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# A new foundation for the study of bird behaviour: Konrad Lorenz's 'Kumpan' paper of 1935

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## Abstract

The Nobel Prize in Physiology or Medicine was awarded to Konrad Lorenz, Niko Tinbergen and Karl von Frisch in 1973 for their pioneering work during the 1930s and 1940s, in the study of animal behaviour. Lorenz established the foundations of ethology in 1935 in what has become known as his “Kumpan paper”. The paper focussed on the social relationships between conspecifics (i.e. ‘kumpans’, companions) and provided a much-needed conceptual framework for the study of animal behaviour. We describe the origins and immediate reception of Lorenz’s paper using his correspondence with colleagues, mainly Erwin Stresemann who was then the influential editor of *Journal für Ornithologie*. The Kumpan paper was notable for its extraordinary originality, but also for its length and—in parts—its incomprehensible language. Most of Lorenz’s concepts were rapidly superseded as the field of Ethology/Animal Behaviour developed over the following decades. The paper (translated in full into English only in 1970) is rarely read today, but as we show, many of Lorenz’s observations of birds are both timeless and highly original and have the potential to inspire further research today.

**Keywords** Konrad Lorenz · Ethology · Journal of Ornithology · Erwin Stresemann · Nobel Prize

## Zusammenfassung

### Eine neue Basis für die Verhaltensforschung bei Vögeln: Konrad Lorenz' „Kumpan“-Aufsatz von 1935

Der Nobelpreis für Physiologie oder Medizin wurde 1973 an Konrad Lorenz, Niko Tinbergen und Karl von Frisch für ihre bahnbrechenden Arbeiten in den 1930er und 1940er Jahren zur Erforschung des Verhaltens von Tieren zuerkannt. Lorenz hatte 1935 mit seiner als "Kumpan-Arbeit" bekannt gewordenen Publikation die Grundlagen der Ethologie gelegt. Diese umfangreiche Arbeit konzentrierte sich auf die sozialen Interaktionen zwischen Artgenossen und lieferte den von vielen erwarteten konzeptionellen Rahmen für die Erforschung tierischen Verhaltens. Wir beschreiben Hintergründe und Anfänge als auch die unmittelbare Rezeption der Kumpan-Arbeit anhand der Korrespondenz zwischen Lorenz und Erwin Stresemann, dem damals einflussreichen Herausgeber des Journals für Ornithologie, sowie einiger Briefe der Amerikanerin Margret Morse Nice. Der „Kumpan“ beeindruckte durch seine Originalität, allerdings auch durch seine Länge und streckenweise unverständliche Ausdrucksweise. Die meisten von Lorenz' Konzepten wurden allerdings in der nachfolgenden Entwicklung der Ethologie (in Deutschland zunächst als Tierpsychologie bezeichnet) wieder fallen gelassen. Die Abhandlung (die erst 1970 in vollständiger englischer Übersetzung vorlag) wird heute nur noch selten gelesen, hat aber das Potential, auch jetzt noch aktuelle Forschung zu inspirieren, weil so manche der Vogelstudien von Lorenz zeitlos bleiben und originell sind.

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*An incredibly fertile mind ... constantly bubbling over with new ideas, good ones and bad ones.*

Ernst Mayr to Erwin Stresemann (Mayr 1997)

## Introduction

In 1973, Konrad Lorenz (1903–1989), together with Niko Tinbergen (1907–1988) and Karl von Frisch (1886–1982), received the Nobel Prize in Physiology or Medicine, for

launching the study of animal behaviour during the 1930s and 1940s.

Lorenz's Nobel nomination stated:

“When Konrad Lorenz in the twenties started his studies on the “instinctive” activities of the birds, he found that they consisted to a large extent of “fixed action patterns” that were elicited by specific “key stimuli” only, and performed in a robot-like way. By studying “naive” animals (e.g. young birds hatched in an incubator), he was able to show that these fixed action patterns appeared as reactions to key stimuli without any previous experience, i.e. without any learning. ... Lorenz [also] studied one, quite specific type of learning, called “imprinting”. During an early critical period of life, a definite type of stimulus may be necessary for normal development. Such stimuli elicit behaviour patterns that are irreversible. The newborn duckling will be imprinted to follow the first moving object it sees, whether it is the mother, a cardboard box or a balloon. An animal's sexual attitudes later in life may be determined by early experiences of this type” (Karolinska Institutet 1973).

These key concepts were first articulated by Lorenz in a monumental paper published in 1935. That paper, referred to here and elsewhere, as ‘the Kumpan paper’ established the foundations of ethology (i.e. the study of animal behaviour) (Burkhardt 2005; Kruuk 2003).

The term ‘Kumpan’ has no satisfactory English translation, but essentially means ‘companion’ and refers to the social relationships between conspecifics, such as between parents and offspring, males and females in sexual relationships, and so on (Burkhardt 2005).

Lorenz was 32 when his Kumpan paper was published. It was the product of many years of observing captive animals and thinking carefully about their behaviours. Submitted to *Journal für Ornithologie*, the paper was accepted for publication by its open-minded and innovative editor Erwin Stresemann (1889–1972). Stresemann was keen to help ornithology expand away from its taxonomic, museum-based roots, towards topics that we now refer to as ecology and behaviour and become part of mainstream biology (Haffer et al. 2000; Haffer 2001). Over the previous 8 years, Stresemann had published other papers by Lorenz (see below), but he recognised the exceptional nature of the Kumpan manuscript (Haffer et al. 2000).

The aim of the present account is first, to provide some historical background to Lorenz's paper—based in part on unpublished correspondence, mainly between Lorenz and Stresemann, but also with Margaret Morse Nice—and hence, the foundations of animal behaviour as a distinct discipline.

We also consider the relevance of the Kumpan paper to animal behaviour researchers today.

## Background

Konrad Lorenz produced his first scientific paper—on the social behaviour of jackdaws *Corvus monedula*—at the age of 24 in 1927 (Lorenz 1927). This was followed four years later with an update and intellectual development, entitled [in English] ‘Contributions to the study of ethology of socially living corvids’ (Lorenz 1931). Lorenz co-opted the term ‘ethology’ from either Heinroth (1911) or Portielje who published several papers in the 1920s with ‘ethologie’ in the title (see Burkhardt 2005:598). A further paper followed in 1932: ‘Considerations of methods in identifying species-specific instinctive behaviour patterns in birds’ (Lorenz 1932). Then, in 1933 he published a substantial paper on the anatomical and physical aspects of avian flight based on his work at the Anatomical Institute in Vienna where he was then employed (Lorenz 1933). His fourth ethologically oriented work, published in 1935, was “Der Kumpan”. This massive paper was a synthesis of all Lorenz's behavioural observations and ideas to date. Thus, over an 8-year period (1927–1935) Lorenz developed a complete concept of ethology. Since his papers were all published in *Journal für Ornithologie* (JfO hereafter), Lorenz played a major role in shaping the journal.

It is well-recognised that Lorenz was the pioneer in the field of ethology. It is also recognised that in creating ethology as a discipline, Lorenz stood heavily on the shoulders of others (Burkhardt 2005; Schulze-Hagen and Birkhead 2015). Although Lorenz freely acknowledged those, who like Jakob von Üxküll (1864–1944) and Oskar Heinroth (1871–1945), inspired him, he was nonetheless, a master of taking ownership of, and developing others' ideas and—as a result—eclipsing them (Schulze-Hagen and Birkhead 2015). Even in the 1930s, he was criticised for such behaviour, and in the introduction to the Kumpan paper he justifies himself by saying:

“I make a habit of not claiming merit for ideas and opinions which are not my own but which I took over from great men. However, it is not only the creator of a new idea who acquires merit, but also the man who realizes its importance and who ‘puts it on the map’” (Lorenz 1935).

The extent to which Lorenz's Kumpan paper was inspired by the work of others can be gleaned from Lorenz's (mostly unpublished) letters to Erwin Stresemann during 1933 and 1934.

“... Before Easter we had two visits from Üxküll, who is incredibly nice and clever and really knows a lot about animals (which is so evident from his publications!).” [Lorenz to Stresemann 22.4.1933]

Baron Jakob von Üxküll was a German physiologist at the University of Hamburg best known today for his concept of *Umwelt* and the way animals perceive the world (von Üxküll 1920). That is, an animal’s perceptual world in which it exists. A key feature of an organism’s world is of course, the other individuals (conspecifics) with which it interacts: their kumpans or ‘companions’.

In the same letter to Stresemann, Lorenz wrote:

“... I am insanely lazy and lie in the grass while poor Gretl [Lorenz’s wife Margarethe] is so hard working in the hospital. I feel a certain inner emptiness because I have nothing planned for the time being. Should I now start a little project, e.g. “The innate recognition of warning-coloured insects by birds”, “Contributions to the ethology of *Nycticorax*” or should I now start “My life’s work”, for example “The behavior of higher animals”?

What I wanted to confide in you, Professor, ... and to instill gently, was above all that I am already writing again in incurable graphorhœa on a thing entitled: “The kumpan in the bird’s environment”. I wanted to tell you about it in a similar way as I told you, when you were my defenceless victim, all the stuff about the ms on flight in birds in my parent’s dining room in Altenberg in the evening from 7 to 12 o’clock. [during a visit by Stresemann to Lorenz’s home in 1932] ... I can [now] confess my intention! The hook in the above-mentioned work, which may prevent you from including it in the JfO, [*Journal für Ornithologie* that Stresemann edited] lies in the fact that in it, because it is supposed to be written for psychologists and environmental researchers, I have to go over things that are self-evident to ornithologists. Of course, finding the right way in these difficulties would have been much easier orally than by letter. *Quae cum ita sint* [In this situation] I shall therefore make the first part of the ms readable and send it to you, Professor, on a trial basis! If you should take the stuff after all, I will then finish it and submit it as a habilitation thesis [necessary to become a lecturer]. The fact that it would already be sufficient for this, if only the ms would have been accepted by the JfO. When it will finally be printed, that is irrelevant for the purpose of obtaining a lectureship. I’ve probably already told you how I came up with the idea for this thesis??!

Ah, only four times!! So: Saint Jakob von Üxküll in persona suggested and ordered this compilation of all bird kumpans and coined the title, thus avoiding any accusation that I am only giving this nonsense for the sake of being a lecturer! For the purpose of showing off, I enclose the Üxküll [book], which you can send back to me occasionally! ...” [Lorenz to Stresemann 17 July 1933].

This letter provides two key pieces of information regarding the paper’s origin. First, that Lorenz was writing, in part at least, for psychologists. That is, to the American behaviourists whose view of animal behaviour was predominantly laboratory-based, and hence to Lorenz’s mind, artificial. Lorenz’s objective was to establish a very different behavioural discipline (Burkhardt 2005).

Second, Lorenz emphasises his debt to Jakob von Üxküll for the central idea of the Kumpan paper. Lorenz admired and revered Üxküll as a “Saint”, as he did Immanuel Kant and some other eminent philosophers. Üxküll’s vague, complicated and intricate philosophical style impressed Lorenz, even though anyone attempting to read it today would find it impenetrable. It is perhaps no coincidence that in their vague and complicated way of expressing themselves, Üxküll and Lorenz were very similar.

At the end of February 1934, Lorenz wrote to Stresemann to tell him that he and his wife would be attending the International Ornithological Congress [IOC] in Oxford in July of that year, but wondered what he should talk about. Another person planning to attend was Margaret Morse Nice (1883–1974). She had previously met Ernst Mayr (1904–2005) at a meeting of the American Ornithologists’ Union in 1931. Mayr put her in touch with Heinroth and with Stresemann, who encouraged her by publishing the results of her pioneering studies of the song sparrow *Melospiza melodia* in JfO in 1933 and 1934 (Nice 1933–1934). Lorenz therefore knew of Mrs Nice before they met for the first time at the IOC congress (Burkhardt 2005).

Wondering about the topic of his talk, Lorenz wrote to Stresemann:

“A comparative study on the ethology of colonial nesting birds? Actually, it is more important to me that the German attendants understand what I am talking about. The charming Margret M. Nice has just thrown me into inferiority problems! That’s how I like Field Ornithology. With this amount of patience somebody should have to pounce on some highly social birds. Couldn’t the courageous Mrs. Nice be set on penguins? There’s no idea what interesting things might come out of it. I was very enthusiastic about this lady’s way of

researching. That's how you have to know every animal before you start experimenting on it. ..." [Lorenz to Stresemann, end of February 1934].

Two points are apparent from this. The first is Lorenz's interest in his German-speaking colleagues understanding him. He needed to prepare the ground for the new ethology in Germany where there was some opposition from both psychologists and animal psychologists. The second is the reverence with which he viewed Margaret Morse Nice.

Lorenz continues:

"Although I was hardly able to work on the Kumpan ms for ½ hour a day because of a 9-hour working day in the anatomical institute, "The Kumpan in the bird's environment" is now finished, i.e. yesterday I wrote "The End" under the last page; there is still much polishing to be done. Just now I have been asked to make a contribution to the Üxküll Festschrift. I enclose this letter from which you can see the conditions. I believe that nothing would stand in the way of having the "Kumpan" included in a Festschrift ... Incidentally, I am not at all sure that you, Professor, will really want to accept the "Kumpan" for publication [in JfO]. It has become almost as long as my other ms about the mechanics of bird flight [130 pages; see Lorenz 1933] and it is difficult to shorten it, since its persuasive power lies in the concrete examples of observations that take up most of the space. If you leave them out, you are left with a dull theoretical cabbage! I will now give you the table of contents, so that you can be armed yourself and get rid of this tapeworm from your journal."

He then provides a long list of the projected contents of the Kumpan paper, which he called—metaphorically—a tapeworm ("*Taenia pythionoides*"; Lorenz to Stresemann, 4 March 1934).

Lorenz at this time was employed at the Anatomical Institute in Vienna, but found himself more interested in behaviour than anatomy. He wrote to Stresemann confiding that he was thinking of leaving the institute to be able to pursue his main interest. He felt that as his supervisor's least favourite post-doc, his chances of securing a position in anatomy were not great anyway. "I think I shall take the plunge into the starving existence of a private lecturer. Definitely, there will be a psychological job opening up somewhere. Then I will start at the bottom and work my way still further ahead! The present state of affairs is really untenable, and I have a better chance of doing some work and getting somewhere as a keeper in a zoo than as an assistant to this constantly

easily irritable severe neurasthenic Pernkopf [the director of the anatomical institute]".

He continues (4 March 1934):

"I think you will have a real understanding of my situation. I think I should take this step while I am still young and still have enough money to earn an academic position as a psychologist without salary. There's no other way to become an assistant anywhere. So, enough of complaining".

Stresemann replies emphatically:

"You must give up anatomy. Your talent for the field of animal psychology is such an outstanding trait that it would be equivalent to autotomy (and a biologically harmful one at that!) if you were to allow yourself to be intimidated and act rationally instead of instinctively. Someone in whom the instinctual is still as strongly pronounced as in you should be very happy about this finger of God. Plunge into the water like a young guillemot without worrying; you will be able to swim. If it means some kind of relief to you, feel free to pass on a good part of the responsibility to me, I will gladly bear it." (Stresemann to Lorenz 7 March 1934).

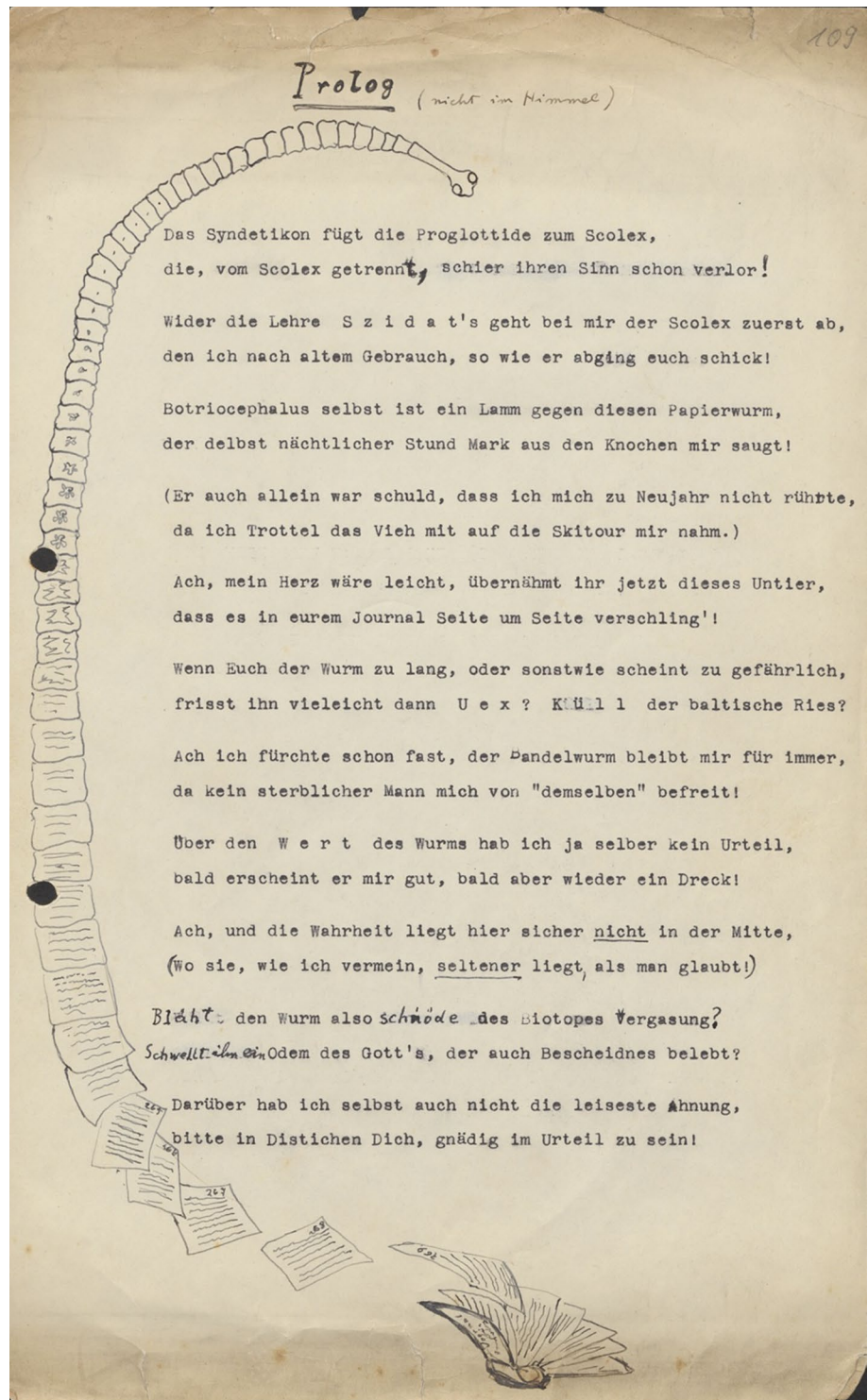
A few days later, Lorenz wrote to tell Stresemann that he had visited Karl Bühler to discuss the possibility of employment in his institute. Bühler (1879–1963) was a psychologist and linguist. The next day Lorenz attended a concert, and "Who was sitting next to me? Bühler! If that wasn't a sign of fate ... After 10 minutes he had already asked why I wasn't doing my habilitation ... he would be so thrilled if a psychological biologist teach [read] a behavioural theory. ..." (Lorenz to Stresemann 11 March 1934).

In June 1934, when Lorenz's submitted the Kumpan paper to JfO, his submission letter to Stresemann took the form of an illustrated poem (Fig. 1).

The poem is virtually impossible to translate into English because the puns work only in German. However, the gist of it is that, as he had intimated earlier, Lorenz felt as though the Kumpan paper was an all-consuming internal parasite eating away at him from the inside. In submitting the paper to Stresemann, he was handing over responsibility for it: "Oh, my heart would be light if you would now take over this beast, that it devours page after page in your journal!" And "Ah, I am almost afraid that the tapeworm will remain with me forever, for no mortal man can rid me of it! ... I beg you in couplets to be merciful in your judgment!"

Stresemann, who also enjoyed writing poetry, responded in a verse in which he presents himself as Zeus or a god of judgement who will decide on the manuscript's fate, but graciously accepts the paper: "nothing better can ever happen to

**Fig. 1** The Kumpan-MS, ingeniously illustrated as a metaphorical “text-tapeworm”. Submission letter from Lorenz to Stresemann, June 1934



me, than to be your Kumpan and vessel and secret breeding chamber”:

“Hail to me, Cestode, multi-limbed one,  
who ripened in long

days and nights in the brain  
of a divine scientist  
until the time has come, and he  
with his quill, gripping thee  
slowly began to turn, and metre

out metre by metre.  
 Willingly, I swallow you up and make  
 The feeding test  
 Whether I am your intermediate host or the  
 The final host for you -  
 Whether after a short stay unharmed  
 you leave me  
 Or your scolex will grab me  
 And never ever let go.  
 Dream indeed, nothing better can  
 ever happen to me,  
 Than to be your Kumpan and vessel  
 and secret breeding chamber  
 spreading far and wide your noble lineage  
 among the people of Achea!”

## Publication

Lorenz’s Kumpan paper was exceptional for several reasons. First, for its sheer size: 209 pages. It was exceptional, too, for its difficult, often incomprehensible philosophical language, and third, it was extraordinary in its vision of a new field of academic endeavour: the study of animal behaviour from a *biological* rather than psychological perspective as others had done and were doing.

Remarkably, given its obtuse passages and Stresemann’s reputation as a formidable critic and uncompromising editor of JfO the paper was accepted with no editorial changes (see: Stresemann 1951, 1975: 362–364; Mayr also reported this often; see also Haffer 1997 who presents the Stresemann and Mayr correspondence on this).

Because of its length, the paper was published in two parts in July and October 1935. It was seen immediately by Margaret Morse Nice in the USA. Nice spoke fluent German and at this time was providing abstracts of German ornithological publications for the American journal *Bird Banding*. She and her sister had shared accommodation in Oxford at the 1934 International Ornithological Congress (IOC) with Lorenz and his wife. Nice and Lorenz therefore had ample opportunity to get to know each other, and presumably for Lorenz to tell her about his Kumpan paper then in preparation. On seeing the first part of the paper published, she immediately set about producing a summary for *Bird Banding*, entitling it: ‘The Kumpan in the bird’s world. The fellow-member of the species as a releasing factor of social behaviour’ (Nice 1935a).

Nice reiterated the fact that Lorenz’s ideas were inspired by Üxküll’s (1920) concept of the ‘Kumpan’, and that the behaviour of individuals often occurs in response to one

particular stimulus. These stimuli can be morphological structures, such as plumage features, or distinctive postures and movements, all of which Lorenz referred to as ‘releasers’. Nice ends her description of this first part of the paper, which is primarily on parent–offspring relations, including imprinting, by saying: “This is a most remarkable paper of fundamental importance” (Nice 1935a).

The second part, as Nice states, “proves easier reading than the first, less space being devoted to theory and more to telling what birds do”—specifically the child-kumpan, sex-kumpan, social kumpan, etc. She ends thus: “Dr Lorenz gives us a solid foundation on which to build; with its illuminating viewpoint we can study bird behaviour intelligently, understand phenomena that before were baffling, analyse our observations, and build up the large body of fact for which there is such a crying need”. (Nice 1935b).

In September 1935, Lorenz wrote to thank Nice for her publicising the Kumpan paper:

“I was very much impressed indeed by the way you reviewed my paper! Not only by the kind reception you have given it and for which I thank you most sincerely, but also by the astonishing celerity with which you have read and so thoroughly understood the whole long story. This is a thing to which I am not accustomed at all. The Kumpan seems to be a somewhat indigestible thing and I am wont to see it treated in a more Friedmannish way”. [Lorenz-Nice 1935a, b-9-19 Cornell via R W Burkhardt, 10/02/2023].

Lorenz clearly recognised that his paper was ‘difficult’, and ‘Friedmannish’ probably refers to the descriptive, atheoretical paper on the displays of the standard wing bird of paradise *Semioptera wallacii* by Friedmann published in the same issue of JfO (Friedmann 1935).

Nice had trained as a psychologist and published several papers on child development. At the time of Lorenz’s paper, she was continuing her study of the behaviour of individually marked song sparrows *Melospiza melodia* and was therefore in a strong position to assess Lorenz’s ideas. It would not have happened had she not been fluent in German, and it is to her credit that she ploughed through and essentially ignored much of Lorenz’s unintelligible ‘philosophical’ comments and focussed on the central concept and his perceptive observations. Indeed, without Nice’s *Bird Banding* review and a subsequent paper, *The social kumpan and the Song Sparrow* (Nice 1939), it is possible that the value of Lorenz’s paper may have been lost, or at least, delayed. Nice was also a realist. After spending a month with Lorenz at Altenberg in the spring of 1938, she wrote to Ernst Mayr about Lorenz: “He is a genius, but he evidently undertakes

too many things and sometimes goes wrong” (quote in Burkhardt 2005: 162).

An abridged, English version of the Kumpan paper, comprising nineteen pages, was published in the *Auk* in 1937, written by Lorenz himself in response to Francis Herrick, the journal’s editor’s, request (Lorenz 1937a, b). In addition, the American zoologist, Gladwin Kingsley Noble (1894–1940), a herpetologist interested in behaviour, had the entire Kumpan paper translated into English in 1937 and circulated mimeographed copies to other American biologists and psychologists (R.W. Burkhardt, pers. comm). Lorenz (1957a, b) later also produced translations of parts of his Kumpan paper. It was not until 1970, however, that an English translation of the entire paper was published (English translation of Kumpan by R. Martin in 1970 *Studies in Animal and Human Behaviour*, Harvard.)

Stresemann accepted the Kumpan paper for publication and was later credited, together with Nice, for promoting it (Curio 1988—see below). Ernst Mayr had met Lorenz in the 1930s through his doctoral supervisor Erwin Stresemann. In 1997, Mayr presented some reminiscences to Jürgen Haffer (Mayr 1997): “Konrad was one of my oldest friends. ... I do know that at the Rouen IOC, 1938, we had long conversations. He was, of course, the protégé if not discovery, of Stresemann and thus I was quickly made aware of his significance. I greatly admired his papers, particularly his Kumpan paper” (1935). Nonetheless, in late 1935/early 1936 when Gretel [Mayr’s wife] and he were asked to translate Lorenz’s paper, they found much of it incomprehensible, and gave up. Mayr states that while he admired the Kumpan paper, he found many of the sentences unclear and when he sent examples to Lorenz to explain, Lorenz said he could not remember what he meant! Reminiscing about Lorenz after his death, Mayr wrote that Lorenz had “an incredibly fertile mind, was constantly bubbling over with new ideas, good ones and bad ones” (Mayr 1997).

“This mixture of good and bad ideas is also characteristic of Lorenz’s popular science books. Particularly the ones meant to be philosophical and it is not surprising that professional philosophers attacked them unmercifully. At the same time, if one reads them with discrimination, one will find quite a few very good ideas in his writings. They are not the careful, scientific, objective, mature writings of a philosopher, but rather the bubbling over of a brilliant, undisciplined, and in many respects rather immature mind” (Mayr 1997).

In a volume celebrating Lorenz’s 85<sup>th</sup> birthday in 1988, Eberhard Curio wrote the following: “When E. Stresemann, friend and early supporter of Lorenz, published

his ground-breaking paper the Kumpan in *JfO* in 1935, he shocked the readers so much that many of them ranted and many of them left the DOG. This classical ethological essay was so new, and so revolutionary, it is doubtful without the foresight of Stresemann it would not have been as powerful as it is”. (Curio 1988).

Shock and ranting are typical of the way paradigm shifts are received, by some at least (Kuhn 1962). “Lorenz’s concepts of releasers, innate releasing mechanisms, imprinting and the roles of each of these in the functioning of animal societies became the core concepts of the new *biological* science of ethology or animal behaviour as it came to be known” (Burkhardt 2005).

In his Introduction in the Kumpan paper, Lorenz states that: “This paper is not a description of a unitary investigation directed at a narrowly defined research problem. It is rather an attempt to arrange a large number of observations, which have previously remained as unrelated entities, within an ordered system. It is in the nature of such an attempt that the result should predominantly have the character of a programme. ...”

When the full translation of Lorenz’s Kumpan paper became available in 1970 thanks to R.D. Martin (above), Jack Hailman (1970) suggested that the paper represented “a major intellectual peak in the thinking of an extraordinarily perceptive man” and must surely stand “alongside Darwin’s *Expression of the Emotions* and Huxley’s study of the great crested grebe [*Podiceps cristatus*] as one of the true classics of ethology”.

Indeed, it was for this conceptual framework for a study of animal behaviour that Lorenz was later awarded the Nobel prize. No one knew better than Margaret Morse Nice in 1935, how valuable Lorenz’s paradigm-shifting vision was in guiding and directing the study of behaviour. Exactly the same thing was to occur forty years later with the new focus on individual selection thinking and the introduction of what was to become behavioural ecology (Parker 2005; Birkhead and Monaghan 2010).



**Fig. 2** The gape of a nestling hawfinch *Coccothraustes coccothraustes*, (photo: courtesy Beata Marlena)



## Lorenz's observations of bird behaviour in the 'Kumpan' paper

It seems likely that very few of those who, today, consider them students of bird behaviour (or animal behaviour) have heard of, let alone read, Lorenz's Kumpan paper. This is not surprising. Knowing the history of one's discipline is rarely deemed essential, not least because things move on, and for the field of animal behaviour this is certainly true (Burkhardt 2005). Indeed, it is ironic that in many cases Nobel Prizes are awarded long after the work on which they are based has been superseded. The conceptual ideas of the Kumpan paper were rather rapidly superseded (Burkhardt 2005; Kruuk 2003) and indeed, Lorenz himself rarely referred to the paper. In contrast, however, the *behaviours* that Lorenz observed and documented have stood the test of time. It is these aspects of the Kumpan paper that make reading it worthwhile today. Lorenz's brilliant and perceptive observations still have the potential to trigger new research. One of the benefits of studying the history of ornithology (and science) is the discovery of earlier observations that can stimulate new research (e.g. Birkhead et al. 2011; Schulze-Hagen and Birkhead 2015).

Here, we briefly consider one example from the Kumpan paper that Lorenz used to illustrate the central concept of a 'releaser'. This is the extraordinarily colourful—yellow, red, blue and purple—mouth markings of the hawfinch *Coccothraustes coccothraustes* (Fig. 2).

Lorenz probably learned about the hawfinch chick's striking mouth markings in 1924 from the illustration in Oskar and Magdalena Heinroth's *Die Vögel Mitteleuropas* (1924 Vol 1, plate XXXVII) (Fig. 3) that Lorenz had been given as a present by his friend Bernard Hellman soon after its publication (Taschwer and Föger 2003; Schulze-Hagen and Kaiser 2020).



**Fig. 3** The illustration of nestling hawfinches from Heinroth and Heinroth (1924)

Lorenz wrote (in Kumpan 1970: 106–107):

“The gape of the nestling Hawfinch, for example, is so unusually colourful for the very reason that it combines with the instinctive gaping pattern to act as a key to the species-specific feeding response of the parents. The biological significance of the colourful pattern lies in the prevention of ‘mistaken’ elicitation by coincidentally similar stimuli from another source. ... The development of a releaser incorporates a compromise between two biological requirements: maximum simplicity and maximum general improbability. An exclamation which is often made by an uninitiated observer seeing the fan-tail of a peacock, the display plumage of a golden pheasant, or the colourful gape pattern of a young hawfinch is: ‘How unusual!’”

In a letter now lost, Margaret M. Nice had evidently queried some aspect of Lorenz's ideas about passerine mouth markings. In his reply, dated 19 September in 1935, he wrote:

“The feeding reaction in many passerines seems to have a rather wide innate releasing pattern. I learned since, that sometimes, young cuckoos too, are raised besides their foster brothers and sisters. Probably the patterns are of quite different width or narrowness in different species. Anyhow I should be surprised if a passerine bird with a very complicated gape pattern like *Astrildids* or *Kernbeißer* (howdoyoucallit!) [the hawfinch *Coccothraustes coccothraustes*,] would accept strange young quite as readily. There is a lot of experimenting still to do ...” [Lorenz-Nice 1935a, b-9-19 Cornell via R W Burkhardt, 10/02/2023].

There is indeed a lot left to do. Given Lorenz's interest in comparative studies and their ability (as first noted by Heinroth 1911) to reveal the evolutionary history of a display, it is surprising, perhaps, that he did not compare the hawfinch's mouth markings with those of other finches (Fringillidae). However, in discussing the role of brood parasites, like the common cuckoo *Cuculus canorus* (above), Lorenz did identify the potential survival value of the hawfinch chick's extraordinary mouth markings, possibly based on a recently published study by Friedmann (1929). Although Lorenz saw the hawfinch chick's mouth markings as a releaser for the parent birds, he seems not to have considered the other, obvious explanation, that bright mouth markings enhance their visibility in a dark nest site. However, among a range of European birds, including finches (but not the hawfinch), Kilner and Davies (1998) found no evidence that mouth colour *per se* enhanced detectability in poorly lit nest sites. A comparative study

of finch mouth markings and their types of nest sites would still be worthwhile.

Another example concerns imprinting. Even though this phenomenon had been known for several centuries, both the layman and the zoologist, Lorenz said, are surprised that most birds do not recognise their own species ‘instinctively’ but must learn it at a specific period of their life, via the process of imprinting. Imprinting was a central tenant of the Kumpan paper, and Lorenz duly became known as its ‘discoverer’. As with his study of releasers, he relied on a combination of observations and studies conducted by others, together with his own observations and small-scale, but revealing experiments, to better understand the process.

His friend and mentor, Oskar Heinroth, he says, failed to breed eagle owls *Bubo bubo* or ravens *Corvus corax*, in captivity because the birds were sexually imprinted on their keepers (i.e. Heinroth and his wife, Magdalena). Similarly, his colleague A. F. (Frits) J. Portielje (1886–1965) had hand-reared a male Fasciated Tiger Heron *Tigrisoma fasciatum*, that when mature, courted humans. When Portielje obtained a female tiger heron, the male initially ignored it, but after leaving the pair together for a time, the male eventually accepted her and the pair bred together. However, if Portielje appeared, the male would ‘drive her roughly from the nest and, turning to his keeper and perform the ceremony of nest-relief, inviting Portielje to step into the nest and incubate!’ (Lorenz 1937b).

One of Lorenz’s key discoveries was the interspecific variation in the predisposition of young birds to imprint on human keepers. He recognised not only the central importance of the different stimuli—the releasers—that allowed the behaviour to occur, but also that some species required very specific stimuli, while others responded to a broad range of stimuli. Curlews *Numenius arquata*, he said, “even when hatched artificially and never having seen any living creature but their keeper, cannot be brought to respond to him with any reactions but those of escape”. At the other extreme, budgerigars *Melopsittacus undulatus* could be imprinted onto a celluloid ball, and providing it was presented at head-height, was treated as though it was the head on a conspecific: “All actions which he performed in connection with it were such as normally directed toward the head of another parakeet [budgerigar]”. Yet, tellingly, when Lorenz placed the ball on the floor of the cage, the bird responded as though its cage-mate was dead, falling “absolutely silent” and adopting “the fright-attitude, with feathers depressed close to the elongated body”. (Lorenz 1937b: 269).

Using observations like these, together with his classic studies of imprinting in ducks and geese, Lorenz was able to emphasise how imprinting differed from associative learning. Specifically, that imprinting was confined to a very definite and brief period of an individual’s life, and

that “once accomplished, is totally irreversible” (Lorenz 1937b: 264).

## Conclusion

Many of the core ideas in the emerging field of ethology had their origin in Lorenz’s Kumpan paper (Tinbergen 1951; Hinde 1966, 1982; Burkhardt 2005). Remarkably, after its publication in 1935, Lorenz himself rarely referred to it again. Indeed, in his ethology textbook, published 1978 (1981 in English), he does not refer to it. One explanation was that he rarely read or cited the literature, especially that of others, but possibly in this case, his own. Another possibility is that his reverence for Üxküll’s ideas was an infatuation and as a result he embraced the ‘Kumpan’ idea somewhat uncritically. Then, finding that few other researchers were as enthusiastic as he had been, decided to drop it. For Lorenz himself, the Kumpan paper was therefore a stepping-stone, since by 1937 he was publishing separate papers on individual topics such as imprinting and instinct.

Perhaps we should not be too surprised by Lorenz’s rapid rejection of the Kumpan concept. Science is a dynamic process and simply by publishing that large, important, but in some ways, indigestible paper, Lorenz was better able to see the way forward. It also allowed him to stamp his authority on the field. There is a certain irony in the fact that Lorenz was inspired to write the Kumpan paper by the groundbreaking ideas of Üxküll, Heinroth and others, yet by doing so and quickly abandoning it, Lorenz left the way open for others to be inspired by it. One of those ‘others’ was Niko Tinbergen. It was through his extraordinary talents that he and Lorenz together developed the field of animal behaviour (Kruuk 2003; Burkhardt 2005). They met in Leiden at the ‘instinct symposium’ in November 1936. As Burkhardt (2005) states, the symposium provided the chance for each of them “to recognise how the other’s strengths complemented their own ... Lorenz’s bold and largely intuitive theorizing dovetailed beautifully with Tinbergen’s strong analytical and experimental talents”. Even though it was Lorenz who kick-started the discipline of animal behaviour, it is Tinbergen whose work has better stood the test of time (Kruuk 2003; Burkhardt 2005).

We allow Hailman (1970) the last word from his perceptive review of the Kumpan paper:

“Perhaps the lesson is that the early phases of a science require the power of a broad, sweeping intellect that has a certain disregard for the formalisms and pedantic, creeping construction of the ultimate scientific edifice”.

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## References

- Birkhead TR, Monaghan P (2010) Ingenious ideas: the history of behavioural ecology. In: Westneat DF, Fox C (eds) Evolutionary behavioural ecology. Oxford University Press, Oxford, pp 3–15
- Birkhead TR, Hemmings N, Spottiswoode CN, Mikulica O, Moskát C, Bán M, Schulze-Hagen K (2011) Internal incubation and early hatching in brood parasitic birds. *Proc R Soc B* 278:1019–1024
- Burkhardt RW (2005) Patterns of behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology. University of Chicago Press, Chicago
- Curio E (1988) In: Schleidt W (ed) Der Kreis um Konrad Lorenz: Festschrift anlässlich des 85. Geburtstages von Konrad Lorenz am 7.11.1988. Parey, Berlin, pp 11–12
- Friedmann H (1929) The cowbirds. A study in the biology of social parasitism. Thomas, Springfield
- Friedmann H (1935) Die Balz von *Semioptera wallacei halmaherae* in Gefangenschaft. *J Ornithol* 83:283–286
- Haffer J (1997) Ornithologen-Briefe des 20. Jahrhunderts *Ökol Vögel* 19:1–980
- Haffer J (2001) Die Stresemannsche Revolution" in der Ornithologie des frühen 20. Jahrhunderts *J Ornithol* 142:381–389. <https://doi.org/10.1046/j.1439-0361.2001.01004.x>
- Haffer J, Rutschke E, Wunderlich K (2000) Erwin Stresemann (1889–1972)—Leben und Werk eines Pioniers der wissenschaftlichen Ornithologie. *Acta Historica Leopoldina* 34, Halle (Saale)
- Hailman JP (1970) Ethology evolving. *Science* 168:700–701
- Heinroth O (1911) Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Ber Int Ornithol Congr* V:589–702
- Heinroth O, Heinroth K (1924) Die Vögel Mitteleuropas, vol 1. Behrmöhler, Berlin
- Hinde RA (1966) Animal behaviour: a synthesis of ethology and comparative psychology. MacGraw-Hill, New York
- Hinde RA (1982) Ethology: its nature and relations with other sciences (masterguides). Oxford University Press, Oxford
- Karolinska Institutet (1973) The Nobel prize in physiology or medicine. Press release. <https://www.nobelprize.org/prizes/medicine/1973/press-release/>. Accessed 18 Feb 2023
- Kilner R, Davies NB (1998) Nestling mouth colour: ecological correlates of a begging signal. *Anim Behav* 56:705–712
- Kruuk H (2003) Niko's nature. Oxford University Press, Oxford
- Kuhn T (1962) The structure of scientific revolutions. University of Chicago Press, Chicago
- Lorenz K (1927) Beobachtungen an Dohlen. *J Ornithol* 75:511–519
- Lorenz K (1931) Beiträge zur Ethologie sozialer Corviden. *J Ornithol* 79:67–127
- Lorenz K (1932) Betrachtungen über das Erkennen der arteigenen Triebhandlungen der Vögel. *J Ornithol* 80:50–98
- Lorenz K (1933) Beobachtetes über das Fliegen der Vögel und über die Beziehungen der Flügel- und Steuerform zur Art des Flügels. *J Ornithol* 81:107–236
- Lorenz K (1935) Der Kumpan in der Umwelt des Vogels. *J Ornithol* 83:137–213, 289–413
- Lorenz K (1937a) Über die Bildung des Instinkt begriffes. *Naturwiss* 25:289–300, 307–308 and 324–331
- Lorenz K (1937b) The companion in the bird's world. *Auk* 54:245–273
- Lorenz K (1957a) Companionship in bird life. In: Schiller CH (ed) Instinctive behavior. International Universities Press, New York, pp 83–128 (translation of parts of Lorenz 1935)
- Lorenz K (1957b) The nature of Instinct. In: Schiller CH (ed) Instinctive behavior. International Universities Press, New York, pp 17–50 (original edition, *Folia Biotheoret*, Der B, 2, 1937)
- Lorenz K (1970) Companions as factors in the bird's environment. Translated by RD Martin. In: Lorenz K (ed) Studies in animal and human behaviour, vol I. Harvard University Press, Cambridge, pp 101–258
- Lorenz K (1978) Vergleichende Verhaltensforschung—Grundlagen der Ethologie. Springer, Wien
- Lorenz K (1981) The foundations of ethology. Springer, New York
- Mayr E (1997) Reminiscences of Konrad Lorenz, 1903–1989, pp 802–803. In Haffer J Ornithologen-Briefe des 20. Jahrhunderts *Ökol Vögel* 19:1–980
- Nice MM (1933–4) Zur Naturgeschichte des Singammers. *J Ornithol* 81:552–595 (part 1) and *J Ornithol* 82:1–96 (part 2)
- Nice MM (1935a) The Kumpan in the bird's world. The fellow-member of the species as a releasing factor of social behaviour. Review of part 1 Lorenz's *Der Kumpan in der Umwelt des Vogels*. *Bird Banding* 6:113–115
- Nice MM (1935b) The Kumpan in the bird's world. Conclusion. Review of part 2 Lorenz's *Der Kumpan in der Umwelt des Vogels*. *Bird Banding* 6:146–148
- Nice MM (1939) The social kumpan and the song sparrow. *Auk* 56:255–262
- Parker GA (2005) Behavioural ecology: natural history as science. In: Lucas J, Simmons L (eds) Essays in animal behaviour. Elsevier, Amsterdam, pp 23–56
- Schulze-Hagen K, Birkhead TR (2015) The ethology and life history of birds: the forgotten contributions of Oskar, Magdalena and Katharina Heinroth. *J Ornithol* 156:9–18. <https://doi.org/10.1007/s10336-014-1091-3>
- Schulze-Hagen K, Kaiser G (2020) Die Vogel-WG. Kneesebeck, München
- Stresemann E (1951) Entwicklung der Ornithologie von Aristoteles bis zur Gegenwart. Peters, Berlin
- Stresemann E (1975) Ornithology from Aristotle to the present. Harvard University Press, Cambridge
- Taschwer K, Föger N (2003) Konrad Lorenz—Biographie. Zsolnay, Wien
- Tinbergen N (1951) The study of instinct. Clarendon Press, London
- von Üxküll J (1920) Theoretische Biologie. Paetel, Berlin

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