Imprinting in an Altricial Bird: The Blond Ring Dove (Streptopelia risoria)

Abstract. *Newborn ring doves were taken away from their parents when they were from 4 to 14 days old. They were then either raised by hand in complete visual isolation from other members of their species or placed in a community cage after weaning. They were tested as adults in a free-choice situation between human beings and ring doves. An optimum period for imprinting was found when they were about 7 to 9 days old. The controls showed that subsequent experiences during the life span of a bird also have an effect on the choice of a mate, and, in this species, imprinting can be said to be reversible.*

Imprinting has been studied almost exclusively in newborn precocial birds ever since Lorenz (*1*) called attention to the phenomenon in the grey-lag goose. Most of the recent papers on imprinting in precocial birds are listed in Gray (*2*). Observations and reports that indicate the presence of an imprinting mechanism in altricial birds (they are unable to follow their parents and must be fed by them for some time after hatching) are few, and their entire life history is known in only a few cases (*3–5*).

In altricial birds there is no response to parents comparable to the following response in precocial birds; however, even in the precocial birds Polt and Hess (*6*) showed that the following response early in a bird's life cannot be equated with imprinting. Ring dove squabs remain in the nest for about 14 days before leaving and must be fed by their parents for at least 21 days.

The test for the imprinting effect was the copulatory response or the immediate precopulatory behavior at sexual maturity as stated originally by Lorenz (*1*). Craig (*4*) found that ring doves raised by their parents but later isolated from all other doves would court human beings and Thorpe (*7*) considered this behavior to be an example of reversible imprinting. Craig's study is the only one in which the entire life cycle from birth to sexual maturity is known and, since Warriner (*5*) did not attempt to analyze the factors affecting the early experience that determined mate selection in the pigeons in his experiments, we have undertaken a more detailed investigation of imprinting in doves.

Because young doves taken away from their parents must be fed by hand, a human being was used as the imprinting object. When the experimental bird was sexually mature at 8 to 9 months of age, the objective scoring of responses in a free-choice situation between a human being and a ring dove of the opposite sex was no problem because the responses were unambiguous.

Birds were taken from their parents at various ages and raised by hand, visually isolated from all other birds. Since Lehrman (*8*) had found that actual participation in courtship and not auditory cues lead to pair formation in ring doves, auditory isolation was not attempted.

Experimental and control groups were established on the assumption that the removal of the squabs from the nest at various ages during the period when they would have normally remained on the nest and raising them by hand in isolation from other doves would have a differential effect on their adult sexual behavior. Since squabs have their eyes closed during the first 3 days of life (Fig. 1), none were removed from the nest during this period.

Group AA consisted of 25 birds isolated in individual cages until they were tested as adults. Squabs were removed from the nest on days 4 to 14, three birds each day, except on days 3, 12, 13, and 14, when only one was removed. Group AB consisted of 11 birds. One bird was removed from the nest each day from day 4 to 14, raised by hand in isolation until they were weaned between 24 to 30 days, and they were then placed in a community cage with other ring doves. Their exposure to human beings was limited to that necessary for feeding and cleaning. Group BA consisted of six birds raised by their parents until weaned and then isolated in individual cages until tested. Group BB consisted of six birds raised by their parents and maintained in a community cage until tested. Exposure to human beings was the same as for group AB.

When tested the birds were sexually mature and were 8 to 9 months old; a few were older. The testing was done in a room 1.8 by 1.5 by 2.1 meters high, illuminated from above by a 40-watt fluorescent lamp. It contained a wooden perch 1.5 meters above the ground that ran the length of the cage and was about 60 cm from the only open side which was covered with 2.5 cm^2 of wire netting. A small nest box was placed on one end of the perch and on the opposite end there was a wire cage (60 by 45 by 40 cm high), with a perch and a nest box, which contained a choice bird of the opposite sex. A chair for the human participant was placed in the corner opposite the wire cage. The observer was about 60 cm away from the wire-covered open side, behind a door with a glass window, and was in contact with the person inside the test cage by an intercommunication system.

After the person and the choice bird were in their places, the experimental bird was placed on the center of the perch. After a few minutes the experimental bird either approached the person or the choice bird. The choice bird was then released from its cage so that it could make advances to the experimental bird as could the person. The observer in the other room noted the behavior on a check list based on an ethogram of the species. A protocol was taken of the behavior of each bird.

The experimental bird being tested could make one of four responses: (i) it could court the person, (ii) it could court the other bird, (iii) it could alternate between the two, or (iv) it could ignore both. In all cases in groups AA and BA the experimen-

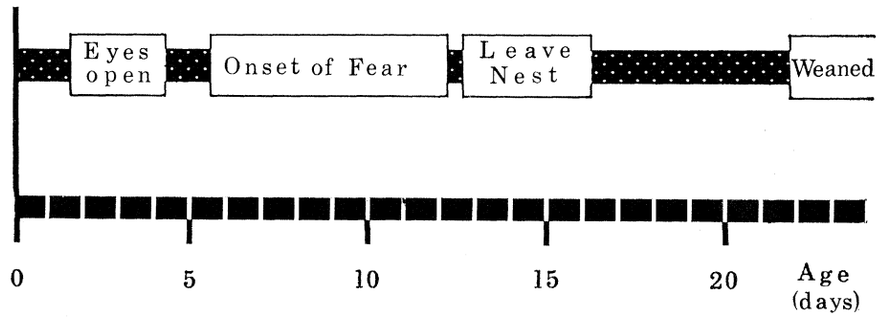

Fig. 1. Normal development of ring doves from the time they hatch until they are weaned.

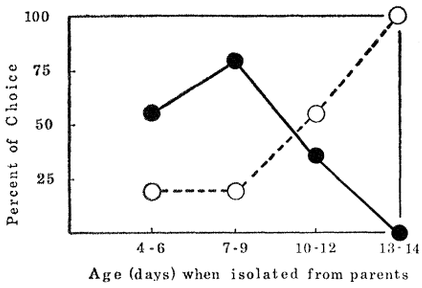

Fig. 2. Percent of choice by 25 ring doves in a free-choice situation between a human being (solid line) and a ring dove (dashed line) of the opposite sex. All birds were kept in visual isolation from other doves from the day they were removed from their parents until they were tested as adults.

tal bird would respond by either assuming the male role in copulation with the choice subjects, showing a decided preference for one, or by exhibiting all courtship behavior except actual copulation. At other times the bird would assume the female role with the appropriate female copulatory behavior patterns. In cases of no preference the choice objects were either ignored or passively avoided. Results for group AA are illustrated in Fig. 2. Only positive choices are included.

The birds in group AB all chose the ring dove. They were so inhibited by the presence of the person in the test cage that they would respond to doves only after the person had left the cage. In group BA two birds chose the human being, two the dove, one bird chose both, and one bird ignored both. Group BB behaved exactly as group AB.

Imprinting occurs in this species of ring dove and the optimum time for its effectiveness seems to be the removal of the young from their parents at 7 to 9 days of age. Squabs removed from their parents after the 12th day chose a dove in a free-choice situation. Only about 50 percent of the birds removed from the nest at days 4 to 6 chose the human being. One might expect that all birds removed before a certain age would choose human beings. The onset of fear lies between the 7th to the 10th day of life (Fig. 1), the period during which the optimum imprinting effectiveness to humans falls. The interaction with a new object, in this case the person who removes the bird from its parents and raises it by hand, may be more effective when this experience is accompanied by fear responses, whereas birds removed earlier have never shown fear to the human. The lack of emotional interaction results in fewer choices for the human being. When all birds are fearful of strange objects, after day 12 the fear is strong enough to prevent establishment of a bond with the human being that might be evident in the adult bird. This hypothesis appears tenable in view of results obtained in chicks by Kovach and Hess (*9*), who showed that more intense arousal, resulting from painful shocks which chicks were given in the presence of the imprinting model, resulted in increased following during and even before the critical period at about 14 to 16 hours.

The birds of group AB behaved similar to birds in group BB. The experience of being raised by hand for several weeks had no detectable lasting effect when these birds again lived with other doves for 7 to 8 months without close contact with human beings. This idea seems to be supported by the behavior of the three birds of group BA who chose the human being. The fact that not all doves in group BA chose the human being may be due to the biologically more adequate object—a dove—competing with such a vastly different one as the human being. This view seems to be borne out by the observation that even human-imprinted birds would nevertheless fight in a species-specific manner with other doves. The competition between biologically appropriate, versus inappropriate, objects may also explain why none of the 11 birds of group AB chose the human being. Another part of the explanation is that in this species, not only the early experience during an optimum period, but also continued experience throughout the bird's life has an effect on adult behavior. That experience around an optimum period between 7 to 9 days of age does have lasting effects is clearly demonstrated by the birds in group AA.

We conclude that imprinting in ring doves is reversible although in some birds its effects are never completely lost. Since both early and subsequent experiences affect the adult sexual behavior, it appears that during evolution two mechanisms evolved which result in pair formation. In nature both must be at work.

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References and Notes

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Eel Electroplaques: Spike Electrogenesis without Potassium Activation

Abstract. *Measurements with the voltage clamp technique demonstrate that only an early conductance increase occurs during spike electrogenesis of eel electroplaques. The delayed increase which is characteristic of spike electrogenesis in many other cells is absent. Instead, the membrane resistance increases two- to threefold above its resting value. The brief initial increase in conductance is due to sodium activation followed by rapid sodium inactivation. The influx of sodium causes an inward current of up to 80 ma/cm². The inward current is abolished by eliminating the sodium from the normal medium (substitution of choline chloride for NaCl); by blocking sodium activation with tetrodotoxin; or by causing sodium inactivation through enrichment of the potassium in the medium. The delayed increase in membrane resistance is not affected by eliminating sodium influx, nor by substituting various impermeable anions for the chlorine of the normal medium. Thus, the increase in resistance signifies the occurrence of potassium inactivation which is unmasked by the absence of potassium activation.*

Spikes are produced in most electrically excitable cells by the same mechanism as that which accounts for the response of squid giant axons to electrical stimuli (*1*). An initial depolarizing electrogenic process, sodium activation, is terminated by a subsidiary voltage-dependent process, sodium in-