SEX – LINKAGE AND AUTOSEXING IN WATERFOWL

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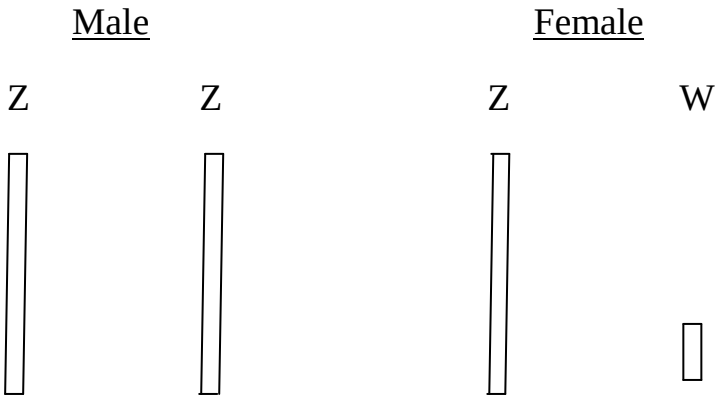
SEX – LINKAGE AND AUTOSEXING IN WATERFOWL

It is only fair to state that the need for early sex determination, through sex linked crosses in waterfowl, is much less than in other classes of poultry. This is because it is easier to vent sex the day-olds of these species with very little training. Moreover, crossbreeding is rarely an option for exhibition and ornamental breeders. The exception is in commercial table duckling production where unfortunately since only white breeds are used, sex-linkage cannot be exploited. There may be some, however, who feel unable to attempt vent sexing, particularly with goslings which are more difficult to manipulate and more vulnerable to rough handling. Others may be interested in sex-linked inheritance for its own sake regardless of any practical advantage.

THE PRINCIPLES OF SEX – LINKAGE

Without going into too much technical detail I would like to explain the principles underlying sex-linkage. For a more detailed account of these principles the reader is referred to the excellent bulletin by Chris Hann (1966). In birds, sex is determined by the number and type of the sex chromosomes. The male bird has two relatively long Z chromosomes, whereas the female has only one Z and a smaller one called W. i.e.



During reproduction the male produces a single type of spermatozoon which always carries one Z chromosome, while the female (who in fact determines the sex of her progeny) produces two types of egg; one with a Z and one with a W. After fertilization, the Z-carrying egg becomes a male (ZZ) and the W-carrier becomes a female (ZW). In mammals, where the situation is reversed, the sex chromosomes are symbolised by X and Y and it is the male which determines the sex of the progeny. i.e. male = XY, female = XX.

The W chromosome carries very few genes for other characters but the Z chromosome is well endowed in this respect, and in the fowl, which is extremely well documented, the positions of large numbers of Z-linked genes are already known. When sex-linked genes occur in pairs (as they do in the male bird) their interactions are important. If one member of a pair of genes masks the effect of the alternative form (allele) when both are present together it is said to be dominant. When the dominant member of a pair of sex-linked genes is present on the single Z chromosome of the dam and the recessive member is found on both Z chromosomes of the sire, we have a potential sex-linked cross where the sexes of the progeny can be distinguished at day old. The rule is that the dominant gene must always enter the cross on the female side. The dominant member of the pair is symbolised by a capital letter, and the wild type allele by a + superscript, e.g. M^+. The following is a classical example from the fowl:

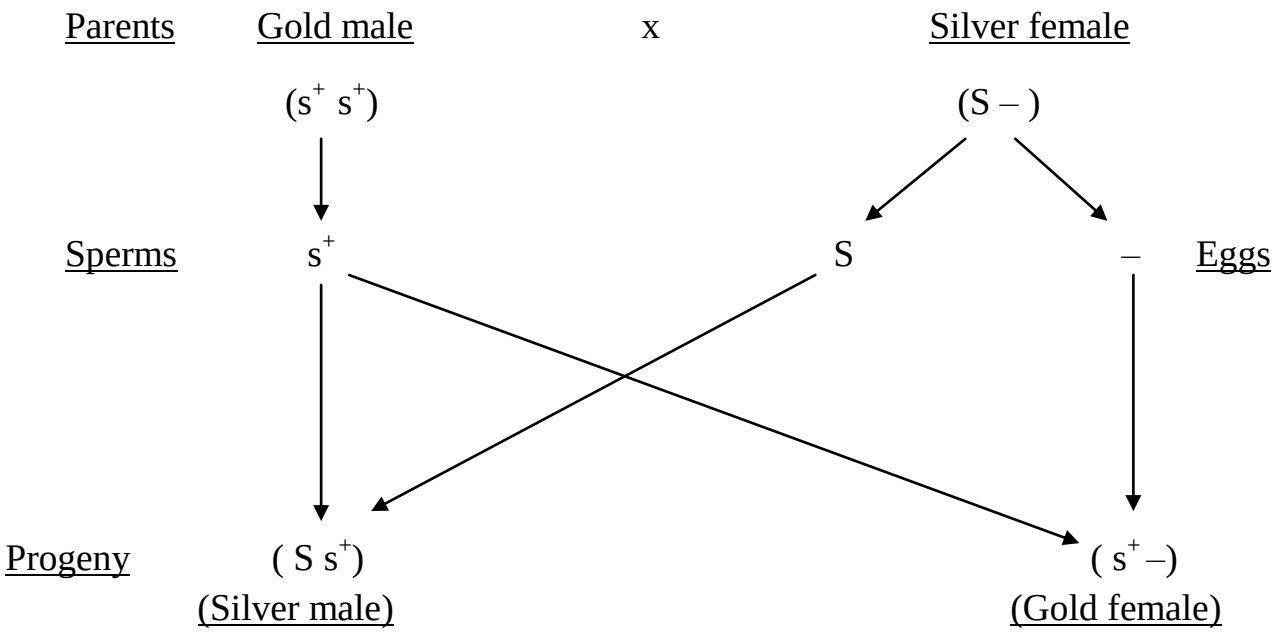
Gold – silver cross

S = silver down (dominant)

s^+ = gold down (recessive)

} Carried by the Z chromosome.

– = the W chromosome



SEX – LINKAGE IN THE COMMON DUCK (Anas platyrhynchos)

There are only two known sex-linked mutant genes in domestic ducks of mallard origin: brown dilution (d) and buff dilution (bu).

1. Brown dilution (d)

Brown dilution, which was first investigated by Punnett (1930 and 1932), and independently by Walther, Hauschildt and Prufer (1932), is found in the following breeds: Khaki Campbell, Buff Orpington, Chocolate Orpington and Fawn Indian Runner. In these breeds black pigment is diluted to various shades of buff, fawn, khaki, brown or chocolate depending on other genes present. Brown dilution is a simple recessive character and therefore the breeds mentioned above must be used on the male side of the cross. The female parent should carry the dominant allele (D^+) which is found in the Rouen, Mallard, Blue Orpington, Dark Campbell and all the black breeds.

To be able to predict and understand the colours of the progeny of these matings, two other pairs of genes must be mentioned. Neither is sex-linked and, therefore, females as well as males can carry a pair of genes in each case. The genes and their symbols, together with breeds carrying them are given below:

Extended black (E) – Black Orpington, Cayuga, Black East Indian.
Non-extended black (e^+) – Rouen, Mallard.

Blue dilution (Bl) – Blue Orpington, Blue Swedish.
Non- dilution (bl^+) – Rouen, Cayuga.

E, which is responsible for solid black pigment, is completely dominant over e^+. The 'wild-type' allele (e^+) allows full expression of the pattern of the wild mallard, where black is restricted to certain specific areas. On the other hand Bl (blue dilution), which dilutes black pigment to blue or grey, is not completely dominant over bl^+ (non-dilution). This means that three different shades of colour can result from combinations of these genes:

Bl Bl (Pale blue or blue-splashed white) Bl bl^+ (Dark blue) bl^+ bl^+ (Black)

Therefore, when standard type (i.e. dark) Blue Swedish birds (Bl bl^+) are mated together they do not breed true and produce the following ratio in their progeny:

Standard Blue Swedish male (Bl bl^+) x Standard Blue Swedish female (Bl bl^+)

Ratio: 1 Splashed White (Bl Bl) : 2 Blue (Bl bl^+) : 1 Black (bl^+ bl^+)

A similar situation is found in the Buff Orpington where the standard requires a deep shade of buff. Buff in ducks is due to the combined action of blue and brown dilution genes (Bl and d) on a non-extended black background (e^+) as follows:

Bl Bl d (d) e^+ e^+	Bl bl^+ d (d) e^+ e^+	bl^+ bl^+ d (d) e^+ e^+
(Pale buff)	(Dark buff)	(Khaki)

Thus, when standard Buff Orpingtons are mated together we obtain:

Male		Female
Dark Buff Orpington (Standard)	x	Dark Buff Orpington (Standard)

Ratio: 1 Light buff : 2 Dark buff : 1 Khaki

[Bl Bl d (d) e^+ e^+] [Bl bl^+ d (d) e^+ e^+] [bl^+ bl^+ d (d) e^+ e^+]

In the adult, the dark buff male has a dark seal-brown head and neck whereas the light buff male has a lighter fawn-buff appearance in these areas.

When the three pairs of genes (Bl bl^+, D^+ d and E e^+) are put together in all possible combinations, eight different colour shades result. These are given in Table 1 together with breed examples. This table also includes all the white breeds which will be discussed later. Lilac*, which appears in the table, is an attractive colour patterns not possessed by any recognised breed and, therefore require description. In Lilac the normal blue colour of the Blue Orpington is further diluted to a pinkish-lavender shade by the action of d. In Blue Mallard the black and dark parts of the normal Mallard pattern are diluted to various shades of blue or grey, but the lighter (brown) areas remain practically unchanged.

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* Since writing this there may now be some new breeds of this type. F.M.L.

Table 1 Classification of Common Varieties of Duck for Sex-linked Matings

Black Group [EE bl^+bl^+ $D^+(D^+)$]
Black Cayuga
Black Orpington
Black East Indian
Black Indian Runner
Black and White Magpie
Black Call
Black Swedish
Black Pommern

Blue Group [EE BlBl $D^+(D^+)$]
Blue Orpington
Blue and White Magpie
Blue Swedish
Blue Bibbed Call
Blue Pommern
Blue Indian Runner

Chocolate Group [EE bl^+bl^+ d(d)]
Chocolate Orpington
Chocolate Indian Runner
Dun and White Magpie

Lilac Group [EE BlBl d(d)]
No breed with this colour combination.

Mallard Group [e^+e^+ bl^+bl^+ $D^+(D^+)$]
Mallard
Rouen
Brown Call
Silver Appleyard
Dark Campbell

Blue Mallard Group [e^+e^+ BlBl $D^+(D^+)$]
Apricot Trout Indian Runner
Apricot Call

Khaki Group [e^+e^+ bl^+bl^+ d(d)]
Khaki Campbell
Fawn Indian Runner*
Fawn and White Indian Runner*
Welsh Harlequin

Buff Group [e^+e^+ BlBl d(d)]
Buff Orpington
American Buff

White Group [e^+e^+ bl^+bl^+ $D^+(D^+)$ cc]
Aylesbury
Pekin
White Campbell
White Orpington
White Indian Runner
White Call
White Crested

* These two breeds in Britain only carry brown dilution (d), but in America they also carry blue dilution (Bl) and should therefore be placed in the buff group. For more comprehensive lists of breeds in all the groups, see Ashton and Ashton (2007)

As a matter of interest the breeds on the left of Table 1, which carry extended black (E), also have white areas or 'bibs' on the front of their breasts, a feature not present in the breeds carrying (e^+) on the right. This is thought to be due to the linkage of the dominant gene for bib (S) and extended black (E) on the same chromosome. Exceptions to this rule are the Black East Indian and the Cayuga where selection has reduced the size of the bib to vanishing point. The hidden presence of this gene can still be demonstrated, however, when Cayugas are crossed with non-extended black, non-bibbed breeds ($e^+e^+ s^+s^+$), such as the Khaki Campbell, when bibs are restored in the progeny. E.g.

Male		Female
Cayuga		Khaki Campbell
(Non-bibbed, black – EE SS*)	x	(Non-bibbed, non-black – $e^+e^+ s^+s^+$)

Bibbed, black
($Ee^+ Ss^+$)

S = presence of bib
s^+ = absence of bib

* latent, i.e.
non-penetrant

In the above case modifying genes introduced from the Khaki Campbell allow the latent gene (S) to be expressed.

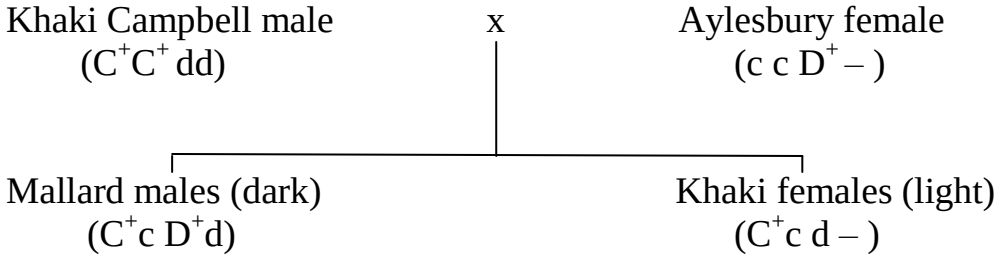
Table 2 shows the results of various sex-linked crosses involving brown dilution (d). There are three complications concerning this table:

a) <u>The use of breeds carrying blue dilution (Bl)</u>
For simplicity all the breeds used in Tables 1 and 2, which carry blue dilution (Bl), are shown to be of the paler shade (Bl Bl). The consequences of using the darker (standard) shade (Bl bl^+) are given later in Table 3 (page 9). Since it is difficult to distinguish between pale blue, pale lilac, pale blue mallard and pale buff at day-old (all carry Bl Bl), matings 7, 8 and 12 cannot be used for sexing at hatching. The colours can, however, be differentiated in the juvenile and adult plumages.

b) <u>The use of white breeds</u>

Most white breeds of duck are non-extended black and non-diluted, i.e. $[e^+ e^+ bl^+ bl^+ D^+(D)^+]$. Colour is prevented from being expressed by the presence of the recessive white gene (c), but when colour is restored by crossing with a coloured breed, whites behave in a similar manner to breeds in the Mallard group in a sex-linked cross:

e.g. C^+ = coloured D^+ = non-dilution
c = white d = brown dilution



Caution is required with this type of cross, because if any cross-breeding has been practiced in the past some white birds may carry E, Bl or d. It is consequently always advisable to test any white birds on a small scale first before using them extensively in a sex-linked cross.

In the commercial production of table ducklings all the breeds used for crossing must be white, so that sex-linked matings are not possible. Unlike chicken broilers, where rate of wing feathering is a sex-linked character and can be used for sexing white day-old chicks, white breed crosses in ducks must be vent sexed. There may be undiscovered sex-linked genes which affect the colour of the day-old white breed duckling. The quest for these could be a profitable line of research. One gene, 'snow-white', is already known which can convert the normal yellow colour of the white breed duckling to pure white. Another, 'pied' can produce a pattern of white markings against the yellow background. Unfortunately neither of these genes is sex-linked. A similar problem is faced with white turkeys where vent sexing is much more difficult.

c) <u>Other pattern genes</u>

Certain pattern genes, (e.g. those responsible for the appearance of the Silver Appleyard, Welsh Harlequin and Fawn and White Indian Runner breeds), can modify the normal mallard pattern and change its basic appearance. These do not greatly affect the outcome of the sex-linked matings mentioned above.

Table 2 Brown Dilution in Sex-linked Matings in the Duck
(From Lancaster, 1963)

Mating Type	Male Parent Group	Female Parent Group	Colour of Progeny Males	Females
1.	Chocolate	Black Mallard White	Black	Chocolate
2.	Khaki	Black		
3.	Chocolate	Blue (Bl Bl) Blue Mallard (Bl Bl)	Blue ($Bl\ bl^+$)	Lilac ($Bl\ bl^+$)
4.	Lilac (Bl Bl)	Black Mallard White		
5.	Khaki	Blue (Bl Bl)		
6.	Buff (Bl Bl)	Black		
7.	Lilac (Bl Bl)	Blue (Bl Bl) Blue Mallard (Bl Bl)	Blue (Bl Bl)	Lilac (Bl Bl)
8.	Buff (Bl Bl)	Blue (Bl Bl)		
9.	Khaki	Mallard White	Mallard	Khaki
10.	Khaki	Blue Mallard (Bl Bl)	Blue Mallard ($Bl\ bl^+$)	Buff ($Bl\ bl^+$)
11.	Buff (Bl Bl)	Mallard White		
12.	Buff (Bl Bl)	Blue Mallard (Bl Bl)	Blue Mallard (Bl Bl)	Buff (Bl Bl)

Table 3 Sex-linked Matings Using Heterozygous Blue (Bl bl^+)

	Males	Females
Matings 3, 4, 5 and 6	50% blue (Bl bl^+) 50% black (bl^+ bl^+)	50% lilac (Bl bl^+) 50% chocolate (bl^+ bl^+)
Matings 7 and 8	25% pale blue (Bl Bl) 50% blue (Bl bl^+) 25% black (bl^+ bl^+)	25% pale lilac (Bl Bl) 50% lilac (Bl bl^+) 25% chocolate (bl^+ bl^+)
Matings 10 and 11	50% blue mallard (Bl bl^+) 50% mallard (bl^+ bl^+)	50% buff (Bl bl^+) 50% khaki (bl^+ bl^+)
Mating 12	25% pale blue mall. (Bl Bl) 50% blue mallard (Bl bl^+) 25% mallard (bl^+ bl^+)	25% pale buff (Bl Bl) 50% buff (Bl bl^+) 25% khaki (bl^+ bl^+)

2. Buff Dilution (bu)

The Buff Orpington is an interesting breed in that in addition to brown dilution (d) and blue dilution (Bl), it also carries another dilution gene (bu) which is sex-linked and further reduces the intensity of pigment. It was first noted by Lancaster (1963) when pale Buff Orpingtons (Bl Bl) were mated with Khaki Campbells (bl^+ bl^+). Both of these breeds carry sex-linked brown dilution (d) and the progeny, of both sexes, should have been uniform dark buff in colour. Instead, although all the ducklings were dark buff and intermediate in colour between the two parents, the males were of a noticeably darker shade than the females indicating the presence of a further sex-linked recessive dilution gene introduced from the Buff Orpington. e.g.

E = extended black Bl = blue dilution
e^+ = non-extended black bl^+ = non-dilution

D^+ = non-dilution Bu^+ = non-dilution
d = brown dilution bu = buff dilution

To avoid confusion in the following diagrams between dark buff caused by the action of blue dilution (Bl bl^+) and the dark shade caused by the presence of Bu^+, the former will be referred to as standard buff and the latter as dark shade. i.e.

Male		Female
Pale Buff Orpington	x	Khaki Campbell
(e^+ e^+ Bl Bl d d bu bu)		(e^+ e^+ bl^+ bl^+ d – Bu^+ –)

Standard buff males (dark shade) (e^+ e^+ Bl bl^+ d d Bu^+ bu)

Standard buff females (light shade) (e^+ e^+ Bl bl^+ d – bu –)

At day-old the sexes are easily distinguished, the dark males (Bu^+ bu) can be separated from the light females (bu –) by the darker down colour and darker bill, legs and feet.

Complications again arise due to the presence of blue dilution. If a standard Buff Orpington (Bl bl^+) male is used, the progeny will include two types of each sex. Provided allowances are made for these differences, however, sexing is still relatively easy at hatching. e.g.

Male		Female
Standard Buff Orpington	x	Khaki Campbell
(e^+ e^+ Bl bl^+ d d bu bu)		(e^+ e^+ bl^+ bl^+ d – Bu^+ –)

50% standard buff males (dark shade) (e^+ e^+ Bl bl^+ d d Bu^+ bu)

50% khaki males (dark shade) (e^+ e^+ bl^+ bl^+ d d Bu^+ bu)

50% standard buff females (light shade) (e^+ e^+ Bl bl^+ d – bu –)

50% khaki females (light shade) (e^+ e^+ bl^+ bl^+ d – bu –)

To date, the buff dilution gene (bu) has only been recovered from the Buff Orpington, but may be present in other breeds. Its use is limited to crosses between breeds carrying brown dilution (d) . This is because in crosses between the Buff Orpington (d d bu bu) and non-diluted breeds (D^+ – Bu^+ –), the

dilution effect of d is stronger than and masks the effect of bu thus making its presence superfluous. To summarise, a Buff Orpington male when mated with a female of any other brown-diluted breed (provided it does not carry bu) should give colour sexing in the day-old progeny.

SEX–LINKAGE IN THE MUSCOVY DUCK (Cairina moschata)

Only one sex-linked gene is known in the Muscovy duck, brown dilution (d), which was first reported by Hollander (1970). The Brown or Dun Muscovy is a rare breed in this country. Appleyard (1949) mentions a Dun and White Muscovy and Peter Scott shows a brown colour variety in the book 'Waterfowl of the World' by Delacour (1964) – (vol. 4, plate 2). Hollander found that brown dilution in the American Muscovy is inherited in much the same way as in the common duck and as a result of crosses between Muscovies and ordinary ducks came to the conclusion that the same gene (or a similar allele) is responsible in both species. To obtain a sex-linked mating the cross should be:

Male	x	Female
Brown Muscovy		Black Muscovy
(d d)		(D^+ –)
Black males		**Brown females**
(D^+ d)		(d –)

In species crosses the d gene of either duck will give sex-linkage in the hybrid:

Male	x	Female
Khaki Campbell		Black Muscovy
(d d)		(D^+ –)
Black hybrid males		**Brown hybrid females**
(D^+ d)		(d –)

or

Brown Muscovy	x	Black Orpington
(d d)		(D^+ –)
Black hybrid males		**Brown hybrid females**
(D^+ d)		(d –)

This knowledge has little practical application, however, unless one wants to rear the sexes separately, since the hybrids are sterile. It is of interest that sex-linked brown dilution genes are also present in the turkey and the domestic pigeon (Columba livia)

SEX–LINKAGE IN THE COMMON GOOSE (Anser anser)

Two sex-linked genes were reported by Jerome (1953, 1954 and 1970) in the goose: Blue dilution (Sd) and buff dilution (g).

1. Sex-linked blue dilution (Sd)

This is an incompletely dominant gene which changes the dark pigment of the Grey Lag to pale grey or white depending on how many doses are present. Its effect is similar to that of the blue dilution gene of the duck except that it is sex-linked. To understand the role played by this gene in present breeds of geese it is necessary to describe another gene pair reported by Jerome, i.e. solid pattern (Sp^+) versus spotted pattern (sp). Breeds such as the Toulouse, Pilgrim, Brecon Buff and Grey Lag carry the dominant solid pattern, but others such as the Roman and Embden bear the recessive spotted pattern.

When the dilution gene (Sd) is present in a single dose with the solid pattern (Sp^+), e.g. in the Pilgrim female, we have a light grey plumage but when a double dose is present as in the Pilgrim male, it produces a white bird. These differences will be examined later under autosexing. However, when the spotted pattern gene (sp) is present, either a single or a double dose of Sd will produce a pure white bird. This is why both male and female Romans and Embdens are white. This type of white is not to be confused with that of the White Chinese which is recessive (c c) and has no connection with Sd. Also Mike and Chris Ashton have pointed out that there is another (autosomal) form of blue dilution present in the Steinbacher, Blue African and Blue Chinese breeds which should not be confused with Sd. This situation is not unusual since there are also two types of blue dilution in the Muscovy duck.

Table 4 gives sex-linked colour differences at day-old following matings between Toulouse males and Embden, Roman or Pilgrim females. Jerome found that the differences at hatching were not as marked as at later stages. Nevertheless, only 5 errors were made at day-old out of 140 goslings sexed (3.3%) and at 3 weeks it was possible to correct these errors.

Table 4 Sex-linked Matings in the Goose using Blue Dilution

Male parent	Female parent	Male progeny	Female progeny
Toulouse (Sp^+ Sp^+ sd^+ sd^+)	Embden/Roman (sp sp Sd –)	Light Grey (Sp^+ sp Sd sd^+)	Dark Grey (Sp^+ sp sd^+ –)
	Pilgrim (Sp^+ Sp^+ Sd –)	Light Grey (Sp^+ Sp^+ Sd sd^+)	Dark Grey (Sp^+ Sp^+ sd^+ –)

2. Buff dilution (g)

Jerome (1970) has shown that buff coloration, which in this country is found in the Brecon Buff and the Buff-backed goose, is due to a recessive sex-linked gene (g) which changes the dark grey plumage of the wild-type Grey Lag pattern to a light reddish buff. To use this in a cross the following matings would be required:

Table 5 Sex-linked Matings in the Goose using Buff Dilution

Male Parent	Female parent	Male progeny	Female progeny
Brecon Buff (Sp^+ Sp^+ sd^+ sd^+ g g)	Toulouse (Sp^+ Sp^+ sd^+ – G^+ –)	Dark Grey (Sp^+ Sp^+ sd^+ sd^+ G^+ g)	Buff (Sp^+ Sp^+ sd^+ – g –)
	Embden or Roman (sp sp Sd – G^+ –)	Light Grey (Sp^+ sp Sd sd^+ G^+ g)	Buff (Sp^+ sp sd^+ – g –)
	Pilgrim (Sp^+ Sp^+ Sd – G^+ –)	Light Grey (Sp^+ Sp^+ Sd sd^+ G^+ g)	Buff (Sp^+ Sp^+ sd^+ – g –)

Sp^+ = solid pattern Sd = blue dilution G^+ = non-diluted
sp = spotted pattern sd^+ = non-diluted g = buff dilution

SEX–LINKAGE IN THE CHINESE GOOSE (Anser cygnoides)

The Chinese is the domesticated form of the wild Swan Goose. No sex-linked genes have been identified separately in this species but since the hybrids between Anser anser and Anser cygnoides are fertile with one another and with either of the parental species, the two sex-linked genes of the common goose (Sd and g) can both be used in crosses with the Chinese.

The Brown Chinese can, therefore, be substituted for the Toulouse in all the crosses above. Similarly the White Chinese, which was mentioned earlier and carries recessive white (c c), can also usually be substituted for the Toulouse since the breed on the other side of the cross restores colour, i.e. its genotype is $C^+ C^+$. As indicated earlier with white ducks a little caution is required in the use of recessive white breeds since earlier cross-breeding may have introduced unwanted genes. e.g. Jerome found a small proportion of his White Chinese carried Sd. He also found that some of his Embdens carried recessive white from earlier crossings with the White Chinese. This latter fault could prevent colour being restored in the cross-bred progeny.

Because of its large size, the African breed was originally considered to be derived from a species cross between the Toulouse and the Brown Chinese. However, recent examination of mitochondrial DNA by Shi, Wang, Zeng et al. (2006) has indicated that its origin is exclusively from the wild Swan Goose and is not a hybrid. Like the Brown Chinese it can be used as a substitute for the Toulouse in a sex-linked cross. The position of another species cross, the Pendle, produced by Will Bradley just before the war, is less certain. Bradley used Embdens, Romans and White Chinese in its production and consequently its genotype is a matter for conjecture.

SEX–LINKAGE IN THE MUTE SWAN (Cygnus olor)

A brief report by Cunningham (1956) suggested that the differences between the two colour phases of the Mute Swan, namely, the Polish and the Royal, were due to a sex-linked pair of genes. Their chief characteristics are as follows:

	Polish	Royal
Day-old down colour	yellow	grey
Juvenile plumage colour	white	grey

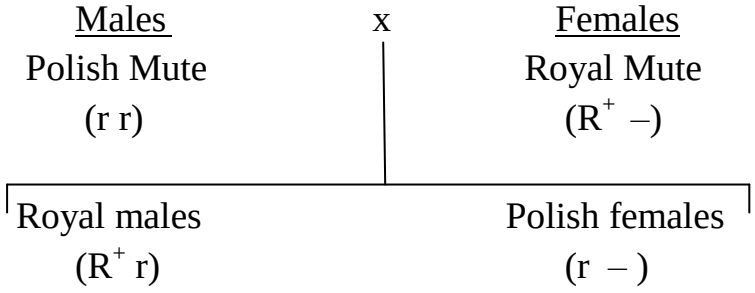
Adult plumage colour	..	..	white	white
Leg and feet colour	..	..	yellowish-grey	black

The two colour phases are illustrated by Peter Scott in Delacour's (1954) 'Waterfowl of the World', volume 1, page 54. Investigations by Munro, Smith and Kupa (1968) confirmed that the differences were sex-linked and showed that 'royal' was dominant to 'polish', Since no symbols were given in either report it is tentatively suggested that the following are used:

R^+ = 'royal'

r = 'polish'

In light of the above findings the appropriate sex-linked cross would be:



The female progeny are pure for the Polish type and can be used to produce pure-bred Polish. The Royal male progeny, however, will not breed true and should not be regarded as pure Royals.

AUTOSEXING IN WATERFOWL

Autosexing breeds of fowl were first introduced by Punnett and Pease at Cambridge in 1929. An autosexing breed is one whose newly hatched offspring can be sexed by their down colours. Unlike ordinary sex-linked matings no crossbreeding is required and autosexing, therefore, is automatic sexing within a pure breed. The main requirements for autosexing are that the gene is sex-linked, incompletely dominant and exerts an effect in the day-old. This means that there is a dosage effect and when two genes are present together as in the male they have a greater influence than when present singly as in the female. The Cambridge autosexing breeds of chicken used the cuckoo barring gene (B) from the Barred Plymouth Rock, which behaves in the way described above:

The Legbar (Autosexing Brown Leghorn)

Legbar male	Legbar female
(B B)	(B –)
Light down	Dark down

The only sex-linked gene in waterfowl which behaves in the same way is sex-linked blue dilution (Sd) in the goose. To be effective, however, Sd must be present with a solid pattern background (Sp^+ Sp^+). This occurs in the Pilgrim and the West of England goose:

Pilgrim male *	Pilgrim female
(Sp^+ Sp^+ Sd Sd)	(Sp^+ Sp^+ Sd –)
White	Light grey

At hatching, the male progeny are yellow and the females are grey-green.* Other breeds bearing Sd are the Embden and the Roman, neither of which has the solid pattern. However, Jerome states that although adult Embdens and Romans are white in both sexes, differences are often apparent in the day-old gosling and because of this some strains can be said to be autosexing. Also, some strains of common English geese possess the same properties. There is no reason why other pure breeds of geese could not be produced bringing together the solid pattern (Sp^+) of the Toulouse or Brown Chinese with the sex-linked blue dilution (Sd) from the Embden, Roman or Pilgrim.

True autosexing as described above should not be confused with sex-linked crosses between different colour varieties of the same breed. Humphreys (1946) produced a Dark Campbell (carrying D^+) specifically for mating with the Khaki Campbell to enable the ducklings to be sexed at day-old without losing their high productivity. This is no different from mating the Chocolate or Buff Orpington with the Black Orpington and is a normal sex-linked cross.

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* Having never kept Pilgrims, I have been told that British Pilgrims are never pure white as adults, having small areas of grey plumage on the rump and thighs and secondary wing feathers. Mike and Chris Ashton tell me that the day-old colours are not always clear cut and that in other autosexing breeds: Normandy, Shetland and West of England; males are significantly whiter than the Pilgrims.

THE Z CHROMOSOME

Few linkage studies have been carried out with waterfowl, but with chickens, detailed maps have been constructed for many of the chromosomes. For example, the positions of at least 15 genes have been located on the Z chromosome alone. This is because chickens are easier to manage for research and are generally more prolific; with the possible exception of the Khaki Campbell and some commercial strains of Pekin. In the colour breeding of waterfowl only three linkage groups are known:

Ducks – d (brown dilution) and bu (buff dilution) – Z chromosome
E (extended black) and S (dominant bib) – autosome

Geese – Sd (blue dilution) and g (buff dilution) – Z chromosome

Genes that are closely linked on the same chromosome do not obey Mendel's Law of Independent Assortment. The closer they are situated, the harder it is to separate them by backcrossing to double recessives. Also, very large numbers of progeny are sometimes necessary to determine whether they are part of a multiple allelic series or are closely linked at different positions on the same chromosome. This is one of the dilemmas of Mendelian genetics.

The d and bu mutations in ducks may well be part of a triple allelic series with D^+ as the true top dominant member. This is because of their similar action in diluting dark pigment and their presence together in only one breed, the Buff Orpington. It was not possible to resolve this in the 1960's due to lack of resources. From test matings, out of 268 ducklings hatched, no crossover combinations were obtained, indicating very close linkage or multiple allelism. However, until further evidence becomes available it is best to regard them as being situated at separate loci.

The distance between Sd (blue dilution) and g (buff dilution) on the Z chromosome of geese was investigated by Jerome (1970). He found they were approximately 1.75 units apart, which is very close. The units of distance are based on the percentage of crossovers (recombinants) following test matings. They are sometimes referred to as centimorgans after the great geneticist T. H. Morgan.

SUMMARY

Six pairs of sex-linked genes are described in waterfowl. The types of crosses required to give sex differentiation at hatching are listed. Only one of the above pairs is suitable for use in autosexing and is found in the Pilgrim goose. The relative locations of sex-linked genes on the Z chromosomes of waterfowl are also discussed.

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