Konrad Lorenz's use of cinematic film for studying dabbling duck courtship behaviour and the availability of historic film materials

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Abstract

During the 1940s and 1950s, Konrad Lorenz pioneered the use of cinematic film for studying bird behaviour, focussing on dabbling duck courtship and the activities of goose species. Observations were made at Lorenz's research station in Germany and also at the Severn Wildfowl Trust (now the Wildfowl & Wetlands Trust) in the UK. This review paper describes how the films contributed to Lorenz's research. Detailed information on Lorenz's editing process and treatment of the data is published separately in the *Journal of Ornithology*. The original film footage is now available at the Austrian Film Museum, Vienna, Austria (http://www.filmmuseum.at/en. Researchers are invited to apply for access to this archive material.

Key words: archive material, behaviour, dabbling ducks, film, Konrad Lorenz.

In 1941, the eminent ethologist and ornithologist Konrad Lorenz, pioneer of studies analysing animal behaviour, published a paper on the comparative behaviour of Anatidae species, entitled "Vergleichende Bewegungsstudien an Anatiden" (Lorenz 1941, 1951–1953, 1971). At the time it appeared to be just another scholarly contribution to ornithology, and a logical continuation of the ground-breaking work of Oskar Heinroth on the biology (particularly the ethology and psychology) of Anatidae (Heinroth 1911); there was no hint of anything exceptional in the data, nor in Lorenz's approach to documentation and analysis. In fact, to this day, the citation frequency of this dabbling duck paper is far below that of many of his other publications. For Lorenz himself, however, the results of this study of duck courtship served to strengthen the concept of "species-specific motor patterns", which formed the basis of his thesis that courtship and other displays are innate behaviour patterns which can be modified by learning. Duck courtship behaviour patterns became fascinating topics for further analysis, and the results of their study are an essential part of the development of Lorenz's ethological research, which led in due course to his being awarded with

Karl von Frisch and Niko Tinbergen the 1973 Nobel Prize for Physiology or Medicine, for their discoveries concerning individual and social behaviour patterns.

Following his release from a Russian prisoner of war camp at the end of World War II, Lorenz returned to his behavioural studies, focussing on the courtship patterns of any dabbling duck he was able to find as a continuation of his 1941 paper. During the 1950s he regularly visited Peter Scott at the Severn Wildfowl Trust (now the Wildfowl & Wetlands Trust) at Slimbridge, England (which had one of the most extensive holdings of waterfowl in the world; Fig. 1), established his own collection of ducks, and patiently filmed duck courtship, to add to his growing archives of 16 mm movie footage. Also during his visits to Britain, he was one of several internationally-renowned scientists (again including Tinbergen) who served on the Trust's newly constituted Scientific Advisory Committee during the mid-1950s (Huxley 1995). This review article aims to describe the contribution that filming made to Lorenz's research, the discovery of this historic material, and how it might be accessed by researchers for future study.

Lorenz's development of the use of cinematic film for behavioural research

Lorenz proposed (following Charles O. Whitman and Oskar Heinroth) that a species' behavioural patterns were as valid as anatomy and morphology as subjects for scientific investigation. Having received an M.D. from Vienna University's School

Figure 1. Konrad Lorenz with Peter Scott at Slimbridge (Photograph: the Konrad Lorenz Archive).

of Medicine, and a few years later a Ph.D. from its Philosophy Faculty, he applied comparative anatomy methods to his behavioural studies. Even though he was a keen observer and excellent draftsman, he supplemented his descriptions with detailed photographic records, tracings, and motion pictures. Discussing the difficulties in developing standard terminology for describing behaviour, he wrote: "Of course, there is only one solution for this problem: the photo, possibly the motion picture. This is exactly the direction of my next step I am planning: a study of the social courtship of the genus Anas" (Lorenz 1937, p. 310).

At an early stage of his dabbling duck studies, Lorenz published a research film on courtship and pair formation in Mallard *Anas platyrhynchos*, with a detailed description of the behaviour patterns of this species (Lorenz 1952a,b, 1982). Thereafter, increasing availability of funds enabled Lorenz to attract Hermann Kacher, a professional illustrator and photographer, to provide splendid illustrations of wildfowl behaviour (Fig. 2) and to act as as curator of Lorenz's photo and movie film collection. These illustrations facilitated Lorenz's ethological investigation of animal behaviour using motion pictures by providing a stepwise record (and ultimately an analysis) of his observations. The stepwise procedure (illustrated in the edited film "Courtship and Pair Formation of the Mallard"; Lorenz 1952a,b), first involved collection of descriptive behavioural data and creating an inventory, the ethogram. Drawings developed from the film footage had the additional advantage that successive stages of a dynamic process (*e.g.* a specific behaviour pattern recorded in both space and time), could be depicted as a superposition of several images (Fig. 3).

Nearly all of the motion pictures were recorded on black and white 16 mm film using a spring-wound Bolex camera (Schleidt & Oeser 2011). Information on Lorenz's careful editing of the film and treatment of the data is described by the authors in a paper recently published in the *Journal of Ornithology*

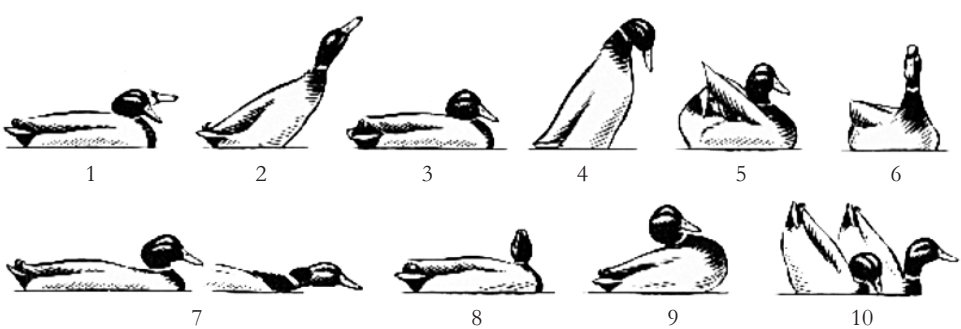

Figure 2. Ten motor patterns of the Mallard, illustrating the core components of the surface feeding ducks' courtship behaviour. 1 = Initial bill-shake, 2 = Head-flick, 3 = Tail-shake, 4 = Grunt-whistle, 5 = Head-up-tail-up, 6 = Turn toward the female, 7 = Nod-swimming, 8 = Turning the back of the head, 9 = Bridling, 10 = Down-up. (Drawings: Hermann Kacher, 1957).

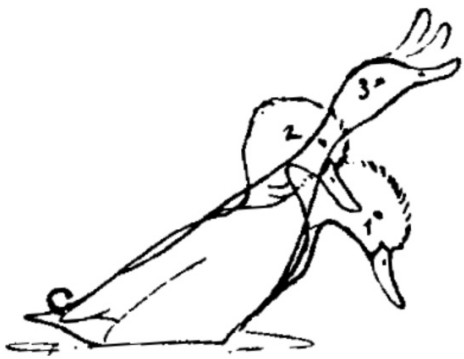

Figure 3. Schematic diagram, illustrating body-shaking movement (from Lorenz 1941, Fig. 54). Note that for better comparison with Fig. 4 the original has been mirrored.

(Schleidt & Oeser 2011), the journal in which Lorenz published his original paper back in 1941 (Lorenz 1941). An early version of the duck courtship pattern reel (A 2.19) has been digitised and is now available as QuickTime movie A_2_19.mov. The film "Courtship and pair formation in the Mallard (*Anas plathyrhynchos* L.)" (published as Lorenz 1952a,b) can be considered to be the first chapter of the duck species reel, but unfortunately this has not been found to date.

Although modern technology such as digital image processing provides additional tools for recording and verifying behavioural patterns, including interactions between individuals, the use of both live observation and video recording continues to be indispensible for ethology. An example of this continuing process is the research into the grunt-whistle display, initiated by Oskar Heinroth in 1911, and included in a study of dabbling duck phylogeny as recently as 1999 (Johnson & Sorenson 1999; Johnson 2000). Lorenz's detailed analyses of the grunt-whistle in the mid 20th century (using both photographs and film footage) found that the lowering of the bill is so pronounced that the bill-tip scoops the water-surface in the first transverse movements, throwing up a shower of droplets in a wide arc (Lorenz 1941; Fig. 4a). This fact had not been recorded by any previous investigators of drake courtship (not even by Heinroth, who had also used photos in his publications earlier in the early 20th century), and Lorenz noticed it only on observing that the "scattered black dots due to faulty emulsion" persistently reappeared in photographs of the grunt-whistle (Lorenz 1941 and Fig. 4b). Several years later it was discovered that this spray of water was always aimed at the target female (von de Wall 1963). In a quantitative analysis of Mallard courtship documented in the research film (Lorenz 1952a,b), two simple features (namely the height of the tip of the bill, and the height of the tip of the tail above the water surface) were found to be sufficient to discriminate between the particular motor patterns; a change in just these two variables provides a unique grunt-whistle signature (Finley *et al.* 1983; Schleidt 1984). More recently, the grunt-whistle display has been used in a study of the evolutionary relatedness (phylogeny) of dabbling duck species (Johnson 2000 and Fig. 5). A phylogeny based on molecular data (Johnson & Sorenson 1999) was used to study the evolution of dabbling duck displays (Foster *et al.* 1996; Johnson 2000) and revealed that overall these displays contained more phylogenetic signal than non-display behaviours (such as male

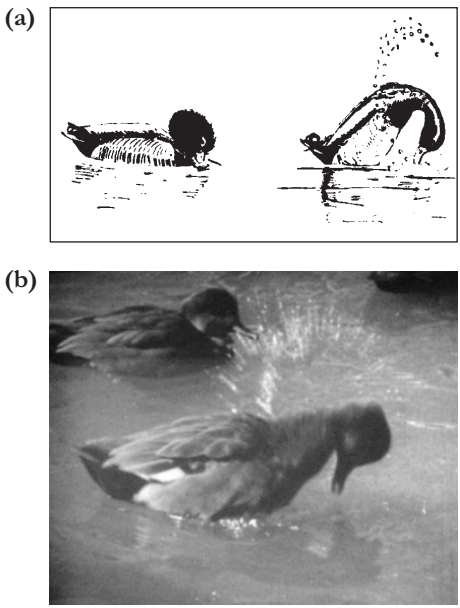

Figure 4. Grunt-whistle courtship display, illustrating the arc of upward-flying droplets. (a) Drawings of two motor phases of the display for a Mallard drake (from Lorenz 1941). (b) Single frame from film footage (Reel A 2.16, at 12.15 min) for an unspecified hybrid.

parental care and migration). However, many displays have been lost from species repertoires, so they provide an imperfect guide to phylogenetic relationships (Johnson 2000).

Several of Lorenz's doctoral students joined the duck research team (*e.g.* Weidmann 1956; von de Wall 1961; Schutz 1965; Kaltenhäuser 1971; Engländer & Bergmann 1990). When *Scientific American* invited Lorenz to write a review of his ideas on the evolution of behaviour, he drew extensively on his new insights gained from the study of dabbling duck courtship (Lorenz 1958). But even though new footage was subsequently added to the collection and various papers were published by his co-workers (Lorenz & von de Wall 1960; von de Wall 1961, 1963, 1965; Weidmann & Darley 1971a,b; Simmons & Weidmann 1973), both Lorenz and Kacher retired without finishing another chapter. Subsequent publications (Lorenz 1971, 1982) were English translations of earlier papers (Lorenz 1941, 1952b, respectively).

Rediscovery of the films and access to the materials

Konrad Lorenz's collection of > 200 16 mm reels of films of ducks and geese, most of them filmed and edited by him personally and accumulated since 1950, were put into storage soon after his death in 1989. In spring 2010, after several years of searching, they were discovered in the attic of the mansion on his Altenberg estate near Vienna (Schleidt & Oeser 2011). The films included those taken of Mallard in 1952 (labelled "Balz und Paarbildung bei der Stockente C 626"; Lorenz 1952a) and also the Greylag Goose *Anser anser* movie of 1950 (labelled Ethologie der Graugans. Hochschulfilm C 560; Lorenz 1950a,b). A detailed review of the material is required, to develop an inventory of which species and behaviours are on record.

The films, now the "Konrad Lorenz Film Collection", are available for further analysis at the Austrian Film Museum, Vienna, Austria (http://www.filmmuseum.at/en). Researchers are invited to apply to the Konrad Lorenz Institute for access to this archive material. For further details please contact the first author (wolfgang.schleidt@univie.ac.at).

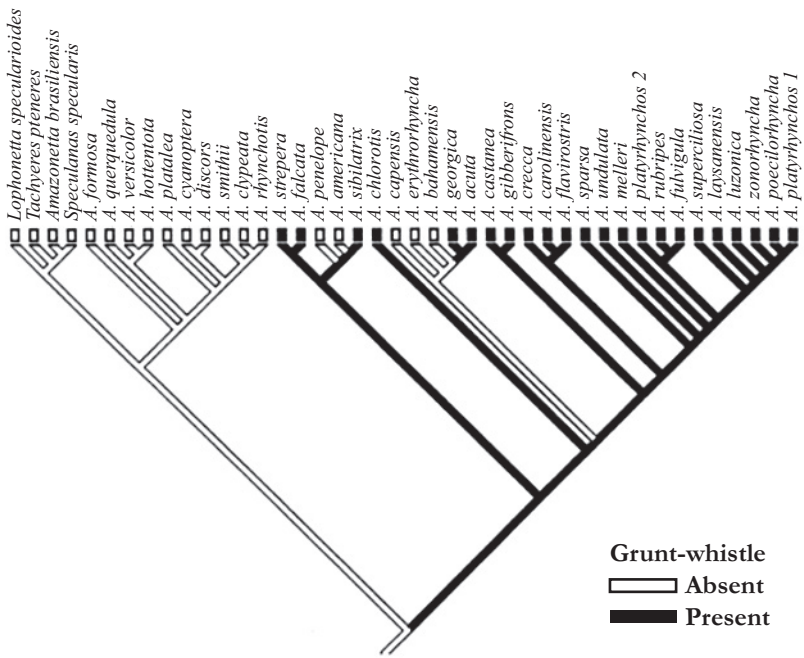

Figure 5. Reconstruction of the grunt-whistle display using unordered parsimony, which minimises the number of gains over the phylogenetic tree used in the analysis. (Tree topology from Johnson 2000.) A. = *Anas*.

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