THE AUK

A QUARTERLY JOURNAL OF

**ORNITHOLOGY**

VOL. 78 APRIL, 1961 No. 2

# THE DEVELOPMENT OF VISUAL DISCRIMINATION PATTERNS IN THE CROUCHING REACTIONS OF NESTLING GRACKLES*

GEORGE B. SCHALLER AND JOHN T. EMLEN, JR.

THE tendency for birds to respond consistently to specific "sign stimuli," and their ability to discriminate between these stimuli and the many other potential stimulus objects of their environment, has given rise to a theory that certain objects are "recognized" innately, *i.e.*, responded to in a specific manner without the intervention of learning processes. Such a theory can be tested only by patiently examining and experimentally analyzing the environmental conditions in which individual birds develop during the periods of sensory maturation. The present study is concerned with the basic negative response (crouching) in nestlings of the Common Grackle *(Quiscalus versicolor)*. Special attention was given to the schedule of maturation of the crouching pattern and of visual competence. Experiments were conducted with various naturalistic stimulus objects to explore the role of individual experience in the development of stereotyped, visual discrimination patterns.

## STUDY AREA AND METHODS

Most of the data for this report were collected between 10 May and 15 June 1958 in a colony of 21 grackle nests located in a stand of small red cedars on the University of Wisconsin Arboretum's Picnic Point at Madison, Wisconsin. Supplementary data were obtained from other nests in the vicinity.

Nests were visited daily or twice daily during the egg stage to determine, as closely as possible, the time of hatching. Ages of young were

* Financial assistance was provided by a grant from the National Science Foundation. University of Wisconsin Arboretum paper No. 44.

recorded in hours posthatching; all age records are accurate to within six hours.

Observations of the responses of nestlings to the arrival of the parent birds were made from blinds at two nests. Tests of responses to artificial stimulus objects were made at 19 other nests. In each test a selected object was slowly raised to the edge of the nest together with a light tapping to simulate the jarring normally accompanying the arrival of the parent. The object was then gently moved about by the observer as he remained quietly hidden at arm's length, his head at the level of or slightly below the rim of the nest. Observations were discounted in all cases where the nestlings were disturbed by a clumsy approach. Test objects were selected that bore superficial resemblance to common bird species of the region; these included: (1) a stuffed male grackle, (2) a stuffed male cowbird, (3) a stuffed female cowbird, (4) a stuffed male cardinal (bright red plumage), and (5) a lifelike, brown latex model of a screech owl.

Nestlings were individually marked as necessary and records kept of the responses of each. Tests were made between 0900 and 1300 hours each day. No more than one test was made on a nest in a given day, and test objects were alternated so that no nest received the same test more often than once in three days.

These field tests were supplemented by experiments designed to interrupt the normal course of environmental experience of nestlings. These were of two types:

1. Temporary withdrawal of nestlings from the nest environment to small, isolation boxes where feeding was done by hand.
2. Temporary blindfolding of nestlings in the nest with a mask of acetate glue mixed with lampblack.

Sample specimens of nestlings were brought into the laboratory at various stages of development for measurements of visual maturation.

## DEVELOPMENT OF THE CROUCHING RESPONSE

The response repertoire of a nestling grackle to the parent birds or other similarly large, stimulus objects appearing at the nest rim consists of two principal motor patterns—gaping and crouching. The former may be regarded as the basic positive response, the latter as the basic negative response.

As in many other altricial birds, the gaping response in the grackle is present at hatching. At that time and for several days afterwards it is apparently the only major response to external stimulation and is given to a great variety of stimulus objects. Studies of the stimuli eliciting the gaping response and its orientation have been made by Holzapfel (1939), Tinbergen and Kuehnen (1939), Prechtl (1953), Messmer and Messmer (1956), and others on a variety of altricial species. The newly hatched grackles in this study gaped to such varied stimuli as touch, shake, sound, and air currents.

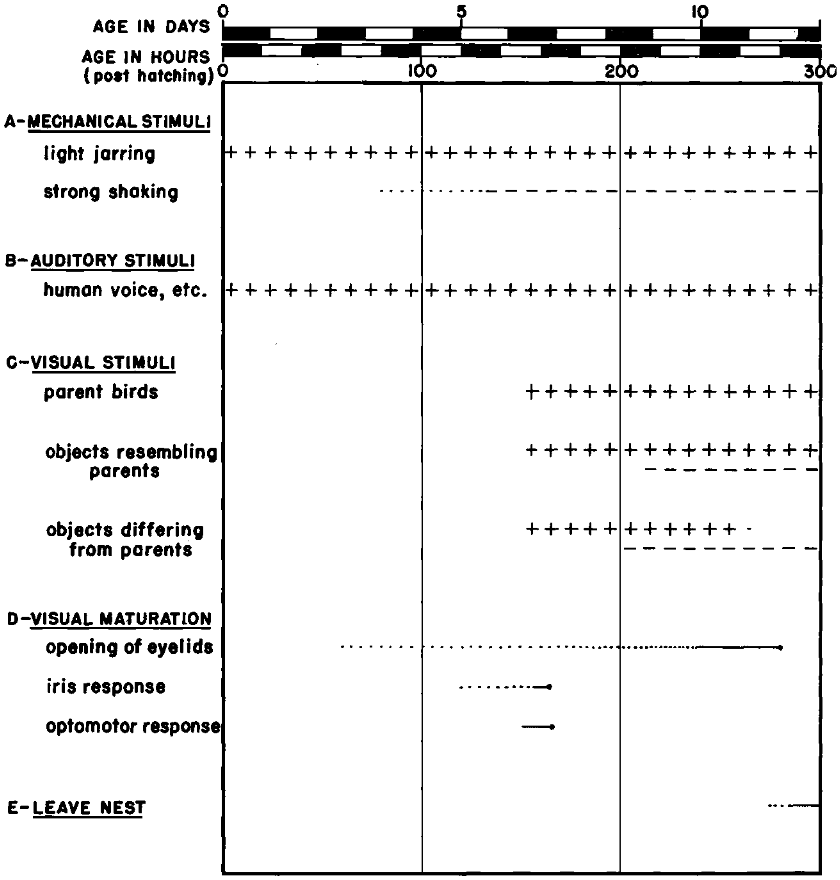


**Figure 1. Time of appearance and development of crouching reactions to various stimuli and stimulus objects as related to the maturation of functional vision in nestling grackles. Plus signs (+ + +) indicate gaping responses; dashes (— — —) indicating crouching responses. Dots (. . . . . .) indicate an incomplete response. In the lower part of the figure a line (————) indicates the span of variation among the tested individuals in acquiring the response. The row of dots opposite "opening of the eyelids" indicates the period during which the eyes were partially opened.**

In contrast to gaping, the motor pattern of crouching did not appear in grackles until about 80 hours of age and did not fully mature until about 130 hours (Figure 1A). With strong shaking of the nest branch, newly hatched young merely rolled around in the nest cup. After about 80 hours a slight tensing was detected, and from then on the crouching response to this rather strong mechanical stimulus developed rapidly to about 130 hours. In young of more than 130 hours of age strong shaking invariably elicited intense crouching. In a full crouch the bird lowers its body into the nest cup, withdraws its head, and hunches its wings upward and forward so that they nearly cover the head. In this position it remains rigid, clutching the nest lining with its feet when the observer attempts to move it. After about 250 hours of age crouching to a disturbance was sometimes accompanied by a tense, partial opening of the mouth; and after 275 hours the birds often left the nest precipitously. Normal departure from undisturbed nests occurred between 275 and 340 hours of age.

Published accounts indicate that crouching characteristically manifests itself rather suddenly in the development of passerine nestlings. The age at which it first appears in several species as recorded in the literature is presented in Table 1. These data are not strictly intercomparable, however, since in most cases the nature of the stimulus producing the crouch is not indicated, and many workers have apparently recorded only responses to visual stimuli.

## MATURATION OF THE VISUAL EQUIPMENT

Crouching to visual stimulus objects does not appear, of course, until the visual equipment has become functional. The maturation of vision in nestling grackles was investigated by several methods.

*The opening of the lids.* The eyes of nestling grackles are closed at hatching. The lids begin to part at about 60 hours, but the cornea is still covered with a watery fluid and the nictitating membrane. The slit widens to 1½ mm. by 130 hours, to 2 mm. by 150 hours, to 3 mm. by 200 hours, and to 4 mm. (fully opened) by 300 hours (Figure 1D). Up to about 180 hours of age the eyes are opened only when gaping; thereafter the eyes remain open for increasingly longer periods to the time of fledging.

*Structural development of the eye.* Opening of the lids is not *prima facie* evidence of complete visual function. Portmann (1938) has shown that the structure of the eye itself in passerines is not fully developed at hatching. In the House Sparrow *(Passer domesticus)* Slonaker (1921) found that the ciliary muscles became functional at

TABLE 1

AGE OF FIRST APPEARANCE OF CROUCHING IN SEVERAL PASSERINE SPECIES

| *Species* | *Age in days* | |
|---|---|---|
| Crow (*Corvus brachyrhynchos*) | 18 | Emlen, 1942 |
| Blue Jay (*Cyanocitta cristata*) | 14 | Ivor, 1944 |
| Black-capped Chickadee (*Parus atricapillus*) | 7 | Odum, 1941 |
| American Robin (*Turdus migratorius*) | 7 | Kuhlman, 1909 |
| Blackbird (*Turdus merula*) | 12 | Messmer and Messmer, 1956 |
| Wood Thrush (*Hylocichla mustelina*) | 9 | Ivor, 1944 |
| Catbird (*Dumetella carolinensis*) | 8–9 | Herrick, 1901 |
| | 6 | Nice, 1943 |
| Loggerhead Shrike (*Lanius ludovicianus*) | 12 | Miller, 1931 |
| Starling (*Sturnus vulgaris*) | 6–8 | Kessel, 1957 |
| Red-winged Starling (*Onychognathus morio*) | 14 | Rowan, 1955 |
| Icterine Warbler (*Hippolais icterina*) | 7 | Heinroth and Heinroth, 1924–33 |
| Ovenbird (*Sciurus aurocapillus*) | 7 | Hann, 1937 |
| | 5½ | Nice, 1943 |
| Redstart (*Setophaga ruticilla*) | 9 | Nice, 1943 |
| Cowbird (*Molothrus ater*) | 7 | Nice, 1939 |
| Common Grackle (*Quiscalus versicolor*) | | |
| To mechanical stimuli | 3.3–5.4 | This study |
| To visual stimuli | 8.3–9.2 | This study |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*) | 8 | Ivor, 1944 |
| Tree Sparrow (*Spizella arborea*) | 7–7½ | Baumgartner, 1938 |
| White-crowned Sparrow (*Zonotrichia leucophrys*) | 5 | Banks, 1959 |
| Song Sparrow (*Melospiza melodia*) | 6–7 | Nice, 1943 |

about six days. Myelinization of the optic nerve is not completed in starlings until the eighth day after hatching, according to Schifferli (1948).

The best indicators of functional vision are behavioral. Accordingly, tests were made of the pupil reflex and the optomotor response.

*The pupil reflex.* The pupil reflex in grackle nestlings was tested in a darkened room by holding the eyelids apart and shining a narrow beam of light from a microscope lamp into the eye. In grackles no response of the iris was noted before 120 hours. Between 120 and 150 hours slight movements were detected, but the pupil did not accommodate. Good light accommodation, presumably related to the attainment of integrated neuro-muscular control, appeared quite suddenly. In 41 tests the earliest definite response occurred at 154 hours and the latest before 163 hours (Figure 1D).

*The optomotor response.* Tests for optomotor responses probably provide the best available indicator of pattern discrimination. In this study the test bird was placed on a stationary platform, and a cylinder, marked with alternating, ½-inch, black and white, parallel, vertical bands, was revolved around it at a constant speed of 12 or 24 rpm. The bird was stimulated to gape and to open its eyes by lightly tapping the apparatus. A following of the moving bands by the head was interpreted as a positive optomotor response; a failure to follow was assumed to indicate lack of pattern vision. In 38 optomotor tests on grackles in the laboratory the earliest positive response occurred at 150 hours and the latest before 163 hours (Figure 1D). The acquisition of the optomotor response thus corresponds closely to the acquisition of light accommodation.

Together these data suggest that functional vision for form or pattern discrimination is attained in the Common Grackle between about 150 and 163 hours of age.

## THE DEVELOPMENT OF VISUAL DISCRIMINATION

### *Tests with Models*

In all observations responses to the principal natural stimulus object at the nest, the parent bird arriving at frequent intervals with food, were positive (gaping) and continued to be positive until the young fledged. Responses to the various test objects presented experimentally at the nest rim were also invariably positive at first and remained positive until the birds were from 200 to 220 hours of age, several days after the attainment of pattern vision (Figure 2). A change from the positive to the negative (crouching) response eventually occurred, however, to all test objects and in nearly all test birds. The shift to a negative response, once made with respect to a given test object, remained negative in all cases where test repetitions were made. The time of shifting varied with the nature of the stimulus object, occurring

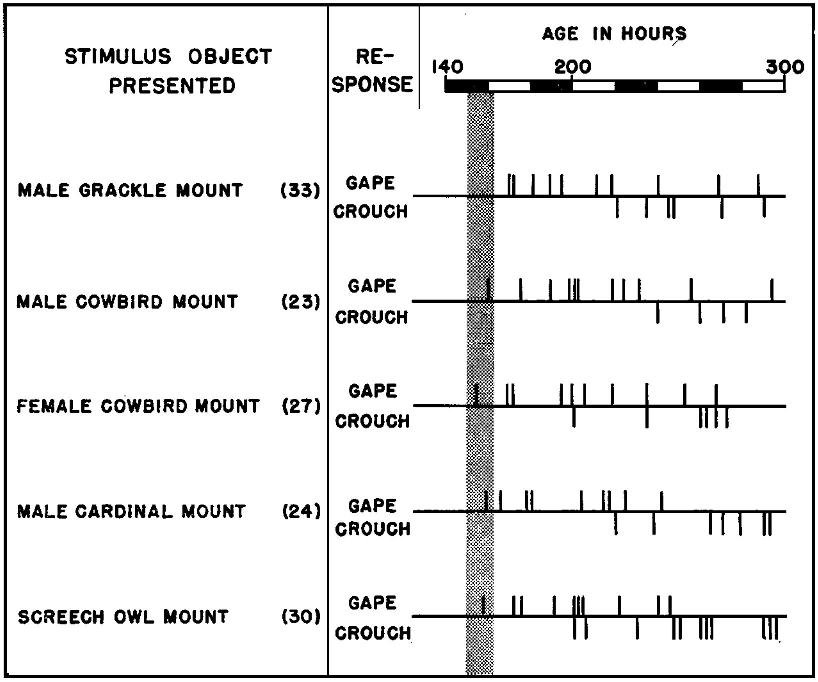


**Figure 2. Record of gaping and crouching reactions of nestling grackles to various naturalistic models presented at the nest rim during the last seven days of nest life. The figures in parentheses indicate the number of tests made with each model. Nestlings were tested no more often than once per day and never more than once in three days with the same model. The shaded band designates the age (150–163 hours) at which functional pattern vision was attained. Each vertical marker represents one to four birds.**

first for objects that resembled living adult grackles (stuffed grackles and cowbirds) and last for the stuffed cardinal and screech owl model.

The occurrence of crouching to the stuffed grackle mount calls for special comment, since, in theory, a perfect model of a grackle, perfectly presented, should give the same consistently positive response as that shown to the parent birds up to the time of fledging. In practice the artificial presentation departed from perfection in a number of ways. Advanced nestlings were alert to minor disturbances in the nest vicinity, and even the most cautious approach by the observer may well have been detected and served to warn the birds in advance of the test presentation. In some cases, furthermore, there was evidence that the parents regularly arrived in a particular manner at one side of the nest; deviations from this norm in the artificial presentation could well influence the response. Soft calls or other warning signals may have been given by the approaching parent, although in our intimate observations from the blind at two nests we did not detect any.

*Experiments with Experience Deprivation*

The delay in the establishment of a negative response to the experimental stimulus objects until several days after they could be seen by the birds suggests that these objects acquired negative valence as sign stimuli only after a period of visual learning. To test this hypothesis a few simple experiments were performed, designed to deprive nestlings of the normal visual experiences of the nest environment during critical periods of development.

In one experiment 12 young grackles were withdrawn from their nests just before the attainment of pattern vision at 150 hours of age, isolated individually in small, solid-walled, open-topped boxes in the laboratory and hand fed for one or two days. They were then returned to their nests and their responses to the test models compared with those of their undisturbed nest mates.

The objective of a temporary deprivation of visual experience was, of course, not completely achieved in this crude experiment; rather, there was a substitution of an unnatural environmental situation (laboratory room with human attendant) for the natural, species characteristic situation (nest vicinity with parental attendants). The possible significance of specific features of the unnatural laboratory situation cannot be evaluated at this time.

The results are presented in Figure 3. Although the data are rather meager, it is clear that the appearance of the crouching response was delayed by this procedure by an amount roughly comparable to the period of withdrawal. The effect was strikingly apparent in comparing the responses of experimentals and controls in the same nests; the intense crouching of the normal birds to test objects in no way influenced the uninhibited gaping of their experimentally retarded nest mates.

In the second experiment seven nestlings were blindfolded with a preparation of glue and lampblack, a procedure well tested in our laboratory on various other animals of comparable size. Blindfolded birds continued to gape to all mechanical stimuli at the nests. They were well fed and suffered no apparent injury or disturbance other than that of visual deprivation.

Three birds kept blindfolded from about 60 to about 150 hours of

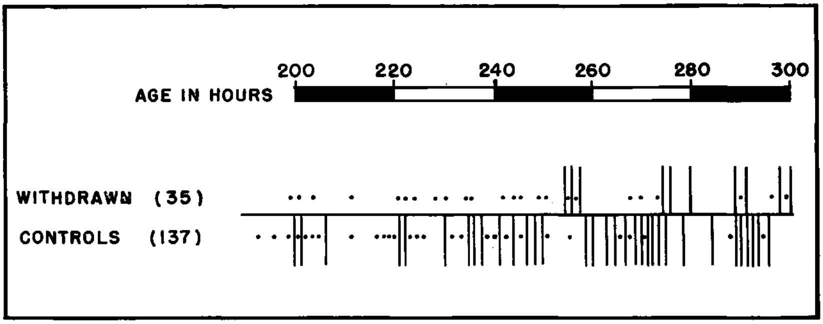


**Figure 3. The effect of an experimental interruption of normal nest experience (temporary removal from the nest) on the time of appearance of crouching reactions to models in young grackles. Gaping reactions are indicated by dots, crouching reactions by bars.**

age showed no delay in the appearance of the crouching response to strong jarring of the nest or, after removal of the blindfold, in the development of visual discrimination to test objects. Another bird, blindfolded from 150 to 275 hours of age, showed complete and normal optomotor response when tested upon removal of the blindfold. The experimental procedure thus had no detectable effect on the maturation of the basic response equipment.

Three nestlings blindfolded from 150 hours to 267–295 hours of age gaped strongly and unhesitatingly to the screech owl model upon removal of the mask, while their untreated nest mates (controls), in striking contrast, crouched tensely on the nest floor. This gaping response to the owl persisted even when these experimental birds were removed from the nest and held in the hand. Discrimination developed rapidly, however, and two of these birds crouched to the owl model within 24 hours; the third continued to gape to the test models until it fledged the next day.

These deprivation experiments, while crude in several respects, suggest that the visual experience ordinarily obtained by nestling grackles in the natural nest environment may be necessary for the normal development of discrimination between parent birds and other stimulus objects that may appear at the nest rim.

## DISCUSSION

The ability to distinguish natural enemies as specific stimulus objects for avoidance responses has been examined in various altricial birds by Nice and ter Pelkwyk (1941), Rand (1941), Kramer and St. Paul (1951), Hinde (1954), and others; and attention has been called to a well-defined ability by some species to discriminate between potentially injurious and harmless forms. Little attention, however, has been given to the early ontogeny of these discriminations and to the relative role of learned and unlearned contributions to their development. Crouching in the nest is a rather specialized form of avoidance behavior with a limited functional duration in the life of the bird. It does, however, bridge the important stage of development during which the motor and sensory mechanisms of avoidance are maturing, and displays in its later phases some clear evidence of object discrimination. Crouching, furthermore, possesses the essential elements of motivation, stereotypy, and adaptiveness that characterize behavior patterns commonly referred to as instinctive.

The observations and experiments described in this report indicate that individual experience played an important role in the development of early visual discriminations shown by nestling grackles in their crouching responses. They suggest, furthermore, that the visual stimulus situations of the natural nest environment, and particularly those associated with the parent birds in their frequent visits with food, could provide the basis for development of the characteristic discrimination patterns displayed by advanced nesting grackles in nature.

Two alternate explanations can be offered for the inhibitory effects of experience deprivation shown by our withdrawn and blindfolded birds: (1) a delay in the development of an ability or readiness to respond to specific sign stimuli of innately determined releasing significance or (2) an interference with the process of discrimination learning by blocking the input of sensory information.

The first of these explanations cannot be properly evaluated at this time, since we do not yet have adequate data on the specificity of the stimulus object necessary to release the initial, visually determined, crouching responses. Knowing the ease with which nestlings of several other species will accept foster parents, however, we tend to doubt that the implied specificity exists.

We therefore favor the second explanation and the view that the crouching (avoidance) response of our grackle nestlings to certain visual stimulus objects was acquired only after several days of experience with pattern vision had provided a basis for distinguishing the consistently rewarding stimulus object (the parent) from other (strange) objects. Thereafter, with a basis for recognizing strangeness in terms of lack of familiarity, the response to new objects as they were encountered tended to be negative until their positive or neutral nature had been established through experience.

This interpretation of our data on grackles differs from that of traditional instinct theory in attributing the delay in visual avoidance responses to the insertion of a learning period in which the bird acquires a basis for distinguishing visually between rewarding and nonrewarding stimulus objects. More work is obviously needed to clarify the significance of the first consistently rewarding stimulus object (the parent) in its functional relation with other objects on their first presentation. According to our interpretation, however, new or strange objects are responded to negatively only because they differ essentially from the one (or several) that have come to be accepted. All objects seem to be accepted (gaped to) by the nestling grackle until after the initial, visual learning period in which the basis for familiarity is established; thereafter, all new or strange (unfamiliar) objects elicit a negative response. Many authors (Nice, 1943; Kramer and von St. Paul, 1951) have noted the role of familiarity and strangeness in determining avian responses; the view here presented merely adds the concept that strangeness is relative and exists only in opposition to familiarity, a characteristic that must be acquired through experience. This theory shares elements with that of Hebb (1946) in which fear (the motivational basis for avoidance behavior) is regarded as arising from the disruption of established behavior (neural) patterns.

The uniformly consistent positive response of advanced nestling birds to the parent on the one hand, and the equally consistent negative response to a strange and potentially dangerous object, such as an owl, on the other, suggests a basic discrimination that one is tempted to regard as innate. The data obtained in this study, however, support a learned basis for the phenomenon in the Common Grackle. The interpretation proposed recognizes a very general basis for avoidance response based on familiarity and strangeness as derived and elaborated in individual birds through experience. It is proposed that the stereotypy and specificity of the stimulus selection patterns characteristic of advanced nestling birds may well be due to the basic stereotypy and specificity of the nest environment rather than to similarities of genetic constitution.

## ACKNOWLEDGMENTS

We are grateful to Mr. John L. Kaspar for help in collecting field data; to Dr. K. S. Rawson for technical advice; and to Drs. N. Tinbergen, F. Sauer, and N. E. Collias for suggestions on the manuscript.

## SUMMARY

Nestlings of the Common Grackle in 21 nests at Madison, Wisconsin,

showed crouching (responses) to mechanical stimuli well before the maturation of pattern vision, but did not crouch to visual stimuli until two or three days after pattern vision has been acquired.

Experimental withdrawal of nestlings from their nests for one or two days produced a comparable delay in the acquisition of crouching responses to visual models.

Temporary blindfolding of nestlings did not affect the maturation of crouching to mechanical stimuli or of the optomotor response to moving patterns. When extended into the visual discrimination period (after maturation of the optomotor response), however, it did postpone the onset of crouching to visual models.

It is proposed that in grackle nestlings crouching responses are given to visual stimuli only after a period of visual learning has provided a basis for discriminating between the consistently rewarding parent and other objects.

## LITERATURE CITED

BANKS, R. C. 1959. Development of nestling White-crowned Sparrows in central coastal California. Condor, **61**: 96–109.

BAUMGARTNER, A. M. 1938. A study of development of young Tree Sparrows at Churchill, Manitoba. Bird-Banding, **9**: 69–79.

EMLEN, J. T. 1942. Notes on a nesting colony of western crows. Bird-Banding, **13** (4): 143–154.

HANN, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull., **49**: 145–237.

HEBB, D. O. 1946. On the nature of fear. Psychol. Rev., **53**: 259–276.

HEINROTH, O., and M. HEINROTH. 1924–1933. Die Vögel Mitteleuropas. 3 vols. Berlin.

HERRICK, F. H. 1901. The home life of wild birds. Knickerbocker Press, New York. xix + 148 pp.

HINDE, R. A. 1954. Factors governing the changes in strength of a partially inborn response as shown by the mobbing behavior of the Chaffinch *(Fringilla coelebs)*. Proc. Roy. Soc. **B142**: 306–358.

HOLZAPFEL, M. 1939. Analyze des Sperrens und Pickens in der Entwicklung des Stars. Jour. f. Ornith., **87**: 525–553.

IVOR, H. R. 1944. Bird's fear of man. Auk, **61**: 203–211.

KESSEL, B. 1957. A study of the breeding biology of the European Starling (*Sturnus vulgaris* L.) in North America. Am. Midland Nat., **58** (2): 257–331.

KRAMER, G., and U. VON ST. PAUL. 1951. Über angeborenes und erworbenes Feinderkennen beim Gimpel (*Pyrrhula pyrrhula* L.). Behaviour, **3** (4): 243–255.

KUHLMAN, F. 1909. Some preliminary observations on the development of instincts and habits in young birds. Psych. Rev. (Monogr. Suppl.), **11**: 49–85.

MESSMER, E., and I. MESSMER. 1956. Die Entwicklung der Lautäusserungen und einiger Verhaltensweisen der Amsel (*Turdus merula merula* L.) unter natürlichen Bedingungen und nach Einzelaufzucht in schalldichten Räumen. Zeitsch. f. Tierpsych., **13** (3) : 341–439.

MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes *(Lanius)*. Univ. Cal. Publ. Zool., **38:** 11–242.

NICE, M. M. 1939. Observations on the behavior of a young cowbird. Wilson Bull., **51:** 233-239.

NICE, M. M. 1943. Studies in the life history of the Song Sparrow. II. Trans. Linn. Soc. N.Y., **6:** 1–328.

NICE, M. M., and J. J. TER PELKWYK. 1941. Enemy recognition by the Song Sparrow. Auk, **58:** 195–214.

ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. Auk, **58:** 518–535.

PRECHTL, H. F. R. 1953. Zur Physiologie der angeborenen auslösenden Mechanismen. I. Quantitative Untersuchungen über die Sperrbewegung junger Singvögel. Behaviour, **1:** 32–50.

PORTMANN, A. 1938. Beiträge zur Kenntnis der postembryonalen Entwicklung der Vögel. Rev. Suisse de Zool., **45:** 273–348.

RAND, A. L. 1941. Development and enemy recognition of the Curve-billed Thrasher: *Toxostoma curvirostre*. Bull. Am. Mus. Nat. Hist., **78:** 213–242, **79:** 517–524.

ROWAN, M. K. 1955. The breeding biology and behaviour of the Red-winged Starling, *Onychognathus morio*. Ibis, **97:** 663–705.

SLONAKER, J. R. 1921. The development of the eye and its accessory parts in the English Sparrow. Jour. Morph., **35:** 263–357.

SCHIFFERLI, A. 1948. Über Markscheidenbildung im Gehirn von Huhn und Star. Rev. Suisse de Zool., **55:** 117–212.

THORPE, W. H. 1956. Learning and instinct in animals. London, Methuen and Co., viii + 492 pp.

TINBERGEN, N., and D. J. KUEHNEN. 1939. Über die auslösenden und richtungsgebenden Reizsituationen der Sperrbewegung von jungen Drosseln (*Turdus m. merula* L. und *Turdus e. ericetorum* Turton). Zeitsch. f. Tierpsych., **3:** 37–60.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull., **60:** 6–51.

*University of Wisconsin, Madison, Wisconsin.*