All organisms have the desire to breed and pass on their genes to the next generation; it is the ultimate means of ensuring survival.

REPRODUCTIVE TIMING
Female wolves usually become sexually active in their second year, although in captivity this can be seen at a younger age. Males usually become fertile by the age of 22 months. In captivity, breeding has been documented as early as nine to ten months, the earliest documented wild breeding is two years. Wild wolves may not breed until four or five years of age. This reproductive capacity still puts them ahead of the grizzly bear which does not breed until eight years old. This may be due to factors such as an inability to care for pups due to underdeveloped hunting expertise and parental skills learnt from older pack members. Wild wolves need to wait until vacant territory is available with ample resources and suitable environmental conditions. This may take time in saturated wolf populations, thereby prolonging the age of breeding.

During autumn hormone levels begin to rise, preparing the body for the reproductive cycles to follow. Female wolves come into oestrus once per year in late winter. This period lasts roughly five to seven days, the female being most receptive in the latter half. Breeding females will usually come into oestrus before other females in the pack, ensuring male interest, whilst suppressing reproductive cycles in other females through physical and mental harassment. Established pairs tend to scent-mark more frequently during this period with newly-formed pairs marking most often.

Wolves mate anytime between January and April with late February to early March being most common for North American wolves. Wolf populations in southern portions of their range tend to breed earlier than those further north. Records exist of Arizona wolves breeding in December and Abyssinian wolves anytime from August to December.

COURTSHIP
In late winter a pair may begin to court, forming a strong bond.

The process is affectionate. Wolves will approach one another whilst quietly whining. Noses touch, muzzles are mouthed, bodies bump, mutual grooming and nibbling of coats ensues whilst the pair become acquainted, often walking closely and even sleeping side by side. Courting pairs will follow each other closely two months prior to oestrus. This early courtship phase is known as the pre pro-oestrus.

After time, males will begin to smell the female genital area, investigating for traces of sex hormones. If she is not sexually receptive, the male is declined with growls and snaps of the jaws. During the pro-oestrus period females undergo physiological changes preparing the body for breeding. Courting behaviour becomes more frequent and levels of female sex hormone oestrogen increase. Males are receptive to these changes. When the female is in oestrus, ready to breed, copulation will occur.

COPULATION
Females give visual and olfactory cues to indicate receptivity.

She will avert her tail to the side (flagging), standing still when the male mounts. An inattentive male is encouraged by the female pawing, rubbing and even mounting him. The physical act occurs with the male mounting from the rear. A copulatory tie results after male ejaculation due to swelling of the males' penile bulb gland and muscular tightening of the females' vaginal tract. This literally ties the wolves together. This tie aims to ensure successful fertilisation, increasing successful passage of sperm and ensuring a lack of competition from other males by preventing further copulation. During attachment wolves often turn to face end to end, ensuring protection from potential intruders during this vulnerable
time. Ties last from five to 36 minutes. Wolf copulatory ties more readily separate than those of domestic dogs, offering obvious survival advantage should danger present itself. Wolves may copulate between one and eleven times during oestrus.

Unfortunately for romantics among us, myths of wolves mating for life are untrue. Lasting attachments are formed but widowed wolves are known to breed with another. Some males bond with different females in different years. Potentially this could occur due to lack of previous breeding success.

PREPARATION FOR PUP BIRTH
After copulation metestrus occurs whether the female falls pregnant or not.

This period prepares the female for pup rearing. Physical changes such as the growth of mammary tissue and loss of belly hair, along with behaviours such as den construction, are elicited by the metestrus phase. Females failing to become pregnant sometimes express this in “pseudo-pregnancies”.

Preparation for pup care may begin well before birth. Dens may be dug as early as autumn. All pack members participate in den digging and provisioning for the pregnant female. Den locations vary depending on availability but are rarely near peripheral territory areas where conflicts are likely. Most natal dens are near water and elevated to allow detection of danger. Dens may be found in crevices, caves and under trees, to name but a few. Dens are not lined with any material. Birthing chambers are normally located at the end of a tunnel up to 15 feet long, often being slightly elevated above the rest of the tunnel. The chamber is approximately 3 feet in diameter and 2 feet high. Females often localise near a den site for a month prior to birth. All pack members protect the den site, the adult male being particularly protective.

Just prior to birth and for a few days after, the female will be alone in the den. Gestation in wolves, similarly to dogs, lasts 60-63 days. Pups are born in early spring (late April/early May), which coincides with birth pulses of herbivores providing a means to cater for their nutritional needs. Again variances can be seen to coincide with alternative breeding patterns of wolves in different environments. Pups are born after the worst of winter and are almost completely physically developed by the time winter comes again.

Wolf litter sizes average five or six pups but range from one to 11. In areas with high mortality rates or larger prey biomass available per wolf, litter sizes tend to be higher.

FACTORS AFFECTING BREEDING

Most wolf packs comprise pups (largest proportion), yearlings from previous breeding, and the parent pair.

Packs may include one or more two- to three-year-olds. Usually, all young are offspring of the breeding pair. Some packs contain a post-reproductive female (old breeding female succeeded by a daughter) or wolf adopted from another pack. Male/female pack composition tends to be even.

Adult wolf mortality peaks during late autumn and winter; also the most major times of dispersal. During this period young adults may leave their pack to find a mate and form their own. Winter hormonal changes preparing for the breeding season stimulate dispersal behaviour. Males are much more likely to fight during this period.

In most situations the parent or Alpha pair mate. Occasionally subordinate breeding or multiple pack pair mating occurs. Multiple litters are more common than initially thought. These situations are seen as a response to severe winters when prey becomes vulnerable creating a more readily available food source. Periodic disturbance or culling of wolf populations can lead to a temporary increase in numbers. Wolf reproduction rates react accordingly to factors in their environment. Subordinate females may successfully mate after pack hierarchy has been disturbed.

Non-reproductive pack members provide indirect pup care for many reasons. At the present time it may be the best course of action to promote the genes which they share with their kin. Their actions reinforce social bonds enhancing survival and juveniles gain valuable experience for when they eventually breed themselves. Issues relating to co-parental care are complex and many hypotheses are untested.

Inbreeding has been observed in wolves both wild and captive. The degree to which this is harmful is not clear. Populations can suffer from inbreeding depression and negative physical effects. Isle Royale (Michigan, USA) wolves show a high degree of inbreeding due to their inability to migrate. This population are suspected to suffer from reproductive failure, population decline, decreased genetic diversity, physical abnormalities and decreased longevity.

Inbreeding occurs due to a lack of choice; similarly, when lacking potential mates, wolves are known to settle for domestic dogs. In most wild situations the opportunity for input of new genetic material is high enough to prevent inbreeding. Social processes causing dispersal and prevention of inter-pack breeding are pivotal.

Factors such as dispersal through connected habitat areas (containing genetically diverse populations), availability of suitable mates and habitat in which to raise young, impact upon breeding processes and thus population viability. To maintain stable and suitable wolf breeding processes, factors determining them must be preserved.

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Pete is currently assisting with educational work at the Trust and is collaborating with Josip Kusak on a project the UKWCT supports. Pete hopes to soon begin a doctorate of biology.