Part I Research background

JOSEF HEMETSBERGER, BRIGITTE M. WEIß AND
ISABELLA B. R. SCHEIBER

1

Greylag geese: from general principles to the Konrad Lorenz flock

Over many years, greylag geese (*Anser anser*) have inspired much long-term scientific research. Thanks to this continuing work, our knowledge of social organisation in birds has greatly improved. Before presenting the latest findings in greylag goose research over the remainder of this book, we therefore introduce the reader to the species – its taxonomic affiliation and geographical distribution – as well as providing information about goose biology in general, and greylag goose biology in particular. This book focuses on a remarkable greylag goose flock at the Konrad Lorenz Research Station (Konrad Lorenz Forschungsstelle, abbreviated as KLF) in Grünau (Upper Austria), where much of our understanding of greylag goose biology has come together over the last 40 years. The origins of this flock, at that location, date back to the time of the late Konrad Lorenz (1903–89). We describe the KLF and also summarise the kind of research questions that can be addressed using this semi-tame goose flock, pointing out its distinctive features relative to wild goose populations, which may be relevant in the interpretation and generality of our findings.

1.1 TAXONOMY

Together with the Galliformes, the order Anseriformes (waterfowl) belongs to one of the oldest lineages of modern (neognathous) birds.

The Social Life of Greylag Geese: Patterns, Mechanisms and Evolutionary Function in an Avian Model System, ed. I. B. R. Scheiber *et al.* Published by Cambridge University Press. © Cambridge University Press 2013.

Recent evidence suggests that they originated during the Cretaceous period (Clarke *et al.* 2005). Although waterfowl phylogeny is still partly unresolved, one extinct (Cnemiornithidae, New Zealand geese) and three extant families are recognised: the Anhimidae (screamers), Anseranatidae (with a single representative, the magpie goose, *Anseranas semipalmata*) and the Anatidae, which includes over 140 species of ducks, geese and swans.

Livezey (1996) divides the Anatidae into five subfamilies: the Dendrocygninae (whistling ducks and allies), Anserinae (true geese, swans and ducks), the monotypic Stictonettinae (with a single representative, the freckled duck, *Stictonetta naevosa*), Tadorninae (shelducks and allies) and Anatinae (surface-feeding ducks and allies).

The subfamily Anserinae is then subdivided into one extinct (Thambetochenini) and three extant tribes: the Cereopsini (with a single representative, the Cape Barren goose, *Cereopsis novaehollandiae*), the Anserini (true geese), and Cygnini (swans). Within the true geese, there are two extinct and 16 extant species in three genera: *Anser* (grey geese), *Chen* (white geese; nowadays usually considered as a subgenus of, and included in, *Anser*) and *Branta* (black geese).

The greylag goose (*Anser anser*), the largest and bulkiest of the grey geese (length 75–90 cm; mean mass: males 3.5 kg, females 3.0 kg; Beaman & Madge 1998), is the type species of the genus *Anser* and also the ancestor of the domestic goose (*A. a. domesticus*) in Europe and North America. It is probable that two isolated populations of greylag geese existed in the late Pleistocene: one in coastal south-western Europe and one in inland south-eastern Europe and Asia, evolving into the three extant subspecies: *A. a. sylvestris* (Iceland, Scotland, Norway), *A. a. rubrirostris* (south-eastern Europe and eastwards) and *A. a. anser* (between the other two subspecies), respectively. The nominate *A. a. anser* from central Europe may be considered as an intermediate between *sylvestris* and *rubrirostris* but, because of an overlap in bill length with *sylvestris*, north-western and central European populations are often treated as single subspecies, *anser*. There are several populations in Europe – some discrete, others overlapping – and most populations are at least partially migratory. The 'lag' part of the name 'greylag goose' is derived from its habit of being one of the last of the migratory geese to move south in the winter.

1.2 HUMAN–GOOSE RELATIONSHIPS

Geese and their eggs have been an important human food source for thousands of years, which may have been the reason why geese were

among the first domesticated birds. They were fully domesticated approximately 3,000 years ago to provide meat, eggs and feathers (Todd 1996). Furthermore, it is known that geese were kept in ancient Egypt, approximately 4,500 years ago: in a burial site in Medum (Egypt), a fresco depicts greylag and red-breasted (*Branta ruficollis*) geese so perfectly that the birds must have been at least semi-tame (Burton & Risdon 1987; Todd 1996); the painting is included in *Meyers Blitz-Lexikon*, published in Leipzig (Meyers, 1932). Geese were also mentioned in two poems by Homer (see discussion in Pratt 1994). Apart from their value as food, humans have also used domesticated geese for other important tasks; because geese are naturally vigilant and domestic geese can be relatively aggressive, they have been used as 'watchdogs' as far back as 390 BC, when sacred Roman crested geese warned the Roman garrison of the attacking Gauls (Aicher 2001: p. 48). Geese also carried out this task at the Dumbarton grain whisky distillery from 1959 until the closing of the premises in 2002 (the 'Scotch Watch'; see Todd 1996). 'Weeder' geese have been used with great success in the USA since the 1950s to control and eradicate troublesome grasses and weeds in a variety of crops and plantings, such as strawberries and cotton plants.

As their traditional wintering grounds have been taken over by agriculture, a number of goose species have started to feed on farmland instead. This rich food supply seems to be a major reason for the increasing numbers of most Eurasian geese. They can cause serious damage to crops (Madsen *et al.* 1999; Gauthier *et al.* 2001; Bowler *et al.* 2005), making them unpopular with farmers. Recently, conflicts have also arisen between the increasing number of summer-staging geese and farmers, and damage compensation claims have risen not only for the wintering period but also during the summer (Feige *et al.* 2008). Therefore, in many European countries, hunting is often allowed in order to protect pastures, at least during certain times of the year (Madsen *et al.* 1999). Greylag geese, in particular, have been – and still are – hunted extensively over most of their range (see Bowler *et al.* 2005). The drainage of wetlands, in addition to human persecution facilitated by the accessibility of nesting sites, especially during moulting when they are flightless, has led to extensive local declines in many populations. For example, in the Netherlands, the greylag goose was a common breeding bird until the beginning of the sixteenth century. From then on, its numbers started to decline continuously until it disappeared as a regular breeding bird in the first half of the twentieth century (Feige *et al.* 2008). After reintroduction programmes in the 1960s and 1970s, and the construction of large nature reserves,

the number of breeding pairs started to rise enormously, from an estimated 150 pairs in the 1970s to 25,000 pairs in 2005 (Voslamber *et al.* 2007; Feige *et al.* 2008). Data from the Netherlands reflect the overall population increase: northern European numbers have been growing quite dramatically (Kampp & Preuss 2005; Austin *et al.* 2007; Voslamber *et al.* 2007; Farago 2010; Fox *et al.* 2010; Mitchell *et al.* 2010), whereas the eastern European populations are more fragmented and relatively small, although they are also on the rise, at least in some countries. This is not true for *A. a. rubrirostris*, which is thought to have declined quite substantially in numbers because of intense habitat fragmentation and its susceptibility to hunting pressure (Madge & Burn 1988).

1.3 DISTRIBUTION

Geese are cosmopolitan, but are absent from continental Antarctica and some islands, with the highest concentration occurring in the Northern Hemisphere. Most species in Europe, Asia and North America are facultative or obligatory migratory, and some species may breed as far north as the Arctic Circle (up to 66° 33′ 44″ N). The brant goose (*B. bernicla*), for example, breeds farther north than any other goose species, with its breeding habitats being located in Siberia and along the northern coast of Alaska and western Canada. It winters in coastal areas of Europe, North America and Japan.

Both the breeding and the wintering ranges of the greylag goose tend to be more southerly than those of the other *Anser* species. It breeds throughout northern Eurasia: from Iceland, Great Britain, Scandinavia and the Netherlands, east across Russia, and south into Mongolia and northern China (Sibley & Monroe 1990). Birds from Iceland overwinter in Britain, where they join with the resident population. Scandinavian birds migrate south-west over Europe to winter mainly in France and the Iberian Peninsula, while central and southern European populations overwinter around the Mediterranean basin, including some lakes in northern Africa. Birds that breed in eastern Europe migrate to the Black and Caspian seas and into northern Iran and Iraq. Even farther east, there are wintering grounds in northern India into Myanmar as well as the lowlands of southern China and central Asia.

1.4 GEESE: GENERAL BIOLOGY OVERVIEW

As a group, geese are easily distinguishable from other waterfowl by their size, long necks, honking calls and sociable nature. Sexes of *Anser*

and *Branta* are monomorphic, with males generally being slightly larger than females (Madge & Burn 1988). On the whole, they are medium-sized (e.g. lesser white-fronted goose, *A. erythropus*; Ross's goose, *A. rossii*; length: 53–66 cm) to large (e.g. Canada goose, *B. canadensis maxima*; length: 90–110 cm), aquatic and terrestrial herbivorous 'grazers' and strong swimmers (Beaman & Madge 1998). As geese assimilate only a small proportion of their plant food, they may spend up to 80% of the daylight hours feeding (Ogilvie & Pearson 1994) and might also feed at night (Ydenberg *et al.* 1984), thereby exposing themselves to predators quite extensively. Much of the remaining time is typically devoted to resting and preening, as well-ordered and oiled feathers are a prerequisite for keeping waterproof. Outside the breeding season, geese are highly gregarious and frequently feed and roost in large flocks, with some species congregating in groups of many tens of thousands during migration and on staging and winter grounds (Todd 1996). Geese migrate in their well-known chevron pattern ('V'-formation), often flying at high altitudes. They migrate southwards on traditional fly-ways in the autumn in large and dense flocks, and stop at well-established staging grounds such as the Neusiedlersee in eastern Austria. Here, one might find a total of 35,000 bean (*A. fabalis*), greater white-fronted (*A. albifrons flavirostris*) and greylag geese gathered together (relative to around 300 greylag breeding pairs; see Ogilvie & Pearson 1994; although the newest estimates are based on the assumption of more than 1,000 breeding pairs in 2012; M. Dworak, BirdLife Austria, personal communication). At their staging grounds they remain for several weeks in large numbers. In some species, the final destination for overwintering is often reached only after a cold spell has occurred (Beaman & Madge 1998). Arrival back at the nesting grounds of northern-breeding forms greatly depends upon weather conditions, so geese will wait out the cold weather at their stop-over sites until the breeding grounds are mostly snow-free (Madge & Burn 1988). Some species, such as the bar-headed goose (*A. indicus*), nest in dense colonies, where nests are as close as the pecking distances to neighbours will allow. In other species, such as the swan goose (*A. cygnoides*), several nests may be located in favoured areas; while other species, such as the bean goose, maintain nesting territories. Greylag geese, the most southerly breeding of all the 'grey' geese (Madge & Burn 1988), mainly nest in isolated pairs, but are known to sometimes nest in colonies with nests as close as 2 metres apart (Madge & Burn 1988; Todd 1996).

Geese are well known for their strong family ties; goose pairs are long-term monogamous and may sometimes remain bonded for

life. They are mostly seasonal breeders with highly synchronised laying periods in arctic species. Nests are usually built near water on the ground in the open or in vegetation. Clutches usually have 4–7 eggs in *Anser* and *Branta*, but are smaller in high-latitude forms, where also no replacement clutches are produced. Eggs are laid at intervals of 1–2 days and are incubated solely by the female for 24–30 days. Upon hatching, the downy young are tended by both parents, with the exception of 'brooding' (i.e. keeping the goslings warm for the first few weeks after hatching, when they are still unable to maintain their body temperature, particularly during cold weather), which is almost exclusively done by the female. Newly hatched goslings respond to parents with 'vee-calls' and outstretched neck for greeting. The herbivorous, precocial young leave the nest and follow parents from the second day post-hatching. Fledging periods are relatively short in high-arctic breeders, which utilise the long arctic days and great abundance of food for fast growth. For example, in snow geese (*A. caerulescens*) the young are fledged in approximately 40 days, whereas temperate species take longer (e.g. around 70 days in Canada geese). Non-breeders form moulting flocks in the summer, when they become flightless, and are joined by breeders a few weeks later. Some species perform a moult migration, which is a move to safer waters for moulting (Madge & Burn 1988). Young stay with their parents after fledging, at least through their first autumn and winter, and in some species through the spring migration. Furthermore, they may reunite with their parents at the end of one or more subsequent unsuccessful breeding seasons. Geese mature sexually at 2–3 years of age but may form durable pair bonds well before sexual maturity. They may also maintain family bonds, particularly with female kin, for many years (Frigerio *et al.* 2001a; Waldeck *et al.* 2008; Anderholm *et al.* 2009a), as discussed later in the book (Chapter 6).

1.5 GREYLAG GEESE

As with the other 'grey' goose species, greylag geese are typically grazers in open countryside (Madge & Burn 1988). They consume a wide range of food (Voslamber *et al.* 2004) and seem to prefer to feed from croplands and grasslands rather than from natural food sources (van der Wal 1998). They do not favour any particular crop but are flexible in adjusting to yearly crop rotations, as they have a high degree of site fidelity (Rutschke 1997; Feige *et al.* 2008). Greylag geese are also quite flexible in choosing breeding sites, as long as they are close to easily

accessible bodies of water: they nest in natural habitats such as reedbeds, marshy swamps and small islands, as well as along estuaries and lakes (Sibley & Monroe 1990), but also on meadows and pastures. They have adjusted their breeding behaviour to the cultivated landscape that exists today in many locations (Berndt & Busche 1991; Rutschke 1997; Kalchreuter 2000; Bauer *et al.* 2005; Feige *et al.* 2008).

Greylag geese seem a little less distrustful of humans than other goose species: reintroduced feral populations tolerate the close proximity of towns and villages (Madge & Burn 1988). They appear to withstand a certain level of human and other disturbances, such as grazing of cattle or mowing. Because of grazing by cattle, the plants tend to be much younger and more palatable, and are higher in protein, which seems to be beneficial to the geese (Owen 1990; Feige *et al.* 2008).

In greylag geese, lifelong monogamy is the rule, with males and females associating all year, even when sexually inactive (Lorenz 1991; Kotrschal *et al.* 2006). The reproductive output of waterfowl may vary considerably not only between, but also within, species (Johnson *et al.* 1992), and greylag geese are no exception. Depending on nest site and location, average hatching success, for instance, may vary from about 30% to 80% (Nilsson & Persson 1994; Kristiansen 1998). Determinants of breeding success include predation on eggs and goslings (Sargeant & Raveling 1992) by both mammalian and avian predators (e.g. red foxes, *Vulpes vulpes*: Kristiansen 1998; hooded crows, *Corvus corone cornix*: Kristiansen 1998; Zduniak 2006), and also weather conditions (Wright & Giles 1988) and other environmental factors. Outside the breeding season greylag geese, like most other geese, are highly gregarious, with strong pair and family bonds. Moreover, shortly after their young hatch, parents may sometimes join together, forming large groups that are able to defend all the offspring by mobbing and attacking predators (Todd 1996). The young of each year group fledge at approximately 60–70 days of age, at the same time as parents regain their ability to fly after a one-month moult of their wing and tail feathers. Fledged goslings remain with their parents until the next breeding season. Adult and first-winter survival rates range from 40% to 90%, depending on populations and their wintering grounds (Nilsson & Persson 1996; Frederiksen *et al.* 2004; Pistorius *et al.* 2007). Parents and their subadult offspring leave the wintering areas together in the spring, but the latter move elsewhere when their parents return to the breeding grounds.

When observing a greylag goose flock, one will find that the leading edge contains a higher proportion of young geese, as they

move and feed faster than adults, pulling their parents with them (Ogilvie & Pearson 1994). On closer inspection, it is possible to identify families: the young with their respective male and female parents nearby. Within a greylag goose flock there is a stable – but not strictly linear – rank order, with individual ranks mainly being conditional upon bonding status (see Chapter 7): families dominate pairs, who – in turn – outrank singletons. This keeps the flock relatively peaceful – most of the time. One goose will move towards another with an outstretched neck and head held low. Should the encountered goose be subordinate, it will simply move out of the way. However, if the encountered goose is dominant, it may not give way and a fight could develop (see Chapter 7).

1.6 THE GREYLAG GOOSE FLOCK AT THE KONRAD LORENZ RESEARCH STATION (KLF) IN GRÜNAU, UPPER AUSTRIA

The greylag goose is the most-studied *Anser* species, with most of the studies being performed with semi-tame flocks or under feral conditions. As a scientific model species, greylags are well known as the birds that the late Konrad Lorenz, one of the founders of ethology, used for his major investigation of the behavioural phenomenon of imprinting (Lorenz 1935). In 1973 he was awarded the Nobel Price for Physiology and Medicine, together with Karl von Frisch and Nikolaas Tinbergen, 'for their discoveries concerning organisation and elicitation of individual and social behaviour patterns' (from a press release of the Karolinska Institute in 1973). Lorenz' contributions stem mainly from his findings on greylag goose behaviour. Among his many books, two are devoted to 'his' geese: *The Year of the Greylag Goose* (Lorenz *et al.* 1978; English translation: Lorenz *et al.* 1979), a popular science account; and *Here I am: Where are You*? (Lorenz 1988; English translation: Lorenz 1991), which includes the detailed greylag goose ethogram still in use today.

Konrad Lorenz and his co-workers carried out a 'longitudinal study' of the social developments in the long-lived greylag geese, which was initiated in 1950 in Buldern (North Rhine–Westphalia, Germany) and continued at the Max Planck Institute for Behavioral Physiology in Seewiesen (Bavaria, Germany) from 1956 onwards, until our flock was established at the KLF in Austria in June 1973. For this purpose, a total of 148 geese – including near-fledged, human-raised juvenile geese as well as pairs with offspring and moulting adults – were transferred from southern Germany to Austria. After 2 years, approximately 75 of

those remained in Grünau instead of flying back to Germany or elsewhere (Hemetsberger 2002). These formed the ground stock for the present KLF flock, which has ranged in size from 110 to 180 individuals ever since, including about one-third of individuals raised by human foster parents. From 1973 to 2011 we have collected standardised life history data for a total of 982 geese. These comprise the adult individuals transferred from Seewiesen to Grünau in 1973, 12 immigrants to the flock, the hand-raised geese, and a total of 562 fledged goslings emerging from the KLF flock during this time (mean ± standard deviation (SD) 15 ± 10.7 per year, range 0–44). Of the goose-raised fledglings, 479 hatched in the valley around the research station, while 83 goslings hatched elsewhere, for instance the Traunsee, approximately 20 km to the west, or the Chiemsee in Bavaria, Germany, some 200 km to the west, but came to the flock in the autumn with their parents.

The flock is completely unrestrained throughout the year, but is supplemented with pellets and grain twice daily on the meadows around the research station, with low quantities from spring to autumn, and with sustaining amounts during the winter. These regular feedings and the fact that several water bodies do not freeze up in winter, and hence provide night roosts safe from terrestrial predators, keep the flock in the valley and accessible for research throughout the year. Accordingly, this flock has never adopted a migratory tradition, although once in a while it happens that geese emigrate/disperse, or 'strangers' immigrate into the valley. As in other populations, natural predation (mainly by red foxes) is common and may account for the loss of up to 10% of the adult flock per year (Hemetsberger 2001). Most predatory events occur on the nests during laying and breeding in March and April, which is the most important cause of the often male-biased sex ratio in the flock (50–65% of males over the years). Predation and the often harsh weather conditions in spring also cause high rates of pre-fledging mortality; while up to 100 goslings may hatch each year, gosling survival to fledging rarely exceeds 25%.

All geese are marked individually with a unique aluminium ring from the Vogelwarte Radolfzell (Institute for Ornithology, Germany) as well as with coloured leg bands, which are also coded for year of hatching, family affiliation, as well as whether the goose is hand-raised or goose-raised. This allows detailed information on individual life histories to be recorded, including survival and reproductive success. The mean age of the geese in the KLF flock is 7.5 years, but some individuals live well beyond 20 years of age. The greatest recorded age was attained by a male called *Herr Viel*, who was almost 27 years old when