The Social Life of Greylag Geese

Patterns, Mechanisms and Evolutionary Function in an Avian Model System

The flock of greylag geese established by Konrad Lorenz in Austria in 1973 has become an influential model animal system and one of the few worldwide with complete life history data spanning several decades. Based on the unique records of almost 1000 free-living greylag geese, this is a synthesis of more than 20 years of behavioural research. It provides a comprehensive overview of a complex bird society, placing it in an evolutionary framework and drawing on a range of approaches, including behavioural (personality, aggression, pair bonding and clan formation), physiological, cognitive and genetic.

With contributions from leading researchers, the chapters provide valuable insights into historical and recent research on the social behaviour of geese. All aspects of goose and bird sociality are discussed in the context of parallels with mammalian social organisation, making this a fascinating resource for anyone interested in integrative approaches to vertebrate social systems.

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Preface
The social life of greylag geese: patterns, mechanisims and evolutionary function in an avian model system

KURT KOTRSCHAL

A book on the social fabric of greylag goose communities would be worth writing and interesting to read simply by virtue of the historical role played by these geese in the development of behavioural biology. Geese were one of the favourite subjects of Konrad Lorenz, one of the major founders of ethology (Tinbergen 1963). But there is much more to geese than this historical aspect. Konrad Lorenz' appreciation of the social complexities (defined by long-term dyadic, valuable and mutual relationships) of greylags and other geese was not all based on systematic data collection (Lorenz 1988). He was a keen observer and had a remarkable mental ability to identify, analyse and compare patterns. Therefore, much of his evidence was truly 'anecdotal'. This approach has certainly changed over time, not least because the standards of data gathering in science have definitely become more rigorous. This will be illustrated in the second chapter of this book.

In our book, we summarise more than 20 years of observational and experimental work on the 'Lorenzian geese' at the Konrad Lorenz Forschungsstelle (Konrad Lorenz Research Station; KLF) in Grünau, Austria. From the time of Konrad Lorenz onwards, this field station has been located in a picturesque valley of the Northern Alps. Substantial progress has been made with the semi-tame, free-roaming flock of geese living there. Several dozen colleagues and students, as well as a considerable number of volunteers, have contributed to our results over the past two decades, and we are very grateful to them all.

Our recent findings indicate that Konrad Lorenz underestimated, rather than overestimated, the complexity of the social life of geese. This book is a synthesis of social organisation in geese, mainly based on our own results, but embedded in the causal and functional

knowledge acquired by others and framed by contemporary biological theory. Although this is a monograph on goose sociality, it is also relevant as a data point for comparing the structure and functions of social organisation in birds and mammals.

Jane Goodall's (1986) ground-breaking description of the social complexity and skills of wild chimpanzees motivated many biologists to come out of the laboratory and into the field. Konrad Lorenz was deeply impressed by her observational approach, which was just as keen but more systematic than his own. When they met, they enthusiastically agreed on the immense value of long-term studies on the social behaviour of animals, whether geese or chimps. From a present-day perspective we could not agree more. It took a while, however, before substantial scientific results started to be produced.

To an even greater extent than Konrad Lorenz, Jane Goodall opened a new window in animal behaviour research, which permitted animals to be approached as individuals who can think and have feelings. After decades of an extremely Descartian, automaton-like view of animals, which also prevailed in ethology, it again became possible to investigate cognition and emotions in animals without the risk of one's work not being taken seriously (Panksepp 1998; Aureli & Schaffner 2002; Aureli & Whiten 2003). In some instances it even became acceptable for scientists to become involved socially with their experimental animals; for example, by personally hand-rearing greylag goslings in order to obtain trusting partners for experimental work (Hemetsberger *et al.* 2010). Women such as Jane Goodall, Irene Pepperberg and Sue Savage-Rumbaugh demonstrated that rigorous scientific methods and compassion and empathy for one's study subjects do not have to be mutually exclusive. Konrad Lorenz is still the prime male example of a researcher having empathy with 'his' animals to such an extent that he was always opposed to invasive work with geese, while remaining a keen observer of their behaviour.

Ever since the time of Darwin (1872), it has been increasingly appreciated that the principles of social complexity may not be exclusive to human societies, and since the publication of Wilson's textbook (1975a), the functional rules governing social systems have become apparent. Primarily, the 'social brain hypothesis' (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998), developed using primates, made the connection between social complexity and cognitive development. The belief in primate–mammalian cognitive supremacy was deeply rooted in the Darwinian continuum. Birds, in particular, were not seriously considered to be candidates for the study of intelligence and complex social

systems. This was a consequence of the long-standing misconception that birds' forebrains consist mainly of striatal rather than pallial components (Edinger 1929), which doomed birds to be perceived as relatively instinctive and 'non-cognitive' creatures. This may even have been one of the reasons why birds became the prime research models in classical ethology, with its traditional focus on the instinctive, stimulus–response components of decision making, although this may have been different in disciplines with a different focus, such as comparative psychology or cognition research. Today we know that bird forebrains, although lacking layered and columnar structures, still feature a similar proportion of pallial components as mammals (Güntürkün 2005; Iwaniuk & Hurd 2005; Jarvis *et al.* 2005), and that corvids rival apes in relative brain size (Emery & Clayton 2004). Even the primatologists finally seem to accept that birds are capable of top-rate cognitive performance.

In fact, we can learn a great deal about the conditions and constraints for the development of complex social systems through comparison with phylogenetically distant taxa. Apes are in some respects strikingly similar to humans, simply because our ancestry diverged only about 6 million years ago. Hence, a substantial amount of common social dispositions within the apes may be due to evolutionary inertia. It would be surprising to find fundamental human traits that are not also basically represented in chimps. To explain the selection pressures acting towards the evolution of social complexity and intelligence, comparisons with birds may be even more relevant than those with chimpanzees, because the common ancestor of apes and birds was probably a generalised reptile living in the late Palaeozoic, some 280–300 million years ago (Jarvis *et al.* 2005). Therefore, if common patterns are found in geese and primates, these are very unlikely to be due to direct common descent ('homology'), especially as our common reptile ancestor was probably not a genius at social cognition. Hence, if such close similarities are found in primates and in birds, simple phylogenetic inertia is probably not the answer. Evolutionary constraints of a conservative central nervous system may have had a role in the shaping of parallel structures in birds and mammals, for example the similarities in the expression of individual behavioural phenotypes ('personality'; see Chapter 3). In general, however, parallels in psychological, behavioural and social structures must have formed due to similar selection pressures from ecological and/or social sources in an 'analogous' manner. Hence, a comparison between geese and primates may be revealing in pinpointing such common selection pressures.

The parallels between goose and mammalian social organisation are indeed striking. They include long-term dyadic and parent–offspring relationships, alliance formation, female bonding and emotional social support, among others. The main topics covered in this book could just as well appear as chapters in a book that discusses mammalian social systems.

There are three main sections to this book: on the biological and historical basics (Chapters 1 and 2); on social patterns (from individual to clan, Chapters 3–6); and on the causes and consequences of social organisation (Chapters 7–10). This means that we treat social patterns and social physiology as a single unit of conditions and constraints, which are congruent with evolutionary function. For example, the social patterns of the monogamous pair and the clan are the structural background for the expression of social support which, as a consequence, will affect individual social efficiency and, ultimately, reproductive success.

We cover goose individuality and personality (Chapter 3); stability and synchrony in the crucial long-term valuable partnership, the monogamous pair bond (Chapter 4); alternative reproductive strategies (Chapter 5); clan formation and extended family bonds (Chapter 6); causes and consequences of dominance and aggression (Chapter 7); the costs (Chapter 8) and benefits of social life achieved through a variety of patterns of social support (Chapter 9); and, finally, cognition in a complex social society (Chapter 10). The relevant biology of geese, as well as specific information about the greylag geese at the Konrad Lorenz Research Station are summarised first (Chapter 1), followed by a chapter on the historical role of geese in science (Chapter 2).

The parallels between the social organisation of birds and mammals, as described in this book, may still be surprising, as these two phyla have had independent evolutionary histories for approximately 300 million years (Benton & Donoghue 2007 and references therein). The motivation for summarising more than 20 years of goose research at Grünau came with the realisation that not only human and chimpanzee societies are similar, but that we can also find similarities in birds and very likely throughout all social vertebrates. Therefore, goose social patterns will be put into perspective with other bird and vertebrate social systems throughout the book and, in particular, in the final chapter (Chapter 11). A doctoral student once commented jokingly to Konrad Lorenz that: '*Gänse sind auch nur Menschen*' (Rost 2001: p. 192) or – loosely translated – '*Geese are only human too*'. Although today we would consider this too

sweeping a statement, some similarities are indeed there, because sociality not only carries benefits but also entails costs, which can be quite high – and this is true for 'everybody', whether fish or human. Therefore this book should cater to anyone with an interest in social systems.

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