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HISTORIOGRAPHIC ESSAY

# Karl von Frisch and the Discipline of Ethology

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**Abstract**
In 1973, the discipline of ethology came into its own when three of its most prominent practitioners—Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch—jointly received the Nobel Prize for Physiology or Medicine. Historians have shown how Lorenz and Tinbergen were central to the practical and theoretical innovations that came to define ethology as a distinct form of animal behavior research in the twentieth century. Frisch is rarely mentioned in such histories. In this paper, I ask, What is Frisch's relationship to the discipline of ethology? To answer that question, I examine Tinbergen's relationship to Frisch's grey card experiments between Tinbergen's time as a student at the University of Leiden in the mid 1920s and his 1951 publication of *The Study of Instinct*. In doing so, I highlight previously neglected affinities between Frisch's early career research and the program of classical ethology, and I show how Frisch's research meant different things at different times to Tinbergen and others working in the ethological tradition.

**Keywords** Ethology · Karl von Frisch · Nikolaas Tinbergen · Grey Card Experiment · Reductionism · Holism

## Introduction

In 1973, the discipline of ethology came into its own when three of its most prominent practitioners—Konrad Lorenz (1903–1989), Nikolaas Tinbergen (1907–1988), and Karl von Frisch (1886–1982)—jointly received the Nobel Prize for Physiology or Medicine. The award was unusual because, instead of commending a particular discovery of major importance, the citation seemed to broadly endorse a disciplinary style of investigating animal behavior (Hinde and Thorpe 1973; Marler and Griffin 1973; Nobel Media1973; Hein 1976, p. 243; Burkhardt 1981, p. 65; Lorenz 1985, p. 283; Kruuk 2003, pp. 268–269). Tinbergen called the Nobel Foundation's decision "unconventional" and reasoned that "Since at least Konrad Lorenz and I

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could not really be described as physiologists, we must conclude that our *scientia amabilis* is now being acknowledged as an integral part of the eminently practical field of Medicine" (1973, p. 113). I begin with Tinbergen's reaction to the Nobel Prize because it illustrates the primary question motivating this paper.

What is Frisch's relation to the discipline of ethology? In the above quote, Tinbergen singled out Frisch for being more of a physiologist than he or Lorenz. That compartmentalization is also reflected in the historiography of ethology. Others have shown how Lorenz and Tinbergen's work was central to the practical and theoretical innovations that came to define ethology as a distinct form of animal behavior research in the twentieth century (Burkhardt 1981, 1983, 1997, 1999, 2005; Beer 1975; Kalikow 1975; Heinroth and Burghardt 1977; Burghardt 1982; Baerends 1991; Jamieson and Bekoff 1992; Dewsbury 1992; Brigandt 2003, 2005; Kruuk 2003; Beale 2008; Munz 2011; Schulze-Hagen and Birkhead 2015, pp. 14–15). Frisch is rarely mentioned in such histories (Jaynes 1969; Beer 1975; Heinroth and Burghardt 1977; Lea 1984, chap. 1), and when he is, he is often framed as an expert practitioner of ethology rather than a founding influence (Bates 1953; Thorpe 1979; Dewsbury 1992; Jamieson and Bekoff 1992, pp. 111–112; Kruuk 2003; Greenberg 2012; Radhakrishna 2018).

However, as this paper demonstrates, Frisch's relationship to ethology is not that of an acolyte or skillful early adopter. Frisch was 17 years older than Lorenz and 21 years older than Tinbergen. By the time Tinbergen and Lorenz began promoting ethology in the 1930s, Frisch had already developed his own experimental approach to animals and established himself as a prominent academic. The most obvious alternative—that Frisch was a co-founder of ethology alongside Tinbergen and Lorenz—also seems to be ruled out. As Burkhardt wrote in the introduction to his comprehensive history of ethology, Frisch "essentially took no direct part in the efforts that constituted ethology as a new discipline in the middle decades of the [20th] century" (2005, p. 6). There is a substantial body of work on both ethology and Frisch, but to date there has been no sustained examination of the historical connections between Frisch's work and that of the ethologists, and likewise no detailed comparison of the similarities and differences between their ideas and their practices. This paper sets itself the task of providing such an examination and comparison. I begin by exploring the idea that Frisch was an *exemplar* for the nascent discipline of ethology.

By questioning whether Frisch was an exemplar for classical ethology, this paper uncovers previously neglected affinities between Frisch's early research and the program of classical ethology. In the 1930s and 1940s, Tinbergen and Lorenz were eager to frame ethology as a discipline that reconciled certain reductionist and holist commitments. On the one hand, Tinbergen and Lorenz promoted reductive, causal-physiological explanations of behavior over psychological explanations. On the other, they saw animals as complex collections of interdependent parts whose behaviors bore nuanced relationships to environmental context and phylogenetic history, and they were keen to incorporate an awareness of those relationships into behavioral studies. Frisch's grey card experiments, performed in the 1910s, modeled how productive a reconciliation between such reductive and holist commitments could be. To complement that conceptual perspective on the history of science with a more concrete examination of interpersonal relationships, I also demonstrate how

Frisch's grey card experiments influenced Tinbergen while he was a university student and early career academic in the 1920s and 1930s.

All this seems to indicate that Frisch was an exemplar for classical ethology. His experimental approach had action-guiding force for young Tinbergen and demonstrated the reconciliation of reductionist and holist commitments that Tinbergen and Lorenz promoted as a hallmark of their new science. However, the problem with this conclusion is that Tinbergen did not treat Frisch as exemplary of the ethological program. That is, after Tinbergen joined forces with Lorenz and began promoting ethology, he did not reference Frisch's work in the way one would expect a discipline-builder to reference an exemplar. Instead of asking What is Frisch's relationship to ethology?, the question now becomes more pointed. Given these significant affinities with Frisch, why did Tinbergen not present Frisch as an exemplar of ethology?

To this end, I examine Tinbergen's references to Frisch's grey card experiments between 1938 and 1951 and show how Tinbergen and Lorenz's vision for ethology differed from Frisch's work in key respects. Those differences concerned the proper way to interpret experimental results, preferred animal subjects, the use of conditioning in experiments, the choice of explanatory targets, and the practice of reconstructing phylogenies through behavioral traits. Put briefly, Frisch performed his most famous work on honeybees, which required him to condition the bees to perform learned behaviors. His experiments produced evidence about the physiology underlying sensory capacities, and he did not engage in the project of reconstructing phylogenies through behavioral traits. These aspects of Frisch's research did not cleanly mesh with Tinbergen and Lorenz's vision for ethology.

I first introduce the notion of a scientific exemplar and clarify what it would take for something to achieve this status. Then I provide a close examination of Frisch's grey card experimental technique that demonstrates how his approach to animals reconciled holist and reductionist commitments. I show how Frisch's grey card experiments influenced Tinbergen and emphasize the affinities between Frisch's early career research and the program of classical ethology. Finally, I answer the question, Given these affinities, why did Tinbergen not treat Frisch's work as exemplary? I conclude by exploring the multifaceted relations Frisch holds within the discipline of ethology.

## What Does It Mean to Be an Exemplar for a Developing Scientific Discipline?

Nikolaas Tinbergen and Konrad Lorenz are generally acknowledged as the two primary figures in the founding and promotion of twentieth century European ethology. In examining the emergence of ethology as a distinct scientific discipline, Burkhardt employed an ecological perspective in which scientific disciplines occupy niches and compete for resources (Burkhardt 1981). For instance, Burkhardt wrote that "The history of scientific disciplines, it would seem, involves the carving out of niches, the defense and expansion of territories, the management of boundary disputes with neighbors, and the placing of demands on contemporary and future resources" (1981, p. 63). Applying that perspective to the emergence of ethology, Burkhardt believed that "instead of viewing the ethologists as having simply moved into a previously unoccupied niche in the domain of scientific knowledge, it appears more instructive to think of them as having actually *constructed* a niche, and shaped their own ideas in the process" (Burkhardt 1983, p. 440; emphasis in original). This paper adopts Burkhardt's ecological perspective to explore whether Frisch's work played an exemplary role in Tinbergen and Lorenz's early efforts to construct a niche for ethology.

To judge whether or not Frisch's work played that exemplary role, I use Andrea Woody's definition of a scientific exemplar: "Exemplars … display, without explicitly articulating, what a scientific community judges to be explanatory, what model of intelligibility it has chosen to embrace.… An exemplar is an example that, through community sanction, we are urged to follow. It has action-guiding force" (Woody 2003, p. 24). The traditional home for scientific exemplars is textbooks. To reproduce themselves, scientific disciplines must familiarize students with the methodological practices, habits of reasoning, and types of explanations that the discipline deems appropriate. Identifying exemplars is especially important for young disciplines because they need to inculcate new students to persist and grow. Additionally, exemplars can lend credibility by demonstrating a discipline's ability to successfully solve scientific problems. Exemplars show how the practitioners of a discipline achieve their epistemic aims and, in doing so, they communicate practical details often left unarticulated by general disciplinary definitions.

Using this definition of exemplar, I will argue that Frisch's grey card experiments exemplified a reconciliation of reductionist and holist commitments that corresponded to Tinbergen and Lorenz's vision for ethology. However, there are a plurality of ways for scientific investigations to be reductive or holistic, and scientific investigations are only reductive or holistic relative to other scientific investigations. Therefore, to highlight how the practices and habits of reasoning that comprised Frisch's grey card experiments reconciled reductionist and holist commitments in their own time, I compare Frisch's grey card experiments with the experiments of two of his contemporaries.

Multiple animal researchers in the beginning of the twentieth century sought a middle path between controlled experiments directed at reductionist explanations and naturalistic observations that remained sensitive to holistic aspects of animals.[1] What makes the two comparisons I draw in the next section especially relevant to a practice-based analysis of Frisch's grey card experiments is how uncannily similar they are to Frisch's experiments. Each experimentalist examined sought to answer the same question using the same animals via similar methods within five years of each other. Comparing and contrasting these experiments highlights the different ways Frisch could have implemented and interpreted his experiments on animal sensation and therefore provides contemporaneous benchmarks for assessing what was reductionist and holistic about the investigative decisions Frisch made with his grey card experiments.

[1] See, for example, the work of German scientist Wolfgang Köhler (1971) and American scientist Gladwyn Kingsley Noble (Noble 1939; Milam 2010, pp. 55–57).

## Can Fish and Honeybees See Colors? How Frisch's Grey Card Experiments Reconciled Reductionist and Holist Approaches to Animal Sensation

In the early 1910s, multiple researchers were asking the same questions: Can fish see colors? Can honeybees see colors? Frisch is remembered for answering both questions in the affirmative. To defend his finding that fish and honeybees can see colors, Frisch engaged in a public and well-documented feud with the German ophthalmologist Carl von Hess (1863–1923) (Hess 1912a, b, 1913; Frisch 1912, 1913a, b, c, 1914; for commentary, see Warner 1931; Frisch 1967, pp. 48–49; Thorpe 1983, p. 198; Hölldobler 1985; Menzel and Backhaus 1989; Autrum 1990; Backhaus 1993; Kelber et al. 2003; Kelber and Osorio 2010; Munz 2016, chap. 2; Dröscher 2016). By contrast, Frisch was largely unaware of the work of Charles Henry Turner (1867–1923), an American comparative psychologist whose experiments on honeybee color vision anticipated Frisch's own experiments (Turner 1910, 1911; Frisch 1914, pp. 79–80; West-Eberhard 1986; Wehner 2016). Using Hess's and Turner's approaches as a historically relevant comparison class allows one to make more concrete, practice-based claims about what exactly distinguished Frisch's investigations as being reductive or holistic.

Frisch employed multiple experimental strategies aimed at producing evidence for different sorts of explanations throughout his career. Here, I focus on Frisch's grey card experiments, a strategy that Frisch used to investigate color vision in honeybees and fish. Frisch's grey card experiments were well received by fellow zoologists and influenced other researchers to execute their own versions of the grey card experiment, especially in Germany during the 1920s and 1930s (Kelber et al. 2003). In fact, animal behavior researchers throughout the twentieth century continued to perform variations of Frisch's grey card experiment, solidifying the strategy's reputation as a scientifically respectable means of answering questions about animals' sensory capacities (Kelber et al. 2003; Horridge 2009, chap. 1; Kelber and Osorio 2010, p. 1621).

Frisch's grey card experiment allows researchers to make inferences about animals' sensory capacities by observing animals' orientation behavior under controlled circumstances. To begin, researchers need an animal that will reliably orient itself toward a target in a reproducible situation. Often, researchers accomplish this by training animals to orient toward a feeding site. Once the animals are primed to orient themselves to a feeding site, researchers begin training the animal to associate food with a particular color. To achieve this, researchers set out a series of potential food-holders at the feeding site, all of which are various shades of grey except for one potential food-holder that is colored. When feeding the animals, the researchers only put food in the colored food-holder. If the animal can indeed see the color in question, researchers reason that the animal will come to associate the color with food. Alternatively, if the animal cannot see the color in question, the animal should systematically confuse the colored food-holder with the grey colored food-holder of corresponding brightness. After training the animal to associate the colored food-holder with food, researchers perform

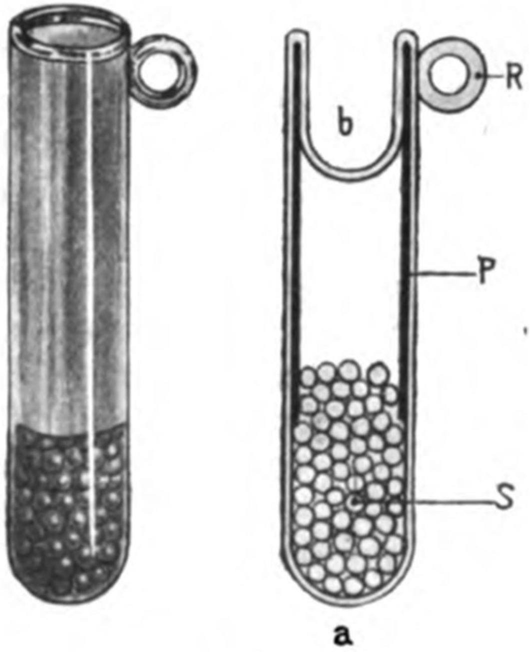



**Fig. 1** A black and white illustration of Frisch's custom glass test tubes. One of the test tubes gives the reader a cross-section view. The small well labeled *b* is where Frisch placed the food; *R* is the eyelet that allowed Frisch to hang the test tubes on a wire. The black line along the walls of the tube labeled *P* represents the colored paper melted into the glass. The little balls at the bottom of the tube labeled *S* indicate the balls of shot Frisch used to weigh down the tubes and keep them upright in the water. (Frisch 1913a, p. 47)

the decisive experiment by presenting the animal with the multiple grey and one colored food-holder; this time, however, none of the food-holders contain food. If the animal still orients to the colored food container, researchers have good evidence that the animal can recognize the color in question. That is because the color was the critical cue directing the animal toward the colored food-holder as opposed to some confounding cue emanating from the food.

## Can Fish See Colors? Contrasting Frisch's Grey Cards with Hess's Light Box

After defending his thesis in the winter of 1909/1910, Frisch, now a research assistant to Richard Hertwig at the University of Munich's Zoological Institute, demonstrated that freshwater minnows (*Phoxinus laevis*) can recognize colors by performing the grey card experiment. To train the fish, Frisch used "rather expensive" custom glass test tubes (Fig. 1) that had either greyscale or colored pieces of paper melted into the walls of each tube. Frisch purchased the paper from Ewald Hering's laboratory, where they produced standardized colors for experiments on color perception (Frisch 1913a, pp. 47–48; Munz 2016, p. 41). The tubes had little eyelets at the lip so that Frisch could hang them in a row by threading a wire through them. To ensure that the tubes stayed right side up when submerged in water, Frisch weighted the bottom of each tube with balls of shot. He then trained the fish for "a few weeks" in diffused daylight coming from the window of his laboratory by submerging the tubes in his fish tanks with food in the colored tube (Frisch 1913a, pp. 44, 48). In

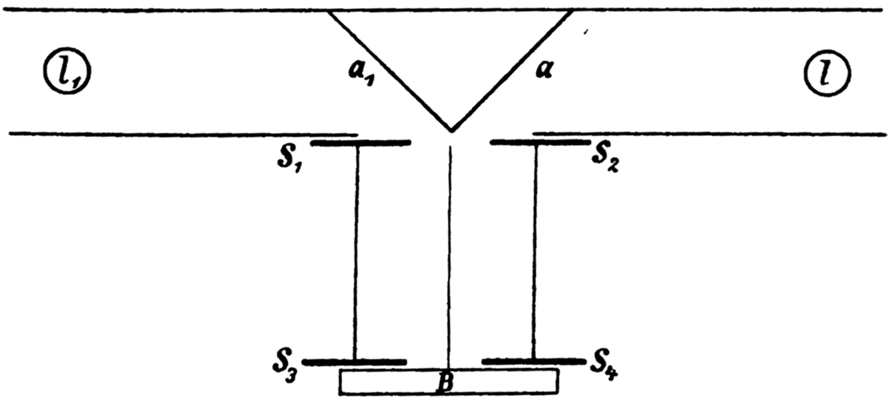



**Fig. 2** An illustrated cross-section view of the T-shaped device Hess used to direct different sources of light in the same direction (Hess 1909, p. 31)

his research report, Frisch informed the reader that "shy" fish are unsuitable, but that such fish can be made tame by keeping them in glass tanks that have no hiding places (Frisch 1913a, p. 46). He also advised readers not to house too many fish per tank lest the fish begin orienting toward the excited movements of other fish and not the color in question. Once Frisch had trained the fish to associate a particular color with food, he submerged the tubes with no food and found that the fish reliably swam to the colored tube. Thus, Frisch concluded that fish possess color vision.

That result squarely contradicted the work of Hess, whose experiments on the Mediterranean sand smelt (*Atherina hepsetus*), carried out at the Anton Dohrn Zoological Station in Naples, had indicated that fish do not possess color vision. For his experiments, the Station provided Hess with one hundred or more fish every two or three days over a period of weeks, so that by the end of his trial he had worked with over a thousand fish (Hess 1909, p. 2). Hess used young fish because older fish tended to be too shy to properly participate in his experiments. He required fresh fish every two or three days because many of the fish died after a day of being held in captivity and those that survived were often too weak to use in further experiments. Hess's general experimental strategy involved keeping fish in tanks and subjecting them to a dark environment "for at least thirty minutes." Then, using tightly controlled sources of artificial light (including incandescent light bulbs, arc lamps, and Nernst lamps), Hess illuminated different portions of the tank with light of varying color and brightness. By observing where the fish swam under different lighting conditions, Hess made inferences about their capacity to see colors (Hess 1909, p. 3).

One of the most striking versions of Hess's experiments involved a T-shaped device that allowed him to direct light from two different sources in a common direction while keeping the two lights distinct (Fig. 2). To use the device, Hess shone light into the two openings facing each other ($l$, $l_1$). Two surfaces sprayed with magnesium oxide ($a_1$,$a$) then reflected the lights in a common perpendicular direction. The channel into which the light was reflected had a dividing wall that kept the reflected lights separate until they exited the opening. Hess directed the divided lights at his fish tanks and systematically manipulated the color and brightness of each light. He found that the fish generally swam to the brighter of the two lights, irrespective of color, such that he could manipulate the movements of the fish through subtle contrasts in brightness. In Hess's words, "All the facts so far established by us would be in good standing with the assumption that the examined fish are totally color blind, indeed, according to such an assumption one could have predicted the behavior actually observed in detail" (Hess 1909, p. 35).[2]

Hess's and Frisch's different experimental strategies led to conflicting results regarding color vision in honeybees. Frisch found honeybees could discriminate between colors, while Hess found they could not. In hindsight, the dispute largely resulted from both researchers' failure to contextualize their findings (Tinbergen 1942, p. 45; 1951, p. 8; Hölldobler 1985; Menzel and Backhaus 1989, p. 281; Menzel 2004, p. 466; Dröscher 2016, p. 4; Gadagkar 2018). In his light box experiments, Hess had created an emergency situation in which the animals fled toward the brightest source of light. Frisch's grey card experiments, on the other hand, caused animals to exhibit feeding type behavior. Taken together, Hess's and Frisch's results showed that in the context of feeding, fish and honeybees exhibit an ability to discriminate between colors; in the context of fleeing, fish and honeybees seem to disregard color and move in the direction of the brightest light. In short, fish and honeybees can see colors, or, more precisely, under some circumstances their behavior indicates that they can distinguish different colors of the same brightness.

Since Hess and Frisch's dispute centered on the question of whether fish and honeybees can see colors, commentators acknowledge Frisch as the winner and attribute his success to his differing methods. For instance, Dröscher noted that Frisch's and Hess's approaches were "profoundly different." Hess, she argued, "acted as an experimentalist, measuring reactions and drawing reductionist conclusions," while Frisch "acted as a naturalist" and tried to keep the fish "in an environment that was a natural as possible" in order to "pose biologically meaningful questions" (Dröscher 2016, pp. 3–4).

Hess's and Frisch's experimental strategies did differ, but the difference, I suggest, does not come down to one being a reductionist and the other a naturalist. Both were reductionists. Both Frisch and Hess deployed their respective experimental strategies as part of research programs that sought reductionist explanations of animals' sensory capacities. As an ophthalmologist, Hess was deeply familiar with the physiology of eyes and sought to understand how the histological and physiological properties of eyes enable and constrain sensory capacities (Hess 1902, 1905, 1911, 1912b). Frisch received his doctoral training in zoology, but he came from a family of academics who had made significant contributions to neuro-sensory physiology and color theory (Exner 1881, 1885, 1889, 1891; Exner and Exner 1902, 1910; Frisch 1989; Coen 2006, 2007). Indeed, Frisch performed his first formal university

[2] "Alle von uns bisher ermittelten Thatsachen würden gut in Ein klang stehen mit der Annahme, dass die untersuchten Fische total farbenblind seien, ja, nach einer solchen Annahme hätte man das thatsächlich gefundene Verhalten in allen Einzelheiten voraussagen können."

research as a first- or second-year university student under the guidance of his uncle Sigmund Exner, the director of the Institute of Physiology at the University of Vienna. Exner guided Frisch through investigations into how nervous stimulation affects eye pigmentation in invertebrates (Frisch 1967, pp. 32–33). Although Frisch is most remembered for establishing the existence of unexpectedly sophisticated capacities in animals,[3] he also sought causal explanations for animal capacities in terms of lower-level physiological dynamics (Frisch 1908, 1910, 1911; Munz 2017). Furthermore, he trained his doctoral students to pursue research oriented towards such reductionist explanations (Baumgärtner 1928; E. Scharrer 1930; Frisch and Dijkgraaf 1935; B. Scharrer 1935, 1937; Löwenstein 1932; Jander and Waterman 1960; Dijkgraaf 1963; Hug et al. 1964; Boch and Shearer 1971). The difference between Hess's and Frisch's work is not that one pursued reductionist explanations while the other did not; both Hess and Frisch sought such explanations.

The key difference between Hess's and Frisch's experiments is rather the degree to which those experiments employed a holistic perspective on animal capacities as phenomena exhibited in particular contexts for adaptive purposes. Frisch's grey card experiments differed from Hess's light box experiments in that they employed more evolutionary thinking. Frisch was initially skeptical of Hess's claim that fish are color-blind because his doctoral thesis research had shown that minnows change color according to luminescent properties of their environment (Frisch 1967, p. 48). Frisch reasoned that an animal exhibiting this capacity would be able to perceive color patterns themselves (Thorpe 1983, p. 198). Similarly, Frisch believed that insects who feed on the nectar of flowering plants would likely possess color vision as a means of recognizing food sources (Frisch 1914, pp. 1–5). In other words, Frisch hypothesized that minnows and honeybees can see colors because the way minnows and honeybees interact with their environment suggested that such a capacity would be adaptive. He then used that evolutionary reasoning to design experimental situations that caused minnows and honeybees to exhibit their color discriminating capacity.

A brief anecdote from Frisch's time as director of the Zoological Institute of Rostock University in the early 1920s further illustrates the sense in which his research was holistic in its incorporation of evolutionary reasoning. Because the ears of fish lack any structure analogous to the cochlea of terrestrial vertebrates, many scientists at the beginning of the twentieth century believed fish were deaf. In his autobiography, Frisch remembered how one such scientist "whistled to them [catfish] in many different ways, with his mouth, through his fingers, on penny whistles, high or low, but in vain. He even asked a famous singer to sing to them, but the fish were no more moved by her trills and shakes than by his own common or garden whistling. They did not give the slightest sign of sound perception" (Frisch 1967, p. 83). In response, Frisch reasoned that, "If I were a small fish, I should be interested in earthworms and other delicacies of the kind,

[3] Minnows change body pigmentation by perceiving light through a translucent window in their cranium; honeybees can perceive ultraviolet and polarized light, and communicate the distance and direction of food sources to nest mates via a "dance language."

but hardly in the coloratura of a famous soprano which normally would not be in the least relevant to my survival" (Frisch 1967, pp. 83–84). By blinding a captive catfish and training the fish to associate his whistling with food, Frisch was able to demonstrate that catfish can hear (Frisch 1923). He did not go on to investigate the specifics of how hearing contributes to the fitness of catfish. He used basic evolutionary reasoning to design an experiment that established the existence of a sensory capacity because the establishment of such a capacity had interesting implications for research on the physiological mechanisms underlying hearing.

The sense in which Frisch's grey card experiments exhibited a holistic understanding of animals is also reflected in his use of relatively natural environments. As a background condition, keeping aquatic animals in tanks requires extensive maintenance (Muka 2014). Frisch kept his freshwater minnows alive for weeks as he trained them, and he attempted to modify the environments of shy fish in a way that would make them experimentally useful. Hess discarded shy fish and was less successful keeping his Mediterranean smelt alive, a species accustomed to brackish water. Nevertheless, Hess overcame this limit on his control by persistently resupplying his stock, a strategy that required the extensive resources of Anton Dorn's Zoological Station and the labor of the "extraordinarily accommodating gentlemen" who worked at the station and supplied him with fish (Hess 1909, p. 2). Frisch's ability and desire to acclimate his fish to his laboratory environment makes his experiments more holistic than Hess's in the sense that he attended to the relationship between his experimental subjects and their environment. However, there is still quite a difference between the paradigmatic image of the naturalist as observing animals in their naturally occurring environment and Frisch's grey card experiments. Like Hess, Frisch required the artificial technologies of the laboratory to exert the kind of control necessary for his experimental strategy.

When considering Frisch's and Hess's means of controlling the independent variable of colored light, one can reach a similar conclusion. Both Hess and Frisch invested in custom technologies to manipulate light. Hess employed multiple sources of artificial light and light manipulating devices, such as arc lamps, Nernst lamps, filters, mirrors, and lenses (Hess 1909). Frisch commissioned custom feeding tubes exhibiting standardized colors for vision research (Frisch 1913a, p. 48). The difference is that Frisch conducted his experiments in diffused daylight from his laboratory window. By allowing his fish to become familiar with their laboratory environment and subjecting them to normal daylight, Frisch was able to make his fish exhibit feeding behavior as needed for his experimental training and trials. Hess's finer control over properties of light allowed him to quantify his results along an extra dimension. But the extreme lights to which he subjected his fish, paired with the fact that his laboratory environment caused fish to die within a few days, likely contributed to the outcome that his fish performed fleeing type behavior and did not exhibit their capacity to distinguish colors. Frisch's experiments were more holistic in the way they attended to the relationship between animals and their environment, but again, keeping fish in aquaria next to a laboratory window is significantly less naturalistic than experimenting on minnows in the freshwater lakes they naturally inhabit.

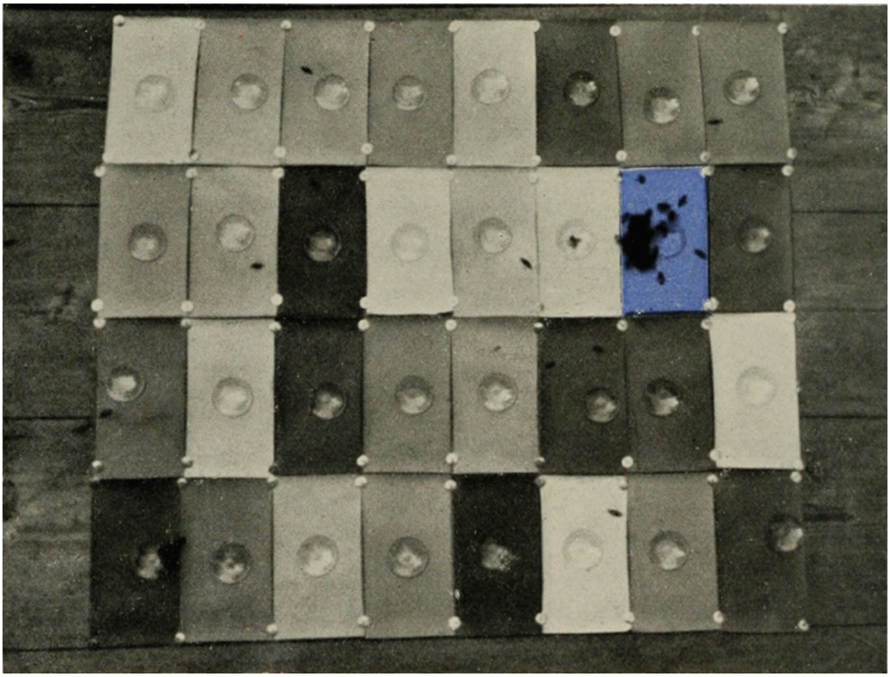


**Fig. 3** A photograph of the feeding station used in one of Frisch's grey card experiment trials. The photograph is black and white and depicts an array of grey scale tiles laid on a table, except for one tile that is colored blue. A little glass food bowl has been placed in the center of every tile. When the photograph was taken, Frisch had already trained honeybees to associate the blue tile with food. The experimental trial captured in the photograph depicts a group of honeybees congregating exclusively on the blue tile feeding bowl they had been conditioned to associate with food, despite the fact that all of the food bowls on the grey scale tile contain sugar water while the bowl on the blue tile is empty. (Frisch 1914, p. 190)

## Can Honeybees See Colors? Contrasting Frisch's Grey Cards with Turner's Colored Cornucopias

The Frisch-Hess comparison highlights holistic features of Frisch's work. The next comparison highlights reductive features of Frisch's work. Though Frisch was unaware of it at the time (Frisch 1914, pp. 79–80), the American comparative psychologist Charles Henry Turner was performing experiments in St. Louis, Missouri that also indicated honeybees can see color and were very similar to the grey card experiments.

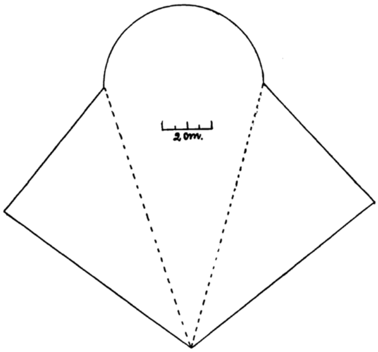
Frisch's grey card experiments on honeybees closely resembled to his previously described experiment on minnows. To train the bees to associate some color with food, Frisch set out greyscale or colored tiles from Hering's laboratory on a table and placed little glass bowls on the tiles (Fig. 3). He then placed honey or sugar solution in the bowls on top of the non-grey tiles. Once Frisch had trained the honeybees to associate a particular color with food for a few days, he set out empty bowls or no bowls at all on the grid. The honeybees reliably navigated to the colored square to which they had been trained, demonstrating an ability to discriminate colored squares from grey squares of corresponding brightness. Thus, Frisch concluded that, like minnows, honeybees can recognize colors.

Unlike his minnow experiment, Frisch performed his grey card honeybee experiments outdoors at his family's summer property in Brunnwinkl, Austria (Frisch 1913b, c, 1914). Beginning a pattern that he continued for much of his career, Frisch studied honeybees when they were active in the summer and fish in the winter. The honeybees Frisch experimented on came from the domesticated hive of an apiary. In his Munich laboratory, Frisch was able to feed his captive minnows whenever he wanted, but the honeybees presented more of a challenge. If he filled the feeding bowl every time the foraging honeybees emptied it, he found that his feeding site attracted an unmanageable number of foraging bees (Frisch 1914, pp. 11–12). However, when the feeding bowl became empty, he found that most bees quickly flew away from the site. By marking each bee that came to his feeding site with paint to avoid double counting, Frisch determined that by refilling the bowl every thirty minutes, he could repeatedly attract the same group of roughly 200 individual foragers. To record every instance of a honeybee landing on any of the tiles, Frisch enlisted help from friends and family vacationing at the Brunnwinkl property (Frisch 1914, p. 9; 1967, p. 56). In this way, he was able to manipulate honeybees' foraging behavior into discrete experimental trials whose results could be quantified with reasonable accuracy.

In stark contrast to Frisch, who was born into the scientific dynasty of the Exner family in fin de siècle Vienna (Coen 2006, 2007), Charles Henry Turner was an African American born in Cincinnati, Ohio in 1867, two years after the end of the American Civil War (Turner 1902; see also Abramson 2003, 2006, 2009). Turner was probably the first African American to publish in *Science* (Turner 1892), and when Turner earned his Ph.D. in zoology from the University of Chicago in 1907, he was probably the first African American to earn such a degree from that institution (Abramson 2009, pp. 346). He was trained in the tradition of American comparative psychology, and much of his work involves behavioral experiments on insects. Contrary to many of his entomologist contemporaries, Turner believed that insects like ants and honeybees were capable of learning and intelligent action, a view that is widely accepted today. Nevertheless, due to the pervasive racism of American academics, Turner was unable to secure a professorship at a major research university (Du Bois 1929; Abramson 2009, pp. 348–350). Securing a position as a science teacher at the segregated Sumner High School in St. Louis, Missouri, Turner performed a series of experiments on honeybee color vision.

Rather than work with honeybees from an apiary, Turner sought to attract wild honeybees for a series of experiments he performed over the course of five consecutive summer days (Turner 1910). He began by placing honey on red cardboard discs that he either pinned to existing plants at various heights or attached to stem-like rods he staked in the ground. Initially, the honeybees ignored his feeding site, even after he caught a forager in a bottle and attempted to force the bee onto his honeyed disc, but eventually Turner succeeded in attracting foragers. He used red colored discs and blue colored discs, but he only placed honey on the red discs. Before ending his first day of experiments, he left three red discs in the field with all

**Fig. 4** A black and white illustration of the cardboard cornucopia vessels used by Turner. Turner constructed the vessels by folding along the dotted lines and fastening the overlapping corners to each other to form a funnel with a protruding, semicircular lip. (Turner 1910, p. 268)



the honey they could hold. When he returned the following day, the honey was gone. Over the next four days, Turner continued to reinforce the association between food and the color red by placing honey on red feeding vessels but rarely placing honey on his blue or green vessels. After using discs, he designed cardboard *cornucopia* vessels (Fig. 4) that resembled flowers and also cardboard boxes with little portico entrances. Turner found that when he did put honey on blue or green vessels, the bees nonetheless mostly ignored them in favor of the red vessels. When he presented the bees with two empty vessels, one red and one green, they tended to avoid the green one while the red vessel became "packed almost full" of bees so that "it was impossible for those that reached the inner depths to leave" (1910, pp. 270–271).

Turner conceded that his results could be explained by honeybees' ability to discriminate between different shades of grey rather than possessing true color vision. But because he had observed honeybees fly directly to his red vessels when the vessels were in the shade, direct sunlight, or cloud-diffused sunlight, Turner reasoned that the bees could recognize the color red as distinct from blue or green by means that did not rely on discriminating different shades of grey (1910, p. 278).

In comparing Turner's and Frisch's experiments, the most striking contrast has to do with available resources and experimental control. In a footnote, Turner explained that "When these experiments were first planned, it was my intention to mark each bee that participated; but, at this stage of the work, I realized that such a procedure would be impracticable and my paint and brush were put away" (1910, p. 264). Such a procedure was quite practicable for Frisch, who used a paint dot notation technique and timed interval feedings to structure the foraging runs of a known quantity of bees. Like Frisch, Turner attempted to count the number of bee-landings on each of his feeding vessels to quantify his results into tables. However, unable to produce discrete foraging runs with wild honeybees, and lacking assistants to help him count the number of bees landing on his various vessels, Turner had fewer and less reliable quantifications. For instance, the tables Turner produced contain X's to designate "that the bees were so numerous that it was impossible to make an accurate count" (1910, p. 269). Finally, although both men worked outside, Frisch used standardized colors and grey-scale tiles to systematically control for the possibility that honeybees discriminate colors solely according to brightness. Turner crafted flower-like feeding vessels, pinned them to existing plants in the honeybee's environment, and relied upon naturally occurring variations in brightness. Frisch's enhanced control allowed him to produce more decisive, quantitative results; Turner's use of happenstance variations in brightness and wild honeybees made his experimental conditions more similar to conditions in nature, but his results were less decisive and quantitative.

A subtler contrast between Frisch and Turner concerns their willingness to make claims about the mental experiences of animals. At the end of his paper on honeybee color vision, Turner wrote, "These experiments prove that, to the bee, my colored discs, my colored cornucopias, and my colored boxes were something more than mere sensations; it seems to me that they were true percepts. To the bees those things had acquired a meaning; those strange red things had come to mean 'honey-bearers,' and those strange green things and strange blue things had come to mean 'not-honey-bearers'" (1910, p. 279). Based on his observations of sophisticated behaviors in ants and snakes, Turner also ascribed "practical judgements" to those animals, a notion he described in one paper as "[responding] to stimuli, not as ends in themselves, but rather as means to ends" (Turner 1907, p. 343, 1909). Turner's willingness to make inferences about mental operations driving the behaviors of animals he observed is in keeping with his admiration of George Romanes, an evolutionary biologist whose book, *Animal Intelligence*, contains the following dictum: "Starting from what I know subjectively of the operations of my own individual mind, and the activities which in my own organism they prompt, I proceed by analogy to infer from the observable activities of other organisms what are the mental operations that underlie them" (Romanes 1883, pp. 1–2). Turner's esteem is exhibited by the extraordinary name he gave to his second son: Darwin Romanes Turner.

Frisch, by contrast, displayed a career-long reluctance to make claims about the mental life of animals. As Munz argued, Frisch "believed that the workings of other minds, be they human or non-human, were not accessible to reliable scientific methods, which for him amounted to those of experimental physiology" (2007, p. 47). In a pronouncement characteristic of his stance on animal minds, Frisch wrote, "If I have taken to speaking of the psychology of the bees, I still want to make one thing clear up front: I cannot speak of what goes on in the bee's soul, but only of those things which manifest themselves externally" (Frisch 1937, p. 9; cited in Munz 2007, pp. 42). This reserved attitude toward the mental life of animals is also evident in the way Frisch wrote about his most celebrated and sensationalized discovery. Although Frisch dubbed certain communication behaviors between honeybee nest mates "the dance language," he was always careful to put the word *language* in scare quotes lest he be interpreted as making deeper claims about honeybees' mental faculties.[4] Unlike Turner, Frisch's work on honeybee color vision does not speak to what colors may mean "to the bee" (Frisch 1914).

In summary, comparing Frisch's grey card experiments with the work of Hess and Turner shows how Frisch reconciled reductionist and holist approaches to the problem of animal sensation. The Frisch-Turner comparison highlights Frisch's

[4] For an explicit discussion of Frisch's justification for using the term *dance language*, see Frisch's (1953) response to a critic who argued that honeybees' communication behaviors do not fulfill the criteria of a true language.

reductionist commitment to explaining animals' sensory capacities in terms of their underlying physiology, and it shows how he used domesticated animals in a tightly controlled environment to generate decisive evidence for those explanations. The Frisch-Hess comparison, on the other hand, highlights how Frisch's holistic understanding of organisms as entities affected by environmental context and evolutionary history helped him design experiments that caused animals to exhibit the capacities under investigation.

## The Case for Frisch as Early Exemplar of Ethology: How Frisch's Experiments Influenced Young Tinbergen and Embodied an Important Element of the Ethological Program

Progressing in roughly chronological order, in this section I establish the influence of Frisch's grey card experiments on young Tinbergen. Then I examine the conceptual affinities between Frisch's grey card approach to studying animals and the disciplinary niche Tinbergen and Lorenz sought to claim for early ethology.

In 1925, Tinbergen was eighteen years old. He was unsure about attending university until his parents sent him to an ornithological field station for the summer, an experience that helped convince him to enter the University of Leiden as a zoology student (Tinbergen 1985, p. 437; Burkhardt 2005, p. 190; Munz 2005, p. 543). Frisch, by contrast, was thirty-nine years old. He had just replaced his former mentor, Richard Hertwig, as the director of the Munich Zoological Laboratory and, during the previous year, had co-founded the *Zeitschrift für vergleichende Physiologie,* a journal that continues to thrive under the title *Journal of Comparative Physiology* (Heldmaier et al. 2014). When Tinbergen was just beginning his academic training in zoology, Frisch had already established himself as one of the most prominent researchers in the field.

Tinbergen's first contact with Frisch came through Frisch's research reports. As a university student, Tinbergen was generally more interested in observing animals and performing experiments than reviewing scientific literature on animal behavior and identifying influences (Baerends 1991, pp. 3–4; Burkhardt 1999, pp. 504–505; Kruuk 2003, pp. 58–59, 78–81). In light of that tendency, Tinbergen's explicit identification of Frisch as an early influence during his time as a student is all the more striking. In an autobiographical essay, he recalled reproducing some of Frisch's experiments on animal sensation as a student, experiments that "seemed (and still seem) to me methodologically faultless and beautifully elegant in their sophisticated simplicity.… I had a tremendous admiration not only for his style of research, but also for the way he described it" (Tinbergen 1985, p. 440). As shown in the previous section, Frisch persistently refrained from making inferences about the subjective experiences of animals. This omission must have further endeared Frisch's research to Tinbergen the student, who was developing a suspicion, which he harbored for the rest of his life, that the subjective experiences of animals are inaccessible to scientific investigation (Tinbergen 1985, pp. 439–440; Burkhardt 1997; Kruuk 2003, pp. 76–81). Contrary to Dutch animal psychologists like Johannes Abraham Bierens de Haan, Tinbergen sought causal, physiological explanations of animal behavior over psychological explanations. The action-guiding influence of Frisch's research became especially evident in Tinbergen's PhD thesis on the orientation behavior of the digger wasp *Philanthus triangulum*, a thesis that Tinbergen published in Frisch's *Zeitschrift für vergleichende Physiologie* (Tinbergen 1932).

Digger wasps reproduce by laying eggs in small, self-made burrows that they supply with honeybees they have paralyzed and captured. When the wasp's eggs hatch, the larvae eat the paralyzed honeybees. In his thesis, Tinbergen investigated the sensory capacities that enable digger wasps to identify both their honeybee prey and their nest burrows. Tinbergen explicitly stated that his experiments were inspired by Frisch's grey card training method (Tinbergen 1932, pp. 312, 320) and called Frisch's (1914) research on color vision in honeybees a "classic work" (Tinbergen 1932, pp. 310, 312, 320), an honorific not bestowed on any other citations. By marking wasps using Frisch's paint dot technique, Tinbergen was able to keep track of individual wasps and observe that they make multiple burrows (Tinbergen 1932, p. 307; Burkhardt 2005, p. 194). That observation further supported Tinbergen's hypothesis that wasps require some means of remembering and recognizing the locations of their hidden burrows.

To determine whether the wasps used visual cues to recognize their burrows, Tinbergen waited until the wasps constructed a burrow. Then, he placed pine cones around the burrow in a circle. If the wasps used visual cues to identify their burrows, then Tinbergen reasoned that the wasps should come to associate the pine cone formation with their burrow. After allowing the wasps time to make this association in their coming and going from the nest, Tinbergen created a decoy burrow about 30 cm away and moved his pine cone formation to the decoy burrow. When wasps returned, they oriented to the decoy surrounded by pine cones, not their actual burrow. In an attempt to control for the possibility that the wasps used scent cues emanating from the pine cones to orient to their burrow, Tinbergen repeated the experiment, but instead of training the wasps to associate a pine cone formation with their burrow, he attempted to train wasps to associate pine-scented oil with their burrow. In another experiment meant to control for scent cues, Tinbergen employed Frisch's method of using "bee scissors" to amputate the antennae of the wasps (Frisch 1921). Both the pine oil and amputated antennae experiments indicated that wasps do not use scent cues to orient to their burrows.

Finally, in a clear reproduction of Frisch's grey card experiments, Tinbergen used the same standardized colors and grey-scale tiles from Hering's laboratory to test whether the wasps can discriminate between colors (Tinbergen 1932, p. 320). He trained wasps to associate a colored square with the location of their burrow. Then, he replaced the colored square with a grey square of corresponding brightness and placed the colored square next to a decoy burrow. The wasps continued to orient to the real burrow with the grey square, indicating they may not be able to recognize colors. However, Tinbergen remained cautious and avoided the over generalizations that characterized the Hess-Frisch feud. As he wrote, "It must be emphasised that this in no way implies that *Philanthus* is unable to perceive colour; it is quite possible that, with the aid of 'natural' landmarks, colour vision could be demonstrated" (1932, p. 324; translation from Tinbergen 1933, p. 122). This seemingly minor divergence between the way Tinbergen and Frisch interpreted their grey card experiments came to play a major role in the way Tinbergen referenced Frisch after he partnered with Lorenz to promote ethology.

After completing his doctorate, the newly married Tinbergen left for an expedition to Greenland with his wife, Elisabeth Amélie Rutten. When he returned in the fall of 1933, Tinbergen stayed on at the University of Leiden as an assistant. There he began training his own group of university students. He established a summer field site at Hulhorst, where he brought students to continue digger wasp experiments along the lines of his thesis work (Tinbergen 1935; Tinbergen and Kruyt 1938; Tinbergen and van der Linde 1938; Baerends 1941). One of Tinbergen's students during this time, Gerard Baerends, remembered how the work of Frisch influenced their studies:

> For the study of causal mechanisms, the work of behavioural physiologists such as Von Uexküll and Kühn, but above all that of Karl von Frisch, was even more important. Von Frisch can be said to have founded the art of making an animal answer questions; this was exactly what Niko needed and wanted to extend to his own experiments. Von Frisch's approach inspired various studies of the Leiden group on how animals perceive and recognize those stimulus situations in their environment that are of biological significance to them." (Baerends 1991, pp. 12–13)

Frisch's work had action-guiding force, not just for Tinbergen during his doctoral research but also for the community of young researchers coalescing around Tinbergen immediately after his doctorate (Baerends 1985, p. 18). In addition, there existed an affinity between the way Frisch reconciled holistic and reductionist approaches to animal behavior and Tinbergen's (and especially Lorenz's) theoretical characterization of ethology. Tinbergen began the project of promoting ethology as a distinct discipline in 1936 after meeting Lorenz, who had already formulated the theoretical basis for the new discipline of ethology prior to their meeting.

Lorenz received his first doctorate in medicine from the University of Vienna in 1927 and his second doctorate in zoology from the same institution in 1933. Like Tinbergen, as a student Lorenz was an unsystematic reader (Brigandt 2005, pp. 580–581; Burkhardt 2005, p. 142). He drew more from personal mentors like the anatomist Ferdinand Hochstetter and the ornithologists Oskar Heinroth and Erwin Stresemann. In contrast to Tinbergen, whom his colleagues described as "pathologically modest" (Kruuk 2003, p. 11), Lorenz developed an early conviction that he "knew animals" to a greater degree than most scientific authorities and that he possessed an extraordinary ability to observe and make intuitive judgements about animal behavior. In a monograph published in 1935, Lorenz wrote that outside his own observations of animals, he could only trust the observations of a few animal researchers whom he personally knew and trusted (Lorenz 1935, p. 151). Tinbergen quickly became one of those trusted researchers after the two met at a 1936 symposium on instinct at Leiden University. The two agreed that Tinbergen's experimental work provided an ideal counterpart to Lorenz's theoretical work,[5] and they began to plan future collaborations that would further Lorenz's well-developed programmatic ambitions to develop ethology into a major discipline.

A key element of Lorenz's vision for ethology was a reductionist commitment to causal physiological explanations over psychological explanations. In tracing the influences behind this commitment, Ingo Brigandt suggested that Lorenz's training in medicine at the University of Vienna predisposed him to favor physiological explanations (Brigandt 2005, p. 593). In light of that claim, it is interesting to note that, like Lorenz, Frisch also began his university studies as a medical student at the University of Vienna before switching to zoology. Concerning his time as a medical student at the same institution a few decades earlier, Frisch recalled that "What one is taught about the histology, anatomy, and physiology of the human body during the first 2 years of a medical course is far more detailed and thorough than anything one learns about any one animal in the course of normal zoological studies, and I have always rated this knowledge as pure gain. It provided me with a solid foundation and a permanent point of reference for all investigations into the structure and function of animal organs" (Frisch 1967, pp. 33–34). Though Lorenz's research was more observational and much less experimental than either Frisch's or Tinbergen's, Lorenz characterized ethology as a discipline that could produce decisive evidence for causal physiological explanations. As demonstrated in the previous section, Frisch and his students were already performing that kind of research.

Tinbergen also stressed the link between ethology and reductive physiology. In a 1939 practicum he designed for his animal behavior students at Leiden University, he wrote: "The scientific approach of this analytic ethology, as it is used in this practicum, is thus in principle the same as that of physiology, when this is viewed as the study of the actions of the animals, and there is no objection to considering this ethology a branch of physiology" (quoted in Burkhardt 2005, pp. 218–219, 530–531). Additionally, Tinbergen's last publication before becoming a prisoner of war during the Second World War, entitled "An Objectivistic Study of the Innate Behaviour of Animals, featured many explicit arguments tying ethology to physiological reduction (Tinbergen 1942). Finally, Tinbergen and Lorenz's efforts to associate classical ethology with experimental physiology also bolstered their discipline-building efforts in a more sociological way by conferring the prestige of experimental physiology on the new science of ethology (Burkhardt 1981, pp. 79–80; 1999, p. 502; 2005, p. 218). In an unpublished and undated manuscript for a talk Lorenz delivered at the end of his career, he stated: "The further progress of ethology was due mainly to Niko Tinbergen whose inspired yet circumspect experimentation did much to make ethology recognized as a 'respectable' branch of biological science" (quoted in Burkhardt 2005, pp. 203, 526). The respectability of reductive experimental physiology served as an important counterweight to another

[5] In an interview with Burkhardt, Tinbergen remembered that upon introducing Lorenz to his experimental work, Lorenz exclaimed, "This is just what *I* need!" (Burkhardt 2005, pp. 203, 526; emphasis in original).

key element of Lorenz's vision for ethology: the importance of a holistic perspective and naturalistic observations.

One month before meeting Tinbergen for the first time, Lorenz sent a letter to Erwin Stresemann in which he lamented the fact that so many physiological chemists are unable to see animals as an "organic whole."[6] The word *Ganzheit*, which was translated as *whole*, often appears in Lorenz's arguments for a holistic conception of animals (Brigandt 2003), especially in Lorenz's Russian manuscript, a strikingly philosophical work that Lorenz wrote while a prisoner during the Second World War. The English translator of that manuscript wrote in a foreword that *Ganzheit* might better be translated as *totality* (Martin 1996, p. xxi). Lorenz was quite clear about how overly mechanistic research suffers from an inability to view animals in their totality, and he situated the ethological approach to animal behavior as a middle ground between excessively mechanist schools and the vitalist school: "If the vitalists created a supernatural 'factor' on the basis of the holistic Gestalt or organic phenomena, in the face of which any attempt at analysis would have been tantamount to sacrilege, the mechanists retreated almost voluntarily into blindness to the Ganzheit accompanied by an extreme, methodologically fallacious atomism" (Lorenz 1996, p. 209). Despite the failings of such mechanistic approaches, Lorenz was clear about his own desire to reconcile holistic understandings of behavior with reductionist analyses:

> Because of their [the mechanists] fearless—one is almost tempted to say disrespectful—causal analytical approach to the most complex of problems, indeed because of their conscious simplism, they have achieved major and lasting success in their research. Seen merely as a working hypothesis, mechanism is not only enormously fertile; it is simply the only legitimate approach available to the research worker .... It is a *question of belief* whether one feels in one's heart that there is something supernatural that is immune to research. As a *researcher*, however, one *must* be a mechanist." (Lorenz 1996, p. 195; emphasis in original)

As demonstrated by the Frisch-Hess comparison, Frisch's research successfully incorporated a holistic understanding of animal behavior in the sense that when he designed his experiments, Frisch considered the effect that environmental context has on animal behavior. He also considered how a particular behavior or capacity fitted into an animal's general life strategy, and this holistic perspective informed the way Frisch formulated and tested hypotheses.

The major conclusion, then, is that Frisch's work influenced young Tinbergen and prefigured two key elements of the ethological approach to animals that Tinbergen and Lorenz championed in the 1930s and 1940s. Thus, there seems to be a strong case for viewing Frisch as an exemplar for early ethology. The problem with this

[6] The original text of the passage in the letter from Lorenz to Stresemann, 4 October 1936, is cited in Brigandt (2005, p. 588, n. 46): "Ich kenne aber so viele Physiologische Chemiker, die alle ganz unfähig sind, im Tier eine organische Ganzheit zu sehen.".

assumption, as I will show in the next section, is that Tinbergen did not treat Frisch's work as exemplary.

## Why Did Tinbergen Not Treat Frisch as an Exemplar of the Ethological Program? A Multifaceted View of Frisch's Relationship to the Discipline of Ethology

As we have noted, scientific exemplars achieve their exemplary status when a scientific community urges its practitioners to follow them. Moreover, exemplars are likely to appear in textbooks or other places where disciplinary programs are summarized and promoted. Given the trajectory of my argument so far, it is surprising to see that, although Tinbergen referenced Frisch's work after joining with Lorenz to promote ethology, Tinbergen did not refer to Frisch's work as exemplary. Instead, he framed Frisch's interpretations of grey card experiments—the same experiments Tinbergen had recreated as part of his doctoral thesis—as an object lesson in what not to do. Specifically, Tinbergen invoked Frisch's feud with Hess as a cautionary tale about the mistakes experimentalists make when they do not adopt the ethologist's observational methods or holistic approach to behavioral analysis.

Classical ethology lacked works that were comprehensive and accessible enough to qualify as textbooks prior to the Second World War. The best candidate for ethology's first textbook comes after the war in the form of Tinbergen's 1951 book, *The Study of Instinct*. Tinbergen referenced Frisch's work in a section entitled "Ethograms" (Tinbergen 1951, pp. 7–8). Ethograms describe and catalogue an animal's behavioral repertoire, or the actions an animal normally performs in a variety of natural situations. As characterized by Tinbergen, a properly ethological approach to animal behavior begins with the creation of an ethogram. Without a baseline understanding of an animal's behavioral repertoire, researchers are ill-equipped to analyze the significance of any particular behavior type.

Tinbergen used the Frisch-Hess feud over color vision to illustrate this point: "Special emphasis should be placed on the importance of a complete inventory of the behaviour patterns of a species. It is a natural tendency of the experimental worker to select a special problem, as, for instance, colour vision, or homing, or the delayed response. This specialization is often accompanied by a narrow point of view and a neglect of other aspects of behaviour. The resulting generalizations, based on too limited a foundation, may give rise to sterile controversies" (Tinbergen 1951, pp. 7–8). Then, after summarizing Frisch's and Hess's approaches to the problem of color vision, Tinbergen concluded that "a species may be able to distinguish between colours and, in a way, be colour-blind as well.… Knowledge of the whole behaviour pattern helps us to recognize the relative value of each one of these conclusions and prevents us from describing as incompatible the conclusions drawn from the study of what prove to be two different sorts of behaviour" (1951, p. 8). Frisch considered the adaptive value color vision would have for foraging honeybees and feeding minnows, and he used these considerations to design experiments that demonstrated the animals' capacity to discriminate between colors. He did not, however, acknowledge the possibility that these animals exercise that capacity in all behavioral contexts.

Although *The Study of Instinct* may have been ethology's first textbook, it was not the first place Tinbergen used the Frisch-Hess controversy to construct a niche for the new discipline of ethology. In 1938, two years after meeting Lorenz, Tinbergen became the first person to promote European ethology in the United States when he presented at a conference on Plant and Animal Communities at the Biological Laboratory, Cold Spring Harbor, New York (Burkhardt 2005, pp. 215–217). Tinbergen's presentation, published one year later, referenced the Frisch-Hess dispute to make the point that "no experiments should be started before simple observation of behavior in natural surroundings has discovered the outlines of the behavior pattern" (Tinbergen 1939, p. 228). Tinbergen also referenced the Frisch-Hess dispute over color vision to make the same point in his 1942 paper "An Objectivist Study of the Innate Behaviour of Animals" and in the inaugural lecture he gave upon assuming the chair of experimental zoology at the University of Leiden in 1947 (Tinbergen 1947). As I have argued, the Frisch-Hess comparison highlights the holistic aspects of Frisch's experimental approach to animals, and yet when Tinbergen, as discipline-builder, looked back on that conflict, he judged that Frisch's approach was not holistic enough.

There are several other broad differences between Frisch's research and the disciplinary niche Tinbergen and Lorenz sought to claim for ethology that help explain why Frisch was not explicitly identified as an exemplar of early ethology. First, Tinbergen and Lorenz promoted ethology as a discipline that investigated instinctive or innate patterns of behavior. In order to produce evidence about such behaviors, they championed the study of wild, undomesticated, or unconditioned animals (Lorenz 1935, 1937; Tinbergen 1942; Tinbergen 1985, pp. 444–446; Brigandt 2005). Much of Frisch's work, on the other hand, focused on sensory physiology, and to produce evidence about animals' sensory capacities, he designed behavioral experiments that required researchers to train animals to perform conditioned behaviors. Thus, both the explanatory target and the methodology of Frisch's work were askew from the promoted focus of early ethology.

Second, Lorenz was clear that part of the theoretical foundations of ethology included the idea that instinctive behaviors could be used to reconstruct phylogenies in the same way biologists used morphological traits to reconstruct phylogenies (Lorenz 1932, 1935, 1955; Burkhardt 2005, p. 134). After World War II, and in collaboration with one of his students, Frisch hypothesized about the phylogenetic age of different versions of the honeybee dance language (Frisch and Lindauer 1956, p. 48); but reconstructing phylogenies via instinctive actions was not a major part of Frisch's research. By contrast, the two men Lorenz credited with the insight that instincts can be used to reconstruct phylogenetic relationships—Charles Otis Whitman and Oskar Heinroth—were often framed as exemplary forerunners of classical ethology.

The final difference between Frisch's work and the program of early ethology is highlighted by contrasting the organisms studied by Frisch with Whitman and Heinroth. Although ethology was never promoted as a science that focused exclusively on bird behavior, birds were nonetheless among the most favored animal subjects of early ethologists, especially Lorenz (Burkhardt 2005, pp. 140–141, 147; Munz 2011). Many of Lorenz's early manuscripts were published in the *Journal für Ornithologie* (Lorenz 1927, 1931, 1932, 1933, 1934, 1935). Whitman and Heinroth, the two men Lorenz referenced as forbearers of ethology, also specialized on birds. Frisch, by contrast, primarily worked with fish and honeybees.

So far, this paper has focused on fleshing out Frisch's relationship to ethology via his relationship to Tinbergen in the period between Tinbergen's doctoral work in the 1930s and his publication of *The Study of Instinct* in 1951. I have argued that Frisch's grey card experiments influenced Tinbergen prior to his 1936 encounter with Lorenz. Once Tinbergen became a fellow discipline-builder alongside Lorenz, however, Tinbergen began referencing Frisch's work as a cautionary tale that served to highlight one of ethology's methodological contributions to animal behavior studies.

Before concluding, I will briefly look forward to make the point that Frisch not only meant different things at different times to Tinbergen but also to different researchers working under the ethological banner. The subject deserves a paper of its own, but it is clear that Frisch is regarded as a pioneering figure by a German-speaking tradition of social insect researchers who continue to direct prominent research programs. This lineage largely passes through Martin Lindauer, one of Frisch's most influential students who completed his doctoral training in 1947 (Marler and Griffin 1973, p. 464; Seeley et al. 2002; Menzel 2004, p. 464; Wehner 2013, p. 3). In the 1960s, Lindauer mentored Berthold Hölldobler, Rüdiger Wehner, and Randolf Menzel, three prominent social insect researchers who explicitly view Lindauer and Frisch as exemplary figures for their style of investigation (Hölldobler 1985; Lindauer 1985; Menzel 2004, 2007; Smith 2013; Wehner 2013; Dyer et al. 2015; Dhein 2017). The disciplinary label of *ethology* continues to be promoted by Wehner and Menzel, who claim the title of *neuroethologist*.

Finally, to include one more strand of the story, it is interesting to see how, after the Second World War, Lorenz looked back to Frisch's research program and, as he did with many things, attempted to incorporate its success into his own overarching theory of animal behavior research (Burghardt 1982; Burkhardt 2005, p. 179; Schulze-Hagen and Birkhead 2015, pp. 14–15). Arguing for the importance of animal watching via his theory of Gestalt perception, Lorenz wrote:

> The accumulation of facts stretching across long periods of time which represents the analogy of the inductional basis for the ratiomorphic perceptional achievement, offers an explanation of the fact that great discoveries by the same scientist dealing with the same subject are often several decades apart. For example, Karl von Frisch published his first work on bees in 1913; in 1920 he wrote for the first time on their ability of communication by dances; in 1940 he discovered the mechanisms of orientation according to the position of the sun, which presumes an "inner chronometer," as well as a means of indicating direction in the hive. (This operates through transposing the direction of the sun by "symbolizing" it in the dances by the vertical direction.) In 1940 he discovered the amazing "computer" which can ascertain the position of the sun by the polarization plane of the light from the blue sky. However much diligent

> experimenting and conscientious verifying is contained in these great discoveries of a great scientist, it is not accidental that they took place during the scientist's vacation and were made with his own beehives in his summer home [Brunnwinkl]. For one of the most pleasant properties of gestalt perception is that it is most active in gathering information when the perceiver, absorbed in the beauty of his object, imagines himself to be enjoying the most profound spiritual peace. (Lorenz 1962, p. 53)

Lorenz's narrative represents a reflexive reinterpretation of Frisch's work.

Whereas Tinbergen criticized Frisch between 1938 and 1951 for not bringing a holistic understanding of an animal's behavioral repertoire to bear on the interpretation of grey card experiments, Lorenz looked back on Frisch's research in the 1960s to exalt his supposedly immersive style of animal observation and thereby bolster his own theory of gestalt perception. Surely, one of the reasons why Tinbergen and Lorenz's relationship to Frisch's research changed over time is because Frisch's research also changed and developed over time. This paper has largely focused on Frisch's grey card experiments early in his career. But after 1946, Frisch became tightly associated with his discovery of the honeybee dance language, a discovery that was widely popularized outside academia (Munz 2016). Given Frisch's rise to prominence, it makes sense that Lorenz sought to capitalize on Frisch's increased celebrity. The way Tinbergen and Lorenz related to Frisch's work was historically mobile and defies easy encapsulation.

## Conclusion

So, what is Frisch's relationship to the discipline of ethology? The conclusion of this paper is that there is no single category that captures Frisch's multifaceted relationship to the discipline. Although Frisch never seems to have used the term *ethology* himself (Thorpe 1979, p. 64), his work meant different things at different times to different figures within the ethological tradition. For Tinbergen the university student and early career academic, Frisch's grey card experiments were a formative influence. Then, once Tinbergen assumed the role of fellow discipline-builder alongside Lorenz, Frisch's interpretation of the grey card experiments became a cautionary tale that helped Tinbergen claim a disciplinary niche for ethology by highlighting the need for a properly ethological approach to animal studies. While Tinbergen became the figurehead of ethology after the Second World War (especially in the English-speaking world), Frisch produced a lineage of students, some of whom currently identify as neuroethologists and regard Frisch as a pioneering figure. Finally, for Lorenz in the 1960s, Frisch's research program was a case study whose illustrious reputation reinforced Lorenz's own theory of animal behavior research. This paper has provided grounds to support the pervasive sense that Frisch was important to the discipline of ethology and furthers the project of specifying exactly how he fits into the larger story of ethology.

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