of classical almond to rich kite.

The linkage has been broken between (St) and $(+)^b$, both ash-red almonds,StB^A , and brown almonds, Stb, have been produced. The development of ash-red and brown kites has also been accomplished, so at this time, classical almonds exist in blue-black and the crossover types.

The flecks on almonds are usually of the sex-linked basic color or colors related to the genotype. A blue-black almond of the genotype, St +//+ B^A, will have ash-red flecks, due both to the dominance of B^A to $(+)^b$ and the tendency of

the sex-linked color gene on the opposite chromosome to be expressed in almond cocks. This "flecking-oriented" mutation will show more flecking with age, often approaching black. In this poorly understood flecked condition, a strange phenomenon, often occurs; instead of black flecks appearing, faded black flecks are expressed. There is no explanation, at this time, for this strange expression similar to almond's alternative (faded, St^F,)in an almond phenotype.

Sandy

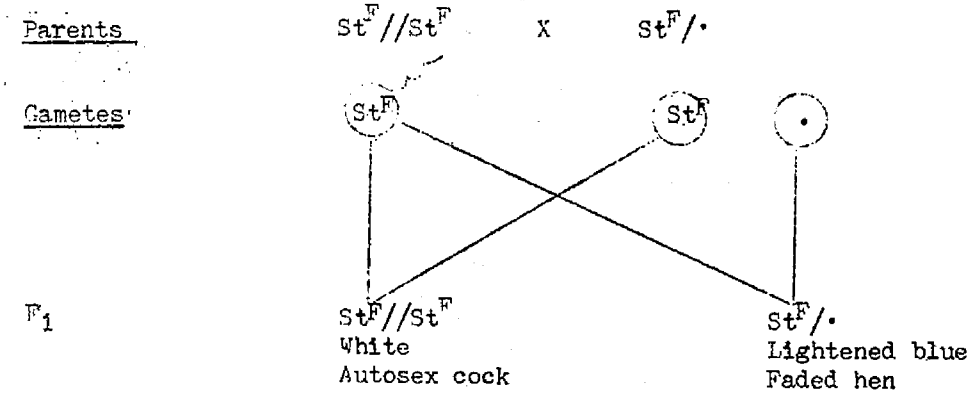
Sandy, (no symbol), is a rare, highly flecked almond type, which occurs from time to time. I have always called this phenotype "gray almond", because it lacked all the almond ground color (rust-yellow) of the typical almond, but otherwise behaved as almond (St). It is a sex-linked mutant, and in my opinion, is the identical almond gene (St), but with a peculiar set of modifiers.

Faded (St^F)

Faded (St^F) is a dominant sex-linked mutation which lightens or fades the pigmentation of a typical blue.

It has been demonstrated to be an alternative (allele) of almond (St), and therefore closely (linked) positioned on the sex chromosome, near to the brown locus $(+)^b$.

The homozygous faded cock birds, $St^F//St^F$, are nearly white, with occassional flecks of the sex-linked basic color. The hemizygous hens, $St^F/\cdot$, show the mild lightening effects of the mutation. Because a clear color difference is noted between $St^F//St^F$ cocks and $St^F/\cdot$ hens, faded has become the basis of auto-sexing breeds of pigeons. The mating of a homozygous faded cock to a faded hen produces:



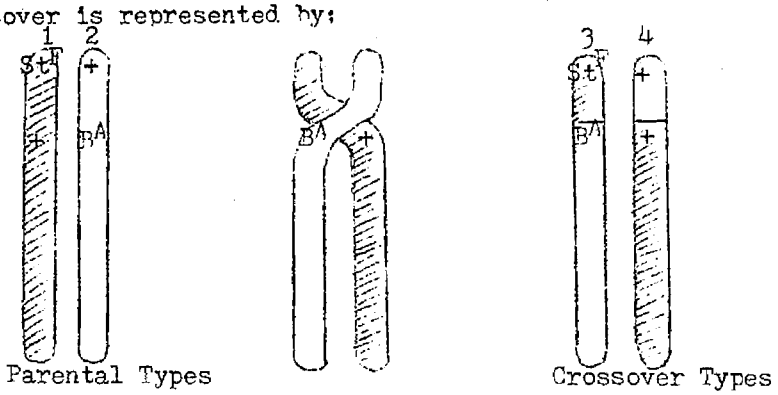
This mating is referred to as an autosex mating; all offspring are identified by color as to their sex, i.e., white cocks ---faded hens. The homozygous faded $St^F//St^F$ cock has somewhat delayed eye pigmentation, and a pinkish beak as a nestling. To the experienced breeder of fadeds, the sex of the squab is known prior to feather development by these characteristics. In commercial squab production, as with chicken production, there are practical advantages in knowing the sex of offspring prior to maturity. Squabs are marketed at about four weeks

of age, and the program of selecting pairs for new breeding stock can be a problem. Obviously, using faded (St^F) in autosexed matings solves the problem completely.

The challenge of breaking the linkage between faded (St^F) and wild type $(+)^b$, is identical to that problem in almond. For both almond and faded, this has been accomplished for brown (b) and ash-red (^{BA}). Essentially, the crossover for a sex-linked gene arrangement can only occur in the cock where two sex chromosomes pair in the formation of male gametes (sperm).

Starting with a faded blue, a mating to ash-red will produce cocks that are faded blue-black on one sex chromosome, and non-faded ash-red on the other. It is this cock, $St^F+//+^{BA}$, mated to any hen, which will eventually produce a faded ash-red hen or a non-faded blue hen.

This crossover is represented by:



A zygote formed by chromosome (3) from the cock and no (·) sex chromosome from the hen, will be a hen $St^F{}^{BA}/\cdot$, a faded ash-red hen. Once the crossover has been made, $\underline{St^F{}^{BA}}$ will stay together and remain as tightly linked as the original $\underline{St^F(+)^b}$ condition.

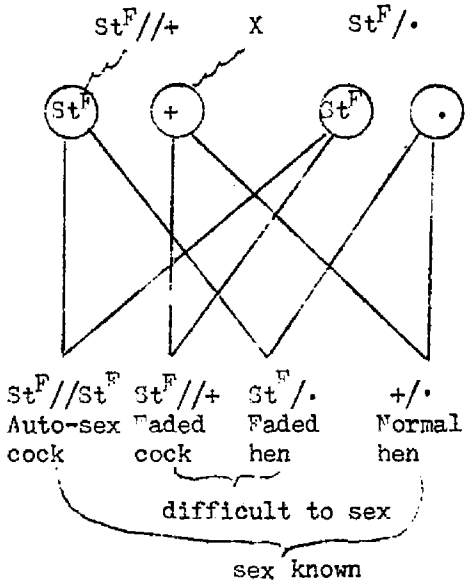
The crossover with brown (b) has been also achieved. In this case, the required cock would have to have a genotype, $St^F+//+b$, in order to produce the desired crossover. It should be quite apparent that the sex chromosome carrying the crossover arrangement, will in one-half of the cases, combine with the sex chromosome from the hen, producing a cock. The question should be asked, why do I keep looking for that strange colored hen? Both almond and faded influence the expression of the sex-linked color gene on the same chromosome, which consequently permits the alternate gene on the other chromosome to be expressed, even if that gene happens to be recessive. Almonds carrying brown show much expression of the recessive sex-linked gene for brown (b).

Almonds, $St+//+b$, show extensive brown flecking in combinations with brown. A blue carrying brown will show no traces of this recessive gene. As almond or faded "turn off" the sex-linked color gene near them, the alternate on the other chromosome expresses itself. In dealing with these two "overprinting" types of dominant sex-linked genes, we find wide variation of expression. Because of this, we can't be absolutely sure we have the crossover till we produce the hen of the crossover type. The hen only has one sex chromosome, and when her phenotype is faded ash-red or faded brown, we know we have succeeded. Each cock produced because of the difficulty in clearly recognizing the new arrangement, would have to be tested.

It is simpler to wait for that "one in a hundred" hen, than to test 100 cock birds for the one chance bird that has one of a pair of chromosomes with a new arrangement. The non-faded blue hen produced by the same crossover mechanism (4) is important in the calculation of the crossover rate. For our goal oriented purposes of breaking the linkage, this blue is an ordinary blue (wild type) hen, produced by a very strange reshuffling mechanism operating in the formation of gametes.

In auto-sexing breeds, it is common to call the $St^F//St^F$ homozygous faded an autosex cock. Its mating to a faded hen $St^F/\cdot$ is called an autosex mating (100% auto sex). The mating of a heterozygous faded cock, $St^F//+$, to a faded hen $St^F/\cdot$, is called a semi-autosex mating. In this mating, some of the squabs can be sexed immediately.

Semi-Autosexed Mating



The student with special interest in the autosexed aspect is referred to an excellent work titled, "Sample Color Charts for Use with Auto-sexing Breeds of Pigeons" , written by Bob Clark of Livermore, California. The colored figure representation of matings and resulting progeny simplifies the learning procedure. The costs of color printing are very prohibitive. Possibly, breeder demand will one day permit Bob Clark's valuable addition to pigeon literature to be "press printed", rather than hand-colored, for breeders.

White

Introducing the complex phenomenon called white is a difficult assignment. The development of pigment cells, their migration and proliferation, is one of the most technical areas of pigmentation study. The breeder can not be concerned with these "single or clonal distributions of melanocytes." The whole matter relates simply to the formation and functioning of a strange type of cell which produces the pigment in animal and bird integuments.

Four general observations are in order:

Observation 1:

Pigment cells develop in great numbers in the neural crest of the pigeon embryo. These cells, like sperm cells, have the power of movement. The peculiar melanin-producing cells migrate in all directions from this neural crest. As if water "draining off a duck's back", the cells move in a downward direction enveloping the embryo. Generally, the cells take up residence in different densities related to the distance traveled. Once established, they divide and saturate a definite area with melanocytes (pigment-forming cells). In turn, the feather follicles incorporate the pigment into developing feathers through a network of fine tubes.

Observation 2:

Pigment cells are very sensitive to small changes in tissue environment and many factors may alter the pigmentation process. In pigeons, egg temperature, disease, tissue damage and other conditions, may enhance or surpress pigment formation. Both nutrition and gene action can play a role and the impact can occur at any time from the cells formation in the neural crest, to its functioning existence throughout the epidermal layers. Pigment cells may be thought of as tiny factories subject to many production problems.

Observation 3

The genetic determination of white is therefore a multifacet problem. There are as many kinds of white as there are genes or conditions that influence this group of chemical-synthesizing units. In pigeons, I suggest at least forty separately-caused white conditions exist. Each form of white has its own peculiar impact-time, action-site and mode of effect. Breeders should handle white phenotypes with great care, least they compound several forms in the same phenotype and produce unbelievable variations in expression. The prevalence of white in pigeons is so extensive, that the breeding art requires some understanding of this complex subject.

Observation 4:

Different areas of the pigeon tend to have different pigmentation densities and the distribution tends to be symmetrical. The migration of pigment cells is clearly a timed process. It must take place within a specific time phase of embryonic growth. If migration is slowed for some reason within this time phase, certain areas will not have resident cells and white will result. Since some migrational or environmental changes take place after hatching, a few white forms are related to the aging process. In this case, changes in the local tissue environment are usually responsible for the white expression.

Some order may be established in this matter, if we try to imagine gene or environmental action occurring at one of the following times:

1. At the development of pigment cells in the neural crest.
2. In the migration, at any point from the neural crest to the destination.
3. In the immediate area of the functioning melanocytes, initially, or at any point in maturation.
4. In the immediate area of the functioning pigment cells during growth and aging of young and adult pigeons.

Conclusion

The nature of pigment cell development, migration and functioning, permits interference by a wide variety of factors across an extensive time-related period. There are as many forms of white as there are factors which interfere with the development or production phases of these tiny melanin-synthesizing units.

White is not color. White is the absence of color. The phenotype white, does not alter the basic sex-linked color genes or other mutants present in the pigeon's make-up. White is that unusual form of epistasis, which masks all mutant color expression by preventing pigment formation, and thereby, preventing phenotypic expression. Matings of white to wild type will usually unmask the hidden basic color and pattern, at least in some feathers, to permit their identification. The potential genotypes for a white self pigeon are only limited by the variation of mutant types in the species. We know less about a given white, than we do about any other pigeon phenotype.

Further understanding of white must await testing by breeders. Erratic white conditions are a constant problem to most breeds. It might clarify somewhat the breeder's understanding, if we were to describe a sampling of the white forms found in pigeons.

Albino (al) White

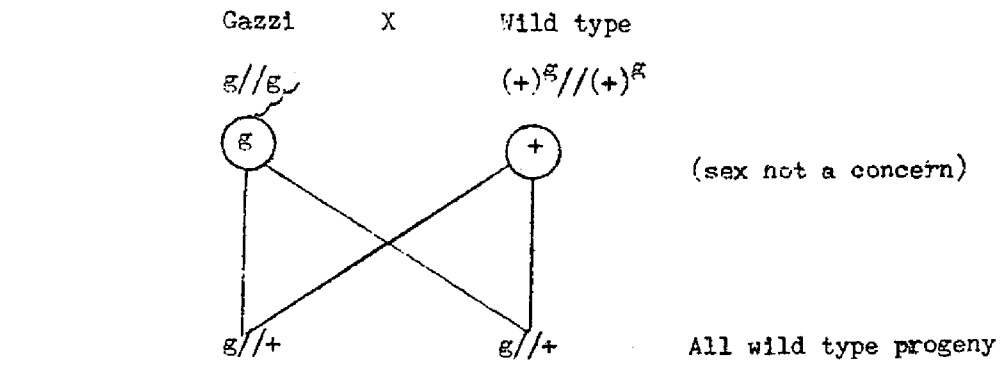
Albino white (al), is produced by a recessive autosomal mutation from wild type. Pigment cells are altered in early development in the neural crest. Pigment cells develop and migrate, but the impact of the homozygous, al//al, albino gene is so great that these cells have no potential to produce melanin granules. In all animals and birds, albino is an autosomal recessive factor which produces typical pink eyes, white skin and white hair or feathers. Several forms of albino are presently being studied in the pigeon.

Pattern White

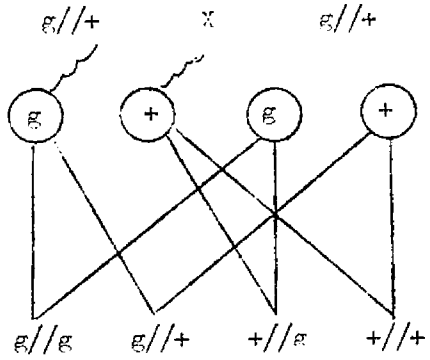
Pattern white is a gene-produced form, which acts in a rather distinct manner in matings. Several of these conditions may be produced by one or more genes. They differ from piebald forms, in that the areas of white are relatively constant. Pattern whites appear in Turbits, Swallows, Shields and other breeds. This form of white is variable, but generally specific for the area of depigmentation. There have been very few studies conducted in pattern white breeds, but at least one factor, gazzi (g), has been demonstrated to be a simple autosomal recessive alternative to wild type.

The gazzi factor in Modenas, when homozygous g//g, produces a pigeon colored in head, shield, flights and tail feathers, with the remaining plumage of a brilliant white condition.

Matings of gazzi g//g to wild type will yield:



Matings of F_1 individuals will produce:



The wild type progeny of this mating carrying gazzi, +//g, show no traces of white. Piebald conditions have a tendency to show progressive expression of increased white areas. Pattern whites are deserving of study, because they show promise as being distinct gene-produced forms.

Migrational White

This condition, is usually the product of an accidental or gene-caused restriction of pigment cell migration. It usually occurs at the extremities. The white "boots" in kittens, the white "blaze" on a horse's head, the white stripes down an animal's underside and the white tip of a puppy dog's tail, are common examples of migrational white conditions. The extremities, located at a great distance from the neural crest, often contain fewer successful migrant cells. Animals and birds generally show lighter colorations on their undersides because of the lowered density of pigment-forming cells. The occassional white in the first flights (most outer) and tail feathers that occur in self-colored strains of pigeons, are probably of this form.

Directional Mutant White

White phenotypes may be produced by many known genes such as almond (St) and faded (St^F) in homozygous cocks, St//St and $St^F//St^F$. Homozygous grizzle G//G produces the white stork-marked grizzle in wild type $(+)^b$ and brown (b) pigeons. The white self, with colored eyes, is usually ash-red (B^A) and G//G in combination.

Indigo (In) and reduced (r), acting together, produce a frosty-white phenotype called "platinum". Dominant opal (Od) and indigo (In) heterozygotes in ash-red (B^A) bar pattern, will produce the beautiful "oyster white". Directional mutant white is merely the additive influence of known depigmenting color mutations.

The stencil factors of Oriental Frills, German Toys and Lebanons, all produce white in the phenotype. These gene oriented white forms are usually related to spread areas (coarse or smooth) and require a "turning on" and "turning off" of the interference, to produce clear areas of pigment and white on the same feather. Dominant opal (Od) acts in a similar manner, producing white bars and checkers on wild type.

Our knowledge of these mutant genes, permits breeders to exercise some control of the expression of mutant related white forms.

Piebald White

Piebald is a loosely defined term, describing the alternation of two colors. Pigeon breeders use the term collectively to identify a series of white forms that have been somewhat standardized by generations of selection. Segregation of phenotypes in piebald matings to wild type, is difficult to analyze. There is a tendency for a progressive increase in white in successive generations.

Baldhead, is most likly, a mutation of the dominant type. The offspring of a bald X wild type mating, usually show some white about the head, flights and tail. The expression of white flights and white tail in baldheads, may or may not be related to the condition of white on the head. The failure to produce baldheads in recessive red, e//e, suggests possible linkage of these genes.

White flights are probably produced by a gene or genes of a dominant type. The chance condition of ten white primaries and ten colored secondaries, occurs far too frequently to be accidental.

White tail is a condition produced by many piebald combinations. White-tailed breeds have been developed. The white tails of piebald phenotypes show a marked tendency to produce mixed tails (colored and white) in crosses to wild type. White-tailed breeds mated to wild type, show a tendency to produce white or colored tails, with fewer mixed tails.

Badge, Beard and Band markings of the head, show some inclination to be gene-produced. The markings consistently reappear in F_2 and backcrosses, but clear segregation has not been found.

Reversion to White

The process of reversion to white, associated with the reduced pigment reservoirs of recessive red pigeons, is called acromatosis. The natural reversion to white in Whiteside Tumblers and the artificial reversion through plucking, in the color pigeons, exemplifies this form. Very little is understood about the pigmentation process or genes involved.

Recessive White

Recessive white is a condition of white found in some domesticated fowl, where the heterozygote is fully colored and the homozygote is pure white. Such a condition in pigeons has been reported, but testing is not yet completed. Apparently, segregating 3:1 as a simple recessive, this white self is produced from self-colored parents and acts in the manner described for gazzi.

Extreme Dilution White

A condition found in some white doves has been demonstrated to be produced by the sex-linked recessive gene ($\underline{d^W}$). The blond ringneck dove is dilute. Hybridization with pigeons show it to be homologous with dilution (d) of the pigeon's set of sex-linked dilution alleles. In this set of alleles, pale (d^P) has not been found in doves and ($\underline{d^W}$) extreme dilution has not yet been found in pigeons. The homozygous extreme dilute $\underline{d^W}//\underline{d^W}$ ringneck dove is pure white with colored eyes.

Review

We understand very little about white, because the phenotypic expression can be the result from a wide variety of genetic and environmental conditions. There are as many forms of white as there are different genes or conditions that influence the development, migration or maturity of the delicate pigment-forming cell

In many breeds, white forms may be expressed that have several causitive agents. Testing of such combined genotypes produces highly confusing results. We have only one practical way to proceed. The testing must take place in highly inbred strains, where only one or two possible causes is operating. At one time, the same confusion exsisted with the phenotype bronze. In this case, at least some progress has been made by testing breed type bronzes separately.

White feathers generally grow longer than colored feathers and wear or frazzle more rapidly, if allowed to get wet. White feathers are a poor protection from sunlight and white selfs suffer skin burns from long exposure to bright sunlight. White offers the breeder a contrast for pigmentation, which can be manipulated through selection, to produce beautiful phenotypes. Piebald white tends to be highly variable and tends to increase in expression in successive matings. All piebald expressions with white about the head, tend to have dark (bull) eyes and present a real challenge to breeders desiring colored eyes on white-headed phenotypes.

Several breeders have in recent years, begun programs to analyze white expression. Progress is slow, but progress is being made. A broader effort by more fanciers might provide solutions to the white mysteries in rapid order. Mating a Turbit to wild type would be a start. The F_1, F_2 and backcrosses, could help clarify matters concerning <u>that</u> form of white expression. Testing other breeds in succession, would certainly add valuable knowledge to help other breeders in the problem-ridden area called white.

Testing Unknown Factors

1. Describe in detail the observed oddity and all related information.
2. Mate to wild type, using both sexes if possible.
3. Observe and record all differences from wild type in progeny.
4. Mate several pairs of F_1 progeny together and record observations of 20+ offspring, classifying as to phenotype and ratio.
5. Backcross F_1 individuals to unknown and wild type. Raise a dozen of so from each mating and compare results with F_1 and wild type.
6. Review the program for sex differences, analyze ratios and classify phenotypes.
7. If results suggest clear segregating differences, tentatively symbolize and name the mutant. Verify the evidence by raising fifty or more birds from the several matings.
8. Record information and report clearly the evidence to a magazine.

<u>Note:</u> The numbers suggested in testing often frighten the breeder. Actually, two pairs of mated F_1 birds will in several seasons, produce the numbers required. After classification, these offspring can be culled, kept or utilized as food. If the reader reaches the place of naming the new mutant, I'm positive he will have little trouble finding ways to verify his results with the additional birds required.

Let us look at an expert's statement of what he observed and did to produce the "pastel" of the pigeon world ---reduced (r).

A boy Carl Graefe had helped in starting in Rollers, brought him a pair of birds and asked, "What color are they?" Carl answered, "I don't know." The chance mutation, coupled with the odds against it being reproduced in a homozygous cock, seems fantastic, when we consider that the pair is presented to one of the few men who might recognize their value. An attempt was made to trace the birds, but to no avail.

Carl describes the pair, "as apparently blue pigeons --- the cock was pied (about half white) and the hen was white flighted. The bars were somewhat washed out and the blue pigment somewhat diluted." He proceeded to mate the hen to cocks of several intense basic colors --- ash-red (B^A), wild type $(+)^b$ and brown (b), with resulting progeny all like the sire. The cock was mated to wild type and produced daughters like himself, and cocks of wild type.

It was clear to Carl at this point, that the factor (?) was sex-linked and recessive to wild type. He, at first, assessed it to be in the $(+)^d$, d^P, d series and mated the hen to a dun cock. This mating produced black cocks and dun hens, and he therefore concluded that it was not an allele in that series. The black cocks mated to reduced hens produced approximately $\frac{1}{2}$ reduced, both $\sigma\sigma$ and $\varphi\varphi$. The segregation ratios in F_2, indicated a simple recessive which is sex-linked. The black cocks produced two kinds of daughters (dilute and reduced intense) and he began to see then that the new factor was closely linked with dilution, as no crossover types occurred. The F_1 cocks from ash-red (B^A), wild type $(+)^b$ and brown (b) matings with (?/.), showed marked crossover types and it was concluded that (?) was widely separated from this locus. Reduced influenced all the basic colorations. The first dilute reduced produced happened to be recessive red e//e, and he called it "Isabelline" (light yellow). Carl's choice of name for this new color as reduced (r), has been questioned often. Others have suggested "pastel" titles to describe its appearance. Aside from his scientific perogative to name it anything he wanted, reduced is far more descriptive,in that the pigmentation distribution is different in coarse spread, smooth spread and blue areas, and reduction in pigmentation is observed in all phenotypes. In the intervening thirty years, we are really still discovering reduced, and that rather odd roller pair has descendants in nearly every breed known to pigeondom.

The Breed Milieu

The breed milieu is that mixture of genes called a breed. Establishment of a breed requires many generations. In the case of the 400+ breeds of domestic pigeons, there has been extensive selection for various, so-called, quantitative genes for size and type, in addition to the collection of modifiers for the known mutations. It is not surprising to find that each breed has a distinctive genetic makeup. In the process of transferring a desired gene from one breed to another, a few surprises usually await the experimenter.

For example, dominant opal (Od) produces a white bar on a typical blue Roller. For the most part, we can identify (Od) quite reliably in most breeds where it occurs by examination of phenotype. If we were to transfer this gene to a breed such as Catalonian Tumblers (Spanish) or Syrian Swifts, it would be unreasonable of us to expect the exact expression of phenotype in this new mixture of genetic modifiers. Naturally, the basic characteristics of the mutation limits the diversity of expression, but we should be conscious always that our descriptions

of mutations are compared to "wild type". If the breed we are considering differs from"wild type" at a great many loci, combination of modifiers may alter significantly the expression of the gene. It may take a great deal of "grading-up" to develop a typical expression of a pattern or color in a new breed. Recessive red has been transferred to Racing Homers, but the rich red of the Tumbler will require years of selection to produce.

Breed milieu is a fact. Breeds have been developed by selection for differences from wild type. Breed out-crosses are important to development within a breed, but it should be understood that they require special treatment and long periods of "grading-up" before the benefits desired from the cross may be obtained.

The mutation called gazzi (g) in Modenas is a simple autosomal recessive. Birds of g//g genotype have colored heads, wings and tails,with the remaining plumage being white. The gazzi pattern of the Strasser is identical, except for the show standard requirements which specify the Strasser to have a colored back. The Modena standard requires white in this area. Genetically speaking, both are (g//g) homozygous gazzi. My observations of crosses of gazzi Modenas and Strassers indicate that this mating does produce colored-headed, winged and tailed birds as expected, but foul feathers abound. Colored feathers in white areas and vice versa, indicate the near identical pattern development of these two breeds was accomplished by slightly different selective procedures.

Even with identical phenotypes and genotypes for gazzi, the differences in breed milieu, impose time consuming restrictions on gene transfer from breed to breed. Transferring barless to Turbits was an accomplishment of merit. The reduced Giant Homer is a far cry from the original mutant Roller, yet, Giant Homers would be something less as a breed, without the varied and beautiful expression of this sex-linked recessive gene (r).

Creative breeding is part of the art, breed milieu is part of the challenge.

Illegitimacy in Pigeons

In every conversation with breeders, the scientist always hears of the blue checkers and ash-reds produced by pairs of blue bars. The typical scientist responds with, "Were the pairs individually cooped?" Somehow, this interchange always creates an antagonistic mood, which prevents further discussion. Let us look at a brief "home type" bit of research to evidence the need for individual cooping, where accuracy of pedigree is necessary. In scientific study, we must control the elements that might influence results. Individual breeding coops, an essential requirement of the scientist, are rather expensive and unnecessary to the general breeding of pigeons. Since records and pedigrees are the foundations of the breeding art, we should look at the problem of illegitimacy in pigeons, and make adjustments in breeding practice wherever necessary.

There has been no research on the consistency of legitimate progeny from mated pairs of pigeons. Several years ago, as the breeding season approached, I attempted to arrange matings in two identical coops in such a manner that each illegitimate offspring would be immediately detected genetically by the phenotype of the offspring. This was only possible to a limited degree. In coop A, which contained the maximum number of genotypes, 18 pairs of breeders produced 66 squabs, of which 8 offspring were clearly illegitimate. Coop B contained 18 pairs of breeders, whose genotypes could only guarantee accurate detection of illegitimacy to approximately 80% of that of Coop A. In coop B, 74 squab were produced, with

12 squabs clearly illegitimate. Both coops were equipped with open front nests. The coops and fly pens were adequate by normal standards for space in breeding Rollers. I have reported that open nest arrangements will yield about 12-17% illegitimacy. It should be understood that these percentages are actual cases noted, for example, a pair of barless producing a checker, and the real illegitimacy rate is greater than this by the mathematical interpolation of the possible undetectable illegitimate offspring which were possible in each coop.

To further test this matter, the following season I arranged three smaller identical coops:

Coop C ---open nests,as in Coop A and B.
Coop D ---an open shelf and nest for each pair.
Coop E ---a closed shelf and nest with a single perch entrance.

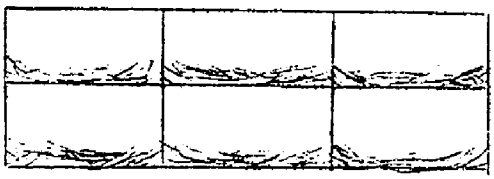
Into each coop, I placed seven pairs of breeders of known genotype, in such a manner, that at least 80% chance of illegitimacy detection was possible.

In Coop C ---16 progeny were produced, with three illegitimate offspring; two of them in the same nest.
In Coop D ---21 progeny were produced, with two illegitimate offspring.
In Coop E ---27 progeny were produced, with one illegitimate offspring.

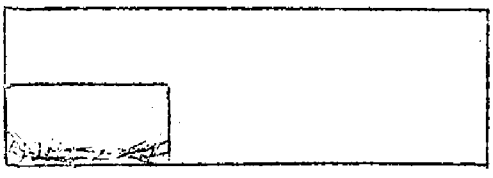
I felt that this research lacked many of the basic controls necessary for a scientific study, but it supports the several general statements I offer to breeders on this matter.

1. The fidelity of pigeon pairs is highly over-rated.
2. Illegitimacy of offspring is directly related to privacy in the nest area.
3. Increasing spacial pressure on pairs by crowding in the loft, increases the chances of illegitimacy.
4. Privacy in nest arrangement will also notably increase squab production, due primarily to less frequent infertile or broken eggs.

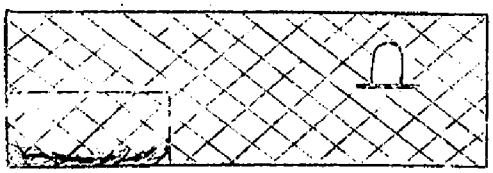
All evidence tends to support the necessity of adequate nest space, with nest privacy being an important part of good loft arrangement. My general conclusions reported in 1967, indicated the following:



Open Nest Arrangement
(12-17% illegitimacy)



Nest and Shelf Arrangement
(6-8% illegitimacy)



Sheltered Nest Arrangement
(2-3% illegitimacy)

I feel the short duration of matings in Roller breeding, probably increases the incidence of illegitimacy over the situation where pairs are life-mated. The problem of the reliability of any pedigree for birds not raised in individual coops should be apparent. In pigeons, a 12-17 % illegitimacy rate destroys the foundation for keeping records of pedigree in the first place. A basic understanding of pattern and color genetics will help identify a portion of these offspring that would otherwise be considered legitimate progeny of the nest parents.

All my remarks on illegitimacy are to be interpreted as conservative. The estimates did not include the possibility of eggs being laid in the wrong nest by the hen or the undetectable illegitimacy potential, present in each of these brief experiments.

By arranging our loft in a manner that reduces illegitimacy to a minimum, we approach an answer to the scientists' question, and willingly concede that in those special matings, so important to our goals, the prize pair will be individually cooped for both personal and scientific reasons.

Suggestions For Further Reading

It is difficult to select from the vast array of scientific works written in recent years, a few publications which would satisfy all student needs. I personally have found the following publications of value in the study of pigeon science, because the authors have paid special attention to communication with student readers. The science texts listed do not take up pigeons as such, but concisely state biological information in a manner that both college students and breeders have found understandable.

Science Texts

Hutt, Frederick B., 1964. Animal Genetics. The Ronald Press Company, New York.

Keeton, William T., 1967. Biological Science. W.W. Norton and Company Inc., New York.

Srb, A.M., R.D. Owen and R.S. Edgar, 1965. General Genetics. 2nd Edition. Freeman and Company, Sanfrancisco, California.

Welty, J.C., 1962. The Life of Birds. Sanders Company, Philadelphia, Pennsylvania.

Pigeon Texts

Clark, G.L., 1965. The Long Face Clean Leg Tumbler. E.A. Jordon and Company, Christchurch, New Zealand.

Goodwin, Derek, 1967. Pigeons and Doves of the World. The British Museum (Natural History), London, England.

Kleinpell, George J., 1968. The Turbit Handbook. The Judson-Brooks Company, Cleveland, Ohio.

Levi, Wendell M., 1963. The Pigeon. Levi Publishing Co., Inc. Sumter, South Carolina.*

Levi, Wendell M., 1965. Encyclopedia of Pigeon Breeds. Levi Publishing Co., Inc. Sumter, South Carolina.

Whitney, Leon F. The Basis of Breeding Racing Pigeons. Paul S. Eriksson Inc., New York.

Zurth, Edmund, 1956. Die Welt Der Tauben. Ortel and Spörer, Germany. (In German)

* - the basic pigeon study reference

Pigeon Booklets

Clark, Robert, 1968. "Sample Color Charts For Use With Auto-sexing Breeds of Pigeons". Published by author, 9009 Tesla Road, Livermore, California 94550.

Hollander, W.F. and Ray E. Gilbert, 1950. "Project on Genetics". National Pigeon Association Information Booklet #1.

Pigeon Periodicals
(recommended for their scientific concern)

"American Pigeon Journal" Warrenton, Missouri 63383.

"The American Racing Pigeon News" 2421 Old Arch Road, Norristown, Pennsylvania 19401.

"Deutscher Kleintier Züchter". Reutlingen , West Germany.

"Geflügel-Borse". Munchen, Germany.

"Racing Pigeon Pictorial". Coo Press Ltd., 19 Doughty Street, London WC1, England.

"Raceduen" % Strugård, 3670 Veks% St. Denmark.

Pigeon Bulletins

Students of pigeon science are clearly concentrated in several breed specialties. The associated clubs and their bulletins are a valuable source of information.

Clubs associated with the following breeds show some scientific concern.

German Beauty Homers	Modenas
American Giant Homers	Pouters
Show Racers	Turbits
Racing Homers	Tumblers

Conclusion

By way of apology, I should indicate that it was a problem deciding what topics would constitute a proper introduction to pigeon science. In this notebook, I have included only a few of the many possible topics. This attempt at "saying it simply" required the deletion of interesting details. Scientifically, this same impulse, initiated the taking of certain liberties with accuracy. Primarily, this fault is one of neglect. I neglected to include those exceptions to rules that nature always provides. These rare cases are usually a concern to specialists in the topic field.

Attempts at simplicity, distort the image of science by suggesting a rigid and mechanical organization of practices. Science dies as regimentation grows. Scientific research in all areas should have the same creative flexibility that is found in the behavior of a curious child. Successful pigeon breeders have most of the elements of scientific method necessary to become breeding artists. The problem in pigeon breeding is a matter of freedom. The freedom to experiment, to question established ideas and to communicate openly new information. If there is no group incentive to try new ways, there will always be strong social forces working for the sentimental protection of old ideas. The opening line to an enjoyable pigeon story could be, "I wonder what would happen if ....!"

Pigeons rise above our hobby in a circle of challenge, if the breeder has the courage to look closely, experiment and create. The "art of breeding" is the breeder's personal way of expressing his curiosity in a meaningful and lasting way.

"A great love springs from a deep knowledge
of the thing that one loves, and if you
do not know it, you may love it but little
or not at all!"

Leonardo da Vinci (Treatise, fol. 74)
(Bird breeder - Scientist - Artist)
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