FERTILITY ISSUES IN DOMESTIC X WILDCAT HYBRIDS

One factor influencing hybrids is their fertility (or lack thereof). This is related to the **chromosome complement (karyotype)**. Geoffroy's cat (and the related Tiger Cat and the larger Margay and Ocelot) has 36 chromosomes. The domestic cat and its relatives have 38 chromosomes. The F1 hybrid offspring of the Geoffroy's Cat and a domestic cat have 37 chromosomes - 18 from the Geoffroy's cat parent and 19 from the domestic cat parent. One could reasonably expect these offspring to be infertile. In fact feline hybrids have proven remarkable fertile with most female hybrids being able to breed with either parent species. The male hybrids are less likely to be fertile. Some of the second generation F2 hybrids (i.e. F1 hybrid is back-crossed to the parent species, usually to the domestic cat to create a domestic-type temperament) also have 37 chromosomes while others have a count of 38. This is apparently because the F1 hybrids are heterozygous, and can produces eggs or sperm containing either 19 chromosomes or 18 chromosomes. F1 hybrids tend to be large while F2 and later generations are the same size as domestic cats. By testing for chromosome count, it is theoretically possible to select and breed hybrid cats which consistently have 38 chromosomes (like the wild ancestor) to maintain the size and appearance of the initial hybrid.

Another problem with hybridization is illustrated by the Savannah, a hybrid between the domestic cat and the much larger Serval (serval/domestic matings have occasionally been attempted in the past). This breed is currently in its infancy and the problems encountered indicate that such a hybrid is unlikely to occur without human intervention. The most obvious is size difference. Typical domestic cats weigh between 8 - 14 lbs with a few reaching 20 lbs. Servals are in the 30 - 40 lb range although the race known as the "Servaline" is smaller as well as being paler, usually with smaller spots.

Unless he has been raised alongside domestic cats, it is not easy to persuade a male serval to mate with a domestic cat since the smells and cues are wrong. If is willing, he must then work out how to get things in the right place with a much smaller female! It is possible to mate a domestic male with a serval female if the female is co-operative though domestic females are used by most, if not all, Savannah breeders.

If mating is successful, there is a problem with gestation period. A domestic cat pregnancy is (on average) 63 days. A serval pregnancy is (on average) 74 days i.e. 10 days longer. The hybrid kittens are larger than pure domestic kittens and the domestic female often goes into labour at her normal time - which is about 10 days premature in serval terms. The more "overdue" she can made to be, the better chance the kittens have of surviving. If a serval female is bearing the young, the hybrid kittens are much smaller than serval kittens and she may kill them accidentally or her maternal instinct may fail to recognise them as kittens allowing her predatory instincts to take over. A domestic cat foster mother may be needed. Premature or undersized newborn kittens cannot suckle properly. They will weigh only a couple of ounces and are extremely fragile. They must be bottle fed every two hours, round the clock for the first two weeks of their lives, and then every four hours until they are weaned onto solids. Some must be tube fed or dropper fed until they are able to suckle from a bottle. By the time they are strong enough to suckle from the mother, her milk will have dried up. Other Savannah breeders have reported that they have experienced none of these problems and that all kittens have been born on time and raised by their natural mother.

At the end of all this, only the F1 females are fertile and F1 males are almost always sterile. The male kittens of the first three or four generations are usually infertile (with one or two exceptions due to close genetic relationship of the 2 species used); since they cannot be used to breed further Savannahs they are homed as pets. It is possible to backcross the hybrids repeatedly to a pure-blooded domestic or pure-blooded serval to get a fertile F1 hybrid male; it is fertile because it is either more than 90% serval or more than 90% domestic. The servals used are all captive bred (servals are bred for the exotic pet market); wild servals are not used.

Regarding Caracal x domestic hybrids; the Savannah gives an indication of problems breeders would face should they choose to pursue this as a breed. Caracals have a comparable gestation to servals. Servals and caracals can interbreed and both species can produce offspring with domestic cats, therefore caracal x domestic hybrids are feasible. There has apparently been one attempt at a caracal x domestic hybrid; a male caracal was housed with a female Snowshoe, but the pair failed to mate. To regard a domestic cat as a mate, the caracal would have to be raised with domestic cats. The lack

of interest in "Caracats" (name posited on this site in 2003) seems related to the current trend for breeding wild-looking striped and spotted cats; the caracal is more reminiscent of a large Abyssinian with long black ear tufts. "Caracat" hybrids (caracal male x Abyssinian female) were apparently been bred using that name in 2007.

Savannah photographs provided by:
http://photos.yahoo.com/jewelsofthenilesavannahcats & http://www.junglecats.com

Serval x domestic kittens can apparently only survive with human intervention so if nature takes its course, the domestic mother will miscarry the kittens before they are viable or the serval mother is unlikely to successfully rear the under-sized hybrids. I have received one report of a female serval who rears hybrid offspring with ease, but this may be individual variation. If nature takes its course, the cat and the serval don't even recognise each other as potential breeding partners. The likelihood of serval hybrids in the wild is therefore extremely remote.

Haldane's Rules

Haldane's Rule states that in animal species whose gender is determined by sex chromosomes, when in the first cross offspring of two different animal species, one of the sexes is absent, rare or sterile, that sex is the heterogametic sex. The "heterogametic sex" is the one with two different sex chromosomes (e.g. X and Y); usually the male. The "homogametic sex" has two copies of one type of sex chromosome (e.g. X and X) and is usually the female.

Haldane's Rule for Hybrid Sterility states that a race of animals could diverge enough to be considered separate species, but could still mate to produce healthy hybrid offspring in a normal ratio of males and females. If any of the hybrid offspring were sterile, the sterile offspring would be the heterogametic offspring (males). If the heterogametic offspring was fertile, it produced the normal 50:50 ratio of X and Y sperm.

Haldane's Rule for Hybrid Inviability states that if the divergence between the species became large enough to generate genic differences, but not to prevent mating, then parental gene products may fail to co-operate during development of the embryo, resulting in hybrid inviability (the hybrids are aborted, stillborn or don't survive to maturity). In this case, the male to female ratio of hybrid offspring is skewed with more homogametic offspring while the heterogametic offspring (males) are absent or rare.

Haldane considered the speciation process (i.e the "growing apart" of one species into two species) to occur in stages. The first stage of this process was complete if the two species could mate and produce healthy but sterile hybrids. As the species continued to diverge, they became genetically less compatible; they could mate but hybrid embryos either could not be formed or they died before maturity - it didn't matter whether or not they were sterile since they would not survive to breeding age. These are called "**post-zygotic barriers**" because a zygote (fertilized egg) is formed, but the offspring (particularly the males) do not breed.

As species differentiation progresses even further, it results in anatomical (body shape), physiological (body function e.g. mismatched pregnancy periods) or psychological (behavioural) differences which prevent the two species mating with each other. Haldane called these "**pre-zygotic barriers**" because they prevent offspring from being conceived in the first place.

Speciation is not always the gradual process Haldane described. It can involve big jumps as well as gradual shifts. Fertile hybrids are more common than Haldane realised since pre-zygotic barriers can be overcome and there are intermediate stages in post-zygotic barriers. This is because the species involved have been kept separate by other means e.g. physical separation.

Male Geoffroy's cat raised with domestic cats will view them as mate, but male Geoffroy's reared apart from domestics will kill female domestic cats presented to them. This is a psychological (pre-zygotic) barrier, but the offspring are fertile so there is no post-zygotic barrier - this is the reverse order to that described by Haldane. Geoffroy's cats are from South America while domestic cats are from Africa/Europe; the species were kept separate by an ocean and had no need to develop other barriers. Servals and domestic cats have some physical barriers (size), but these can be overcome; male offspring are sterile, though female offspring are fertile (pre-zygotic and post-zygotic barriers). In some hybrids of domestic cats with small wildcats, a proportion of hybrid males are claimed to be *partially* fertile (incomplete post-zygotic barrier) and though the hybrid females are fertile they may not successfully raise their young - a psychological barrier, but one which does not prevent mating/conception.

In addition to Haldane's Rules, the viability and fertility of hybrid offspring can depend on which species is the male parent and which is the female parent since some embryo developmental effects come into play depending on which genes come from which parent (e.g. giantism in ligers [lion x tigress], but not in tigons [tiger x lioness]). In Beefalo, Domestic cows may can be impregnated by Bison, but have an immune response against Bison/Cow hybrid calves in utero (physiological barrier), but Bison cows don't have this immune response against hybrid calves and hybrid Beefalo males can be fertile.

Crossing the Species Boundary

According to H C Brooke in Cat Gossip during 1926, the recently held Vienna cat show had included a litter of kittens said to have been sired by a Civet-cat on a domestic female. Herr Joe Lesti attempted to learn more about the remarkable kittens as well as details of a reported Marten-cross. Brooke was dubious that such hybrids were possible. At that Vienna show there were Tibet Cats, Civets or Genets (Dr Alder had exhibited a Genet at the 1923 Croydon cat show). Brooke himself had exhibited a Civet and an Egyptian cat at Croydon and attracted a great deal of interest. Confusingly, the term "Civet" has been applied to African Wildcats although it is the viverrine civet that is indicated in the reports. At the time, some cat-fanciers, and even some naturalists, genuinely believed in hybrids between true cats and cat-like viverrids.

Lilian J Veley, in 1926/7, claimed to have seen, in a Zoo (probably a continental zoo though she could not remember which and it was never traced!) a litter of Civet/cat hybrids. The mother was a large mackerel tabby and the presumed father was a Civet with whom the mother was "certainly on good terms". The alleged results most resembled the cat, but with longer faces, more bushy tails and more blotchy markings. At the time, some authorities were claiming the Siamese to be the product of a mating between a viverrine Civet and the Bay Cat. Cat-fancier, breeder and writer HC Brooke doubted that the two could interbreed, being from different families. He added that even if they could interbreed, they were unlikely to "fix" a new type since the offspring would breed with either their civet ancestors (losing the feline type) or with cats (losing the viverrine type). Dr P Chalmers Mitchell, Secretary of the Zoological Society responded that hybrids of cat and Civet, and of cat and Genet were unknown at London Zoo. He also disabused fanciers of the conceit that the Siamese cat was a hybrid between domestic cat and the wild Bay Cat. Capt J G Dollman, Assistant Curator of the Natural History Museum, South Kensington (London) added that the Siamese cat and the Bay Cat were unlikely to interbreed and produce fertile offspring and that the Siamese was most unlikely to have been the product of a cross between a viverrine (identified as the Indian (or Yellow-throated) Marten) and a Bay Cat. Siamese cat fancier Lilian J Veley (1926), however, remained adamant that the Siamese was had traits inherited from some type of viverrine, possibly unknown to science, that lived in the region.

Thanks to our better understanding of genetics since the 1920s, it is generally accepted that different species usually cannot mate and reproduce - this is called "reproductive isolation". The exception is closely related species which can produce hybrids, although those hybrids have reduced fertility. The more easily two species form hybrids, the more closely the species are related in evolutionary terms. Static species are a human concept; hybridization is more common in nature than previously

realised. Species are kept separate by several different typess of reproductive isolation:-

Physical separation: *the species live in different geographic locations or occupy different ecological niches in the same location and so never have the chance to meet each other.*
Temporal isolation: *the species mate during different seasons or different time of day and cannot breed together; this can be overcome in captivity by using artificial light or hormones to manipulate the breeding cycle.*
Behavioral isolation: *members of different species may meet each other, but do not mate because neither performs the correct mating ritual. Imprinting by fostering the young of one species on a female of the other species can overcome this in some cases.*
Mechanical isolation: *copulation may be impossible because of incompatible size and shape of the reproductive organs.*
Morphological isolation: *copulation may be impossible because of the difference in body size or shape.*
Gametic isolation: *the sperm and egg may not fuse and hence fertilization cannot occur; if it does occur then the embryo fails to get past the first few cell division.*

In addition, **physiological factors** can prevent hybridization: the mother's immune system may reject the hybrid embryo; differences in gestation (pregnancy) time mean offspring are born prematurely or greatly overdue (both of which cause the offspring to die). **Genomic imprinting** - the unequel expression of genes depending on parent of origin i.e. whether certain growth genes are inherited from the male or the female - can affect the health and lengevity of the offspring and may cause **growth dysplasias** (giantism or dwarfism) with potentially crippling or lethal results. Growth dysplasia due to the mismatch of genes on the maternal and paternal chromosomes affect the embryo's growth rate and the size of the placenta (causing miscarriage). An affected embryo may be aborted at an early stage due to abnormal growth, the offspring may be stillborn or may only survive a few days. The mother may die if the offspring are too large to pass through the birth canal.

Hybridisation is usually considered a dead end because the hybrids are not fully fertile; if they are fertile, the hybrids are usually absorbed back into the population of one or other parent species and most of the alien genes are bred out. More rarely, hybrids can become new species or new sub-species. In the hands of breeders, some domestic/wildcat hybrids can become breeds; these are not new species because the wildcat genes are largely bred out by crossing with domestic cats, until only the wildcat pattern remains.

In the wild, hybridisation is part of evolution. Most hybrids face handicaps as a result of genetic incompatibility, but the fittest survive, regardless of species boundaries and may contain a combination of traits which allows them to exploit new habitats. In experiments with sunflowers, successful hybrids could evolve into new species within 50-60 generations. Life may be a genetic continuum rather than a series of self-contained species. Usually, where there are two closely related species living in the same area, less than 1 in 1000 individuals will be hybrids because animals rarely choose a mate from a different species. Otherwise, genetic leaks would cause species boundaries to break down altogether. In some closely related species there are recognized "hybrid zones".

For example, in Heliconius butterflies, hybrids are common, healthy and fertile - hybrids can breed with other hybrids, or with either parent species. Genes are leaking between the two parent through regular hybridisation. Predators avoid eating the parent species because they have wing patterns warning that they taste bad. The hybrids are disadvantaged because their intermediate patterns are not (yet) recognised by predators. In mammals, hybrid White-Tail/Mule Deer are disadvantaged because they don't inherit either parent's escape strategy (White Deer dash, Mule Deer bound) and are easier prey than the pure-bred parents. Cats, however, are predators and apart from specialists such as the fast-running cheetah and the pride-living lion, they have relatively similar hunting strategies.

Finally, what happens if two species previously kept separate by geographical boundaries suddenly meet up? The hybridisation of the native European Red Deer and the introduced Chinese Sika Deer means that pure Red Deer risk being hybridized into extinction. While humans want to protect the Red Deer; evolution wants to utilise the Sika Deer genes. The same is happening in Europe between introduced Ruddy Ducks and native White-headed Ducks. Nature always selects for the fittest genes; hybridization is just another way of shuffling genes into winning combinations.