

# The Hawk/Goose Story: The Classical Ethological Experiments of Lorenz and Tinbergen, Revisited

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We present a historical account of the story behind the famous hawk/goose experiments of Lorenz and Tinbergen in a wider context of cognitive ethology. We discuss their significance, for ethological experimentation in general, and specifically for understanding innate constraints on cognition. As examples of the continuing significance of the hawk/goose paradigm of selective habituation, we discuss its relation to “exposure therapy” of human phobias and the use of hawk silhouettes as deterrents for songbirds. Finally we rephrase Uexküll’s thesis of taxon-specific worlds (“Umwelten”) as a “Theory of World.”

*Keywords:* selective habituation, hawk/goose experiments, cognitive ethology, theory of world, phobias, predator-prey

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Based largely on the involvement of the senior author of this paper in his 1961 attempt to replicate the famous 1937 hawk/goose experiments (Figure 1) of Lorenz and Tinbergen (Lorenz, 1939; Tinbergen, 1939; Schleidt, 1961a, 1961b, English translation, Schleidt, 1974) we present a historical account of the story behind these experiments within a wider context of cognitive ethology.

At the 1936 Leiden Instinct Symposium, Konrad Lorenz concluded his all-out critique of the contemporary teachings about learning and instinct with these words:

I do hope and believe . . . that investigations of the instinctive behavior patterns is not an area for highly complex philosophical speculations but a field in which (at least for the time being) *only experimental investigation of individual cases is decisive*. (Lorenz, 1937b, p. 315; our emphasis)

More than half a century later, Richard W. Burkhardt, Jr. wrote:

The symposium was not of equal consequences for all who attended. It did not alter the thinking or change the careers of the older

scientists, who were already well set on their individual courses. For Lorenz and Tinbergen, however, it proved pivotal . . . The symposium’s significance was that it provided the occasion for Lorenz and Tinbergen to meet one another. Each of them had the chance to begin to recognize how well the other’s strength complemented his own. (Burkhardt, 2005, p. 200).

The special strengths of Lorenz, who trained as a comparative morphologist, were his acuity of observation and skill in dissecting complex systems, whereas Tinbergen’s were his talents for planning and conducting experiments.

Lorenz had established a diverse collection of tame animals at his home in Altenberg, Austria, and invited Tinbergen to come and combine their skills in the “experimental investigation of individual cases” (Lorenz, 1937b, p. 315). In the spring of 1937, Tinbergen visited Lorenz in Altenberg (Burkhardt, 2005, pp. 205–213), and during his 3-month stay, they focused on two

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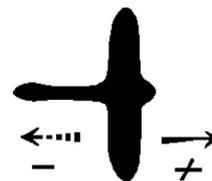
\**Author’s Note.* Text set in [ ] contains additions for increased clarity.

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*Figure 1.* Tinbergen’s famous 1951 rendering of the “hawk/goose dummy” supposedly used by Lorenz and Tinbergen in their 1937 experiments. Such a silhouette released escape behavior in young, experimentally naïve turkeys when flown to the right (as “hawk”): “fixating, alarm calling and marching off to cover” (Lorenz, 1939). No escape behavior was released, however, when the model was flown to the left (as “goose”). (Image reprinted from N. Tinbergen, *The study of instinct*. Copyright 1951 by Oxford University Press. Reprinted with permission.)

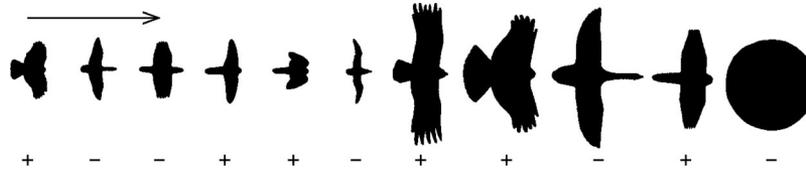


Figure 2. Bird models, pulled high up across the sky by Lorenz and Tinbergen in their 1937 experiments to test the reactions of various birds to raptors. Tinbergen (1948a) claimed that only those models marked + released escape responses, whereas Lorenz (1939) reported that the shape of the models was irrelevant for all species tested except for turkeys (Image modified from N. Tinbergen, *Social releasers and the experimental method required for the study*, *Wilson Bulletin*, 60, pp. 6–51. Copyright 1948 by Wilson Ornithological Society. Reprinted with permission.)

projects: an experimental analysis of egg-rolling behavior in the greylag goose (Lorenz & Tinbergen, 1938) and the responses of various young birds to cardboard dummies of raptors and other flying birds (Figure 2).

The question as to how birds are able to distinguish between life-threatening raptors and harmless flying creatures, or irrelevant objects crossing the sky, had been debated for some time, and Friedrich Goethe apparently was the first to fly cardboard silhouettes of raptors, harmless birds, and geometric shapes over experimentally naïve chicks (Western capercaillie *Tetrao urogallus*, age 51 days; Goethe, 1937). According to Lorenz (1939, p. 94), Oscar Heinroth had observed that domestic chickens are more alarmed by short-necked, long-tailed birds than by long-necked ones: “Many birds in the Berlin zoo reacted by escape to sailing swifts in the first days after the latter’s arrival in spring” (Tinbergen, 1951, pp. 30–31). Thus, inspired by Heinroth’s hypothesis that a short neck and long tail are salient features of raptors, Lorenz and Tinbergen used a reversible model (see Figure 1): wings with a short protrusion on one end and a long one on the other. Thus, depending on the direction of movement, it could be seen as either a flying raptor or a goose.

However, the precise shape of the silhouette of the reversible “hawk/goose dummy” used in the original 1937 experiments by Lorenz and Tinbergen remains a mystery. Lorenz never published a figure of the “hawk/goose dummy,” and Tinbergen depicted three different shapes in his 1939, 1948a, and 1948b papers (Figure 3a–d). The figure in Tinbergen 1948b (our Figure c) carried in its caption the acknowledgment “after Krätzig, 1940,” indicating that this was not his own design, and, since Krätzig did his experiments in September of 1938 (Krätzig, 1940, p. 154) it was probably not the exact shape used in the 1937 experiments. Tinbergen used this design as Figure 65 in his 1951 *Study of Instinct*, now (incorrectly) referenced as “after Tinbergen, 1948a” (our Figure 3d), even though it did not resemble the one depicted in 1948a. But, because it appeared in Tinbergen’s “Study of Instinct,” this shape was generally assumed to have been used in 1937.

The results of the 1937 experiments in Altenberg varied with species, prior experience of the individuals tested, and shape of the models. Tinbergen saw Heinroth’s short-neck hypothesis confirmed:

Some ducklings, which were reared by man and never had any experience with birds of prey, showed intense flight reactions to many

different shaped models, such as circles and triangles. Other species displayed their ‘predator-reactions’ (crouching, running for shelter, threatening) to every birdlike form moving along the sky, provided it had a short neck! (Tinbergen, 1939, p. 23).

Lorenz, also in 1939, gave a more detailed report of these experiments. He discussed especially the importance of “slow relative speed” of the model for eliciting a typical antipredator response, that is, “fixating, alarm calling and marching off to cover,” and emphasized that the shape of the models was irrelevant for all species tested except for turkeys:

“While the form of the model is indifferent, or at any rate does not have a statistically reliable effect on greylag geese and ducklings (for technical reasons we were unable to experiment with adult hand-raised ducks), the contrary could be proven in young turkeys. These experiments were based on Heinroth’s observation that domestic chickens are more alarmed by short-necked, long-tailed birds than by long-necked ones. Our model had a symmetrical pair of wings and, on the longitudinal axis, a short protrusion on one end, and a long one on the other, functioning as its head and tail respectively. The young turkeys actually reacted much more vigorously when the model was propelled with the short end forward. This was well quantifiable in the number of alarm calls uttered.” (Lorenz, 1939, pp. 93–94, translation<sup>1</sup> cited from Lorenz, 1957, p. 256).

Tinbergen and Lorenz never reconciled their different views of the results of the hawk/goose experiments they had performed together, most importantly the effectiveness of the shape of the models, and, especially, of the hawk/goose model. Thus, when they started using the results in their subsequent publications, not only did a difference in emphasis emerge, but also a striking contradiction: While Lorenz reported that only in turkeys is the short neck a salient feature of the flight response (e.g., Lorenz, 1939), Tinbergen claimed that “The reactions of young gallinaeous birds, ducks, and geese to a flying bird of prey are released by the sign-stimulus ‘short neck’ among others” (Tinbergen, 1951, p. 77). As Tinbergen’s 1951 book “The Study of Instinct” became the bible of classical ethology, his sweeping statement turned into an undisputed truth for believers.

That “truth” persisted. In 1967, 30 years after the Altenberg experiments, 16 years after Tinbergen’s sweeping generalization,

<sup>1</sup> Claire H. Schiller’s translation was slightly improved, for example, for *graugänse* “greylag geese” instead of “grey geese” and for *truthühner* “turkeys” instead of “turkey hens.”

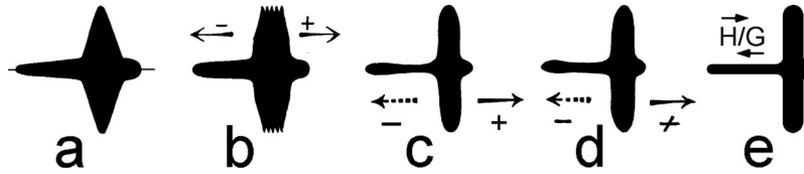


Figure 3. The four versions of Tinbergen's rendering of the "hawk/goose dummy": Tinbergen, 1937(a), 1948a (b), 1948b(c) and 1951(d), and the silhouette as Konrad Lorenz remembered it in 1961 (e). (Image a reprinted from N. Tinbergen, *Why do birds behave as they do?* (II), *Bird Lore*, 41, pp. 23–30. Copyright 1939 by National Audubon Society. Reprinted with permission. Image b reprinted from N. Tinbergen, Social releasers and the experimental method required for their study. *Wilson Bulletin*, 60, pp. 6–51. Copyright 1948 by Wilson Ornithological Society. Reprinted with permission. Image c reprinted from N. Tinbergen, *Physiologische Instinktforschung*, *Experientia*, 4, pp. 121–133. Copyright 1948 by Birkhäuser GmbH. Reprinted with permission. Image d reprinted from N. Tinbergen, *The study of instinct*. Copyright 1951 by Oxford University Press. Reprinted with permission. Image e reprinted from W. M. Schleidt, Über die Auslösung der Flucht vor Raubvögeln bei Truthühnern, *Die Naturwissenschaften*, 48, pp. 141–142. Copyright 1961 by Springer Verlag GmbH. Reprinted with permission.)

and two years after his retracting it and accepting the "selective habituation hypothesis," the cover of the first edition of the ethology textbook by Manning (one of the doyens of ethology) still depicted the hawk/goose silhouette, and reprinted the 1951 version of the story (Manning, 1967, 1979).

### Reexaminations of the Hawk/Goose Paradigm

During the turmoil of World War II, ethological research had come to a standstill. Afterward, while Lorenz was still stuck in a Russian POW camp in Armenia, "Tinbergen set about reviving ethology internationally" (Burkhardt, 2005, p. 283). He reworked his paper "An Objectivistic Study of the Innate Behavior of Animals" (Tinbergen, 1942) into a series of invited lectures he presented across the United States, and cast it as a review of ethological concepts for the *Wilson Bulletin* (Tinbergen, 1948a), complemented by an abbreviated German version (1948b). Thus, in 1948 when Lorenz came home to Altenberg, the stage was set for a good start. Tinbergen's 1948 papers were welcomed with great enthusiasm by Lorenz and his students in Vienna. With respect to the hawk/goose experiments, however, the discrepancy between Tinbergen's 1948 version and Lorenz's of 1939 was spotted instantly. Thus, a reexamination of the 1937 experiments became a matter of high priority.

In 1951, after Lorenz had obtained funding for his germinal ethology group at "Schloss Buldern" in Westphalia, Germany, with the senior author of this paper as his first assistant, the replication of the hawk/goose experiments ranked high on the list of projects. Because Lorenz had found that only young turkeys responded differently to the hawk/goose models depending on the models' direction of movement, the establishment of a breeding stock of turkeys was pursued with the same vigor as the acquisition of geese and ducks. Unfortunately, the turkey flock repeatedly suffered severe losses due to histomoniasis infection (blackhead). Only after moving the animals in the spring of 1956 to the newly established Max Planck Institut für Verhaltensphysiologie in Seewiesen, Bavaria, did Wolfgang and Margret Schleidt succeed in building and maintaining the flock of turkeys needed to put Lorenz's and Tinbergen's claim to a rigorous test. The report that chickens did not respond differently to the two versions of the hawk/goose model

(Hirsch, Lindley, & Tolman, 1955) became an additional incentive to repeat the original experiments with turkeys.

The 1961 "Hawk/Goose Project" had four objectives: First, to learn more about the responses of free-ranging geese, ducks, and turkeys to various "flying objects" they encountered in their natural environment; second, to test free-ranging turkeys under seminatural conditions with various types of "flying objects"; third, to replicate the 1937 hawk/goose experiments of Lorenz and Tinbergen with turkey poults under "controlled laboratory conditions" that matched the original procedure and setting in Altenberg as closely as possible to that at the Max Planck Institut in Seewiesen. But ultimately, the 1961 "Hawk/Goose Project" was intended to explore the texture of an animal's world (as sketched in Figures 5 and 6), and not merely to be an experiment to find out what is innate and what needs to be learned.

Because the exact shape of the original Hawk/Goose dummy was dubious, as discussed above, the senior author of this review (W.M.S.), in preparing for his 1961 studies, discussed with Lorenz the details of the 1937 turkey experiments. Lorenz recalled that the type of dummy he had used best resembled the one pictured in Tinbergen 1948b, and suggested corrections that resulted in the shape depicted as "hawk/goose dummy" in Figure 3e.

### Effects of Naturally Occurring Flying Objects

With respect to the more or less free-ranging fowl on the grounds of the Max Planck Institut in Seewiesen, namely various species of geese, ducks, chickens, and turkeys, the only birds of prey appearing regularly were buzzards (*Buteo buteo*), a species specialized in hunting small mammals. The two other endemic raptors known to hunt fowl, the goshawk (*Accipiter gentilis*) and peregrine falcon (*Falco peregrinus*), were seen only rarely, and no actual attacks on fowl by any raptor were ever observed. However, all these raptors elicited vigilance and, depending on the distance, alarm calls in our fowl. "Vigilance," in turkeys and other fowl, is expressed by freezing in an upright posture and fixing a distant object monocularly (see Schleidt, 1961b, p. 538, Abb.2, and Supplemental Materials Fig. S11). This behavior is highly contagious,

especially when accompanied by alarm calls,<sup>2</sup> and thus helps the human observer detect the object of concern.

Strangely, the strongest reactions to flying objects were evoked not by a raptor, but by two separate and completely harmless events, a meteorological balloon descending nearby, and two storks passing high overhead. In both cases, geese, ducks, and turkeys displayed intense vigilance with monocular staring straight up into the sky, and, in the case of the turkeys, voiced occasional “singing” calls. Such calls are typically emitted in response to very small, slowly moving objects (subtending an angle of about 1° and moving with about 10 diameters per second, or less). The meteorological balloon was red, in the shape of a cylinder, slowly rotating in its descent, and was apparently designed to attract the attention of human observers, who could find it on the ground and return the attached electronic gear to the authorities for a reward. Airplanes and helicopters were largely ignored; only the rare appearance of a blimp elicited increased vigilance and an occasional alarm call. The great attention the two storks elicited among the fowl was especially noteworthy in view of the old “short neck hypothesis”: storks fly, like geese, with the neck stretched forward, and their long neck and beak constitute the antithesis of the short neck of a hawk.

### Experiments With Free-Ranging Fowl

To test free-ranging geese, ducks, and turkeys under seminatural conditions with various types of “flying objects,” closely resembling the conditions (especially the geometry) of the original 1937 Altenberg experiments, a funicular was built 8.3 m above ground level of a test pen (6 by 7 m) within which the experimental subjects could be contained and exposed to dummies of various shapes (for details of the experimental setup see Supplemental Materials, Fig. SI 1). The only change, seen as an improvement, was that while a clothes line was used for the funicular in the Altenberg experiments, a much thinner Perlon monofilament, barely visible from the ground, was sufficient to support the dummies in the Seewiesen experiments.

Various dummies, closely resembling the shapes used by Lorenz and Tinbergen in 1937 (see Figure 2), moving along the funicular elicited vigilance and alarm calls among a variety of fowl, but no statistically significant differences between the responses to the two forms of presentation of the hawk/goose silhouette were found. Surprisingly, the detailed silhouette of a buzzard, and even a plain black disk of equal area had the same effect, initially eliciting an equally strong response. However, when the presentations were repeated, habituation set in, independent of the shape of the dummy.

These results not only falsified Tinbergen’s general short-neck hypothesis but also failed a first attempt to replicate the result of the 1937 experiments with free-ranging turkeys in Altenberg as reported by Lorenz (1939; Schleidt, 1961a, 1961b).

However, Lorenz’s contention that “slow relative speed” of a flying object is a salient feature for eliciting a typical antipredator response was confirmed. The effect of slow speed was especially striking when minute dummies (7.5 mm in length, at a height of 8 m subtending an angle of 3'13") were used, which allowed also presentations at very high relative speeds (up to 0.5 m/s, 66 diameters/s). The alarm call typical in response to high-flying raptors was reliably elicited only in the range between 3 to 6

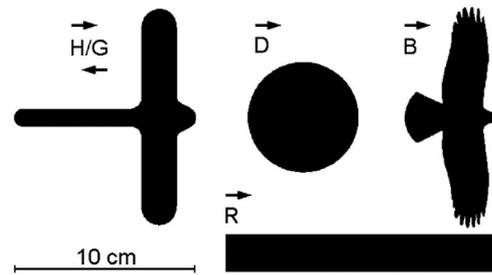


Figure 4. Shapes of dummies used in the 1961 experiments: the hawk/goose H/G, disk D, buzzard B, and rectangle R, all of equal area (28 cm<sup>2</sup>), made of black cardboard, and presented 2.3 m above ground (after Schleidt, 1961a). The original dummies and related materials are deposited at the Vienna Museum of Natural History, Division of Ecology. (Image modified from W. M. Schleidt, *Über die Auslösung der Flucht vor Raubvögeln bei Truthühnern*, *Die Naturwissenschaften*, 48, pp. 141–142. Copyright 1961 by Springer Verlag GmbH. Reprinted with permission.)

diameters/s (Schleidt, 1961b, Table 5). The small dummies at high speed, fitting the range of flying insects, were ignored.

### Replication of the 1937 Hawk/Goose Experiments Under Controlled Laboratory Conditions

The free-ranging turkeys in Seewiesen had ample exposure to a great variety of flying objects. Their equally strong responses to the two forms of presentation of the hawk/goose silhouette, as well as to a detailed silhouette of a buzzard and a plain black disk of equal area, indicated that the salient feature of these dummies was novelty. Thus, the ultimate test of an innate predisposition to respond differently to the feature “short neck” was to experiment with turkeys which had no prior experience with flying objects.

To exclude any uncontrolled experience with flying objects, five bronze turkeys were raised indoors (windows covered with parchment), and tested in an experimental cage (1 by 2.5 m), with a built-in funicular (height of the Perlon monofilament 2.3 m above ground level). For details of the experimental setup see Supplemental Information Fig. SI 3). In addition to the “classical” hawk/goose dummy (after Tinbergen, 1951), a disk, a silhouette of a buzzard, and a rectangle were used (Figure 4).

This experiment was performed in three phases. In Phase I, the first testing phase, on Days 1 and 2, the shapes D, B, G and H each were shown, one at a time, at 5-min intervals, only once. Each presentation elicited very strong alarm on Day 1 and strong alarm on Day 2, irrespective of the shape of the dummy (see Figure 5).

In Phase II, the habituation phase, 11 presentations of the H/G dummy were conducted each day at 5-min intervals, 10 times as G and, inserted on a random schedule, once as H, as the “rare shape.” The mean value of the alarm calls in response to the 10 presentations of G, shown in Figure 5 as the encircled goose icon, was in

<sup>2</sup> Turkeys, like many other species of fowl, emit two different types of alarm calls: “*prr*” and “*singing*.” *Prr* (a loud, rattling call, a rhythmical “clucking”) is emitted in response to sudden disturbance, as an approaching predator, and *singing* (a soft, long drawn-out call) in response to slight disturbance, as a high-flying raptor. See Hale, Schleidt, & Schein, 1969, Figure 102, and Supplemental Materials Fig. SI 2.

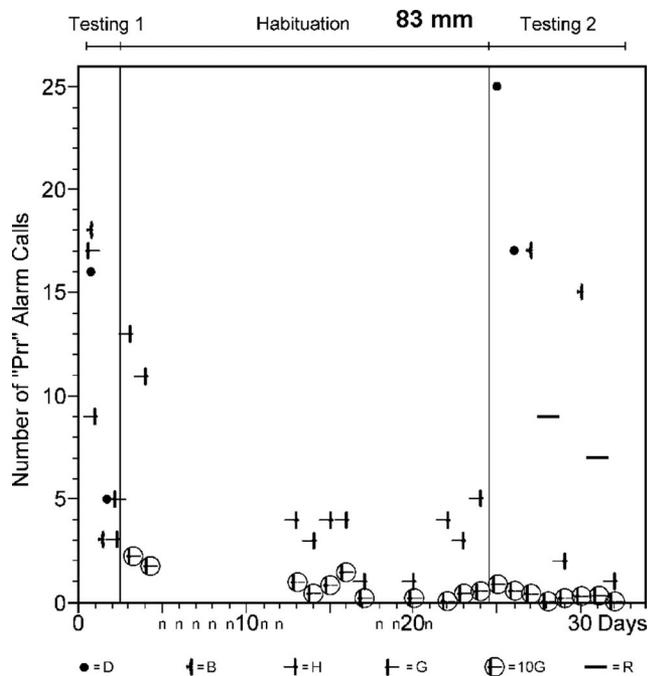


Figure 5. Changes in the response of turkey poult to various shapes of dummies (see Figure 4) over a time span of 32 days, depending on shape and frequency of presentation. The location of the various icons indicates the number of “Prr” alarm calls elicited, and in the case of the encircled goose icon, it indicates the mean number of prr alarm calls in response to 10 presentations of G in phase II and III. Note that because of unforeseen logistical problems, no experiments were conducted on Days 5 to 12, Day 18, 19, and 21. (Image modified from W. M. Schleidt, Über die Auslösung der Flucht vor Raubvögeln bei Truthühnern, *Die Naturwissenschaften*, 48, pp. 141–142. Copyright 1961 by Springer Verlag GmbH. Reprinted with permission.)

all 11 trials significantly less than the number of alarm calls elicited by H ( $p < .001$ ).

In Phase III, the second testing phase, 11 presentations were again conducted each day, but now the disk was inserted once within 10 presentations of G. The disk evoked the strongest response ever observed in this group of turkeys. On the following day when the same schedule was repeated, the response to the disk was slightly less than on the preceding day, but, nevertheless, as strong as on Day 1, when the disk was first presented. On the next day, when the buzzard silhouette was shown, imbedded in a sequence of 10 Gs, the response, once again, was very strong (as strong as the response to the disk on the preceding day, and similar to that on the very first showing).

The results of phases II and III strongly supported the “selective habituation hypothesis,” and created a stir among the scientific community at the Max Planck Institute. Lorenz welcomed the result as an important advance, but Erich von Holst, dean of behavioral physiology, refused to accept the implications: in his view an innate releasing mechanism of an antipredator response that did not include some feature of “Gestalt” would, in terms of evolution, make no sense. He pointed out that any random movement of a leaf on a tree, or of a falling branch, would elicit alarm, and when a predator appeared, it would be ignored. So, W.

Schleidt asked him what kind of shape he would propose to be tested. Von Holst suggested testing the effect of a “flying stick,” a rectangle moved along its main axis. A new dummy (R) was cut to von Holst’s specification and shown on the following day, imbedded in a sequence of 10 Gs. The response to R (9 prr calls), once again was remarkably strong (as strong as to H on Day 1, and considerably stronger than to H, when tested the next day). The response remained high when R was tested again two days later. An annotated English translation of the original paper (Schleidt, 1961a) is available as Supplemental Materials (AI 1).

**Replications of the Replication**

The 1961 replication, reviewed above, was intended as only the first part of a series of experiments. The plan had been to repeat the first experiment with other groups of turkey poult under identical conditions, except that in phase II, the habituation phase, the ratio of the presentations of the H/G dummy was reversed: G, as the “rare shape” was inserted into 10 presentations of H.

Because of space limitations, it was impossible to conduct both experiments in parallel under identical conditions, as would have been most desirable. Therefore, when the experiment with the second group was started, the poults were already 17 weeks old, and when an experiment was started with a third group, the poults were then 23 weeks old. Furthermore, again because of space limitations, the poults of groups two and three had to be raised

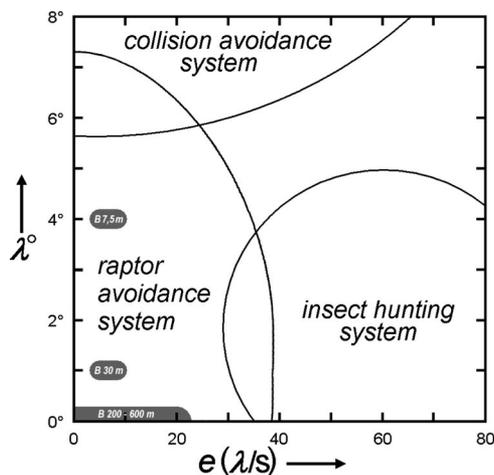


Figure 6. Within a feature space of apparent size  $\lambda^\circ$  (visual angle subtended by an object) versus relative speed  $e$  (apparent size  $\lambda$  per s) of an object in the sky, the salient features for eliciting raptor avoidance, insect hunting and collision avoidance occupy discrete but overlapping areas. The most common raptor in the study area in Seewiesen, Germany was the buzzard (*Buteo buteo*), circling high up in the sky from 200 to 600 m ( $\lambda < 15'$ ,  $e = 0$  to 20), indicated by gray shading, inscribed B 200–600 m, in the left bottom corner of the graph. Occasionally a buzzard swept by just above the tree tops at 30 m ( $\lambda = 1^\circ$ ,  $e = 6$ ), once again indicated by gray shading, inscribed B 30 m. For comparison, a raptor at 7.5 m ( $\lambda = 4^\circ$ ,  $e = 6$ ) has been entered by gray shading, inscribed B 7.5 m. (Image modified from W. M. Schleidt, Reaktionen von Truthühnern auf fliegende Raubvögeln und Versuche zur Analyse ihres AAM's, *Zeitschrift für Tierpsychologie*, 18, pp. 534–560. Copyright 1961 by Blackwell Verlag GmbH. Reprinted with permission.)

under more limited conditions (less floor space, less contact with humans).

When the poults for experiment two were placed in the experimental cage, they were extremely agitated, unlike the birds in the first experiment. During the presentations of the dummies, they spread their tail feathers in silence in response to all shapes, only occasionally emitting a few alarm calls—insufficient for any analysis. Experimentation was aborted after Day 6.

The birds of experiment three also were extremely agitated and, during presentation of the dummies, rarely vocalized. Since, once again, tail fanning in response to the dummies was elicited by all shapes (B, G, D, R, H), it was used as an indicator in subsequent trials. During the following 12 days, the buzzard dummy (B) was presented 10 times each day, with one of the other shapes (G, D, R, H) inserted in a random order. The poults quickly habituated to the buzzard dummy, but continued to respond to the other shapes. On each of the 12 days, the mean value in response to B was less than that to the rare shape ( $p < .001$ ), thus supporting the habituation hypothesis.

In summary, the results of the 1961 “Hawk/Goose Project” were in good agreement with those Lorenz had reported, including the response of his turkeys to the hawk version of the hawk/goose dummy. They did not support Heinroth’s short-neck hypothesis or Tinbergen’s generalization. Within the framework of classical ethology, selective habituation to common objects has been shown to be a potent mechanism for tuning innate releasing mechanisms of predator avoidance to specific features of objects in the individual’s world. In addition, the strong response to slow-moving tiny objects in the sky—evident in baseline observations of fowl under natural conditions and in various experiments—supported Lorenz’s 1939 contention that “slow relative speed” is a salient feature of an avian predator. Thus, within a “feature space”<sup>3</sup> of apparent size versus relative speed of an object in the sky (see Figure 6), the various behavioral elements of raptor avoidance are elicited by objects within the lower left quadrant, grading to the right into insect hunting (elicited by small fast moving objects), and toward the top into collision avoidance (evading large objects).

The kind of collision avoidance referred to here is not only the response of a stationary potential prey (a standing turkey poult) being rapidly approached by a flying predator (a hawk), but to any approaching object of an apparent size, or an increase in apparent size, exceeding a certain value, for example, another turkey descending from the roost. In our experiments, we carefully avoided getting into the range of collision avoidance by using small models at relatively great heights. In this way, the “looming effect” of a moving dummy was minimal and, therefore, ignored in our schematic representation of the feature space (see Figure 6). The basic geometry of a turkey watching a moving object overhead is illustrated in Schleidt, 1961b (Figures 2 and 3) and discussed in greater detail on pp. 538–540. For a recent review and experiments concerning the neurophysiology of the response to looming objects, see Münch et al. (2009). Note that in natural situations, an expanding retinal image can result not only from object motion but also from observer motion, for example, a bird in flight trying actively to avoid collision with stationary objects. The latter situation will be discussed in the section entitled “Abuse of Raptor Decoys.”

Thus, not only was an answer provided to the original question as to whether or not a specific shape—short neck—can be a feature, preprogrammed “center of crystallization” of an innate releasing mechanism (IRM) for predator avoidance, but also the scope has been widened to the role of selective habituation and to the relationship between other behavioral systems: insect hunting and collision avoidance.

### Subsequent Reexaminations of the Hawk/Goose Paradigm

The results of the 1961 study (Schleidt, 1961a, 1961b) settled the issue, and even though it was published only in German, it was cited in various textbooks of that time (e.g., Marler & Hamilton, 1966; Hinde, 1966). Even Tinbergen accepted selective habituation as an explanation for the hawk/goose effect and in 1965 he wrote:

The clue to the timid crouching of chicks lies in their innate tendency to do this when anything passes overhead—harmless as well as harmful birds—and even to cringe at falling leaves. As they grow older, they slowly get used to these common objects and lose their fear of them. However, they never become accustomed to the unfamiliar shapes of predators, because these birds are rare. (Tinbergen, 1965, p. 131).

However, because Tinbergen’s “Animal Behavior” appeared as a volume in *Life Nature Library*, a popular series of hardbound books published by Time-Life, his “Study of Instinct” (Oxford University Press) remained the most influential textbook on ethology, and since it was reprinted without updating for many years, his erroneous 1951 version of the 1937 experiments continued to be accepted by many as a striking example of an IRM, responding to a complex configuration. For example, Manning still stated in the third edition of his textbook:

In summary, there is evidence that wild birds do possess an IRM which enables them to respond to birds of prey on the first occasion that they see them. This IRM probably has different properties in different species but short neck and relative speed of movement are among them. (Manning, 1979, p. 85).

Here, we present a few cases illustrating the wide disparity of results. Melzack, Penick, and Beckett (1959) tested ducklings with a rather large hawk/goose model, and found a stronger response to the hawk model in only one of their 24 tests. McNiven (1960) also tested ducklings and found no difference in response. Green, Green, and Carr (1966) reported that ducklings “were more active in the presence of the silhouette of a hawk than that of a goose. However, the Ss were equally responsive to a triangle moving either base-forward or apex-forward” (p. 185). The former result supports Tinbergen’s 1939 claim, and the latter disproves Schneirla’s 1959 hypothesis that

<sup>3</sup> A feature space is a theoretical n-dimensional space occupied by various objects in an animal’s world. When a particular class of objects eliciting specific behaviors, for example, raptors eliciting avoidance and similar actions, such as alarm calling, tail spreading or escaping, cluster within a specific range of the feature space, they can be attributed to a specific behavioral subsystem, in this example, a “raptor avoidance system.”

a different response to the two directions of the hawk/goose silhouette was produced by rapid versus gradual retinal changes. Parenthetically, Schneirla, a vocal critic of ethology, tried unsuccessfully to explain the hawk/goose effect by his approach/withdrawal principle (Schneirla, 1965); for an excellent discussion of this issue see Burghardt (1973).

In a follow-up study, Green, Carr, and Green (1968) tested two sets of ducklings with the hawk/goose silhouette and additional versions without neck or without tail and found, once again, that the ducklings were more active when presented with the silhouette of the hawk. The models lacking neck or tail and moved in either direction had the same effect—lower response—as the goose. In two doctoral dissertations (unpublished), M. Green (1968) and R. Green (1968) used heart rate as an indicator of fear and found a significantly greater increase in response to the hawk model. Helmut Mueller (an expert in raptor biology) tested a variety of behavioral indicators of fear with conflicting results (personal communication) until he monitored the heart rate of his subjects (ducklings: Mueller & Parker, 1980; chicken chicks: Moore & Mueller, 1982). In contrast to the Greens' findings a significant difference in the heart rate increase was observed only in response to the goose model. However, heart rate variance was greater in response to the hawk model, and, "therefore," it was concluded that "variance in heart rate is an excellent measure of emotional response to a stimulus" (Mueller & Parker, 1980, p. 111). This interpretation is not beyond dispute. For example, in an extensive study of free-ranging greylag geese in their natural environment (Wascher, Scheiber, & Kotschal, 2008), the increase in heart rate was the most useful indicator of emotionality, and an increase in variance usually coincided with an increase in rate (Wascher, personal communication). Thus, the increase in variance in response to the hawk model, and an increase in mean heart rate in response to the goose model, observed by Mueller and Parker, 1980, are contradictory. The most recent attempt to substantiate the report of Tinbergen's claim "that goslings respond more to moving hawk silhouettes than to moving goose shapes" was reported by Canty and Gould (1995). Once again ducklings were tested instead of goslings, and the excessive apparent size of the models,  $\lambda = 9^\circ$  (!), was more suitable for investigating collision avoidance than predator detection. Because of the enormous size of their models, as compared to those used by Lorenz, Tinbergen, and Schleidt, their results cannot be compared in any meaningful way. For the same reason, a discussion of the results of Rogers, Zucca, and Vallortigara (2004) and those of Palleroni, Hauser, and Marler (2005), who used models up to a  $\lambda = 20^\circ$ !, resulting in a high looming effect during presentation, exceeds the scope of this paper (see Figure 7, and compare with Figure 6). Of the few relevant investigations in recent years, only two papers (Evans & Marler, 1991; Evans & Marler, 1992) report the use of models in the order of magnitude of those used in the seminal investigations by Lorenz and Tinbergen. These papers yielded very interesting results concerning the role of bystanders in evoking the alarm calls elicited by predator models, but did not address the hawk/goose issue.

We conclude that even though some results suggest that experimentally naive ducklings may respond differently to the two versions of the hawk/goose silhouette, the effects are not striking. Moreover, we cannot exclude the possibility that these differences were due to selective reporting of trials with "statistically signif-

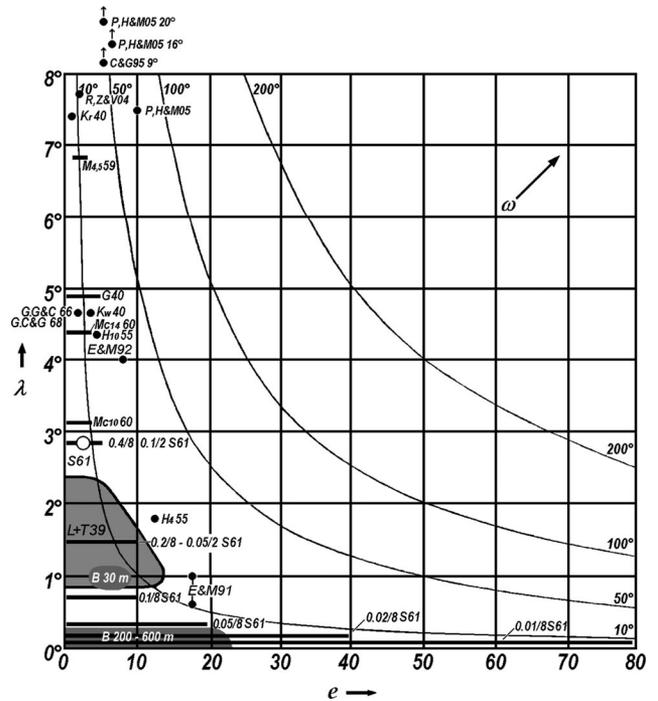


Figure 7. Representation of sizes and speeds of raptors in nature, and raptor dummies used in various experiments—a selective update of Figure 4 in Schleidt, 1961b. The apparent size and speed of objects were standardized to the apparent angle of length ( $\lambda$ ), relative speed ( $e$ ) and, consequently, to angular speed ( $\omega$ ). The most common raptor in the study area in Seewiesen, Germany was the buzzard (*Buteo buteo*), which circled high up in the sky from 200 to 600 m ( $\lambda < 15'$ ,  $e = 0$  to 20) and occasionally soaring just above the tree tops at 30 m ( $\lambda = 1^\circ$ ,  $e = 6$ ); these ranges are indicated by gray shading. Explanation of symbols for each dummy type, as used by various authors, ranked by date of publication: L + T 39 = Lorenz, 1939; Tinbergen, 1939, the shaded area indicates the apparent size and speed of their dummies. G 40 = Goethe, 1940. Kr 40 = *Buteo lagopus*, Kw 40 = *Falco peregrinus*, Krätzig, 1940. H4 55 = 4" dummy, H10 55 = 10" dummy, Hirsch & al., (1955). M4,5 59 = Melzack & al., (1959). Mc10 60 = 10" dummy, Mc 14 60 = 14" dummy, McNiven, 1960. S 61 = Schleidt, 1961a. 0.4/8 0.1/3 S 61, to 0.01/8 S 61 = Schleidt, 1961b (length of dummy/height presented, in m). G,G&C 66 = Green et al., 1966. G,C&G 68 = Green, 1968. E&M91 = Evans & Marler, 1991. E&M92 = Evans & Marler, 1992. C&G95 9° = Canty & Gould, 1995. R,Z&V04 = Rogers, 2004 P,H&M05 = *Accipiter striatus*, P,H&M05 16° = *Accipiter cooperii*, P,H&M05 20° = *Accipiter gentilis*, Palleroni et al., 2005. Note the cluster of dummy dimensions in the upper left hand corner: objects in this range of size as well as the looming effect elicit collision avoidance, thereby being of questionable relevance for understanding the recognition of the shape of predators. (Image modified from W. M. Schleidt, Reaktionen von Truthühnern auf fliegende Raubvögel und Versuche zur Analyse ihres AAM's, *Zeitschrift für Tierpsychologie*, 18, pp. 534–560. Copyright 1961 by Blackwell Verlag GmbH. Reprinted with permission. Copyright 1961 by Blackwell Verlag GmbH. Reprinted with permission.)

icant" results and discarding of results of experiments that did not fit the investigators' expectations as "statistically not significant"—as occurred in the study of Melzack et al. (1959), mentioned above.

## Discussion

Considering the great attention the 1937 hawk/goose experiments of Lorenz and Tinbergen once received, a brief discussion of the wider perspective of cognitive ethology appears in order. To keep it brief, we have hand-picked a few examples in which selective habituation offers a parsimonious explanation and have added some anecdotal evidence. The ultimate reason for the 1937 experiments was to explore the limits of the “inborn” knowledge of an animal’s environment. In what detail does an animal know what a life-threatening predator looks like? What are the salient features of a dangerous object that are missing in a harmless object of similar appearance? Where are the boundaries between a simple stimulus that elicits an unconditioned reflex and a complex “Gestalt” that indicates deadly danger? At a time when comparative psychology was preoccupied with learning processes, the claim that an experimentally naïve bird recognized a raptor by the feature “short neck” was shocking. The idea that the perception of a “Gestalt” could be “innate” was met with amazement by critics of behaviorism, and with disbelief by its supporters.

Thus, the subsequent attempts to falsify the “short neck hypothesis” were actually attempts to falsify the hypothesis of “innate cognition,” and they became embroiled in the “nature-nurture” controversy. During the rare failures to falsify the “short neck hypothesis” it had been overlooked in most cases that there is an innate ability to respond to some simpler features, such as relative speed, size, or contrast, of a moving object, before discrimination between familiar objects and rare ones can be established. Learning something about an object can always be traced to an “innate propensity” of something (of some “thing”) earlier in ontogeny. There is an “Innate Releasing Mechanism,” an “IRM,” as proposed by classical ethology (Lorenz, 1935; Tinbergen, 1942; see also the discussion in Burkhardt, 2005, pp. 203–205), as the center of crystallization for selective habituation to salient features, later expanded (modified?) to an “IRME” or “IRM adjusted by Experience” (Schleidt, 1962).

The discovery of the 1961 replication that selective habituation—getting used to common objects in the environment but avoiding those encountered only rarely—indicates that this is a very efficient mechanism for a young animal to adjust to the specifics of its environment. Although this mechanism has been largely ignored, several exceptions are discussed below.

But first, let us take a brief look at the historical setting of the hawk/goose story in the wider context of the individual organism within its private world, and the amazing match between organism and environment. For most shamans and priests, as predecessors of today’s scientists, “our world” and the match between man and his environment were seen as the result of a willful act of a god. Only since Darwin (metaphorically speaking) have scientists become aware that evolution is the mechanism by which organisms adapt to their environment. But even within biology, “Darwinism” was still ridiculed at the beginning of the 20th century, even by such ingenious scientists as Jakob von Uexküll.

When psychology emerged as a field of science, its pioneers reduced the environment to a mere “world of stimuli,” as illustrated by J. B. Watson’s famous statement:

“Our ‘environment’—our world of stimuli—is not only one of external objects, sights, sounds and smells; it is one of internal objects as well—hunger contractions, bladder distensions, palpating heart, rapid breathing, muscular changes and the like.” (Watson, 1924, p. 59).

Uexküll was the first scientist who posed penetrating questions concerning the world of different organisms, ranging from the “World of the Paramecium” to the “World of the Astronomer” (Uexküll, 1909, 1957; Uexküll and Kriszat, 1934). His distinction between “*Innenwelt*” (internal world) and “*Umwelt*” (the personal environment of an individual organism), and their connection by a control system, “*Funktionskreis*” (functional circuit), were of seminal importance for European ethology. Even though von Uexküll used a stimulus-response paradigm describing the life of protozoa and invertebrates, he described the world of higher animals in terms of objects with multiple features, from which a particular species selects only those of personal relevance to itself. His writings were ignored in his time by the psychological establishment and attracted attention only after Lorenz had dedicated to von Uexküll his well received paper about “the companion in a bird’s world” (Lorenz, 1935, 1937a). Despite von Uexküll’s great knowledge about a wide variety of animals and his ingenuity—for example, he coined the term search image (“*Suchbild*”)—his conceptual framework remained incomplete for two reasons. First, he totally rejected Darwinian evolution, and, second, because of his narrow view of the personal Umwelt, he basically insulated each individual in its own bubble, thus dwarfing the role of communication between organisms and their shared Umwelten.

Even though Watson used here the terms “*external objects*” and “*internal objects*,” they remained vague until Melanie Klein proposed a psychoanalytical theory of an internal world with introjected objects (Klein, 1935), and gave the term “object” a very specific connotation.

Egon Brunswik, at about the same time, was one of the first who criticized the narrow view of stimulus-response theory, and proposed a radical redefinition of “psychology in terms of objects” with due consideration of an organism’s environment (Brunswik, 1934, 1937). His pioneering ideas did not match well, however, with the behaviorism of his time and were rediscovered only in recent years. James Jerome Gibson’s “*Ecological Approach to Visual Perception*” (the befitting title of his 1979 book, but introduced already in his 1950 “*The Perception of the Visual World*”) finally laid to rest the simplistic Watsonian assertion “Our ‘environment’—our world of stimuli.”

Building on the foundations laid by von Uexküll, Brunswik, and Gibson, the senior author of this paper attempted a coherent theory of organisms in their natural environment (Schleidt & Crawley, 1980; Schleidt, 1981, 1985, 1992), leading to a new “theory of world.” For an example, let us take a brief look a newly hatched turkey poult within its natural environment.

## The World of a Newly Hatched Turkey

The “world of a newly hatched turkey” is depicted in Figure 8. The world of a newly hatched turkey, emerging from the dark beneath its mother’s wing, consists of two types of visual “objects” within a space: “individuals” and a clutter of “things.” Individuals (“companions” in the sense of Lorenz, 1935/1937a) are its mother and siblings. Things are 1) small objects on the ground, contrasting with the background and not moving too fast, such as a small seed, a crawling insect, a dew drop on a leaf, a tiny image of the sun reflected on water, and so forth; and 2) larger objects (exceeding a few centimeters in size), to be avoided as potential obstacles. At that age, turkey poult show no phobic responses to specific types

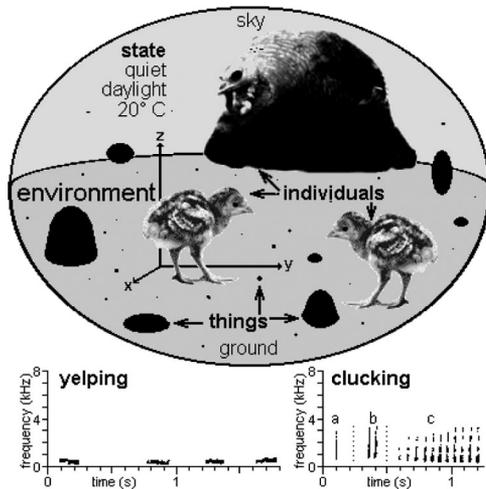


Figure 8. The “World of a Newly Hatched Turkey,” an environment furnished with two types of visual objects: “individuals” and “things.” In the domain of sound, two vocalizations of the mother hen are recognized: yelping, the call of a broody turkey hen serving as a beacon for the poult exploring its environment, and clucking, the general alarm call, eliciting crouching and freezing.

of objects, such as flying predators, furry things, small mammals, or cylindrical shapes of a certain size, like that of a snake.

Within the auditory domain, two types of sound catch the poult’s immediate attention: the hen’s yelping and clucking. Yelping, the call of a broody hen, may occur spontaneously, or be elicited by the poult’s peeping while exploring its environment; in the latter case, it serves as an acoustical beacon to guide the lost poult back to its mother. Clucking, the general alarm call, elicits crouching and freezing.

The behavioral repertoire of a newly hatched turkey is quite precocial. When awake, the poult moves around, actively exploring its environment, picking at everything small contrasting with the background, and within three or four days has learned to fulfill its caloric needs. The mother does not feed her young, and only occasionally supports her poults’ search by scratching in the leaf litter, exposing hidden food. Occasionally, a poult may initiate a chasing game, and fragments of adult behavior may suddenly pop up, like attempting to mount a sibling, or even performing the complete behavior pattern of “strutting” (Schleidt, 1970). When resting in the open, the poult spends most of the time preening its feathers.

It may take hours or even days before obstacle avoidance and visual predator avoidance mature, and weeks before selective habituation results in the avoidance of rare objects (raptors and ground predators, such as mammals or snakes). Predator recognition and avoidance develop as a consequence of individual experience, but also may be facilitated by social stimuli, such as alarm signals or fear responses of others (Curio, Ernst, & Vieth, 1978; Curio, 1988).

### The World of a Grown-Up Turkey

Let us now look at the world of a grown-up turkey, and examine the objects of vital importance—flying, crawling, or stationary. The older turkey’s knowledge of food will vary with the richness of the environment. A wild turkey growing up in the woods of Pennsylvania

learns to discriminate between a variety of specific insects and inert material, avoiding bad-tasting objects and yellow jackets. A domestic turkey, on the other hand, growing up in a warehouse-like enclosure on a farm may be exposed only to cracked corn or pellets of a special turkey ration; nothing moving, practically no variety.

The same applies to a turkey’s knowledge of predators. A wild turkey growing up in the woods shows very different responses to four more or less distinct classes of objects. A “rare flying object,” like the hawk it sees only once every few days or even less often, will elicit alarm calls and escape. A “small furry object,” between the size of a mouse and a weasel, will either be actively avoided or pursued with the intent to kill it either by pecking at the eyes (or in case of a bigger mammal like a weasel, by beating it with its spurred legs). A “large furry object,” a mammal the size of a dachshund and larger, will be actively avoided, and if it approaches the turkey will try to escape by running or taking flight. An “elongated object that resembles a snake” will be actively, but very carefully, pursued, usually along with clucking, which alerts the other members of the flock to join in the pursuit. When the snake curls up, the turkeys take turns trying to strike its head, until the snake has been killed. This obsession of turkeys to kill snakes has even been used to reduce the rattlesnake populations in cow pastures in Colorado:

Domestic turkeys react toward rattlers in somewhat the same manner as the wild ones, except they rarely will attack the rattler . . . but when one was discovered . . . they immediately started to gobble and half a dozen or more turkeys would surround the snake. This commotion could be heard or seen by the herder, who carried a hoe for the express purpose of killing snakes. (Klauber, 1972, pp. 1088–1089).

### Selective Habituation: Shaping the Response to Predators

As for the role of selective habituation of turkeys to any one of the four categories of dangerous objects, we can offer only anecdotal observations from the senior author, based on many years of keeping a flock of about 60 domesticated and up to 15 wild turkeys for behavioral studies under “barnyard conditions” at the Max Planck Institut in Seewiesen and at a farm in Glenn Dale, MD.

The role of selective habituation to flying objects has been discussed above. In regard to habituation to a “small furry object,” the responses are highly variable. In exploratory experiments with dummies selective habituation occurred in some cases within a few trials, in others it took weeks, and in one case a series of presentations of a weasel decoy had to be terminated before the end of the third trial because the turkeys had become so agitated that they were at risk of hurting themselves in panic.

One of the complications in this category of furry objects is that the visual feature variables of a newly hatched, fluffy turkey poult fall into the “small furry predator” category. Only the peeping vocalizations of the poult inhibit the mother from attacking it. A deaf turkey hen, even though appearing fully competent in the daily barnyard routine, and a devoted incubator of her clutch of eggs, cannot differentiate between a small mammal trying to steal her eggs versus a fluffy poult emerging from under her own wings. As a consequence, she kills each one (Schleidt, Schleidt, & Magg, 1960).

Selective habituation of turkeys to mammals the size a dachshund and bigger is best illustrated by the fact that under barnyard conditions even our wild turkeys grew accustomed to the dogs they met on a daily basis, but became highly agitated when a strange dog appeared.

The response of our Seewiesen turkeys to “elongated objects that resemble a snake” could be observed every spring after the danger of frost had passed and a garden hose was rolled out between the “Gänsehaus” (a small building, used primarily as laboratory for poultry research) and one of our turkey pens outside the surrounding fence. The hose resembled a very long snake, between the faucet and the fence. While other fowl ignored this event, our turkeys became highly agitated, approached the hose clucking and gobbling, and stayed about a meter away. At first the hose constituted an obstacle that could not be overcome, except by flying over it (a big effort for a turkey, usually reserved for flying to roost in the evening). But within a few hours, our domestic turkeys had calmed down, and walked across the hose without hesitation. It was not the same with our tame, human-imprinted wild turkey hen, who continued flying over the hose, whenever she wanted to be on the other side.

In turkeys, selective habituation to dangerous objects appears to be a common strategy for adapting to a specific environment, at least to flying objects and big furry objects. In the case of small furry objects and snakes, the response varies between habituation and sensitization.

### Selective Habituation in Other Species

Even though selective habituation to dangerous objects appears to be a very efficient strategy for adapting to a specific environment, we found it well confirmed for only two mammalian species: harbor seals and humans. The first case in which selective habituation has been invoked as the most parsimonious explanation is the account of Deecke, Slater, and Ford for the selective response of harbor seals (*Phoca vitulina*) to specific vocalizations of killer whales, broadcast from underwater loudspeakers. Wild harbor seals in British Columbia responded strongly to playbacks of the calls of local mammal-hunting killer whales, but completely ignored the calls of the local fish-eating population which they encounter frequently. On the other hand, playbacks of calls of fish-eating killer whales from Alaska, which are ecologically similar and close genetic relatives of British Columbia fish-eaters but do not share any of their call types, elicited a strong behavioral response. This response to the calls of harmless but unfamiliar killer whale calls suggests that the seals have habituated to the calls of the local fish-eating killer whale population, but not to the different call types of the local mammal-eaters (Deecke, Ford, & Slater, 2002; Deecke, Ford, & Slater, 2005).

The second case is supported by the effectiveness of “exposure therapy” in healing certain kinds of phobias in humans, a method pioneered by Isaac Marks (1973, 1987; Marks, & Dar, 2000). What makes human phobias so interesting is their amazing similarity to “risk avoidance” (not just predator avoidance) in a wide variety of “higher animals,” as, for example, the different onset ages in various phobias (Marks & Gelder, 1966; Marks, 1987). Just one example: in humans, an aversive response to a snake is not present during the first years and matures about the time the toddler starts to explore the environment beyond the immediate control of its mother. If a strong snake phobia developed in a patient, it usually began before the age of 8. “Exposure therapy” based on selective habituation is the most effective psychotherapeutic method for reducing phobias to a level that allows a rational assessment of a dangerous situation (Marks & Dar, 2000; Schneider, Mateix-Cols, Marx, & Bachofen, 2005).

### The Abuse of Raptor Decoys

Another important area in which selective attention and the hawk/goose paradigm are highly relevant is the persistent use of raptor decoys as potential deterrents against bird collisions with glass panes. Soon after the use of large glass panes in modern architecture became fashionable, it was discovered that huge numbers of a variety of birds fail to see the transparent glass as an obstacle, and die on impact from severe head injuries.

Given what we now know about the glass threat to birds, the one billion U.S. death toll estimated by Klem in the late 1970s may be highly conservative (Klem, 2006). Only in the past few years has the glass menace to birds been acknowledged as a serious conservation issue by more than a handful of people. If one accepts the attrition figure of one billion annual kills in the United States, it would take about 3300 Exxon Valdez oil spills each year to equal the carnage! The Exxon Valdez, which killed an estimated 300,000 birds in Alaska in 1989, is still cited as a horrific environmental disaster. It is ironic and lamentable that the far greater toll extracted by glass window panes every year still goes largely unnoticed (Klem, 2006).

Even though the effect of stationary silhouettes was not investigated in the Lorenz-Tinbergen experiments, the short-necked raptor silhouette became an icon of a “biological deterrent” against birds of all kinds. To this day, raptor silhouettes are affixed on glass panes in various contexts. This is especially surprising since already in 1962 Hans Löhrl wrote a devastating review on the uselessness of such silhouettes. Despite the availability of truly effective bird deterrents, for example, stripes (e.g., Rössler & Laube, 2008), raptor decoys continue to be widely used (e.g., Klem, 1990, 2006).

With respect to the role of “selective habituation” in shaping an individual’s world, collision avoidance is an interesting example of the multitude of variables that ultimately define a class of objects. In this case the object would be a “wall”—in pristine nature, a cliff’s face—contrasting to open space ahead, or to a penetrable object, such as the foliage of a tree. Pasting silhouettes of raptors on glass panes—to catch a bird’s eye—does not turn the invisible glass into a wall. Actually, as a “biological bird deterrent,” habituation to the monotony of the silhouettes will defeat their intended purpose (for an example of excessive abuse of raptor silhouettes on glass panes, see Supplemental Materials AI 2, AI 3).

The age-old practice of “netting” birds has taught us that a net has to be very fine so as not to be noticed and avoided by birds (effective bird catching nets are called “mist nets”). Affixing a subtle line pattern on a glass pane—2-mm Nylon threads spaced 50 mm apart—turns a pane of acrylic glass for a bird’s eye into an impenetrable object (Rössler & Laube, 2008). On the other hand, raptor silhouettes as a “biological bird deterrent” have proven ineffective because of selective habituation: birds habituate not only to the shape, but also to a fixed location (Shalter, 1975), as do certain fishes (Schleidt, Shalter, & Carawan, 1983).

### Closing Remarks

In the early 1950s, ethology emerged as an evolutionary approach to the study of behavior that challenged the narrow view of contemporary psychology, then preoccupied with learning and focused on the laboratory rat. In this historical setting, the result of the 1937 hawk/goose experiments by Lorenz and Tinbergen was viewed as the ultimate proof of complex innate imagery. Despite the fact that the

results of the 1961 experiments offered a relatively simple explanation, that is, a few “innate” features fine tuned by selective habituation, the “myth” of an innate image persisted for many years. Neither the potential of selective habituation as an important mechanism for matching an individual’s needs to its specific environment, nor the wider context of individual- or taxon-specific mechanisms for detecting, recognizing, and classifying potentially harmful or lethal objects have received much, if any, attention.

Our proposal, based on previous works (Schleidt & Crawley, 1980; Schleidt, 1981, 1985, 1992), is to overcome the simplistic attempt trying to reduce our world to a “world of stimuli” and dare to widen our view: to deal even-handedly with the full diversity of objects relevant for survival. We propose a “theory of world” far beyond von Uexküll’s “Umwelt,” a new theory which takes into account not only objects but “everything” detectable by a specific organism’s senses, everything that sticks out from the background noise, and is distinguishable from the clutter as something relevant to that individual’s Umwelt and survival.

Is this an utterly unreasonable proposal? We have an interesting precursor for such an endeavor: Johann Amos Comenius’ (1658) *Orbis sensualium pictus*: “A world of things<sup>4</sup> obvious to the senses drawn in pictures.” (Comenius 1659/1727/1887; see Figure 9).

<sup>4</sup> “A world of things” is an excellent start from the viewpoint of the human observer, but we must be aware of our bias toward visible things and try to compensate by evenhanded consideration of other senses such as touch, smell, hearing, taste, and so forth.



Figure 9. “The World” according to Johann Amos Comenius 1658 *Orbis sensualium pictus*: “A world of things obvious to the senses drawn in pictures; . . . The Heavens, 1. hath Fire, and Stars. The Clouds, 2. hang in the Air. Birds, 3. fly under the Clouds. Fishes, 4. swim in the Water. The Earth hath Hills, 5. Woods, 6. Fields, 7. Beasts, 8. and Men, 9. Thus the greatest Bodies of the world, the four Elements, are full of their own Inhabitants.” (Verbatim quotes from Comenius 1659/1727/1887, woodcut from Comenius 1658/1978).

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