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Variations of geese under domestication

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Man has been in interrelationship with wild water fowl for thousands of years. Yet, in that time, only two species of wild geese have been domesticated (13.3% of all true geese); the Greylag goose (*Anser anser*) in the fourth millennium B.C. and the swan goose (*Anser cygnoides*) in the second millennium B.C. From these two species, numerous breeds (181) have been developed. Compared to other domestic animals, the goose has varied less during domestication, aside from a few modifications in appearance, reproductive traits, internal organs and behaviour. It has increased in body weight, and hence became a non-migratory bird. Compare to the greylag goose (gander 2.8-4.1 kg, goose 2.5-3.8 kg body weight), the body weight of the Toulouse gander has increased by 331-421%, and the Toulouse goose by 286-364%. The African goose developed higher body weights (gander by 285-362%, goose by 292-311%) compared to the weight of the swan goose (gander 3.5 kg, goose 2.8-3.5 kg body weight). Conformation traits have changed, whereby the natural grey feather colour has changed to white in some breeds. Furthermore, sexual maturity has accelerated, and prolificacy increased. Egg production of a significant proportion of the European goose breeds has increased by 600-1000% compared to the greylag goose (5-6 eggs/goose). For example, egg production of the Chinese goose has increased by 875-1200% compare to the wild swan goose (5-8 eggs/goose), and the monogamous partnership typical of wild geese has turned into polygamous matings.

Keywords: wild geese; domesticated geese; domestication; changes of domestication

Introduction

Only about 40 of approximately 50,000 avian and mammalian species traceable in the world have been domesticated: 18 mammalian and 16 avian species have added one site-specific hybrid to both groups. For avian species the following have been domesticated; chick, duck, turkey, goose, Muscovy duck, guinea fowl, partridge, pheasant, quail, peacock, pigeon, swallow, cassowary, emu, nandu and ostrich (Rischkowsky and Pilling, 2007). Some sources consider only the ostrich to be fully domesticated among running birds (Appleby *et al.,* 2004). At the same time the canary, Bengalese, zebra finch (Ellis, 1984) and the Mute swan have been placed among the domestic birds. A widespread inter-specific hybrid among domestic birds is the sterile Mulard duck

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resulting from the crossing of Muscovy duck drake and domestic duck layer (Pingel, 2000). In about 10,000 avian species known in the world, the rate of domesticated breeds is very low (Rischkowsky and Pilling, 2007).

True geese comprise either 14 species (Crawford, 1993) although others mention 15 (Kear, 2005; Owen, 1980). They belong to the geni Anser; the Swan Goose (*Anser cygnoides*), Bean Goose (*Anser fabalis*), Pink-footed Goose (*Anser brachyrhynchus*), White-fronted Goose (*Anser albifrons*), Lesser White-fronted Goose (*Anser erythropus*), Greylag Goose (*Anser anser*), Bar-headed Goose (*Anser indicus*), Snow Goose (*Anser caerulescens*), Ross Goose (*Anser rossi*) or the Emperor Goose (*Anser canagicus*). Corresponding species from genus Branta are the Hawaiian Goose (*Branta sandvicensis*), Barnacle Goose (*Branta leucopsis*), Brent Goose (*Branta bernicla*) or Red-breasted Goose (*Branta ruficollis*) (Scott, 1980). Of these, only two species have been domesticated (Crawford, 1995).

History of domestication of geese

Among birds, geese were the earliest to be domesticated. Their domestication started approximately 20,000 years ago (Camiruaga-Labatut, 2002). Domestic geese have been kept since about 3,000 years B.C. (Crawford, 1984) *i.e.*, having been domesticated about 5,000 years ago (Kear, 2005). The greylag goose (*Anser* anser) was considered to be domesticated first in Southwest-Asia (Crawford, 1984) or in China (Appleby *et al.*, 2004) or otherwise in Southeast-Asia and the earliest date of domestication is the fourth millennium B.C. (Matolcsi, 1975). Geese have undergone multiple domestication processes (Appleby *et al.,* 2004). Early goose depictions in art known from North-Siberia and Mesopotamia suggest that earliest domestication of the goose happened in Asia Minor during the fourth to fifth millennium B.C. thus, the goose was in Egypt as a domesticated bird. Indeed, domesticated variations of the greylag goose can be seen in the Egyptian goose drawings in frescoes where they appear beside Nile geese (Matolcsi, 1975). There is ample evidence that geese had undergone domestication in Egypt. Greylag geese had been fully domesticated by the period of the New Kingdom (1552-1151 B.C.; Crawford, 1993) as seen in Europe (Crawford, 1984). It can be historically justified that more geese breeds were known in ancient Egypt (Matolcsi, 1975). The ancient Greeks had kept the greylag goose as a domesticated bird which additionally played important role in Roman civilisation, cited from around 400 B.C. (Crawford, 1993).

Domestication of the Chinese Swan Goose, ancestor of the Knobbed goose (*Anser cygnoides f. domestica*) started in East-Asia in the second millennium B.C. (Matolcsi, 1975). Probably the bird was bred more than 3000 years ago over many centuries in China from whence these breeds spread to India, Africa and Europe. African breeds are generally considered to have derived from China (Ashton, 1999).

Thus, the two domesticated geese species derive from two different lineages (Crawford, 1995). The European geese derive from the Greylag goose (*Anser anser*), whereas the South-east Asian geese derive from the Swan goose (*Anser cygnoides*). Under the commonly used names ‘goose’ or ‘geese’ (Crawford, 1984) the domestic goose (*Anser anser f. domesticus L., 1758*) and Swan goose (*Anser cygnoides f. domestica*) derive from the above-mentioned goose species (Matolcsi, 1975). The name of the Wild Swan goose probably originates from its appearance, combining the features of the swan and the goose (Ashton, 1999).

Domestication of other geese, *e.g.*, the Canada goose (*Branta canadensis*) stopped during an early stage due to the spread of the fully domesticated *Anser* population after

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their settlement, thus further changes discontinued. Today it can be regarded as a wild or pet bird (Crawford, 1984) or a tamed goose, and crossing the Canada goose with domestic geese results in a sterile hybrid called a 'Mongrel' goose in North-America (Pingel, 2000).

The Nile goose (*Alopochen aegyptiacus*) (Davies, 2005) belongs to genus Alopochen and is probably not classed among the true geese, as it has been a domesticated species in Egypt but today only occurs only in the wild and is not kept as a domestic bird (Schneider, 1995). Most researchers, in turn, qualify the white geese depicted on Egyptian frescoes originating from the second half of the third millennium B.C. as domesticated Nile geese (*Chenolopex aegyptiacus L., 1758*) (Matolcsi, 1975). This was probably the first domesticated bird before any other fowl (Stromberg, 1996). Some believe that the Nile goose was used for meat and as a sacrificial bird, but has never had been a truly domesticated animal (Pingel, 2000).

In Eurasia, other species might have been starting bases of domestication such as the Barnacle, Bar-headed and Red-breasted goose. The Greylag goose had proved favourable for selection and domestication by humans. In Iceland the Pink-footed goose species, in Siberia the Been-goose, White-fronts, Barnacles and Brents goose species served as important food sources but they were only caught and killed in the wild (Ashton, 1999).

Wild species of domesticated geese

Domestic geese have been classified in the order *Anseriformes*, suborder *Anseres*, family *Anatidae*, subfamily *Anserinae* and tribe *Anserini* (genus true geese). The Greylag goose (*Anser L., 1758)* has two subspecies: western (*A. a.* anser) and eastern (*A. a. rubrirostris*). The bill in the former is orange and pink in the latter (Rutschke, 1997). The two subspecies do not differ substantially by body size. The Swan goose (*Anser cygnoides, L., 1758*) has no recognised subspecies (Crawford, 1993).

In true geese, the Greylag goose (*Anser anser*) is the biggest after the Canada goose and the heaviest among the European wild goose species (Rutschke, 1997). Sexes of immature and adult geese are alike, although the male is bigger (Nyeland, 2005). Ganders weighing 2.8-4.1 kg (Crawford, 1993) 3-4 kg (Rutschke, 1997) and layers 2.8-3.8 kg (Crawford, 1993) or 2.5-3.5 kg, but liveweight may differ greatly depending upon the season (Rutschke, 1997).

The hatching weight of goslings is 112.6 g on average (Nyeland, 2005). Goslings grow rapidly; they triple their day-old weight in three weeks and by the 70th day reach 75% of their adulthood weight (Bogenfürst, 1992). They become sexually mature by the age of two years (Serjeantson, 2002). The pair-bond with their mate is strong and long lasting; it usually starts during the second winter (Crawford, 1993). Stable, monogamous pair-bonding is usually formed in geese over 3-4 years (Nyeland, 2005). The monogamous pair is bound for a lifetime for brooding pairs (Rutschke, 1997).

Laying dates differs by latitude. The usual period is late April-mid May in continental Europe, and late March-early April in the United Kingdom (Nyeland 2005). The layer produces 5-6 eggs (Crawford, 1993) or 4-9 eggs (Rutschke, 1997) with a maximum of 12 eggs in a nest, and broods them alone after last egg laid to ensure synchronous hatching at 27-28 days of incubation (Nyeland, 2005). The nestlings usually all hatch in one day (Rutschke, 1997).

Goslings have olive brown upper parts, yellow wing bar and underparts, dark bills and dark greyish legs (Nyeland, 2005). The plumage of adults is paler than other grey geese, with neck feathers barred as if they were striated. Legs are reddish-orange orange (Rutschke, 1997). Plumage colour is evenly greyish-brown except for the underparts

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(belly, lower chest) which are marked with black or dark brown patches. Immature geese lack these darker patches. Flight feathers are dark brown with clear white shaft and the eye ring is pale yellow (Nyeland, 2005).

Newly hatched goslings are covered by down coat that they change from weeks one to three of age. Flight feathers start to grow during the fourth week and fully develop at about eight weeks of age. Geese can fly already a little time before this. After having attained flight, they go through their first moult and, after some weeks, start the second juvenile moult that lasts throughout autumn well into the winter. At this time the whole plumage is renewed except the wing feathers and the pertaining cover feathers. After the age of one-year, wild geese undergo a complete moult (Rutschke, 1997), and moulting happens on two occasions (Serjeantson, 2002). Nesting birds shed first their wing feathers from around mid-June to the time the goslings are already four weeks old. Non-breeders and failed breeders shed their wing feathers between late May and early July. At this time the geese cannot fly for some weeks (Rutschke, 1997) and remain flightless for 20-25 days (Serjeantson, 2002). The wing feathers grow 9-10 mm per day and are renewed after five weeks and only thereafter they begin shedding body feathers, which may last till the winter. During the moulting time the geese migrate to specific sites (Rutschke, 1997).

Grey geese are mainly confined to temperate zone but do extend into arctic and subarctic areas in some places. (Nyeland, 2005). Their nesting area extends from Iceland and western part of North-Scotia throughout the western coastline and South Scandinavia as far as Central Europe, as well as from mid and southern part of Siberia as far as the Pacific Ocean. The wintering sites for birds nesting in North and Central Europe are situated in North Africa and Spain where they arrive at in late summer (Pingel, 2000). They breed in habitats near lakes or streams. After hatching, the families often aggregate into larger flocks and tend to remain gregarious (Nyeland, 2005). They feed on grass, marsh plants, other green forages, cereal grains (Serjeantson, 2002), and pulses and root crops (Schneider, 1995). The natural lifespan of geese is long (Crawford, 1984). Maximum lifespan of UK ringed bird is more than 18 years (Nyeland, 2005). Their lifespan may reach even 40 years, but this does not happen in Nature (Serjeantson, 2002).

The Swan goose (*Anser cygnoides*) is also known as Chinese, Dry-nosed or Siberian goose and many names are given to domestic forms such as the African, Cape, Knob, Spanish or Guinea goose (Callaghan, 2005). These breeds body shape is more swan-like, longish and slender compared to the grey goose (Schneider, 1995). Body weights are about the same as in Greylag geese: ganders weighing 3.5 kg and geese 2.8-3.5 kg. Its long slim neck and gait is characteristic of swans and this carriage is especially visible during swimming (Crawford, 1993). In adults the bill is long and black (Schneider, 1995) with a faint knob at its dorsal base (Crawford, 1993). Feet and legs are reddish-orange; legs are medium in length, making its gait more vigorous (Schneider, 1995). Upperparts are dark chestnut with feathers bordered by white. The rest of head and neck are pale brown, slightly darker at the chest. Flanks are barred dark chestnut, and anterior lower-parts are white. Sexes are alike but the female is smaller with a shorter neck and smaller bill (Callaghan, 2005).

In goslings the head, neck and underparts are yellowish buff, with broad blackish patch over lores and eyes. Upperparts are dusky brown with pale buff patches on hind wing and the sides of back. The bill is blackish-green, with a light tip. Immature birds are similar to adults but have no chestnut barring on flanks (Callaghan, 2005).

Sexually mature geese undergo one body and one wing moult. Non-breeding adult geese moult in early July, whilst nesting geese moult in July-August (Callaghan, 2005). Their behaviour is similar to that of the grey gees on the whole. They reach sexual

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maturity during the second winter, and their pair bond with their mate is strong. They lay 5-8 (Crawford, 1993) or 5-6 eggs per clutch (Schneider, 1995) weighing 160 g and hatch at 28 days of incubation (Crawford, 1993) or 27-29 days (Rutschke, 1997).

Their preferred habitat is near rivers and ponds. They are exclusively herbivorous (Crawford, 1993) and eat various grasses, weeds, mosses, rhizomes of coastal plants. The breeding area of the Swan goose covers the South part of Central-Siberia eastward as far as Kamchatka and Central-Asia and northward as far as Mongolia. It overwinters in areas situated in China and Japan. Its voice is trumpet-blast like call (Schneider, 1995). The principal call is a prolonged, resounding, ascending honk and alarm is signalled by a harsh, short note repeated two or three times. The pre-flight call is low 'ga-ga-ga-ga' (Callaghan, 2005).

Changes under domestication

Domesticated goose species are characterised by the influence of excessive breeding work in an historical scale, resulting in the two wild goose species and their domestic varieties differing today considerably both in appearance and features. All this is due to the fact that man has placed the animals in a new environment and created different rearing and production conditions during domestication, leading to alteration of the animal. Darwin was the first to give a scientific explanation for the biological reasons for changes that have taken place during domestication. He attributed these mainly to the altered living conditions but also attached importance to overuse of certain organs or disuse of others. Thus, under the influence of altered external factors and human selection adaptive changes occurred in the animal mainly through a series of physiological changes. As a result, the traits forming a basis for selection have accumulated from generation to generation, thereby faint differences visible during selection become more obvious. Formation of these changes, *i.e.*, domestication traits, have been facilitated by the great adaptability of the animals (Matolcsi, 1975).

During domestication, a high degree of variability evolved in the animals compared to the wild population - as a result of the primary alteration stage and adopted breeding methods later on. Consequently, body size, conformation and appearance have altered, with modifications in the physiological processes, sexual life, prolificacy and the nervous system (Matolcsi, 1975). However, scarcely any other farmed species has varied so little than the goose under such a long period of domestication (Darwin, 1959). Variability has given to raise numerous breeds of domestic animal (Matolcsi, 1975). Around the world 166 and 181 goose breeds have been registered according to the January census in 2005 and 2006, respectively. In a report comprising the breeds by continent, a total of 158 goose breeds was registered with 10 in Africa, 39 in Asia, 100 in Europe and the Caucasus, five in Latin America and Caribbean, two in the Near and Middle East, none in North America, and two in the Southwest Pacific. Nearly a quarter of the registered goose breeds (24.68%) are in Asia and almost two-thirds (63.29%) are in Europe and the area of the Caucasus (Rischkowsky and Pilling, 2007). However, domesticated geese can be found in every part of the world (Hugo, 1995). In an FAO report of 94 goose breeds recognised around the world, 42 have Greylag goose ancestry, 23 originate from the Swan goose and 10 derive from crossing of the two breeds, while, for 19 breeds, the ancestry is unknown. Many of the breeds are small in number, have poor production performance and limited geographical distribution (Buckland and Guy, 2002; Heikkinen, 2017).

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Appearance

The body size in domestic livestock shows greater variation than in nature (Matolcsi, 1975). In domestic geese body size differs considerably (Schneider, 1995); and is higher compared to that of wild geese (Riddell, 1943). With increment in size, other body dimensions have altered (Pingel, 2000), the body has deepened (Serjeantson, 2002), became more horizontal and the tail has shortened (Tóth, 1956). Among goose breeds descending from the wild Swan goose (*Anser cygnoides*) the African breed has, in turn, a little more upright carriage, rising by 30-40% from the horizontal (Roberts, 2008). Body weight of some breeds can even exceed 10 kg (Pingel, 2000). According to data from ca. 150 years ago, the body weight of the domesticated geese and the Marsh goose amounted to ca. 8 kg and 15-20 kg, respectively. Nowadays, the body weight is ca. 10 kg for some breeds, *e.g.*, the Toulouse of Greylag (*Anser* anser) origin (Schneider, 1995), a French breed used for meat and fattened liver production with a body weight of 11.8-13.6 kg for the gander and 9.1-10.9 kg for the goose, as well the African goose with a body weight of 10.0-12.7 kg for the gander and 8.2-10.9 kg for the goose (Roberts, 2008). Body weight has increased almost in all domesticated geese except the Philippino belonging into species *Anser anser* located in the Philippines - the gander weighs 2.8 kg and the goose 2.3 kg (Buckland and Guy, 2002).

With increase in weight, the load-bearing bones (femur, tibiotarsus, tarsometatarsus) have become more robust in domestic geese. But length measurements of the leg bones seem nearly identical with those of the wild Greylag goose, although differs in breadth (Serjeantson, 2002). Thus, leg bones have become heavier while wing bones have become lighter as domesticated geese walk more and fly less. In spite of this, musculature of the legs has changed little whilst that of the wings and the breast has decreased by about 30% (Pingel, 2000).

Alterations have happened in the integument in the form of skin-folds and outgrowths in certain regions in some goose breeds (Matolcsi, 1975). Some body fat may accumulate in the abdominal skin-folds and the thighs forming peculiar bulges (Schneider, 1995) and abdominal pouches (Roberts, 2008) hanging from the belly, which may be single or double lobed (Bogenfürst, 1992). The recess of the larynx is a consequence of selection (Schneider, 1995), appearing as a dewlap (Holderread, 1993).

The Pomeranian goose has a single lobed abdominal pouch and the Toulouse breed has a well-developed pendulous dewlap (Roberts, 2008). In Cobbed geese, a large cob has developed on the forehead, attributable to domestication since it is absent in its wild ancestor, the Chinese Swan goose (Matolcsi, 1975) or barely visible (Crawford, 1993).

Eye colour relates with the plumage; the iris is brown in geese of grey plumage and blue in those having white plumage. In geese with mottled feathers, the iris may be of mixed colour or the two eyes may differ from each other in colour. Legs and webs are orange, but in geese with grey plumage they seem more intensely coloured. The bill is usually orange with paler spots, regardless the breed. However, in breeds of the grey Swan goose (*Anser cygnoides*) the bill is black with a black bump upon it (Schneider, 1995), and their legs and webs are dark orange-brownish or chocolate-orange. The white Chinese goose has orange-coloured legs, bill and webs (Roberts, 2008).

Plumage

In some breeds a feather crest may develop on the head (Schneider, 1995) such like is, *e. g.*, the Crested Roman goose (Ashton, 1999; Stromberg, 1996). In descendants of the Greylag goose the pattern of the neck feathers are toothed, or crimpy-looking, like its

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wild ancestors, while in descendants of the Swan goose it is smooth - similar to its wild ancestors (Hawes, 1993). In some breeds the so-called 'ruffled' plumage has developed *via* curling and crinkling of the feathers (Matolcsi, 1975) and cluster formation is observable (Pingel, 2000). This is seen in the Sebastopol (Roberts, 2008), and the Frizzled Hungarian goose breeds (Szalay, 2002). This plumage is very fragile and becomes crumbly, rugged and rough in high density flocks (Hawes, 1993).

With access to water, angel wings may develop due to anatomical disorders. This formation may be caused by genetics, rapid feather growing or pecking among birds kept together. By this time, unilateral or bilateral torsion of the wing feathers is visible due to the abnormal twist of the metacarpal bones from their normal positions (Hawes, 1993).

In domestic geese the tail and wing feathers have decreased in number (Kear, 2005). The plumage has altered mainly in its colouration in relation to pigment formation. The grey colour, characteristic in wild geese, has changed to white in some breeds (Serjeantson, 2002). Appearance of the white feather colour may have occurred at an early stage of domestication (Matolcsi, 1975). Some breeds have become partly or entirely white. Certain shade of grey colour still appears on the wings in some goose breeds in the form of combined spottiness or in grey colour in one-third of the neck and head. The white feather colour has evolved in both domesticated goose species. Similarly, there is a pure white-coloured White Chinese breed, a descendant of the Swan goose (*Anser cygnoides*), and the Grey Chinese goose has brown or grey-coloured feathers. The Pomeranian breed has three recognised colour-varieties namely, white, grey and grey-saddleback. There are some domestic goose breeds in which the feather colour differs between the male and female, called 'auto-sex breeds'. Likewise, the Pilgrim geese have a white gander and pale grey ashen goose (Roberts, 2008).

Nervous and digestive system

The skull has become bigger in poultry species compared to their wild ancestors (Matolcsi, 1975), but the brain has reduced in geese by 16.1% (Ebinger and Löhmer, 1987) weighing 12-12.5 g and comprises 0.15% of its body weight. As a result, eye sight and sense of hearing have regressed. During domestication, man removed geese from their natural environment. As a consequence, their behavioural instincts (food seeking, defence against predators and survival) has altered under human influence to which they had to adapt. Waterfowl have a good memory and can quickly recognise the route objects important for them, such as sheds or the pond (Pingel, 2000).

The organs involved in metabolism have altered, *e.g.*, sections of the small intestine have reduced in length: the duodenum to 40-90 cm, the jejunum to 150-185 cm and the ileum to 20-25 cm. The liver, in turn, has enlarged, and may weight even 175 g (Pingel, 2000). Birds living in the wild are disposed to natural hepatic steatosis to create large energy stores for their migration. In domesticated waterfowl, the high fat storing ability of the liver is utilised for producing specialist fatty liver products for human consumption. Force feeding can make the liver enlarge up to tenfold. The fattened liver (foie gras) is a trait of nutritional origin to which modern hybrids used for fatty liver production have been specifically adapted (Guémené *et al.,* 2002).

Reproduction

In wild geese - owing to the life-long pair bond -sexual activity is an annually repeated short phase. They mate only in spring, irrespective of the time of pair-bonding (Rutschke,

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1997). The sexual life in animals living in the wild is controlled by the season, allowing offspring to be born in the period most favourable for their survival. Nearly all domesticated animals have become more prolific as their sexual maturation occurs earlier compared to their wild relatives (Matolcsi, 1975). However, under traditional rearing (when the egg-laying cycle occurs due in spring) sexual maturity and egg-laying does not coincide in the geese (Bögre, 1981). Mating activity is more intensive in domesticated than wild geese (Matolcsi, 1975).

With domestic geese, egg production starts earlier, at the age of 8-9 months, due to sexual maturity occurring by 31-36 weeks of age (Pingel, 2000). Goose breeds differ in egg production considerably. Egg production of the less improved barnyard breeds is similar to their wild ancestor. For example, the Hungarian goose produces 12-15 eggs annually (Matolcsi, 1975) but its upgraded variety (the Babat Hungarian Upgraded Goose) lays 45-55 egg per goose annually (Kozák, 2006). Considerable numbers of European upgraded breeds lay 30-60 (Bogenfürst, 2000) and some breeds lay 60-70 eggs per annum. There are some breeds in China that produce more than 100 eggs per season. In the course of the laying period, geese lay, usually every second day, one egg or two to three eggs in succession and then discontinue their egg production for some days. Thus, in goose breeding, increased yield has been achieved by extension of the laying period. Under natural light conditions, the breeder geese begin egg-laying in February and continue for 20-24 weeks till end of May or early July. Using appropriate technology and constant 9-11 hour lighting, the laying period can be extended by 30-40 days compared to the natural lighting. Hence, the egg number per bird has increased from 50 to more than 70. Using various technological interventions, a second laying cycle can be induced in the autumn period when egg laying stops and geese are in state of rest under natural conditions (Pingel, 2000). With breeder geese, the cycle can be initiated at any time following the preceding egg-laying period - after sufficient rest and preparation for the next cycle (Bogenfürst, 1992). An 8-10 hour daily lighting period cause extend the laying period by more than six months, resulting in an increased egg yield by 30% in one laying season (Pingel, 2000). Notably, the egg-laying period can be extended to 6-8 months *via* selection and improvements in environmental conditions (Huang *et al.*, 2012). Domestic geese lay more eggs in their second and third year than in the first, yet it is expedient to keep them in production for up to four years (Pingel, 2000). With ageing, reproductive performance declines and number of eggs, fertility and hatchability decrease (Huang *et al.*, 2012). However, there is a precedent for geese laying 25 eggs per bird even in their tenth year. With breeder flocks, a ratio of one gander to five geese is calculated to ensure eggs of suitable fertility (Pingel, 2000).

For eggs weights of 130-200 g, day-old goslings comprise 60% of the egg weight, and their incubation period lasts for 28-30 days (Pingel, 2000) or 28-32 days (Ensminger, 1992). The egg laying capacity over the quantity needed for reproduction is a new heritable quantitative trait that evolved under domestication (Matolcsi, 1975).

Care of offspring

With wild geese, parental care is a long-lasting bond. Goslings can walk, swim, submerge and feed already 2-3 hours after hatching. Parents ensure successful raising of offspring by searching and defending feeding sites from when the young hatch until wing feather emergence. Filial bond to parents occurs by imprinting (Rutschke, 1997) which is remarkably developed in goslings, and is especially strong in the immediate *post-hatch* period (Pingel, 2000). Imprinting is a kind of learning realised in the first few hours of life and determines species-specific behaviour of animals. This enables goslings

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to recognise their parents and follow them after hatching. However, directly after hatching, goslings can accept a wide choice of objects or individuals as parents (Hawkins, 2001). Notably, the gosling becomes imprinted on the first creature it sees, which may be a human (Serjeantson, 2002). In a wild family - the brooding pairs and their offspring remain together during the autumn migration, on the wintering sites and for the return route to the nesting place. This bond ceases when the parents prepare for the next brooding time (Rutschke, 1997).

With wild birds, the nesting instinct is an innate behaviour and, together with parental care of offspring, allows breed preservation. Under domestication, and later on due to selection for egg production, brooding behaviour has disappeared in certain goose breeds and today is observable only in some goose breeds (Pingel, 2000). Owing to artificial hatching of eggs and commercial rearing of day-old goslings there is no need for broody geese or parental care. Hatching goose eggs by broody hens was common up until the mid-20th century. Artificial incubation has become an important prerequisite of large-scale systems (Magyari, 1971). Unlike other poultry species, natural hatching has been retained in the goose (Schneider, 1995) and some breeders have exploited brooding and natural incubation (Crawford, 1984). Some goose breeders combine natural brooding with artificial incubation (Pingel, 2000).

Increase in body weight

The goose is one of the most rapidly growing domesticated poultry species (Huang *et al.,* 2012). Growth rate of domestic geese is rapid and they soon provide meat products, (Crawford, 1984) and are marketable from 10-18 weeks of age, depending upon feeding regime (Huang *et al.,* 2012). They reach a live weight of 4.5-5.5 kg by 12-15 weeks of age, as they have good gains in weight, adipogenesis and fatten well. Selection for these traits has led to an increase in the size and depth of the body (Serjeantson, 2002). For meat production, there is a large variety of suitable goose breeds (Huang *et al.,* 2012). Domestic geese reach 70-80% of their adult weight by 7-8 weeks of age, thereafter the pace of gain slackens. However, meat production amongst goose breeds is rather different. Selection for this trait has enabled rapid progress in meat-type breeds (Bogenfürst, 1992).

In the breast muscle of geese, red fibres share 80-90% and white 20-10%. The leg muscle contains 50-60% red fibres. Only a little intramuscular fat is formed, the majority is deposited in the dermal tissue and the abdominal cavity (Pingel, 2000). Domesticated meat-type breeds can increase their muscle mass better than non-meat type ones when fed at appropriate nutritional levels. Animals living in the wild develop only to the weight limit characteristic of the species which is restrained by the nutrient uptake capacity of the animal organism. Rapid growth together with early fattening is a modern physiological trait resulting from domestication (Matolcsi, 1975).

Feather formation

Goslings replace their early ‘natal’ down with juvenile plumage between 3-5 weeks of age. This process is their first moult. The new feathers grow from the same follicular papillae from where the natal down developed. Thus, the natal fluff remains upon the tips of the incoming new feathers until they break done (Bögre and Bogenfürst, 1971).

Growing goslings undergo partial moults regularly, involving the down and cover feathers but not the quill and tail feathers (Mueller *et al.,* 2013). Spring-hatched

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goslings acquire mature plumage between 8-10 weeks of age (if nourished appropriately), and afterwards start their second moult (Bögre and Bogenfürst, 1971). Subsequent moults occur every 6-7 weeks as each feather requires about 44 days for maturity (Schneider, 1995). Other researchers report that feather maturation lasts for eight weeks between the first and second moult and *ca*. 10 weeks between the second and third. Accordingly, growing both of feathers and down is completed by weeks 8-9, 16-17 and 26-27. By this time the blood supply from the follicular papilla to the quill of feather recedes completely (Mueller *et al.,* 2013) and is shed from the body in a short time (Schneider, 1991). Autumn-hatched goslings (coming from the second laying cycle) attain mature plumage by week 11 and begin to moult from the 12th week (Kozák and Monostori, 1992). Breeder geese start to moult after the egg-laying period (Schneider, 1995). Feather growth is affected by the genetic base and the external factors such as nutrition, keeping conditions and climatic factors (Bögre and Bogenfürst, 1971). Notably, the duration and intensity of moulting is greatly differentiated depending upon the environment. The difference in moulting is especially high between wild and domestic geese. All these are attributable to the fact that in the Greylag and Swan goose was domesticated 6000 and 4000 years ago, respectively, and a new trait, namely increased feather production, has evolved via environmental changes and selection (Kozák, 1999). The annual gathering of feathers from live geese has been enabled by the frequent and synchronised moulting of the domestic geese (Ménesi *et al.,* 1965).

Behaviour

Man has exploited his observations on goose behaviour purposely. Peculiar behaviour of geese is determined by the innate attributes of the species, and their experiences acquired by learning (Pingel, 2000). However, well-adapted domestic goose breeds have retained many attributes of the wild species. Geese have not adapted to large-flock keeping and are more sensitive to stock density than chickens, and their performance decreases with increasing stocking density. Crowded conditions cause deterioration in feather quality (Rauch *et al.,* 1993).

The feeding habits of geese are characterised by the intake of large quantities of feed in a short time period, owing to it dilatable gullet (Pingel, 2000). The goose is a grazing bird and feeds for prolonged period, even in darkness, and is good at utilising fibrous fodder (Crawford, 1984). The take advantage of this, producers provide plenty of green forage to young geese to dilate the digestive tract to enable higher feed intake during fattening time (Pingel, 2000).

The high feed input *via* force feeding (cramming) induces surplus fat deposition in the liver, but does not cause fatty degeneration of the liver. Geese can tolerate physiologically excessive feed input, but its effects need to be considered in respect of animal welfare (Rauch *et al.,* 1993).

Geese are semi-aquatic birds, and, if water is available, they spend part of the day swimming and resting on it. However, most feeding activity takes place on land (Crawford, 1984). Domestic geese walk long distances, maybe in excess of 5 km, to feeding sites and back to their berth (Guémené *et al.,* 2012). Their good walking ability is due to anatomic structures and localisation of the legs. This trait was exploited in ancient times when flocks were herded on foot from Germany and Gallia to Rome to be sold (Pingel, 2000). In Tsarist Russia geese were herded from different areas of the country towards the western frontier to be sold to Prussian merchants (Héjja, 1984).

Geese are easy to tame. This has enabled the domestic flocks to be crossed with wild geese (Serjeantson, 2002). However, a long time ago, domesticated geese partly retained

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certain wild-type behaviour; are generally more nervous than other poultry (Hawkins, 2001). Domestic geese have retained the instinct to migrate, but are no longer capable of doing so, as their flight ability has declined, or even disappeared (Pingel, 2000) and inactivity resulted in flightlessness and walking in some breeds (Serjeantson, 2002). Their eating instinct has become more intense (Matolcsi, 1975).

The life-span of geese can be exceedingly long. Anecdotes are cited of individual domestic geese living for more than 100 years (Crawford, 1984). The domestic goose usually lives for 25-30 years (Roberts, 1991), however, there still a precedent set by a gander that died in England at the age of 49 years and 8 months on 16 December 1976 (McFarlan, 1992). The eldest British goose was 51 years old, the eldest goose recorded (unconfirmed) lived with over three family generations for 101 years in the state of Massachusetts in the USA (Roberts, 1991). In commercial breeding, they are kept until at least five years of age, which is different from the situation in other poultry, which are usually discarded after one breeding cycle (Crawford, 1984).

Conclusions

Darwin's statement still holds, namely, that geese have changed less during domestication relative to other farmed animals. Several features have altered considerably during domestication, notably weight gain accelerated, resulting in higher body weight and, in some breeds, the body weight of adult geese greatly exceeds that of the wild ancestors. The breeding characteristics of geese have altered whereby the monogamous pair-bond is now polygamous. Laying periods have extended, resulting in higher egg yields and annual production. The natural grey, greyish-brown feather colour has remained in several breeds, but has changed to white or more colourful in other breeds. The feather maturing process has undergone modification, and become a favourable trait in industrial poultry processing and in feather harvesting from live geese. Several breeds have evolved from the two main domesticated goose species, utilising the higher meat production in some, high fat storing ability in others and allowing liver-producing genotypes to be produced. Enhancement of these traits (surplus egg production, rapid growth and fattening, increased meat production) has resulted from the high adaptability and variability of geese. As a consequence, previously geographically limited habitats have now been extended by domesticated geese to all continents today. Thus, domesticated geese significantly contribute to the human need for end products (meat, fattened liver, feathers and eggs).

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