Imprinting: a comparative study of a range of avian species.

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Imprinting : A Comparative Study of a Range of Avian Species.

This thesis investigates the field of imprinting by comparing the behaviour of a range of precocial, nidifugous avian species, i.e. types of bird which leave their nest soon after hatching. In the first chapter literature relevant to imprinting is reviewed. A fact emerging from this review is the lack of comparability between various imprinting experiments. In this thesis the importance of experimental uniformity is stressed.

It had been thought by Lorenz (1935) that some species of wa~~t~~der, i.e. curlews (Numenius arquata), and godwits (Limosa limosa), could not imprint on an inappropriate stimulus. This suggestion was investigated in the present comparative study in which, for the species studied, the experimental method was kept uniform.

In the second chapter the experimental method is described as is the type of species and the taxonomic group from which they come. The species used were: the domestic fowl; pheasant; partridge; wild mallard; curlew; lapwing and oyster-catcher. The stimulus used to encourage approach from these species was a rotating, white disc, with a 45° red sector.

In the third chapter, four experiements are described. In the first three experiments the effects of various stimuli and training procedure in imprinting, were investigated using domestic

fowl. This was done in order to examine the effectiveness of the stimuli in inducing approach. The fourth experiment compared a range of species responses to a combined visual and auditory stimulus.

In chapter five, two further experiments are described which were conducted on lapwings, extending the generality of conclusions from experiment four.

Chapter six contains the conclusions drawn from the experiments, and the need to consider the natural parent-chick bond is stressed.

IMPRINTING - A COMPARATIVE STUDY OF A RANGE OF AVIAN SPECIES.

ANTHONY CHIVA

Submitted for M.Sc. Thesis to
Durham University, in September, 1975.

CONTENTS

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Chapter One.

INTRODUCTION.

The imprinting process has been considered to take place over a short period of time, and its effects to be permanent and non-reversible (Heinroth, 1911, Lorenz, 1935). The term 'imprinting' describes the attachment of young birds to their parents, which affects their later social, sexual and parental behaviour. Views on imprinting have changed markedly since these early studies. It is for this reason that a brief summary of research findings is presented in Chapter One. This summary describes the many types of experiments, stimuli and species that have been used, which have tended to produce conflicting results. Therefore, any overall conclusions based on different species are extrapolations, often from conflicting results.

Each specie can differ in significant ways. Development may pass through different stages and at various speeds. Innate predispositions to respond may vary from specie to specie as they may vary with the level of hormonal secretions. The interaction of innate and experiental variables is likely to result in different experimental results between differing species. These differences must be considered in any analysis of a range of subjects and species. Yet some similarities will emerge between species because of similar adaptations to the environment.

Rarely have researchers used the same stimulus with a range of species to produce more comparable conditions. It is this failure that has prompted the investigation described in this thesis. A range of species were reared and tested in identical ways. The results for different species were not the same and this would not be expected.

The experimental method used for these experiments is described in Chapter Two. In this Chapter such topics as subjects, incubation, hatching, rearing and general procedure are included. The rationale for the experimental method is also included in this Chapter.

In Chapter Three experiments carried out to select a suitable stimulus are described . This Chapter also includes an account of experiment four, which compares the behaviour of a wide range of species to similar stimuli. One of these species was further studied in order to extend the findings from experiment four. To do this, certain aspects of the experimental procedure were modified. This experiment is fully described in Chapter four.

In the final Chapter an attempt is made to link the differences between species to demands made by their respective environments. The main conclusion drawn is that the feeding of the young may initially be the most important factor determining chick responsiveness to stimuli, both parental and experimental.

Review of Relevent Literature

Imprinting is the process by which the young precocial, nidifugous avian subjects become attached to their parents. The effects of these attachments are so permanent, that even at maturity, their influence on the behaviour of these animals is still felt. One of the first studies of imprinting, or attachment of filial responses, was carried out by Spalding (1873). He noted that chicks of certain species would follow a variety of objects just after hatching. He also noticed these following responses in chicks who were not exposed to a stimulus until a few days post hatch. Prior to Spalding description the following of humans by young birds had been observed. However, Spalding's experiments seem to have been some of the original experiments carried out in imprinting.

Heinroth (1911) published a report on the Anatidae, a family of birds including ducks and geese. Ducks, like other precocial, nidifugous species, include birds that are able to leave their nests immediately after hatching. In this study he discussed a process which he referred to as 'pragen' the German verb meaning 'to stamp'. Later Lorenz (1935, 1937), developed this theory of 'stamping', or the imprinting process and suggested that it had some very definite and precise characteristics. The four main qualities of this unique process were according to Lorenz:-

a) the process of imprinting, not its effects, is limited to a very definite period, early in the animals life. This has been called 'the critical period'.

b) Imprinting once completed, is irreversible and the objects on which the subject is imprinted cannot be changed.

c) Imprinting may influence many forms of later behaviour which were not manifest in early life.

d) Some generalisation of the imprinting object or objects takes place to allow for species, rather than individual, recognition.

These four points will be examined more fully in later sections. A brief explanation of the experimental procedures used to determine the responses of precocial, nidifigous species follows.

Criteria used in Assessing Imprinting.

Responses such as approach, following, discrimination or preferance, later choice of sexual and social companions, have all been used as measurers of imprinting. Guhl and Fischer (1969), have indicated the necessity for adequate tests of these variables. Bateson (1966), stated that approach and following can be viewed as the same process. Following can therefore be considered as a series of approaches. Prior to approach the subject is usually making high pitched sounds termed 'fear chirps'. During approach, 'fear chirps' cease and the bird will run to the stimulus. This applies to domestic chicks and many other species. These initial movements towards a stimulus have recently been studied in detail by Fabricius (1964), Dimond (1970) and Salzen (1970); the subject views the stimulus with side-to-side head movements; the stimulus is then approached in a series of tangential movements, so that a curve in the path of approach may be found. This behaviour can be seen by examining the course of the subjects' approach from above with cine film or video tape recordings. A bird seen to approach and discriminate can be said to have imprinted.

When the subject arrives at the stimulus, a whole series of other behaviours may be initiated. These are often of an emotional nature, examples of which are contentment chirps and nestling behaviour. This is a good indication of the rewarding effects of the imprinting object. When domestic chicks nestle to the mother hen, she protects and warms the chicks. An artificial stimulus may not warm the chick, but the chick will press hard against the stimulus, as though seeking physical contact. Some researchers suggest that a more specific tactile imprinting can take place (Taylor et al 1967). This view would explain the attachment and later preferance for a specific texture of type of contact. In the natural environment this preferance would presumably be formed by the process of nestling and warming.

Lorenz (1935, 1937), Immelmann (1967), and Schutz (1965) have used the later social and sexual responses of subjects such as geese, finches and ducks to confirm the occurrence of imprinting in these species. Their experiments are described in some detail in a later section.

Stimuli Initiating Approach

A great variety of stimuli can initiate approach in precocial species. Experiments have used a wide range of objects and found many of these to be effective. The most effective features common to these objects seem to be movement and contrast. Fabricius (1951), stated that when a moving model is used, and its component parts move and sway independently, the following response is again increased. In fact, anything that draws the subjects' attention can function as an imprinting object.

The types of stimuli used to cause approach have included objects moving in depth, revolving discs (Smith 1960), lights (James 1959) and flashing lights, (Abercrombie and James 1961). Moving models are effective stimuli, but if these are retreating they appear to be more attractive than advancing objects (Bateson, 1966), Rubel, 1970). It may be that a retreating stimulus causes less fear and encourages the chick to approach, whilst an approaching stimulus may tend to induce avoidance responses.

The effects of stimulus contrast on imprinting are examplified by experiments in which stationary stimuli have been used. Bateson (1964), Gray (1960), and Taylor & Taylor (1964,) have shown that stationary objects can cause imprinting. This type of attachment is called 'static imprinting'; Static imprinting could be a form of adaptation to the environment. If a chick becomes imprinted on its surroundings i.e. an area which has been a successful breeding ground for its parents, then if at maturity this organism chooses a similar breeding ground then it too may well be equally successful. This may be the reason why certain species return to a similar habitat, to that in which they were reared. An example of this is the Lapwing (Vanellus vanellus), which, during nesting, has a preference for a certain type of grass height and colour. This preference may well be learned during the juvenile period.

The Effects of Colour on Imprinting.

Many species have been tested with differently coloured stimuli to examine their effects on imprinting. The aim of these tests is to investigate whether a colour preference is a component of imprinting.

In research on colour preferences many inconsistancies occur, as they do in other areas of imprinting. Jaynes (1956), exposed New Hampshire Red chicks to red and green objects. However, as the red object was a cylinder and the green object a cube, the shape and size of the objects differed, introducing additional variables which may have influenced the results i.e. the red object was followed more and more over the 4 days. Schaefer and Hess (1959) exposed White Rock chicks to different coloured spheres and found a slight preference for red and blue over the other colours, green and orange, grey, black and yellow were the least preferred. However, Gray (1961), also using White Rock chicks, exposed them to rotating 5½ inch coloured discs, and found a preferance for red, yellow and black. These colours were more effective in eliciting approach than green, blue and white. Smith and Hoyes (1961), exposed Brown Leghorn x Light Sussex chicks to flashing circles of coloured light. They found red to be slightly more effective than the other colours used (green and white), but the difference was not statistically significant. A clear finding that emerges from the above is that red is an effective stimulus when used in imprinting studies with the domestic chick. Other than this however, no firm conclusions regarding colour preferances can be drawn. Shapiro (1971), suggests that the conflict in results that can occur is often due to the lack of consideration given to the background against which the stimulus is presented.

The Effect of Auditory Stimuli on Imprinting

A combined auditory and visual stimulus tends to be more effective in inducing following responses than either stimulus alone. The domestic fowl, a game bird, prefers the pitch of the auditory component to be between 49 and 392 cycles per second when immature (Collias & Joos, 1935). Sounds outside this range do not initiate a significant approach. The preferred auditory frequency range varies from species to species. Different subjects within the same species seem to vary in their relative responsiveness to auditory and visual stimuli (Klopfer & Gottlieb, 1962). Klopfer and Gottlieb suggested imprinting to an auditory stimulus is of importance in the natural environment, where chicks may lose sight of the parents, but still remain in auditory contact. Thus the chick will not be lost, even when visually isolated from the parent.

Heinz (1973), has studied the effects of conspecific calls, such as the brooding call, on approaching Ring Neck pheasant chicks and has found the brooding call to be effective in eliciting approach. Gottlieb (1967, 1970), has conclusively shown that identification of the species call in the Peking and Mallard ducks, originates from the embryo's 'self-audition' during late embryological development, i.e. after the seventeenth day. This was demonstrated by three experiments:

i) Isolating the batch of eggs from the parents, and finding that the neonates preferred the parental call to that of a Domestic Fowl.

ii) Isolating eggs singly from the batch, and finding that the neonates preferred the parental call.

iii) Isolation of eggs singly and the wiping or brushing of the embryo's vocal chords in order to prevent 'self-audition'. The neonate ducklings of this experiment did not manifest preference for the parental call over the call of a Domestic Fowl.

This shows that auditory imprinting in the Mallard, and possibly other species, takes place during later embryonic development.

However, auditory imprinting seems to be partially modifiable by subsequent experience, (Gottlieb, 1965).

In experiments on Japanese Quail eggs. Vince (1966), has shown that sounds can speed up or slow down the rate of development of the embryo. This maturational effect was produced by the sounds emitted from other eggs and could also be produced artificially by the experimenter. Motor development of neonates could also be affected, (Vince & Chinn 1972). Other research has shown that movement of the embryo may cause parental vocalizations and this may increase the speed of hatching, (Impekoven, 1973).

'Arousel' and Approach

Various experimenters, (Fischer, 1968; James & Binks, 1963; Kovach & Hess, 1963; Pitz & Ross, 1961) have examined the effects of traditional learning techniques, such as conditioned avoidance and selective reinforcement of responses, in the imprinting process, and have compared imprinting with conditioning processes. Pitz and Ross (1961) using Vantress Broiler chicks which were 12-15 hours post hatch, sounded a loud clapper during experimental trials and found that this caused a significant increase in approach. Kovach and Hess (1963), using the same species, used different levels of electric shock to ascertain its avoidance and/or reinforcing qualities. They found that the following responses to a blue ball, emitting the call 'come chick', increased with small shocks and drastically decreased with large shocks. Fischer et al (1965), using electro-convulsive shocks on the domestic fowl chick found that one shock did not have an adverse effect on discrimination but nine shocks prevented approach and produced avoidance. These experiments indicate that arousal rose to an optimal level, thereafter decreasing.

Guhl and Fischer (1969), have suggested that if the emotional state or degree of arousal in humans can be measured so can that of avian species. By the use of such measures as electro encephalography (EEG) recordings of electrical and thermal properties of the skin (GSR) respiration rate and muscle tension, the degree of arousal can be measured (Fischer, 1966). However, these techniques are only just beginning to be used to obtain information on imprinting (Schulman, 1971).

DISCRIMINATION

Discrimination is said to have occurred when the imprinted chick prefers (as measured by approach responses, etc) the familiar or imprinted stimulus, when compared with a novel stimulus that differs in some way from the original. There are several methods of testing for discrimination (Guhl & Fischer 1969). In Simultaneous Discrimination trials both stimuli are presented and the subject may approach one, neither or both. An alternative is the Successive Discrimination method in which two stimuli are presented, one at a time, for a fixed time interval.

In Successive Discrimination trials, the stimulus presented second is usually followed far more than the first. The effect of this 'extra' approach can be avoided by the inclusion of a large number of trials.

The sequence of stimulus presentations may be randomly determined. One of these stimuli would already have been presented to the subject during imprinting trials.

Many imprinting experiments use the discrimination or preference of the familiar over the novel stimulus as a measure of imprinting. Under these circumstances several workers, i.e. Jaynes (1958), Klopfer & Hailman (1964) amd Smith (1962) have shown that the subjects sometimes respond to the novel stimulus. This has often been taken as a lack of evidence of imprinting and/or evidence for the optimal effect of the novel stimulus.

In the above sections some characteristics of the imprinting process have been described. In the next five sections the characteristics of imprinting propounded by Lorenz in 1935, and current thinking with respect to his early views, will be discussed.

CRITICAL PERIOD

As mentioned earlier the critical period, or the time at which the organism could imprint, has been discussed, by other experimenters (Bateson, 1964; Fabricius & Boyd, 1954; Gray, 1962; Hinde et al, 1956; Rubel, 1970; Salzen, 1962; Smith & Bird, 1964; Weidmann, 1958). The length of the critical period varies from species to species. Agreement about any specific species has not always been possible, the reason for this being the use of different rearing and experimental procedures, and disagreement about the type of response, or lack of response, that indicates that the critical period is terminated.

The critical period for the domestic chicken (Gallus domesticus), was said to be from 12 to 36 hours posthatch. Various times have been suggested for the critical period of the mallard duck (Anas platyrhynchos). Ramsey & Hess (1954) state that the optimum time for responsiveness is around 16 hours. Fabricius (1964), suggests that it may be later, between 25 and 30 hours posthatch. Weidmann (1958), estimates general responsiveness to extend from 5 to 40 hours posthatch. Rubel (1970), with a game bird, the Japanese Quail (Coturnix coturnix japonica), showed that exposure to a moving object after the sixth hour posthatch no longer reduced 'fear chirps', the arrest of 'fear chirps' indicating the possibility of imprinting. Another investigator, however, found quail to be responsive at an older age. Ozmon (1973), managed to get 12 hour-old Japanese quail to imprint on a moving, illuminated light bulb. The chicks of Japanese quail are able to locomote efficiently at about 30 to 60 minutes after hatching. This may allow the critical period to commence and terminate sooner in this species than in others. The domestic fowl for example does not locomote successfully until 2 hours posthatch.

Judgement of the length of the critical period is usually based on approach, following, and other behavioural cues such as types of socialization, vocalization, nestling and pecking. Generally the hatched chick will approach and follow a suitable stimulus and subsequently be able to distinguish this from an alternative stimulus. After a certain time any stimulus which does not resemble the familiar stimulus will elicit 'fear' and avoidance from the chick. The close following of the familiar stimulus eventually decreases. This varies with the type of stimulus (Moltz & Rozenblum, 1958; Brown 1964), the degree of socialization of the chick with siblings, (Bateson, 1964; Salzen, 1963; Smith & Bird, 1964) and with various maturational factors.

It has been stated, by several investigators, that the end of the critical period is due to an increase in fear. Moltz (1960), suggested that this increase in fear prevented further activity towards a novel stimulus. Others hold the view that fear is induced when there is a change in the newly learned environment (Bateson, 1966; Dimond, 1968; Hebb, 1946; Hinde 1955; Salzen, 1967; Sokolov, 1960). The initial experience was thought to stimulate sensory development. Without this development fear could not subsequently have occurred.

If increased experience decreases the length of the critical period, Smith & Nott (1970) using socially reared domestic chicks, obtained approach to a visual and auditory stimulus up to 10 days posthatch. Thus though the subjects received sensory experience from peers, they still approached the stimulus, However this stimulus was thought, from previous studies to be extraordinarilly effective in eliciting approach. Other experimenters, using different stimuli with domestic chicks, comment on the decreasing approach responses to stimuli over the first week posthatch (Bateson 1964; Salzen 1963). Then reduced experience should increase the length of the critical period. This has been demonstrated by Bateson (1964^{b}) and Salzen (1962).

Various investigations have shown that the critical period does not begin when the chick hatches from the egg, but has already started during embryonic development (Bateson, 1964^{b}; Dimond, 1968; 1971; Gottlieb & Kuo, 1965; Impekoven, 1973; Vince, 1966). The sensory systems are sufficiently developed a few days before hatching to be capable of responding to stimulation. Gottlieb and Kuo (1965), point out the relationship between the behaviour of the embryo duckling and the subsequent behaviour of the neonate duckling.

Gottlieb (1961^b, 1963), has used the concept of developmental age, which is the age from the start of controlled incubation rather than age from hatching. He suggests this to be an accurate measure of the stage of development reached by the embryo. This is often necessary, as some subjects in the same batch may take much longer than others to 'pip' and hatch. Gottlieb prevented development of the eggs by keeping them for 2 to 3 days at 29 degrees fahrenheit (± one degrees). The eggs could then be incubated and all would begin to develop at the same time.

This technique does not seem to have been adopted generally, even though it may reduce the developmental variability at hatching. This may be important in experiments where the chicks are incubated seperately. However, Vince (1966), using Japanese quail, has shown that developmental age may not be so significant, because inter-egg stimulation co-ordinates the rate of development and the hatching times. This was shown by putting eggs at various stages of ontogenetic development into one batch; after a certain amount of time they all hatched simultaneously. In species such as Japanese quail, where simultaneous hatching and mobility of the clutch as a whole is conducive to survival this is an important consideration.

In conclusion, the critical period seems to be an important factor in limiting imprinting. However, the length is not fixed for any one species, but can be modified by either increasing or decreasing the amount of sensory stimulation. The limiting factor is therefore partly experiential and partly determined by the internal physiology of the animal. The critical period can now be viewed as the interaction between the degree of experience or sensory stimulation and maturation.

The concept of critical period implies that imprinting can only take place within a fixed time interval. Since in fact the imprinting period can be extended or decreased by manipulating experiential factors such as, the amount of sensory stimulation, 'sensitive period' is perhaps a better descriptive term.

IMPRINTING AS AN IRREVERSIBLE PROCESS

The irreversibility of imprinting has been witnessed in cases where imprinting on an inappropriate object has taken place. Lorenz (1935, 1937,) cites many instances where young birds have imprinted on humans and ignored, sometimes even attacked, members of their own species. Lorenz reared goslings in a group so that imprinting could take place and the social and sexual behaviours of the goslings would not be limited solely to him. Immelmann (1967), has stated that imprinting is not reversible because under artificial conditions a less than optimal stimulus is accepted. He has shown this with his work on Estrildine finches, which are altricial birds, i.e. they remain helpless in the nest for over a week after hatching. He cross-fostered zebra finches (Taeniopygia guthata castanotis) with Bengalese finches (Lochura striata domesticata), birds belonging to two distinct genera. When independent of the foster parents, the zebra finches distinctly preferred Bengalese finches for social and sexual companions. This preference lasted for several years. However, the males of the zebra finches would, in the absence of female Bengalese finches, mate with female zebra finches.

Imprinting can be said to be a process having lasting effects on the subjects involved. However, these effects may be reduced. For example Immelmann's cross fostered zebra finches would accept members of their own species, in the absence of the preferred Bengalese finches. Schein (1963) considered that periodic reinforcement was necessary to maintain social and sexual preferences. If this reinforcement was not permitted, species to which the subjects had been 'tamed', would not receive social and sexual responses. Therefore the imprinting process does not seem to be an irreversible process, its effects can be modified by experiences subsequent to the sensitive period.

THE INFLUENCE OF IMPRINTING ON LATER SOCIAL, SEXUAL AND PARENTAL RESPONSES.

Numerous observations seem to indicate that imprinting can affect behaviour in future years (Cofoid & Honig, 1961); (Fabricius & Boyd, 1954; Hinde et al 1956; Lorenz 1935; Moltz 1970). These observations often involve precocial birds addressing sexual responses to humans, usually in preference to their own species.

Different experimental techniques have been used to investigate the sexually determined aspects of imprinting. Most researchers expose the subjects when juvenile, to an imprinting stimulus, and subsequently conduct tests to examine the effects of the exposure to the stimulus. An alternative method is to rear subjects of one species with a different species and record the subsequent socio-sexual behaviour. Tests of subsequent socio-sexual behaviour are either conducted at natural puberty or at artificial puberty, the latter induced by the injection of sex hormones. (All such hormones cause prodigious sexual development and initiate sexual maturity).

The hormonal treatment has been used by G~~r~~uiton (1966). Using the hormone testosterone oenanthate with Domestic fowl chicks, he has shown that chicks imprinted on a yellow glove will show significant sexual preference for this rather than a stuffed pullet. Other studies have yielded similar results; i.e. they prefer the stimuli to which they were originally imprinted.

In order to examine the latent effects of imprinting many researchers have used cross-rearing techniques and have studied the subsequent behaviour, (Immelmann, 1967; Schein, 1963; Schutz 1963, 1964, 1965). Schutz has conducted much of the work in this field, working mostly with the Anatidae and cross-rearing than with species of other orders. He has shown that male mallards reared with different foster species, will prefer the adopted species for later social and sexual companions. The mallard is a dimorphic species (i.e. the male and female are coloured and shaped differently) and the male readily imprints on other species. The female mallard, however, rarely accepts another species for sexual pairing. This difference in behaviour seems to be due to weak physical cues from the female to the male mallard, e.g. a relative lack of colouration of the female. However, the cues for the female mallard, from the male mallard, are very strong due to the distinctive colouration of the male. In some monomorphic species (i.e. where the male and female resemble each other closely), such as the Chilean Teal, both male and female imprint sexually on other species without difficulty.

In the mallard the female does not sexually imprint on other species, but she can be imprinted socially and maternally on other species. Schutz (1971) reared a female mallard with a coot family. The mallard therefore had coots for foster parents and siblings. When mature this mallard would mate and incubate naturally, with other mallards, but rearing of her own ducklings was abandoned in preference for coot chicks. She would attack other mallards and geese which approached the coot chicks, including any ducklings that came too close to the coot chicks. These findings seem to suggest that different types of imprinting processes may be involved in the development of social, parental and sexual behaviour.

Fabricius & Falt (1969) attempted to imprint a female and two male mallards on humans. In fact all the mallards were found at the age of 4-5 months to be sexually imprinted on humans. This includes the female mallard which Schuts (1971) states is non-imprintable on non-appropriate stimuli (i.e. the male mallard). At about one year of age these mallards were placed with a mallard of the opposite sex. Successful matings followed leading to avoidance and fear of human beings.

An even better experiment to show the reversibility of imprinting would have been to expose the human-imprinted mallards to another species of bird i.e. in order to avoid any innate predisposition or responsiveness to the same mallard species.

Two possible interpretations of these results are:

a) Sexual imprinting extends far beyond the sensitive period i.e. up to a year of age; or

b) Constant contact with new objects or species eventually leads to habituation and preferences for these new objects, even when the original object is presented.

The former interpretation seems least likely since there is a definite increase and avoidance of new objects by precocial species as they get older. Also it seems unlikely that the 'sexual' sensitive period lasts for as long as a year or more in this precocial species. Sexual maturity is reached before one year of age in mallards.

The latter interpretation therefore seems the most limely and agrees with the findings of Schein (1963). Sexual fixations therefore, appear to be modifiable by post-imprinting exposure to a non-familiar object or species.

The generalisation of imprinting allows for group or species recognition and also allows for individual recognition. Lorenz (1935), mentions how hand-reared geese could identify him from other people and would produce the 'greeting ceremony' on his approach.

The imprinted object has been shown to elicit approach and following and to affect subsequent social, sexual and maternal behaviour. Any object similar to the imprinting object also elicits the same responses. This has an obvious evolutionary significance; dangers of inbreeding and extinction of the species could be forecast if only the parents or siblings could initiate social, sexual or parental responses. Therefore, the whole species, or the particular sub-group of that species, must elicit the same behavioural characteristics to maintain a normal balance in the breeding population.

PRESENT VIEWS ON THESE CHARACTERISTICS

The original characteristics of imprinting, expressed by Lorenz (1935), have been modified in many small but significant ways. It is now known that the length of the sensitive period can vary according to the degree of sensory stimulation. The view of irreversibility of imprinting has been modified; familiarity with a new object or species can lead to acceptance of that new object as a social and sexual companion. The view that imprinting influences later behaviour patterns, which were thought not to be present at the time of imprinting, such as sexual behaviour, may be partially erroneous. Andrew (1966) demonstrated that some strains of two day old domestic chick will respond sexually to an unusual stimulus. In this experiment a hand was thrust backwards and forwards at the level of the chick's head, and the chick made an attempt to mount it. Andrew also obtained sexual responses from chicks of other precocial species, i.e. pheasant and partridge. The presence of siblings may act as a stimulus for the release of social, sexual and parental responses long before sexual maturity. Therefore, consideration should be given to the fact that innate neural mechanisms, behaviourally representing strutting and mounting, are present in infancy, which gradually mature and then reach their peak of development in adult life.

MODELS - AN EXPLANATION OF IMPRINTING

The study of imprinting logically leads to a discussion of the mechanisms underlying this process. Selection of the stimulus by the chick may be mediated by the responsiveness of the peripheral sense organs or may be more centrally determined. A sense organ may have greater sensitivity to a particular range of sound frequencies. For example, the domestic chick has a preferred range of responses to sounds between 49 and 392 cycles per second, but below 800 cycles per second, (Collias & Jones, 1953). Schwartzkopff (1955) has stated that this preference in chicks changes with the increasing maturity and development of the middle ear. Thus the adult hen responds to a different range of frequencies than the chick. This type of specific sensitivity also seems to apply to the visual system, (Maturana & Frenk, 1963; Sackett, 1963; Salzen, 1967). Maturana and Frenk (1963), have stated that the eyes of many birds have very well developed moving edge and contrast detectors. This has definite advantages for the animals in allowing them to detect small moving objects. These authors have demonstrated that specific retinal detector cells respond to particular stimuli. Hubel and Wiesel (1958) using single cell recordings on the cat, have shown that specific cells in the cat's visual cortex are responsive to stimulus configurations at the level of the retina (see also Salzen 1967, on electrode implantations in the brain of the domestic chicken). Selection of certain stimuli therefore, does seem to take place in the sensory systems and these are associated with specific neural areas. These neural areas may in some cases require priming by sensory experience before they will become functional (Adam & Dimond 1971a, 1971b; Moltz, 1960; Dimond, 1970).

The chick is born with a brain in which some neural pathways are already present; other pathways however, must be formed.

The formation of these involves learning. Different researchers have applied different models to explain this learning process. Salzen (1966),applied the neuronal model originally suggested by Sokolov (1960), to the imprinting situation. The neuronal model is formed by learning e.g. the development of specific neural pathways which correspond to the environmental stimuli around the subject. When a novel stimulus is seen which does not correspond with the neuronal model, an amplifying system is triggered which causes an orienting response. In Salzen's interpretation orientation would take place to the familiar stimulus; whereas according to the interpretation by Sokolov the orientation would be to the novel stimulus, thus leading to habituation. Fear occurs when the neuronal model has formed and novel stimuli appear. The neuronal model therefore explains why sensorily deprived chicks i.e. auditorily and visually isolated, have an extended sensitive period.

Dimond (1970), makes three points in criticism of Salzens interpretation.

i) The familiar object is already part of the neuronal model, so why should the organism orient towards it? According to the simple neuronal model orientation takes place towardsthe novel stimulus.

ii) Orienting is not the same as approach, organisms orient to many things from which they subsequently flee.

iii) When an organism is presented with an unfamiliar object in an unfamiliar environment, why should it approach the unfamiliar object in preference, since neither form a part of the neuronal model.

Dimond therefore criticises the neuronal model as an explanation of imprinting, but agrees with the idea of image formation and an amplifying machanism. He does not link the amplifying system directly with the modeling or learning mechanism as used in the neuronal model He considers, as does Klopfer (1967), that imprinting consists of two phases; the first phase is the primary orientation and approach to one or more stimuli; the second phase is the restriction of approach 'to one object', by learning. The primary approach depends upon the developing locomotor, visual and neural systems. The secondary phase takes place by various forms of learning. Dimond considers there to be an amplifer linked to both the sensory mechanism and the learning mechanism. The amplification function in a newly hatched chick is at a low level and sensory stimulation only causes a little excitation in the neural system. In this situation the chick approaches any object which is 'attention getting'. With maturation of the sensory and neural systems, the amplifer can act on a more organized neural system, and new stimuli cause higher amplification.

After 2 to 3 days the chick avoids and shows fear of novel stimuli. These stimuli, being unknown to the chick, trigger a high amplification, which can lead to fear and immobility. A familiar stimulus triggers low amplification, which may lead to approach. The mechanism of low amplification is preferable to the chick and therefore may act as a reinforcer for the familiar stimulus. High amplification, associated with novel stimuli, causes fear and may act as negative conditioning.

Dimond (1970), using various experimental techniques, tried to influence the amplifying mechanism independently of the learning mechanisms. In the first experiment, he kept one group of domestic chick eggs under constant illumination and another group in constant darkness. After hatching, some differences in behaviour were noticed between the two groups. The light-incubated chicks approached far less readily and avoided far more that the dark incubated group. However, the ability of the former group to discriminate objects was unaffected. These experiments indicate that the chicks' learning system was not affected, but that the amplification mechanism of the sensory system was affected. This could be interpreted as a priming in the development of the sensory systems, facilitating the organisation of the retina and neural pathways prior to hatching. After hatching, sensory cues produce greater excitation, inducing fear at an earlier age and shortening the critical or sensitive period.

The second experiment involved the use of a flickering light on eggs which were incubated for 19 days. A group of domestic chick eggs was exposed to a square wave light, flickering with equal 'on' and 'off' exposure times. This produced neonates which approached flickering stimuli far more readily than a group of chicks which had not been exposed to the flickering light. Dimond interpreted these differences as meaning that the flicker had affected the learning mechanism, rather than the amplification mechanism. Dimond therefore suggests a theory of imprinting, substantiated by experimentation, which appears to overcome the objections to Salzens' (1969) 'neuronal model' as a theory of imprinting.

The learning mechanism, or the formation of specific neural pathways, is somewhat hypothetical as the physiological correlates of such paths have not as yet been demonstrated. A comparison of the learning phase of imprinting with other forms of learning, such as associative and perceptual learning. Associative learning has several specific attributes; it requires reinforcement; the resulting behaviour is overt; the response is generalised to more than one stimulus.

Campbell and Pickleman (1961) successfully used the imprinting object as a reinforcer or reward for securing the choice of a particular path in a 'T' maze by domestic chicks. Abercrombie and James (1961) successfully used a flashing light as an unconditioned stimulus, with domestic chicks. Meyer et al (1970) have used light increment as a reinforcer for domestic chicks and found this to be effective, however light decrement was not found to be effective. Peterson (1960), Hoffman,(1968), Hoffman et al (1966, 1969) have shown that the imprinting stimulus can be used as a reinforcer in both rewarding and punishment situations. Barrett (1972), prevented conditioned pole pecking by adminstering electric shocks. The conclusion he draws from this, is that if conditioning can be reversed in the domestic chicken, then imprinting, which may be a form of conditioning, may also be reversible. Originally it was felt that the imprinting object was not reinforcing and therefore imprinting could not be regarded as a form of associative learning. However, it is now clear that the imprinting object can be used as a stimulus for conditioning chicks to perform diverse activities. Present evidence seems to indicate that the imprinting stimulus has several reinforcing or rewarding properties,(Bateson, 1964b). These reinforcers were not originally obvious to experimenters, and imprinting can now be considered to be a form of associative learning.

Theories of perceptual learning aim at explaining an organism's ability to discriminate between different stimuli. This ability may be directly related to the extent of exposure to those stimuli. The advantage of perceptual learning in describing imprinting is that it avoids postulating a reinforcer. This account of imprinting has been favoured by some researchers (Salzen 1962; Sluckin 1962; Sluckin & Salzen 1961). Salzen viewed the process of imprinting as taking place in the following way; the initial stage of approach behaviour was exploration, this being followed by familiarity with the stimulus or perceptual learning, this corresponds to his description of the neuronal model. Subsequently this learning leads to better instrumental learning, or latent and incidental learning. This particular attachment to a stimulus or configuration of stimuli, would be equivalent to imprinting and similar processes. Sluckin agrees with Salzen on the significance of perceptual learning and relates perceptual learning to the amount of sensory stimulation. As perceptual learning depends on the degree of exposure to a stimulus then a restriction of sensory stimulation reduces perceptual learning. As the organism matures the sensory systems develop and there is an increase in the capacity for perceptual learning. According to Sluckin (1962) sensory stimulation and perceptual learning are interrelated; perceptual learning will take place as the organism receives sensory stimulation. The major criticism of perceptual learning as a theory of imprinting is similar to that raised against the neuronal model, namely, why should the organism orient towards and approach the unfamiliar object in an unfamiliar environment?

Imprinting seems to be the result of a balance between the innate schemata, (information contained in neural pathways, present early in embryonic development), and learning processes. Some researchers have attempted to analyse the contribution of innate schemata to behaviour (Hinde 1955; Immelmann, 1964; Lorenz, 1935; Schutz, 1965; Tinbergen, 1959). These pathways predispose the organism to respond in certain ways, perhaps by approach and following, towards certain physical or behavioural cues which act as an Innate Releasing Mechanism (I.R.M.), when the organism is presented with these cues. In certain cases a supra-normal stimulus could act as the Innate Releaser (I.R.) even if this was not the natural releaser.

Innate schemata may or may not be modifiable as a result of experience. As previously described Schutz's (1965) work on the female mallard resulted in inappropriate social and maternal behaviours, but not inappropriate sexual behaviour. He explains these differences in terms of the 'balance principle'. The resulting behaviour is a balance between innate and learned components. In the female mallard there is less choice allowed on sexual companions. Immelmann (1967) holds a very similar view. He considers that birds, (he uses finches as an example), have a narrow range of stimuli to which they will respond. This range is further narrowed, or the responses become more specific, during imprinting. In cross-fostering experiments Immelmann has shown that zebra finches will initially respond to both zebra and Bengalese finches. Early learning however, tends to restrict this response to one or other of the species.

Lorenz (1935), originally stated that different species of precocial birds will differ in their response to stimuli, according to the completeness of the innate schemata. In some species these schemata limit imprinting, and later socio-sexual responses, to the natural stimuli only, i.e. the same species. He explains the lack of reactivity to non-natural objects during imprinting experiments, in the curlew (Numenius arquata) and the godwit (Limosa limosa), as due to an almost complete innate schema. He termed this the 'Mosaic form' of imprinting. The exceptional reactivity of precocial birds, such as the domestic chickens, mallards and geese, is due to less complete innate schemata, which Lorenz designated as the'regulative form' of imprinting. Lorenz imagined a scale of responsiveness between two extremes, different species occurring at different points along the scale.

In order to verify Lorenz's hypothesis it would seem desirable to conduct similar experiments on a wide range of species. This is necessary due to the variation in experimental procedures used by other researchers e.g. the lack of uniformity in imprinting experiments, types of species; and the time of the experiments in relation to the sensitive period. Lorenz's hypothesis would be correct if the different species fell into the scale specified by him. Lorenz considered the curlew to have a complete innate schema and therefore to be unreactive to non-natural stimuli. However, if some of the curlews react to the non natural stimuli this would appear to disprove some of Lorenz's arguments. In fact Seitz (1949) described how a curlew, being reared in a cage at head height, approached a researcher's head as he moved past the cage. The curlew approached an inappropriate object and therefore the situation cannot be as straight forward as Lorenz initially implied.

SUMMARY OF CURRENT VIEWS ON IMPRINTING

Imprinting remains a unique process. Experimenters cannot neatly place it into other categories of learning. All researchers agree that it is a form of learning, but they cannot agree on the type or mode of aquisition. Two current attitudes on imprinting are, that imprinting is the conditioning of an innate social response; or that imprinting results after the formation of a 'neural model', which then allows comparisons with novel stimuli, if these mis-match, fear, avoidance or immobility may result. Lorenz's (1935,1937) criteria of imprinting have subsequently been modified by other researchers, but his basic hypothesis seems to have been upheld. The main criticisms and modifications of Lorenz's hypothesis are in respect of the critical period. Lorenz said that the critical period lasted only a few days and that if imprinting did not occur during this period it would not take place. This has been shown to be inaccurate. A domestic fowl chick which has undergone sensory deprivation will still approach and imprint ten days posthatch (Smith & Nott, 1970). In view if these results it is felt that the critical period should perhaps become termed the 'sensitive period', because termination of imprinting is dependent on sensory stimulation and not purely internal determinants of the organism.

Imprinting seems to direct later social, sexual and parental behaviours. However, two points should be made. The first is that many of these responses are already present during infancy

(Andrew 1966; Schulman 1970). Therefore they are not later behaviours but neonatal behaviours which develop with the maturing organism. The second point is that once these 'behaviours have developed fully they can be mis-directed to an inappropriate stimulus (Fabricius & Falt 1969); Immelmann, 1967; Schein 1963); therefore the control of these behaviours by imprinting may not be as great as originally inferred by Lorenz.

Imprinting does have characteristic features but these seem to be extreme cases of characteristics found in other forms of learning and behaviour. The extreme nature of these features may be associated with the fact that they are learned at a very early and formative period in the organism's life when other influencing factors are reduced or absent.

CHAPTER TWO

EXPERIMENTAL METHOD AND PROCEDURE

It has been mentioned previously that the problem with many of the experiments carried out on imprinting is that different experiments have used different conditions and different stimuli; the stimuli used in the same experiment are often not comparable (e.g. Jaynes' experiments with colour, 1956, referred to in Chapter 1). As very few studies have conducted psychometric scaling on the parameters involved in imprinting stimuli (Smith 1969) the need for uniformity of conditions for all subjects is essential irrespective of species. Therefore any study intending to compare the imprintability of different species must ensure as far as possible that hatching, rearing and experimental conditions are equivalent for all subjects.

In the experiments reported in this thesis comparability of experimental conditions was ensured in various ways, and in what follows the steps taken to ensure standardization and the experimental procedure adhered to are described.

I. SUBJECTS

Any investigation into imprinting necessitates the study of precocial, nidifugous species. These species include chicks which leave the nest soon after hatching and are classified in the Modern Birds, or Superorder, Neognathae. There are 19 orders of birds of which 6 orders contain nidifugous types. Species from 3 of these orders have been studied. These are as follows:

Superorder Neognathae	Species Studied
Order Anseriformes:	
Ducks and Geese.	Wild mallard (Anas platyrhynchos)
O. Charadriformes	
Waders and gulls	Curlew (Numenius arquata) Lapwing (Vanellus vanellus) Oyster-catcher (Haematopus Ostralegus occidentalis)
O. Galliformes	
Game birds.	Domestic fowl (Gallus gallus) Partridge (Perdix perdix) Pheasant (Phasianus colchicus) (both melanistic and ring neck strains).

All the game bird eggs were obtained from commercial breeders. The wild species were collected specially for the study either personally or from the Slimbridge Wildfowl Trust.

II. INCUBATION

The different species studied required different temperatures and humidities for incubation. This was due to the vastly different natural environment in which they live and breed. The game birds nest in a drier environment than the waders; Waders nest in a variety of places, and many are found in cultivated fields: the difference in incubatory conditions is probably due to the blood temperature and body humidity of the parent waders. Curfew type incubators were set and adjusted for the different incubatory needs of the birds. The eggs of the game birds were incubated at 101°F (38°C), and all the eggs were sprayed with water daily, and turned daily. This was to prevent the embryonic membranes from drying and sticking to the shells. Light entered the incubators only when eggs were being checked, sprayed and turned. Care was taken with this aspect of the incubation as Dimond (1970), has noted that chick behaviour can be affected by exposure to light.

III. HATCHING

The hatching times of the game birds and mallard eggs could be planned and predicted to within a few hours. This was impossible with the waders due to the random mode of collection. Constant visits to the incubators were therefore made to ensure accurate estimations of post-hatch age. This ensured that all birds were tested within the first 6-12 hours post-hatch. After hatching, subjects were allowed to dry until experimentation began, or were removed from the incubators and placed in individual cages in visual isolation from other organisms.

IV. REARING

The rearing cubicles, or cages, were matt grey surfaced, in order to prevent reflections which could have affected the subjects' later responses during experimentation. The cages were 12" long x 9½" wide x 9½" high. Each cage was heated and lit by a 60w. bulb, passed through a 2½" diameter hole at the back of the cage. Water was delivered through 'flomatic' drinking troughs. Food varied from species to species and was placed in small feeding troughs.

The game birds were fed on Chick Starter Mash and/or turkey crumbs. Which of these two foods were given depended on the size of the chicks. 'Chick mash' tended to block the beaks and feet of the smaller birds. Ducks were fed on 'chick mash' mixed thoroughly with water until it was of a mushy consistency.

The waders needed the most varied diet, which included high protein-content foods, such as 'chick crumbs', eggs, fish, meat and invertebrates. Mineral elements, in the form of calcium salts and oyster shells, were also added in moderation. The addition of minerals was necessary to compensate for dietary deficiencies of calcium, which can produce malformation in the wings and legs of chicks. As the feet and leg size of the species differed, the flooring was changed accordingly. This usually involved making the floor firmer. These were the major steps used to ensure similar backgrounds for all species concerned. However, there was no auditory isolation of subjects. This may have introduced unwanted variables to the experiments, since eggs of different species of waders were placed together in the incubator. Also all hatched subjects remained in the same room, irrespective of species. Gottlieb (1965) suggests that exposure to an auditory stimulus after hatching can modify the early learning of self vocalisations of a multitude of species. The auditory stimuli to which the chicks were exposed would potentially cover a wide range of frequencies and might be expected to reduce the importance of self audition.

After experimentation was completed the birds were transferred from a solitary to communal cages. Usually after the third week the cages were moved outside the laboratory, on to a lawn. The change from a solitary to a communal environment often produced interesting results: the behaviour was noted and is described in the appendix.

V. PROCEDURE

Prior to each day's experimentation the subjects were transferred from the rearing room to the experimental laboratory in a dark box, 5" x 4" x 4". Most experiments continued for 5 days. The first 3 days involved the presentation of the 'familiar' stimulus. The 4th and 5th days were used for preference trials. These involved simultaneous presentation of the familiar and the novel, or unfamiliar, stimuli. The exposure trials took place in a rectangular run with the familiar stimulus at one end. The stimulus was changed from one end to the other after each day's experimentation. The rectangular run was 10' x $2\frac{1}{2}$' x 2' (Smith, 1960). The floor was marked at 6 inch intervals, from plus 10 through 0 to minus 10. The chick was placed at 0 at the start of each trial. The run had two overhead lights, which produced maximum illumination at both ends of the run (see figure 1A).

In the discrimination trials the run was triangular (see figure 1B). The stimuli were placed at two of the angles, and the positions were changed after the first day. The floor was graded in semi-circles, marked from 0 to 10 on both sides of the mid-line. The chicks were then placed at 0, in front of the scoring area. If the chick ran to the familiar stimulus, positive scores were gained. Running to the unfamiliar stimulus produced negative scores. The total score was the sum of these two scores. A bird that moved from 0 but did not pass over a grade, did not receive any score. A typical stimulus consisted of a disc revolving twice per second, combined with an auditory stimulus.

FIG. 1A

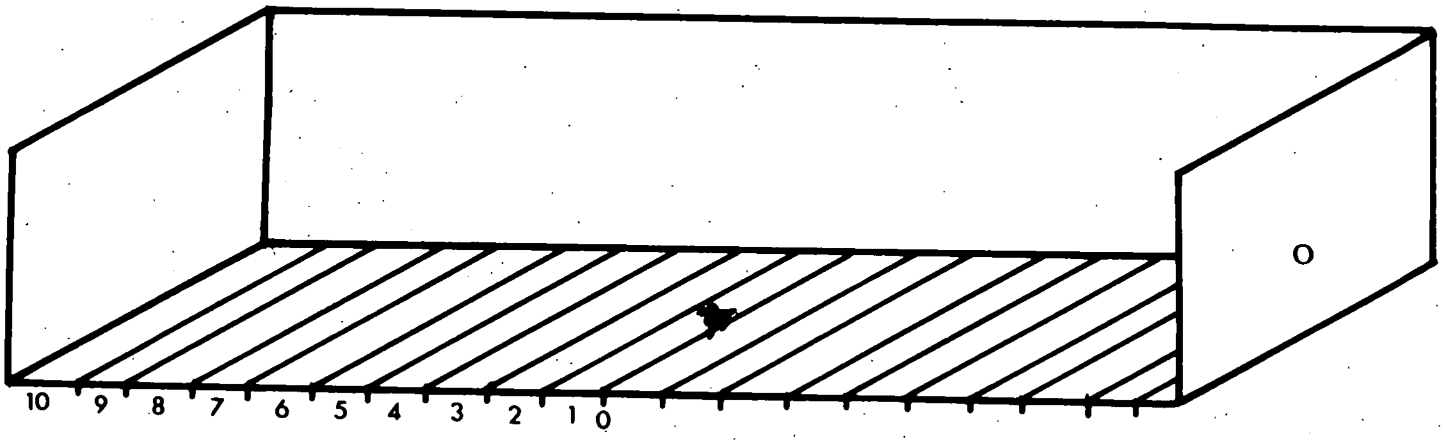


Figure 1A

Diagram of the rectangular run used for exposure (approach) trials in the experiments. The front side has been removed in order to get a better view of the internal plan of the run.

FIG. 1B

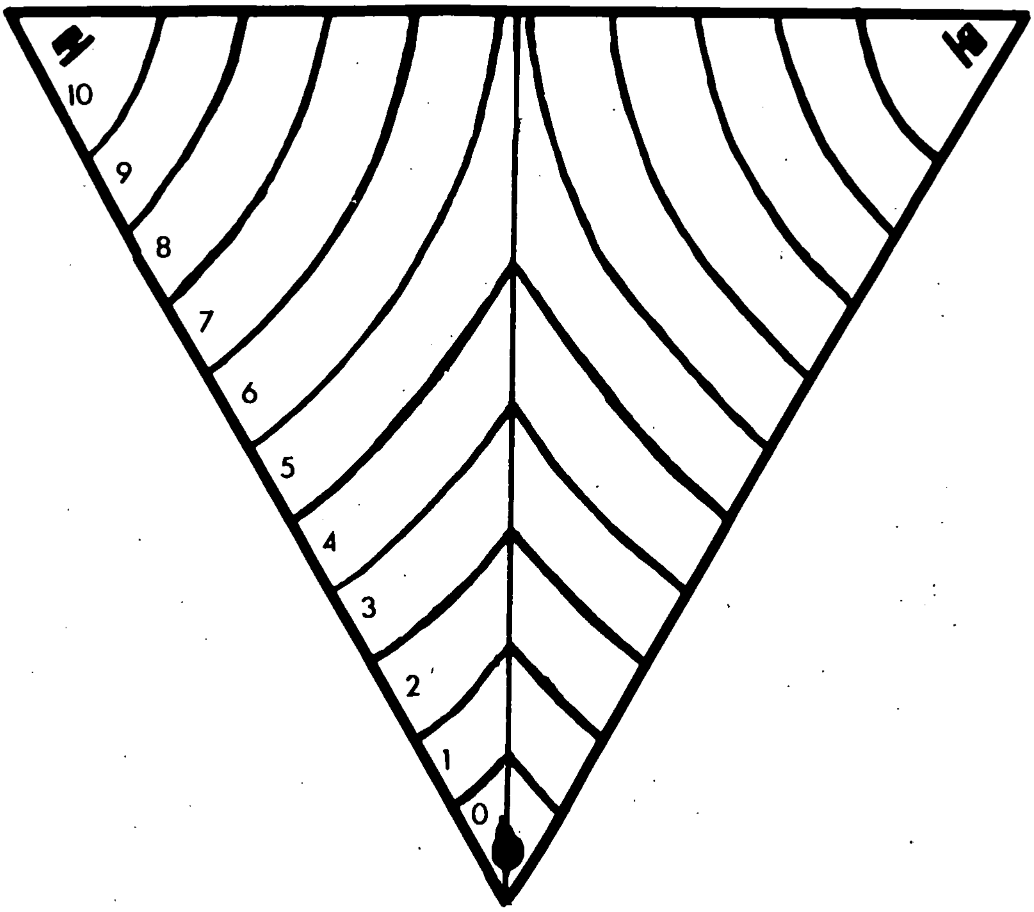


Figure 1B.

Diagram of the experimental chamber used for preference or simultaneous discrimination trials.

During experimentation the chicks were prevented from seeing the observer by the darkness of the laboratory and a double-netted screen above the run. The recording of behaviour was made at 15 second intervals. Behaviour patterns were also recorded where relevant.

Two other practical considerations had to be taken into account. Some species of birds, especially the wader's chicks, slipped on the floor of the experimental chamber. For this reason brown hessian was placed on the floor of the chamber. All chicks were able to walk on this quite adequately. The second point was that for some species, especially oyster catchers and curlews, very few subjects were obtained. The results for these species therefore can only be tentative; however, some indication of their imprintability can be obtained.

VI. EXPERIMENTAL RATIONALE

The major concern of the present research was to investigate the imprintability of different species to stimuli which had been found to be effective when used with domestic chicks and other species in the laboratory. The choice of stimuli was difficult. The stimuli should be effective not only for domestic chicks but for as many other species as possible. Thus ideally the stimuli chosen would be supra-normal in eliciting approach behaviour. Smith and Bird (1964) used a disc, rotating at two revolutions per second, with a 45° red sector as a stimulus. They found this to be effective in eliciting approach and discrimination behaviour in domestic chicks and mallard ducklings. For this reason the same stimulus, (stimulus A), was used as one of the imprinting stimuli in the author's experiments. A second stimulus had to be found for the discrimination trials, which requires two stimuli to be present. The second stimulus must have similar approach eliciting characteristics. Several alternative stimuli were tested. One which proved to be attractive to domestic chicks was a revolving black and white striped disc, (Stimulus B). In the absence of prior exposure the two stimuli should, when paired together in discrimination trials, have comparable effects, i.e. should elicit approximately equal approach and avoidance behaviour.

In Experiment One preference trials were conducted using domestic chicks as subjects. In these trials the visual stimuli were presented simultaneously. Chicks could therefore approach either stimulus. The results showed that stimulus A was more efficient in eliciting and maintaining approach than the black and white striped disc, stimulus B. Stimulus B could, however, be used if training to this stimulus led to it's preference over stimulas A during preferance trials. If ~~significance~~ in preference trials, subjects approach stimulus B, this would be due to previous exposure to B, and not because of any initial preference for either.

In Experiment two, birds were divided into two groups which were either exposed to stimuli A or B, followed by preference trials to examine the effect of prior exposure to stimuli. Part of Lorenz's contention is that curlews will not imprint on anything other than the 'natural' stimulus, i.e. other curlews. Since in the wild the parent curlew vocalizes, these vocalizations may be important in the imprinting process. Therefore in Experiment two, auditory stimuli were combined with the visual stimuli.

In Experiment three, a visual stimulus alone was compared with a combined visual and auditory stimulus to examine their effectiveness as imprinting objects.

Experiments 1, 2 and 3 used domestic chicks as subjects. The aim of this was to provide the experimenter with two stimuli that for the domestic chick at least:

I) were each affective in eliciting approach behaviour during the sensitive period.

II) were comparable to the extent that prior exposure to one of the stimuli, during the sensitive period, would result in approach to that stimulus in subsequent preference trials.

III) contained components that a priori might be expected to elicit approach and discrimination behaviour in species other than those tested.

In Experiment 4, stimuli A and B combined with auditory stimuli were used to examine the type of imprinting taking place in a wide range of species. This experiment was carried out to test Lorenz's hypothesis relating to mosaic and regulative imprinting, that curlews will not imprint on anything other than curlews.

Experiments 5 and 6 were carried out to extend the generality of the conclusions that were drawn from experiment 4.

CHAPTER THREE

EXPERIMENT ONE

An Investigation of stimulus preferences in chicks.

Prior to the experiments by which Lorenz's hypothesis was to be tested, an adequate experimental design had to be chosen. This and the following two experiments were carried out to do just this. Many researchers have shown that different species of birds exhibit preferences for some stimuli over others (Bateson, 1966; Gottlieb, 1963; Immelmann, 1964: Lorenz 1935; Smith 1962). Therefore in this experiment simultaneous preference trials were conducted using two different stimuli.

Subjects

Fourteen domestic fowl chicks (White Leghorn x Light Sussex) were used. The subjects had a post hatch age of 6 - 12 hours at the beginning of the experiment.

Stimuli

The two stimuli were: stimulus A, a 12" diameter disc of white bristol board, with a 45° red sector; stimulus B, a 12" diameter disc with 1" wide black and white stripes, each disc rotated at two revolutions per second.

Procedure

Each subject was placed in turn in one corner of a triangular run (figure 1b), where they were facing the two stimuli. The floor was marked and the subject's performance was recorded, firstly by a letter indicating which of the two discs was approached, secondly by the score it obtained. Trials took place for five days, and there were 3 x 3 minute trials per day. A total of 360 could be scored per day. This score could be either to stimulus A or stimulus B, or a combination of both.

Results

Most subjects approached one or other of the stimuli during these trials. Approach scores tended to increase over the five day period. Only 2 subjects had a total score of less than 10 for the five days' trials. Ten subjects ran to stimulus A, 4 of these had also approached B, but not to the same extent. Two subjects ran mainly to stimulus B, chick 12 had a total score of 22 (182 to B and 160 to A), and chick 24 scored 1068, i.e. ran solely to B (See table 1). The average score over the five day period to stimulus A was 882.2 and to stimulus B was 154.8.

A sign test was used to analyse these results. The two subjects that scored below 10 were considered as 'ties'. The results indicated that these subjects preferred stimulus A to stimulus B (N = 12, +s = 10, -s = 2, P = 0.038 (0.05, two tailed). The apparent preference for stimulus A would seem to be unlearned and may be due to the greater receptivity for the colour red, found by other researchers (Gray 1961; Jaynes 1956; Schaefer & Hess 1959, Smith & Hoyes, 1961). The preference for stimulus A may also be due to the striking contrast to the white area. Disc B on the other hand, when rotating often appeared (to the human eye), to lose contrast and the black and white areas seemed to merge to produce a greyish effect.

Discussion

The results of this experiment indicate that disc A is preferred over disc B. This suggests that the two stimuli could not be used in preference trials without pre-training. For this reason experiment 2 was conducted.

Table One

SUBJECTS	SCORE TO STIMULUS A.	SCORE TO STIMULUS B.	STIMULUS RECEIVING GREATEST APPROACH
8	1,020	0	A
10	1,368	160	A
11	898	46	A
12	160	182	B
13	1,278	0	A
14	1,350	130	A
15	8	2	'TIES'
16	4	0	'TIES'
17	1,360	130	A
18	1,065	350	A
19	1,674	0	A
21	174	8	A
23	392	4	A
24	0	1,068	B

Table One

This table indicates the total score attained by subjects in exposure to stimulus A and stimulus B. (N = 14, Experiment 1.) It can be seen that stimulus A receives the greatest approach score.

Experiment Two

The effects of prior exposure to a particular Stimulus on Initial Preference

Since a preference exists for the 45° red sector stimulus

A, over the black striped stimulus B, for this particular species, these stimuli cannot be used in comparative experiments on imprinting unless previous exposure can be shown to overcome this initial preference. For this reason the effects of prior exposure to, and subsequent preference for the stimuli were examined.

Subjects

The subjects were domestic fowl (White Leghorn x Light Sussex). Twenty subjects were used.

Procedure

The twenty subjects were divided randomly into two groups, ten subjects in each. One group was exposed to stimulus A and the second group was exposed to stimulus B. The visual stimuli were combined with auditory stimuli. This was done to ensure a greater performance in all subjects. With disc A the sound of a clucking hen was added, and with disc B the sound of a male human voice, repeating the words 'Kum, kum, kum'. Both sounds are highly attractive to domestic chicks and ducklings, (Shapiro) 1971).

Exposure trials (see table 2) lasted for three days, with 3 x 3 minute trials per day. The apparatus used was a rectangular run (see figure 1A). Preference trials lasted for 2 days, with 2 x 3 minute trials per day, conducted in the triangular run (see fig. 1B). There were thus 5 days of experimentation for each subject. The stimuli were moved from one corner to the other on each day's experimentation.

Table Two

GROUP	EXPOSURE TRIALS DAYS 1,2, 3.	PREFERENCE TRIALS DAY 4, 5
A N = 10	Disc A + 'clucking' hen call.	Disc A + 'clucking' hen call versus Disc B + 'kum kum' call.
B N = 10	Disc B + 'kum, kum' call.	Disc B + 'kum, kum' call versus Disc A + 'clucking' hen call

Table Two shows the allocation of subjects to two groups, and the stimuli presented to these groups during exposure and ~~presentation~~ preference trials, Experiment 2.

Results

The approach scores of both groups to the stimuli during the exposure trials, were high. All subjects achieved a score of over 260 on their third day of training. Two subjects in group B did not complete the five days experimentation and therefore are not considered in these results. A comparison of the relative performance of the subjects in the exposure trials was made. Each subject's score was summed over the three days (see table 3 and figure 2A) and the scores for groups A and B were compared using the Mann-Whitney U test. No significant differences in approach between groups A and B could be detected ($N1 = 8$, $N2 = 10$, $U =$ ~~33.5~~ 35, $P > 0.05$). Thus the preference for stimulus A, found in Experiment One was not replicated here. This could be due to one or both of two factors:

i) in the present experiment subjects were exposed only to one stimulus and could therefore only manifest a preference for this stimulus; ii) the addition of an auditory stimulus may have enhanced the attractiveness of one or both stimuli.

An additional comparison was made of the results from the preference trials. It was clearly the case that those subjects exposed to stimulus A, in the exposure trials, preferred it to B in the preference trials. Again those subjects previously exposed to stimulus B, preferred it to stimulus A in the preference trials (Mann-Whitney U test, $N1 = 8$, $N2 = 10$, $U = 29.5$, $P > 0.05$).

Discussion

The results of this experiment would indicate that even if an initial preference exists for a certain colour and/or geometric pattern, this preference can be overcome by training. This would seem to be true for the stimuli used in these experiments. Therefore the use of these stimuli in exposure trials (i.e. imprinting trials) is justifiable, for the domestic chicken and presumably other species. These stimuli were therefore used in subsequent experiements.

It is relevant to point out that little or nothing is known of the characteristics of artificial visual and auditory stimuli which would prove attractive to such wild species as the lapwing, curlew and oyster catcher.

While the stimulus combinations already described are clearly effective with domestic chicks, there is nothing to suggest that they would be the optimal stimuli for inducing and maintaining approach and preference in the above mentioned species, although they may well prove effective.

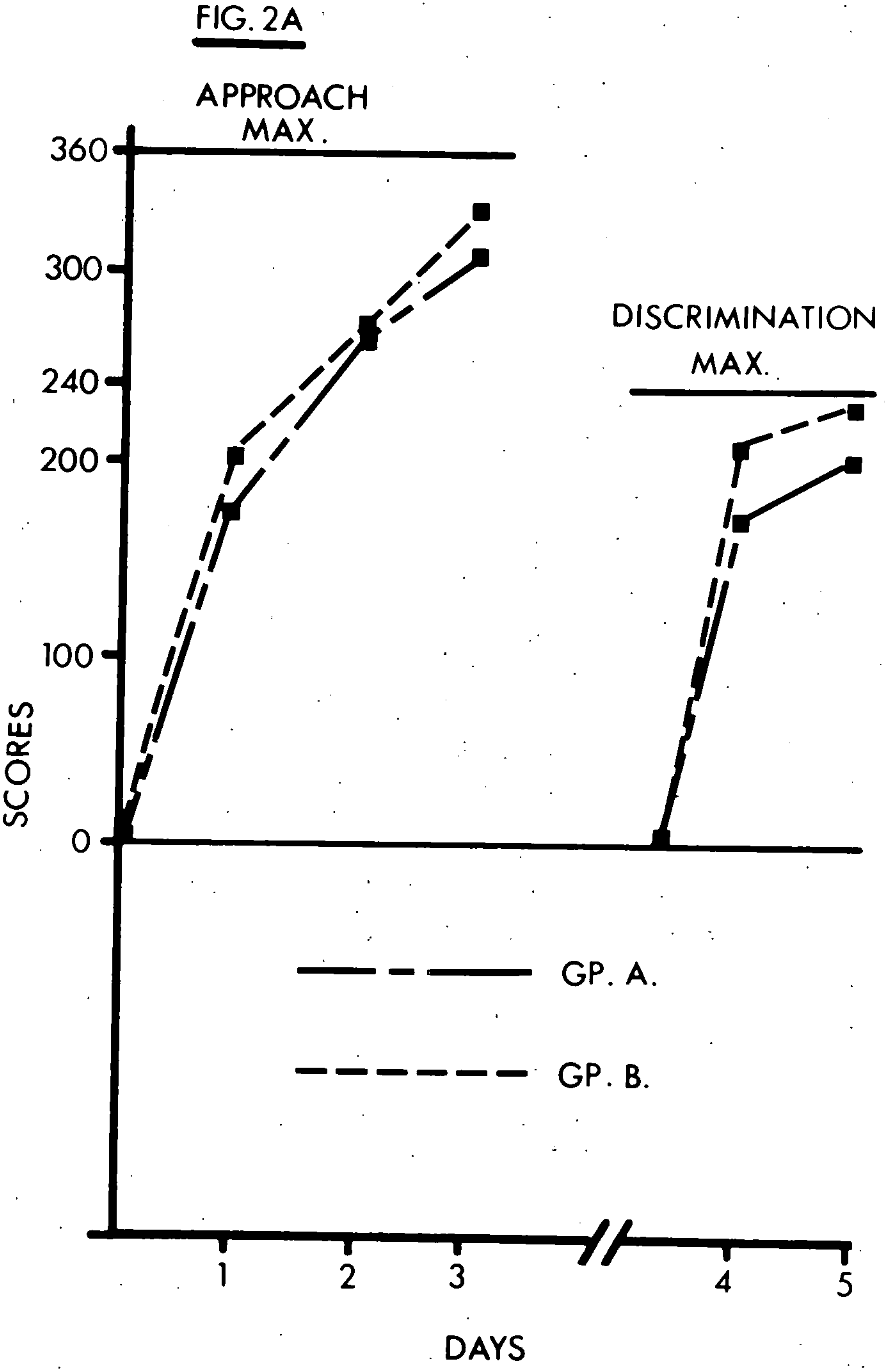


Figure 2 A.

Gives the preference of groups A and B in exposure (or approach) and preference (or discrimination) trials.

Nevertheless, ~~on~~ with the present state of knowledge it would appear to be of some interest to compare how several wild species do react to the same stimuli and perhaps in this way examine Lorenz's differentiation between the 'mosaic' and 'regulative' types of imprinting.

Table Three

Group A N = 10 Subject	EXPOSURE or approach Scores (Stimulus A)	Preference or discrimination Scores (Approach to A in preference to B)
2	1,004	470
4	1,069	480
6	1,036	440
8	1,072	480
10	954	440
11	670	420
13	636	460
15	704	460
17	785	450
19	518	360
	Average = 844.8	Average = 445.0
Group B N = 8 Subject	EXPOSURE Scores (Stimulus B)	Preference or discrimination Scores (Approach to B in preference to A)
1	707	430
3	995	460
5	1,026	480
7	560	480
9	904	470
14	962	420
16	947	330
12	39	0
	Average = 717.5	Average = 421.2

Table Three

This table shows the summed scores for each subject during exposure and preference trials in Experiment Two.

Experiment Three

A Comparison of Visual and Auditory Stimuli with Visual Stimuli alone in Eliciting Approach in Domestic Chicks.

This experiment investigates the effects on Domestic chicks of visual plus auditory stimuli versus a visual stimulus alone.

Subjects

Twenty-six domestic fowl chicks were used. Fourteen of these were randomly allocated to group C, and twelve to Group D.

Procedure

The apparatus used in this experiment was the same as that used in other experiments. Exposure trials again took place in the rectangular run (see figure 1A), and the preference trials in the triangular run (see figure 1B). Group C was given exposure trials with stimulus A (see table 4). In preference trials this stimulus was combined with stimulus B. The second group, D, was given exposure trials with stimulus A and the sound of a 'clucking' hen. In preference trials stimulus A plus the sound of the 'clucking' hen, were presented with stimulus B, plus a human male voice emitting the sounds 'kum, kum, kum', continually. Both exposure and preference trials lasted two days, 3 x 3 minutes and 2 x 3 minutes per day respectively. Each group was thus submitted to four days experimentation.

Results

In exposure trials a difference between the groups' performance was immediately noticeable (see tables 5A, 5B and figure 2B).

FIG. 2B

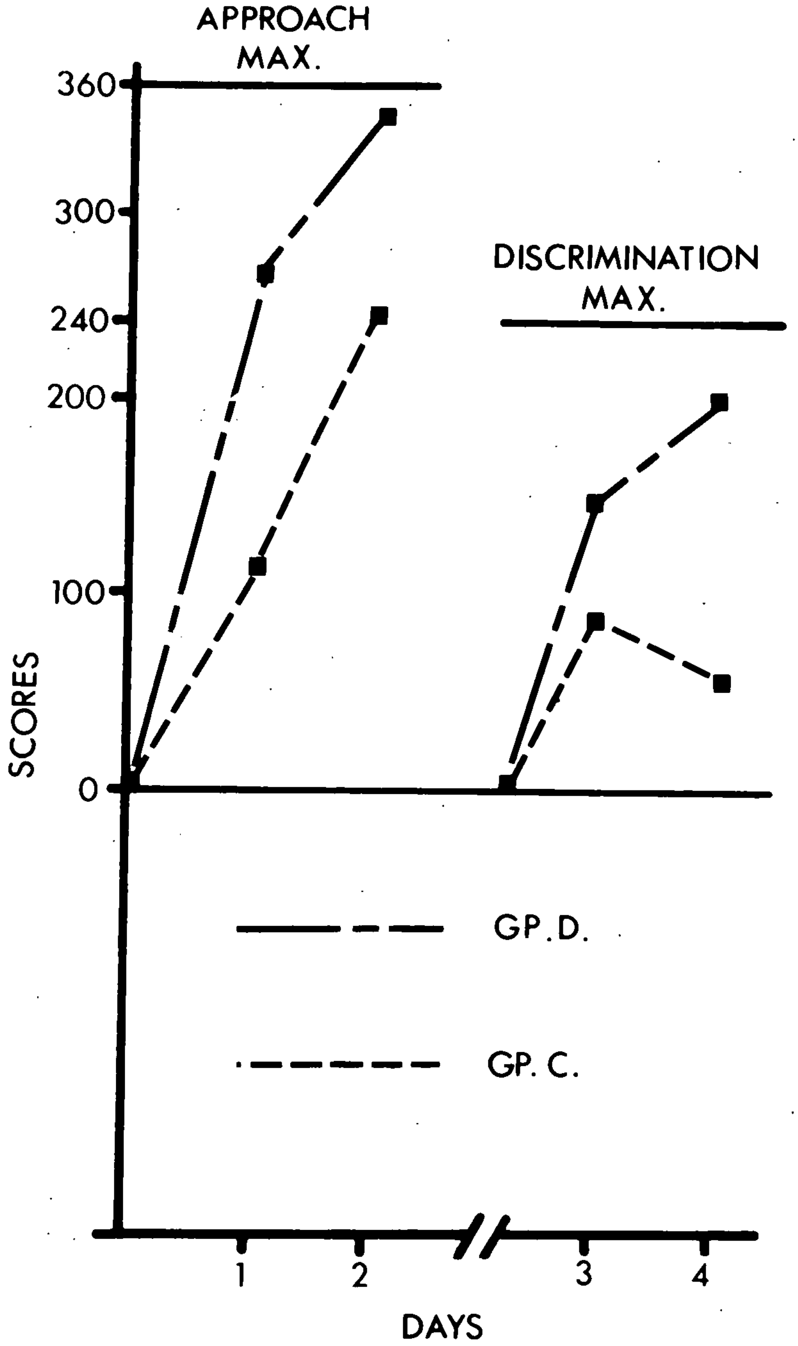


Figure 2B.

The performance of Group C and Group D during exposure (or approach) and preference (or discrimination) trials are shown. Group C were exposured only to a visual stimulus, whilst group D were exposed to visual and auditory stimuli, in Experiment 3.

Table Four

Group	Exposure Trials Days 1 and 2	Preference Trials Days 3 and 4
C N = 14	Disc A alone	Disc A versus Disc B both silent
D N = 12	Disc A + 'clucking' hen call.	Disc A + 'clucking' hen call. versus Disc B + 'kum, kum' call.

Table 4.
The allocation of subjects to groups C and D, and the stimuli presented to the subjects during the four days experimentation, Experiment 3.

Table Five (A)

Group C	Exposure or approach scores	Preference or Discrimination Scores
Subject		
8	272	330
9	545	0
10	-47	0
11	217	140
12	461	450
16	706	-260
18	614	420
19	471	460
20	198	10
22	578	0
23	74	0
25	0	0
26	175	270
27	686	390
Mean	353.5	167

Tables 5A and 5B indicate the scores and mean of scores for groups C and D during the exposure (or approach) and preference (or discrimination) trials, in Experiment 3.

Table Five (B)

Group D N = 12	Approach or Exposure Scores	Preference or Discrimination Scores
Subjects		
1	687	480
2	576	450
3	584	470
4	701	460
5	567	0
6	707	460
7	524	390
28	705	220
29	435	440
30	681	470
31	691	280
32	710	430
Means	630.6	362

Many subjects in group C, those exposed to a visual stimulus alone, did not respond at all during the first day's experimentation. One subject did not respond at all during the first two days. The response of group D during exposure trials was much better than group C. All subjects approached the stimulus by the end of the first day's experimentation. A comparison of the scores of groups C and D during exposure trials was made by the Mann-Whitney U test. This clearly showed that group D approached the stimulus A plus 'clucking' hen, more than group C approached stimulus A alone ($N1 = 12$, $N2 = 14$, $U = 29$, $P < 0.01$ one tailed,) (.02 two tailed).

A comparison of the scores obtained in the preference trials, using the Mann-Whitney U test, clearly indicates that group D not only approached, but also showed greater preference for stimulus A plus 'clucking' hen,than group C showed to stimulus A alone. ($N1 = 12$, $N2 = 14$, $U = 31.5$, $P < 0.01$ one tailed).

Discussion

The results from this experiment, together with those of experiment two, confirm the view already held by many researchers that an auditory stimulus combined with a visual stimulus mediates enhanced approach. It can be inferred that sound plus vision produces maximum effect in approach for most species (Shapiro, 1971). For this reason the stimulus used in experiment 4 contained both visual and auditory components.

Experiment Four

The Imprintability of Different Species of Birds.

In this experiment a range of species was used. The species fall into three main classificatory groups, as indicated in Chapter 2.

The curlew was used in this experiment because of its reputed lack of imprintability to non-natural stimuli (Lorenz, 1935). Lorenz stated that the godwit (Limosa limosa) also would not imprint on inappropriate stimuli, due to complete innate schemata. The godwit could not be obtained for these experiments, and it was hoped that by using two other waders, the lapwing (Vanellus, vanellus), and the oyster catcher (Haematopus ostralegus occidentalis), the situation could be clarified. The use of a wide range of game birds was necessary as a comparison with the highly domesticated domestic fowl.

Subjects

There were 95 subjects in all : 20 domestic fowl chicks; 10 melanistic pheasant chicks; 12 ring neck pheasant chicks; 9 partridge chicks; 21 mallard ducklings; 9 curlew chicks; 10 lapwing chicks; and 4 oyster-catcher chicks.

Procedure

For each subject the experiment lasted 5 days. During the first 3 days post-hatch a single stimulus, with both visual and auditory components, was presented to the subject in exposure trials. The visual component was stimulus A of experiments 1, 2 and 3. This was combined with an auditory stimulus of a male voice repeating the words 'kum, kum, kum'. The use of the 'kum, kum' call for the auditory stimulus, rather than the 'clucking hen' was in order to avoid any chance of an innate or early learned preference for this call. This auditory stimulus produced a noise level of 69 decibels and the background noise was 45 decibels.

During the presentation period the chick was placed in the rectangular run, which has been previously described, for 3 x 3 minute trials, Each trial was interrupted by a return to the box in which they had been carried, for a one minute interval. The range of scores for 3 x 3 minute trials could produce a total score of 3 x ± 120 or ± 360.

Preference trials extended over the following 2 days and involved 2 x 3 minute trials per day. This allowed a total score of 2 x ± 120 or ± 240 for each day. In preference trials the bird was placed inside the triangular run and presented with the familiar and unfamiliar stimuli. The unfamiliar stimulus was stimulus B of experiments 1, 2 and 3. This visual stimulus was combined with a call of a 'clucking hen', which produced a noise level of 65 decibels against a background noise of 45 decibels.

Results

The results of this experiment are shown in Tables 6, 7 and 8. The mean scores obtained for each day are shown, together with the standard deviations. Table 7 gives the mean and standard deviation for the exposure trials, and table eight gives the mean and standard deviation for preference trials. The significance of these scores are examined by the t - test in tables 7 and 8. The

Table Six

SUBJECTS	N	EXPOSURE TRIALS			PREFERENCE TRIALS		
		DAYS			DAYS		
Species		1	2	3	4	5	
Domestic Fowl	20	198.4 118.4	333.0 61.7	354.3 8.8	227.0 21.2	210.9 64.0	Mean StD
Pheasant Mel	10	248.7 53.9	293.9 65.7	342.7 22.6	200.0 64.7	136.8 94.0	Mean StD
Pheasant Rn	12	219.9 111.1	280.7 100.2	288.3 94.3	74.0 110.1	132.5 125.7	Mean StD
Partridge	9	308.8 59.0	303.1 80.1	281.6 98.5	100.8 100.5	119.3 96.8	Mean StD
Wild Mallard	21	95.3 149.6	191.1 155.0	219.9 162.6	64.8 168.2	71.1 163.3	Mean StD
Curlews	9	18.5 39.2	31.4 142.2	33.0 58.4	32.4 42.6	22.0 44.1	Mean StD
Lapwings	10	-12.7 49.9	779.1 138.0	-59.6 212.0	46.0 55.9	1.6 43.1	Mean StD
Oyster Catchers	4	30.7 72.7	126.2 161.6	158.5 151.0	52.0 52.0	77.5 88.3	Mean StD

Table Six In this table the results for each days performance have been summed and the Mean and Standard deviation calculated. This thus acts as a summary of the performance of the different species in Experiment Four.

Table Seven

Species	Means	S.D.	T-test Analysis
Chicken	295.2	103.6	t = 12.74 P〈 0.001
Melanistic Pheasant	295.1	63.6	t = 14.65 P〈 0.001
Ring neck Pheasant	263.0	106.6	t = 8.59 P〈 0.001
Partridge	297.8	81.7	t = 10.93 P〈 0.001
Wild Mallard	168.8	164.7	t = 4.68 P〈 0.01
Curlew	27.6	91.8	t = 0.903, 0.3〈P〈0.4 N.S
Lapwing	-50.4	151.4	t = 1.054, 0.2〈P〈0.3 N.S
Oyster Catchers	105.1	145.0	t = 1.44, P〈0.3 N.S

Table Seven

These figures show the performance of different species during exposure trials of experiment One. The standard deviations and the results of the t-tests indicate the amount of variation and whether the level of approach to stimulus A was significant

Table Eight

Species	Means	S.D.	T-test Analysis
Chicken	218.9	48.3	$t=25.52$, $P<0.001$
Melanistic Pheasant	168.4	86.6	$t=6.144$, $P<0.001$
Ring neck Pheasant	103.2	121.7	$t=2.937$, $P<0.02$
Partridge	110.1	99.1	$t=3.332$, $P<0.02$
Wild Mallard	67.9	165.8	$t=1.876$, $P<0.1$ N.S
Curlew	27.2	43.7	$t=1.867$, $P<0.1$ N.S.
Lapwing	23.0	54.6	$t=1.379$, $P<0.3$ N.S
Oyster Catcher	64.7	73.6	$t=1.759$, $P<0.2$ N.S

Table Eight.

This table shows the performance of the different species in Experiment four, during preference trials.

results are shown graphically in Figures 3 - 17. For each of the species studied, one graph shows the average performance and range of the scores for the group and a second graph shows the performance of the highest scoring individual subjects.

The results obtained by the seven different species will be described individually under seperate headings, and a comparison of these will appear in Chapter 5.

Domestic Fowl

This species performed well, both in exposure and preference trials. These results are to be expected from this species because of previous experimental results. On average the domestic fowl did not move for the first 155 seconds of the first three minute trial. During this period the subjects would either make high-pitched vocalizations, 'fear chirps' or were sleepy. When the subjects approached the stimulus the 'fear chirps' subsided, and softer 'tweetering' sounds were emitted, ('contentment chirps').

On reaching the stimulus a variety of behaviours resulted which were of an 'emotional kind': The subject tries to get as close as possible to the stimulus. This involved either running to and fro in front of the stimulus; jumping at or to the sides of the stimulus; nestling under or near the stimulus. Some subjects also pecked or scratched close to the stimulus. Some of the better performances of domestic fowl chicks can be seen in figure 4. On the first day scores for these subjects were over 290, the average for the group of domestic fowl 198.4 (see table 6). On the second day of exposure trials the mean score for all subjects is much higher, 333.0. Birds 12 and 20 were the best birds overall in approach and they received 360 each on the second day. On the third day of exposure trials these two subjects also maintained this high score, (the maximum possible). The mean score for all subjects was still high at 354.3 (see table 6 and figures 3 and 4). The increasing level of approach over the three days' exposure trials for the domestic fowl is clearly shown by the decreasing level of the standard deviation. On day one S.D. = 118.4, but on day three it had been reduced to S.D. = 8.8 (see table 6). The overall increasing level of approach is indicated by a t - test conducted on these exposure scores, $t = 12.74$, $P < 0.0001$ (see table 7). These results show that the domestic fowl are very responsi~~ble~~ve in terms of approach to stimulus A, as was indicated by experiments 1 and 2. ‡

<u>Footnote</u>:- ‡

Smith and Nott (1970) using socially reared domestic chicks, obtained approach to a visual and auditory stimulus up to 10 days post hatch. Thus though the subjects received sensory experience from peers, they still approached the stimulus. However this stimulus was thought from previous studies to be extraordinarilly effective in eliciting approach. Other experimenters using different stimuli with domestic chicks comment on the decreasing approach responses to stimuli over the first week posthatch (Bateston 1964), Salzen 1963)

FIG. 3

DOMESTIC FOWL

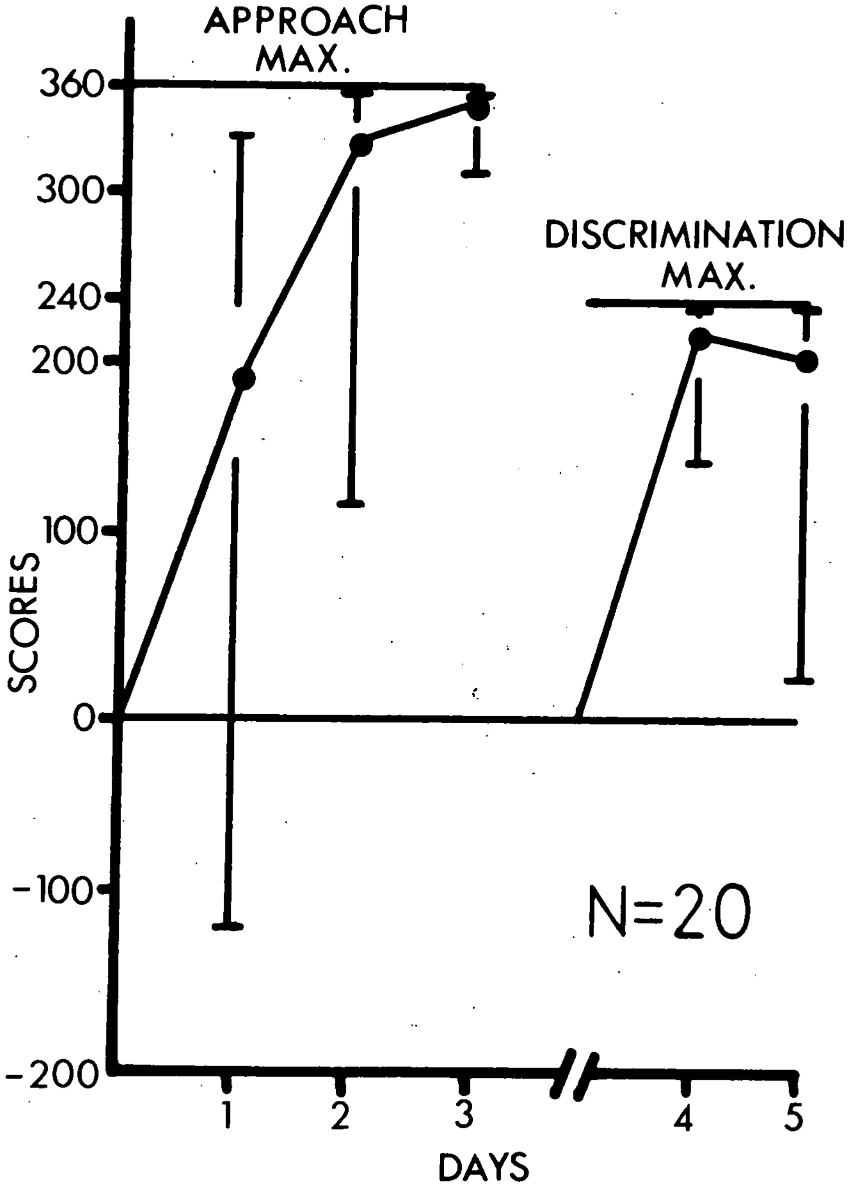


Figure 3.

The performance of the domestic fowl subjects during exposure (or approach) trials and preference (or discrimination) trials, in Experiment 4.

FIG. 4.

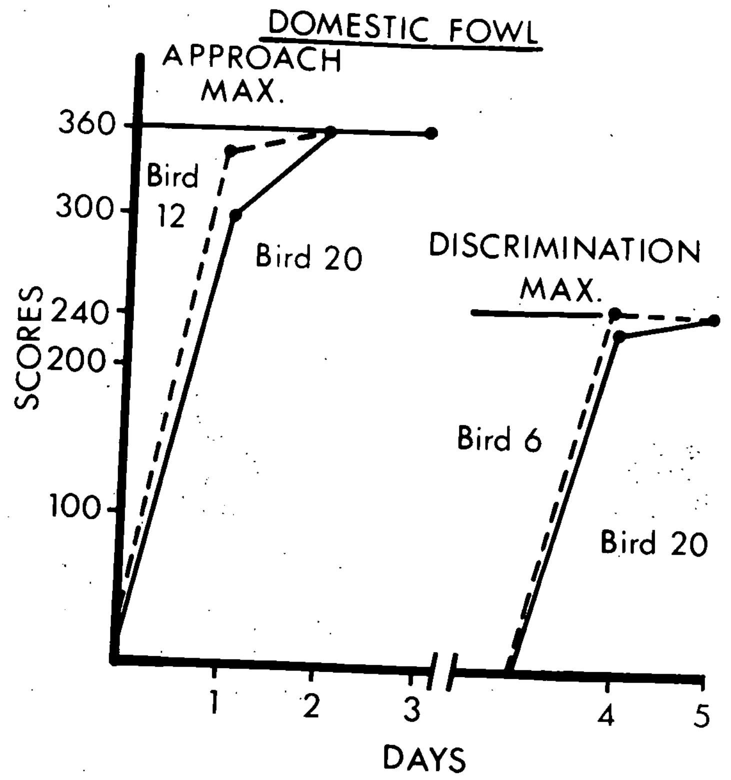


Figure 4.

The performance of some of the best subjects of the domestic fowl species, in Experiment 4 during exposure (or approach) and preference(or discrimination) trials.

In preference trials the approach to stimulus A was high (see table 6 and figure 3). Some approach to stimulus B took place on day 5 and this caused a decrease in the mean and an increase in standard deviation. The range of scores also increased (see figure 3). The level of approach response was high ($t = 25.52$, $P < 0.001$, see table 8).

The response of the domestic fowl was as expected. Approach to the stimulus increased over the days of exposure to a very high level (see figure 3). It was not surprising that the subjects of this species preferred stimulus A, the stimulus presented during exposure trials, rather than stimulus B. These results clearly show that the domestic fowl subjects had imprinted on stimulus A, a rotating disc, with a 45° red sector, and a human vocalization, 'kum, kum'.

Pheasant - Melanistic

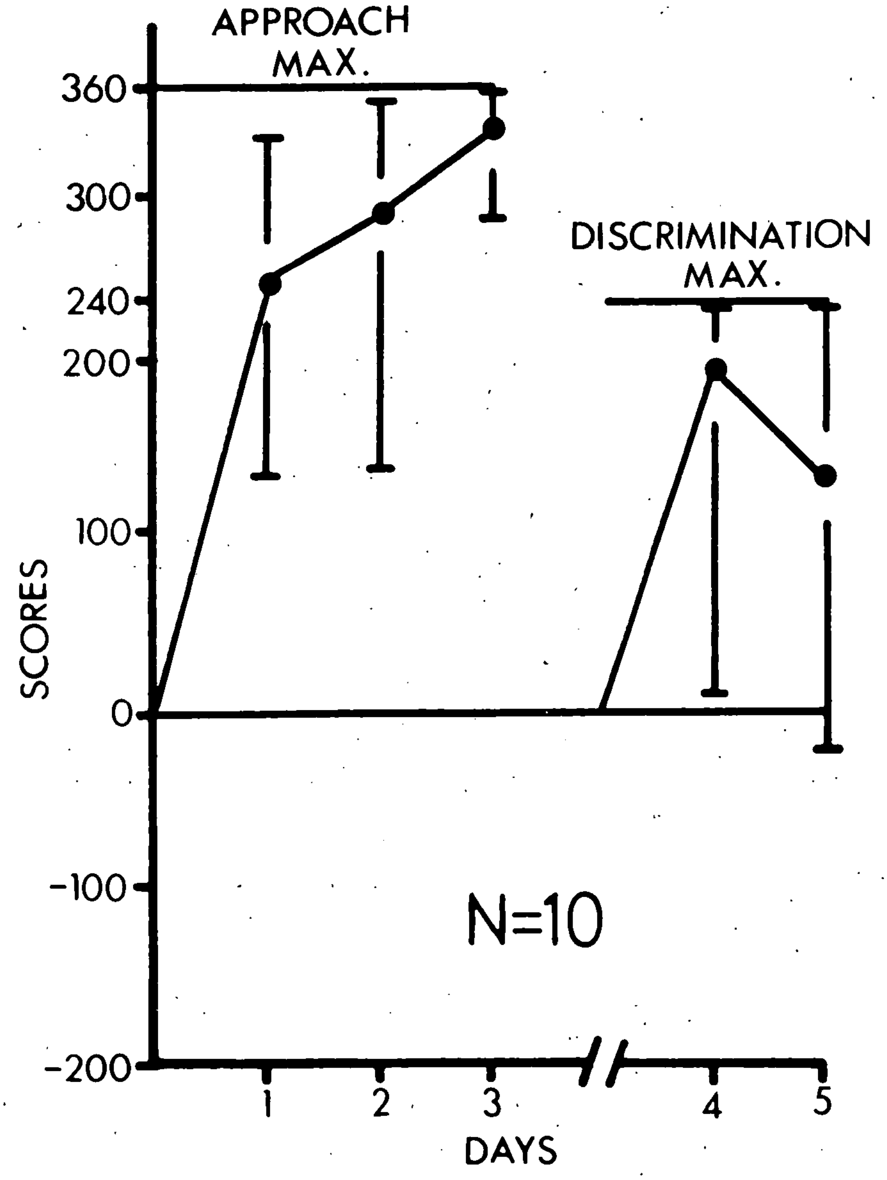
The behaviour of the melanistic pheasants was much the same as the domestic fowl chicks. Responses of these subjects were very spontaneous, i.e. the chicks begain their approach to the stimulus in the exposure trials after an average of 30.8 seconds, and a great deal of pecking took place. In the first day of exposure trials these melanistic pheasants attained a very high level of approach, (higher than that attained by the domestic fowl). In fact the responses over all the exposure trials were very high, (see table 6). Under analysis by the t-test responses were at a significant level of approach ($t = 14.64$, $P < 0.01$, see table 7).

These results are also indicated by the mean score shown in figure 5. Figure 6 gives the performance of the best subjects in approach subject 19 (subject 2 is a ring neck pheasant).

In preference trials the melanistic pheasant did not do as well as expected from their performance in the exposure trials. The mean of the score on days 4 and 5 was lower than 200, and the standard deviation higher, especially on day 5 (see table 6). The high standard deviation is attributable to some subjects running to stimulus B. This would seem to indicate a lack of imprinting, however this response may have been due to lack of discrimination, because of the speed at which the chicks reacted to the stimuli. Only later would a subject perceive its error and then run to stimulus A, the familiar stimulus. This is an explanation of the larger standard deviation. Statistical analysis using the t - test, gives a level of approach of $t = 6.144$, $P < 0.001$.

From these results it is clear that the melanistic pheasants give rapid and sustained approach to a stimulus. However, when the imprinting stimulus is in competition with a novel stimulus, some approach is given to the novel stimulus. Clearly the melanistic pheasants have imprinted on stimulus A, an inappropriate stimulus (the performance of this species is summed up in figure 5). Although some subjects did approach the novel stimulus, B, this was not significant.

FIG. 5



PHEASANT - MELANISTIC

Figure 5.

The performance of the melanistic pheasant subjects during exposure (or approach) trials and preference (or discrimination) trials, in Experiment 4.

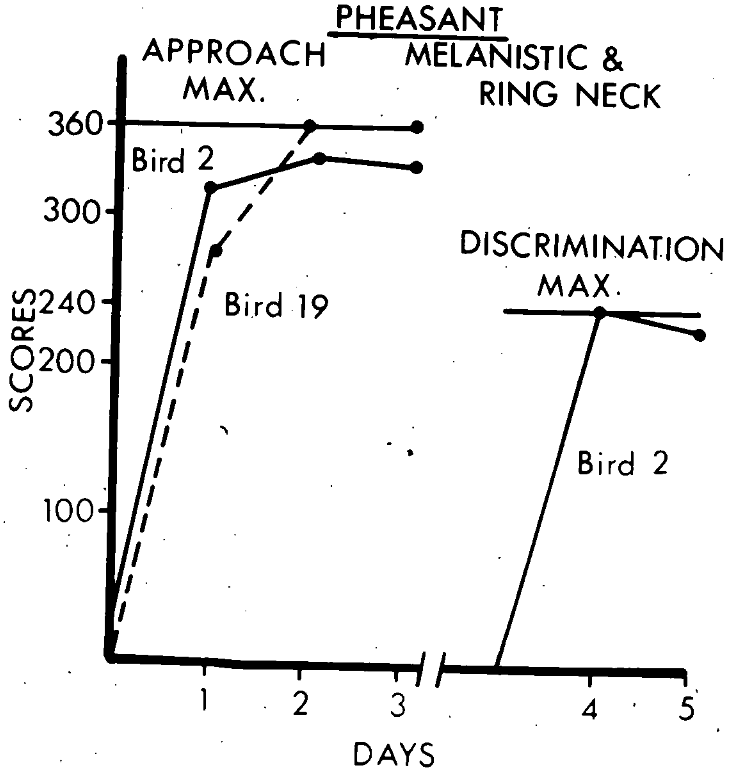


FIG. 6.

Figure 6

The performance of some of the best subjects of the melanistic pheasant (Bird 19) and the ring neck pheasant (Bird 2) during exposure (or approach) and preference (or discrimination) trials, in experiment 4.

Pheasant - Ring neck

The ring neck pheasant chicks behaved in a similar way to the melanistic pheasant with reference to nestling, pecking and vocalizing. Their vocalizations were of a different pitch, but resembled those of domestic fowl, i.e. 'contentment' and 'fear calls', could be identified.

In exposure trials these subjects showed increasing approach responses to the stimulus. The approach on the first day was high, at a mean of 219.9, the best performer of this group, bird 2, receiving over 300 (see figure 6). The standard deviation for subjects was high over the first 3 days of exposure. Although the standard deviation decreased, as in the domestic fowl and melanistic pheasant, the standard deviation for the ring neck pheasant remained at a high level (see table 6) - (figures 3, 5 and 7). The results of the exposure trials are summarised in table seven and indicate that these subjects give a significant level of approach to stimulus A, ($t = 8.59$, $P < 0.001$).

On days 4 and 5 (the preference trials) the responses of the ring-neck pheasants were poor. A large number of the subjects approached the novel stimulus, B, at some time during the preference trials. In fact 8 of the 12 subjects approached stimulus B. This variability is shown in tables 6 and 8 and figure 7. The mean response for these two days is 103.2; S.D = 12.7. Even with this variability the approach to stimulus A is however, still significant ($t = 2.937$, $p < .02$). It can therefore be stated that the ring-neck pheasants have imprinted

FIG. 7

PHEASANT - RING NECK

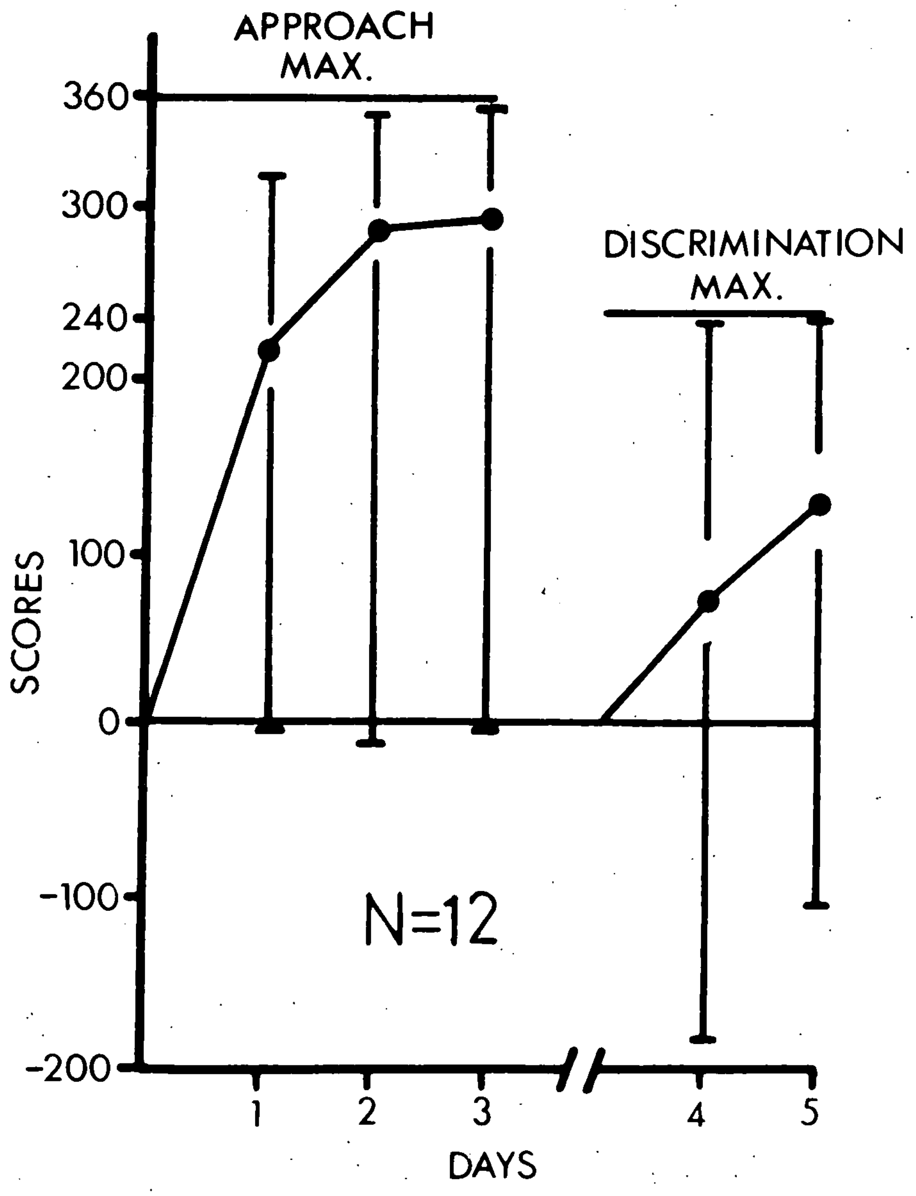


Figure 7.

The performance of the ring neck pheasant subjects during exposure (or approach) and preference (or discrimination) trials, in Experiment 4.

on stimulus A, and prefer this to the novel stimulus, B.

Ring-neck pheasants seem to be less able to discriminate than melanistic pheasants. These results indicate that the degree of imprintability can vary between strains of species. When these two species were compared by the Mann-Whitney U test, N1 = 10, N2 = 12, U = 18, $P < 0.05$. It can be seen (Figure 5) that the melanistic pheasant approaches stimulus A significantly more on day 4, than did the ring-neck pheasant.

Partridge

The general behaviour of the partridge was similar to that of the pheasants. On the first day's exposure trials the subjects achieved a very high mean score of 308.8 (see table 6 and figure 8). This was a higher score than any other game bird species. This high level of approach was not significant in comparison with other species of game bird, except the ring-neck pheasant, at a level of $P < 0.05$ ($N_1 = 8$, $N2 = 9$, $U = 16.0$).

On days two and three of exposure trials the approach remains high (see table 6), this is confirmed as significant by a t - test, ($t = 10.93$, $P < 0.001$ see table 7 and figure 8). Bird 3 attains almost maximum scores on day one (see figure 9), and the maximum score on day two, but the response drops dramatically on day three. This is the reason for a higher standard deviation on day three.

In preference trials the subjects showed a wide range of responses (see tables 6 and 8). Seven of the nine subjects approached stimulus B, at least to some extent. This caused the

FIG. 8

PARTRIDGE

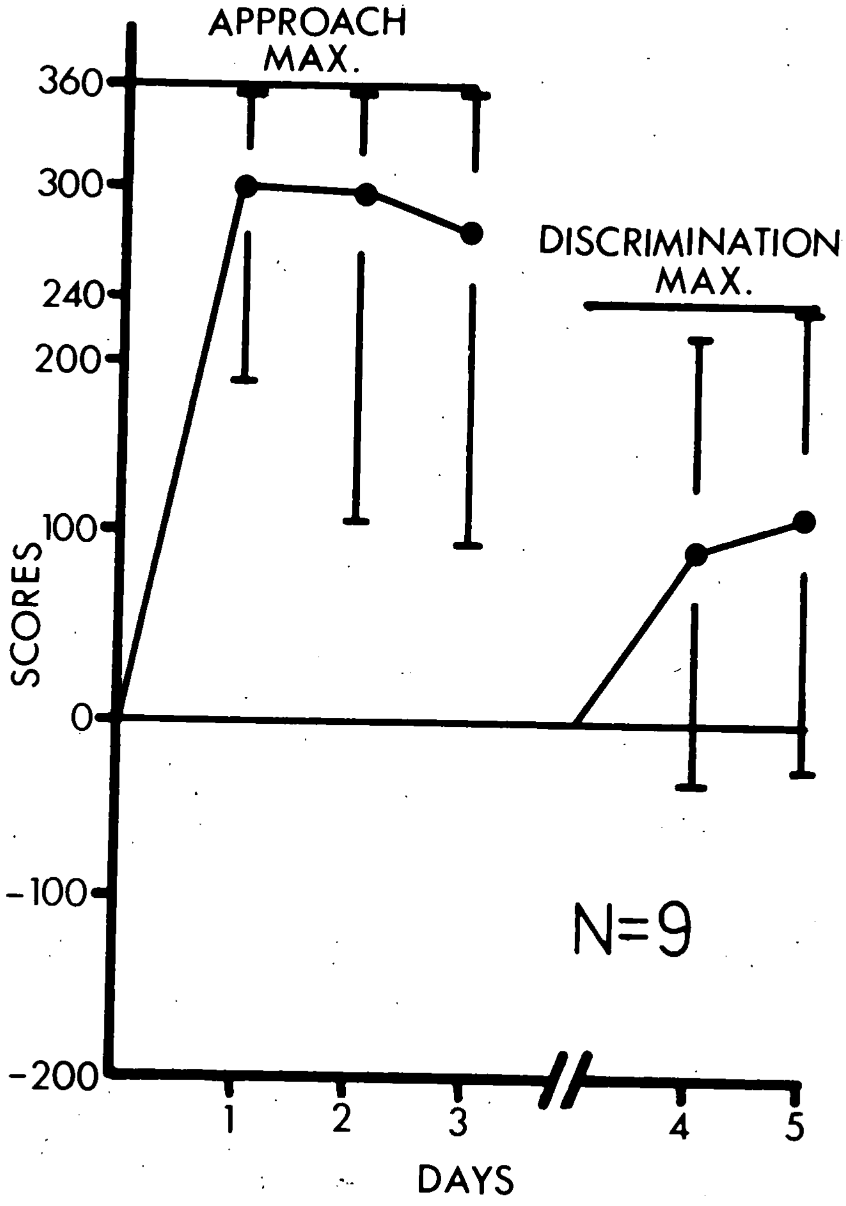


Figure 8

The performance of the partridge subjects during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

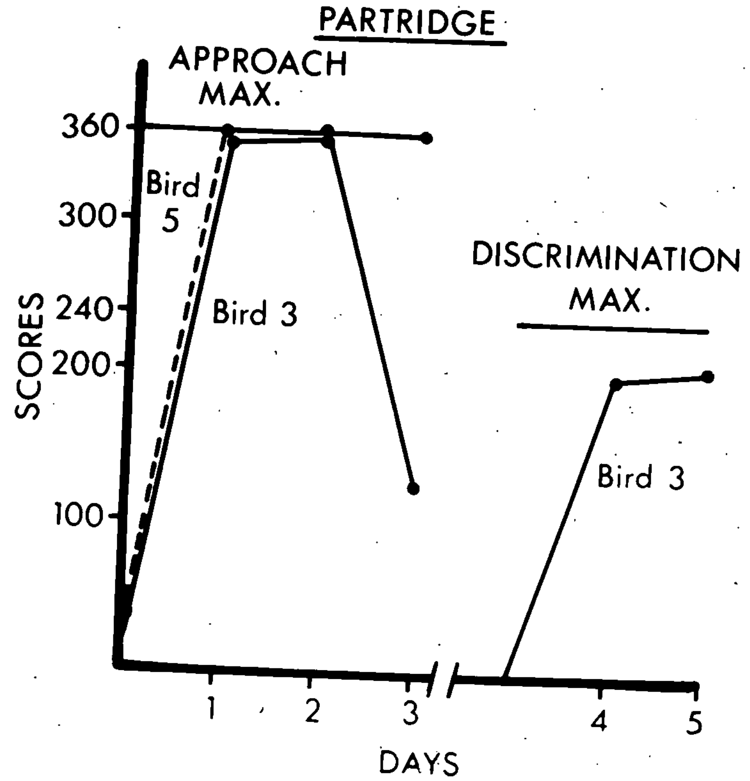


FIG. 9.

Figure 9.

The performance of the best subjects of the partridge species, during exposure (or approach) and preference (or discrimination) trials, in Experiment 4.

high standard deviation and the low approach scores recorded to stimulus A (see figure 8). This subjects performance in exposure trials was not uniform, but it approached better in preference trials (see figure 9). Because of this wide range of responses the results for the partridge attain a low level of significance in approach scores, during preference trials, $t = 3.332$, $P < 0.02$.

These results indicate that the partridge will imprint on stimulus A, an inappropriate stimulus. Their performance in approach and preference for stimulus A is worse than the domestic fowl and melanistic pheasant, but better than the ring-neck pheasant.

A Comparison of the Results of Game Birds

A comparison can be made of the game bird species. Considering the time of first movement on the first day's trial, the partridge (Perdix perdix) gives the most rapid response at 23.4 seconds, on average. Second is the ring-neck pheasant Phasianus colchicus) at 27.6 seconds, on average; third is the melanistic pheasant (Phasianus colchicus) at 30.8 seconds on average; and lastly the domestic fowl (Gallus gallus, Light Sussex x White Leghorn), at 155 seconds on average. These figures clearly show that the partridge gives the most rapid initial approach. It is interesting that this species also gave the highest initial approach and least standard deviation, on day one (see table 6). The speed and rapidity of approach decreases from the melanistic pheasant to the ring-neck pheasants, and the domestic fowl.

Obviously the partridge and pheasant strains have the quickest response time. Presumably their attention is attracted more quickly than other species, and they are sufficiently stimulated by the biologically inappropriate stimulus, A, to give rapid and high levels of approach. Whether these initial movements and approach scores in exposure trials can be related to the level of domestication of the species concerned remains inconclusive, but this should be considered as a possibility.

With reference to the results of the exposure trials, the species with the highest approach levels are melanistic pheasants; partridge; domestic fowl; and ring neck pheasant, (see table 7). The stimulus which was found to be an effective approach inducing stimulus for the domestic fowl was even more effective for melanistic pheasants and partridge. Presumably contrast between the red and white areas of the stimulus, and movement, played a significant part in causing approach.

In preference trials the order of approach changes, the species with the highest approach levels are : firstly the domestic fowl, secondly, the melanistic pheasant, thirdly, the partridge; and lastly, the ring-neck pheasant. Table 6 shows that over the five days experimentation, the domestic fowl chicks' approach responses improve, whereas all other game bird species' approach scores become more variable. This culminates in poorer preference scores. Another factor contributing to a lower score in approach during preference trials, is an increasing tendency to approach the novel stimulus. This is especially true of the ring-neck pheasant. The approach to the novel stimulus B however, is not so great in game bird species as to disqualify statistically the possibility of imprinting (see table 8).

Wild Mallards

The wild mallard neonates were some of the liveliest species used in these experiments, they made a great commotion whenever a noise was made nearby. They would jump and vocalize readily. When placed in the run for their first exposure trial they would immediately emit very high-pitched calls, probably equivalent to the 'fear chirps' of the game birds. The most rapid subject ran to the stimulus after 3 seconds and the slowest did not run at all during the first day's trial ($\bar{x}$ = 117 seconds).

On reaching the stimulus the subject would usually jump up in front of, or to the sides of the stimulus. These jumping actions would subside and the ducklings would nestle close to the stimulus, making 'softer' quacks, or sometimes bill clapping movements. The ducklings would also make a sound intermediate between the high-pitched 'fear chirps' and the 'softer' quack. This vocalization occured in situations where the duckling was not below or to the side of the stimulus, but only close to it.

In exposure trials the degree of approach to the stimulus was lower than any of the game birds, and the standard deviation higher (see table 7). Table 6 gives the performance over the three days of exposure trials. As with the game birds, approach responses increased over the three days of exposure trials, but the standard deviation did not decrease. The overall result in the wild mallard during exposure trials is significant when analysed by the t - test, ($t = 4.68$, $P < 0.01$). Figure ten shows clearly the wide range of scores. Subject 24 gained the maximum score over the three days exposure trials (see figure 11).

During the preference trials a positive score in approach was obtained on day four. This score was maintained on day five (see table 6 and figure 10). On day four one subject obtained the maximum minus score of - 240. In fact 17 of the 21 subjects gave some approach to stimulus B during preference trials. The mean score for days four and five is 67.9, with a standard deviation of 165.8. t - test analysis gave the significance level in approach to be $t = 1.876$, $P < 0.1$ (see table 8). The discrimination, or preference, of this species was therefore poor.

In conclusion the wild mallard approached the stimulus well during exposure trials, though variation in approach scores between subjects is very high (figure 10.) This variation is even more apparent during preference trials. The results do not confirm that imprinting to the stimulus has taken place. Other experimenters have reported that the wild mallard will approach a novel stimulus after exposure to another stimulus (Klopfer & Hailman ,1964).

FIG. 10

MALLARD

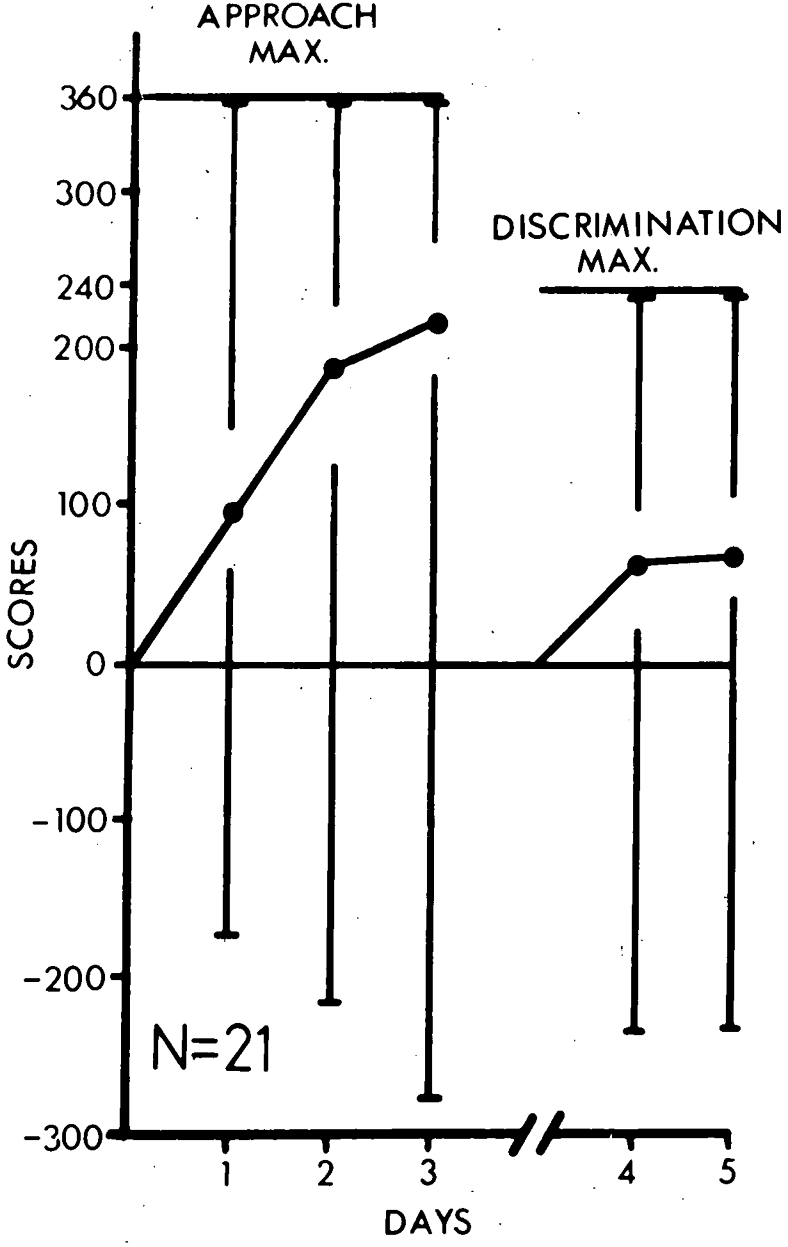
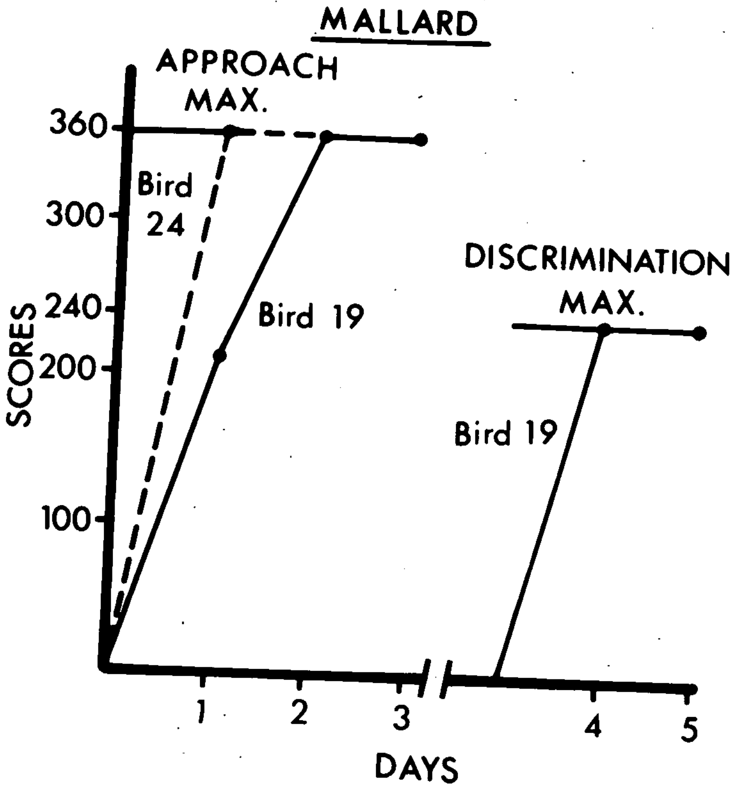


Figure 10.

The performance of the wild mallard subjects during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

FIG. 11.



<u>Figure 11</u>

The performance of the best wild mallard subjects, during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

In the experiments of Klopfer and Hailman, the novel stimulus was considered to be intrinsically more attractive than the familiar stimulus. In experiment 1, on the domestic fowl, stimulus A was more attractive than stimulus B. Perhaps in the case of the wild mallard the red colour of stimulus A is of less importan~~t~~ce.

Curlews

This species of wader produces quite a large neonate chick. The chick when placed in the experimental chamber, emitted a high-pitched whistling sound, which is comparable to the 'fear chirps'. The average time of first movement for this species was 141.1 seconds, a faster response than both domestic fowl and the wild mallard. The subjects would either continue making 'fear chirps', or a softer whistle may be emitted, presumably this is because the chick is less afraid. When this second vocalization or 'soft whistle', is produced the subjects would sometimes peck the floor of the run. Pecking also took place in association with nestling when the subjects reached the stimulus. The subjects that reached the stimulus would emit a very soft whistle which has been called 'contentment chirps'.

During the exposure trials the curlew's approach responses increased (see table 6 and figure 12). Close inspection of table 6 shows that there is a great deal of variation between scores, especially on the second day. The reason for this seems to be the behaviour of two subjects. One approached and maintained high scores to stimulus A, i.e. + 280, whilst the second maintained high negative scores, i.e. - 238, away from stimulus A. The mean for the exposure tr~~ai~~ials, including all subjects, is 27.6, with a large standard deviation of 91.8. This result, when analysed by the t - test, does not indicate a significant level of approach in the direction of the stimulus ($t = 0.903$, $0.2 < P < 0.4$, see table 7).

In preference trials five of the nine subjects showed some approach to stimulus A, and one of the nine approached stimulus B. Thus the reason for the low approach scores in preference trials is the absence of any response, rather than a negative score (see tables 6 and 8). This would also explain the low standard deviation. Some curlew chicks gave more positive responses, and approached stimulus A, in both exposure and preference trials (see figure 13). One of these, bird 5 might have imprinted. Considering this species as a whole however, approach to stimulus A, during preference trials, was not significant ($t = 1.867$, ~~0.5~~ 0.05 $< P < 0.1$ see table 8).

In conclusion, the curlew subjects could not be said to have imprinted on stimulus A, i.e. that results were not statistically significant. However, all of the subjects showed some approach to stimulus A in exposure trials; over half of the subjects showed some approach to stimulus A during preference trials. Some curlew chicks maintained sustained approaches to the stimulus, but this is masked by the other subjects' overall lack of responsiveness to the stimulus. Some subjects were allowed to remain in the run for an extra three

FIG. 12

CURLEW

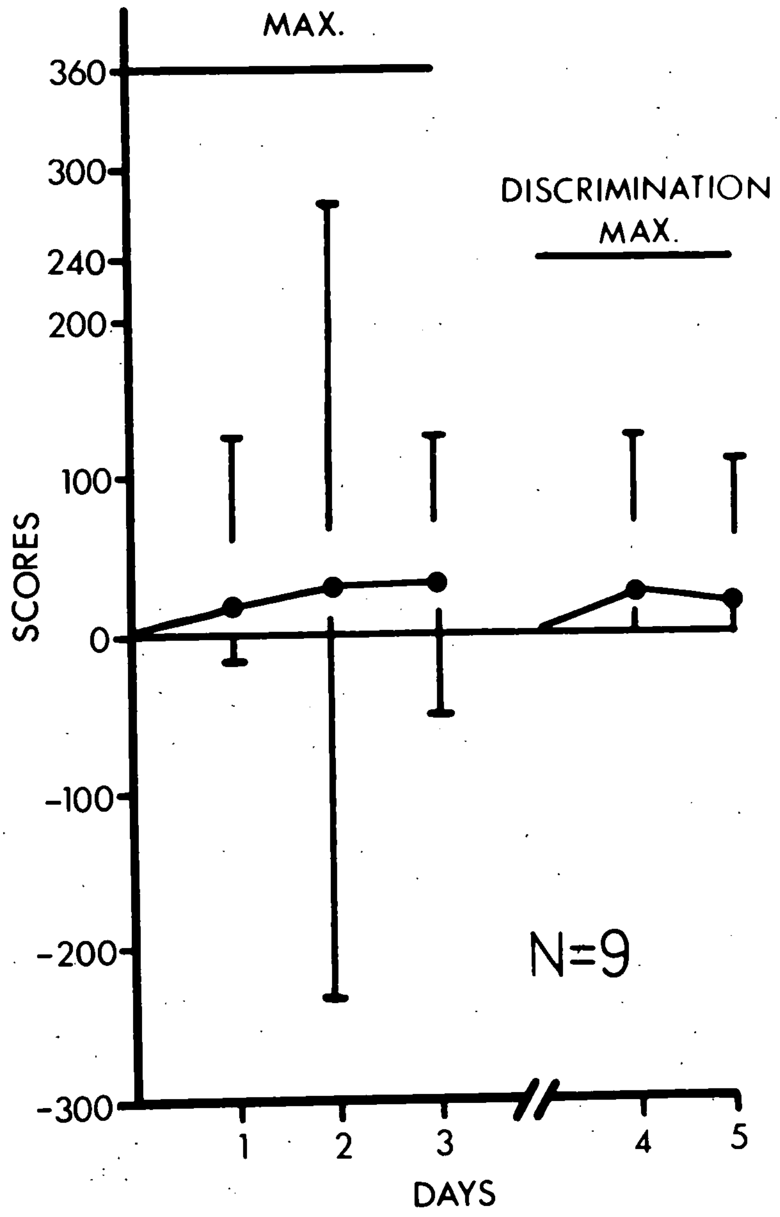


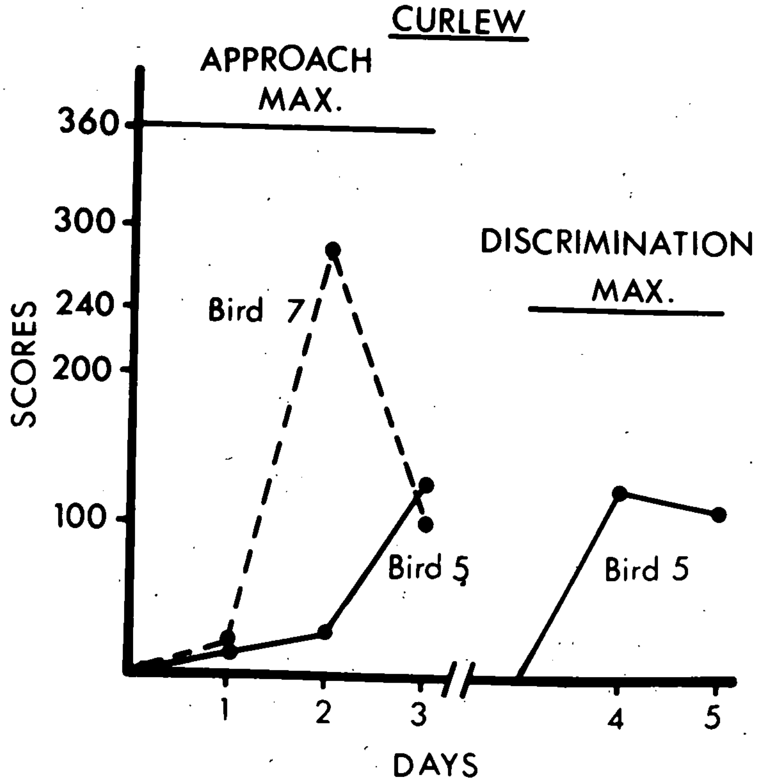
Figure 12.

The performance of the curlew subjects during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

minutes after experimentation had been concluded. ~~In~~ During this time one of the subjects, which had previously scored 0 on day five, gained 82 out of a possible score of 120. This would suggest that imprinting in curlew subjects can take place to an inappropriate stimulus. This was not a conclusive result, but gave an indication of the possible effects of a longer exposure time. (This hypothesis was further examined in part 2 of experiment 5, on Lapwings). A fuller discussion takes place in Chapter 5.

Lapwing (Vanellus vanellus)

The lapwing is another species of wader and from Lorenz's hypothesis it should not imprint. The behaviour of this species resembles that of curlews, especially in terms of vocalizations. The lapwings produce the same range of whistles. Loud, high-pitched whistles resembling those of the attacking adult, during territorial defense, were produced in the most fearful situations. These vocalizations would take place when the chick was first introduced into the experimental chamber, and for some subjects lasted throughout the experimental trials. The ~~average~~ time of first movement to the stimulus was on average 109.0 seconds (a faster time than mallards, curlews and domestic fowl) although some subjects did not approach the stimulus during the first three minutes' exposure. An interesting behaviour sometimes took place just in front of the stimulus, this could be termed 'brooding' or'food seeking' behaviour, which involved the subject crouching in front of the



F I G . 13.

Figure 13

The performance of the best curlew subjects during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

stimulus and quivering its wings (the oyster catchers and moorhens also exhibited this behaviour, directly in front of the stimulus). During 'brooding', or 'food seeking' behaviour the high-pitched whistles would subside and give way to a softer whistle. In the same way as other species, pecking and nestling took place, especially around the stimulus.

During exposure trials 8 of the 10 lapwing subjects made some approach to the stimulus, though this approach score was often negative (see figure 14 and table 6). Over the three days exposure trials approach to the stimulus decreased and there was also running in the opposite direction, i.e. away from the stimulus. This produced an overall mean score for the exposure trials, of-50.4, and a high standard deviation of 151.4. t - test analysis indicated that approach to the stimulus was not significant ($t = 1.054$, $0.2 < P < 0.3$, see table 7). Birds 8 and 12 approached the stimulus favourably (see figure 15). Bird 12 achieved a score of 271 out of a possible 360, on day three of the exposure trials.

On day 4, the first day of preference trials, the subjects approach score reached a mean of 46.0, this decreased on day 5 to a mean of 1.6. Closer inspection of each subject's responses indicates that 8 of the ten subjects gave positive responses to stimulus A, and 4 of the 10 subjects made some approach responses to stimulus B. These results, when analysed by the t - test, gave $t = 1.379$, $0.2 < P < 0.3$ (see table 7). The lapwing, as a species, did not approach stimulus A significantly during preference trials.

FIG. 14

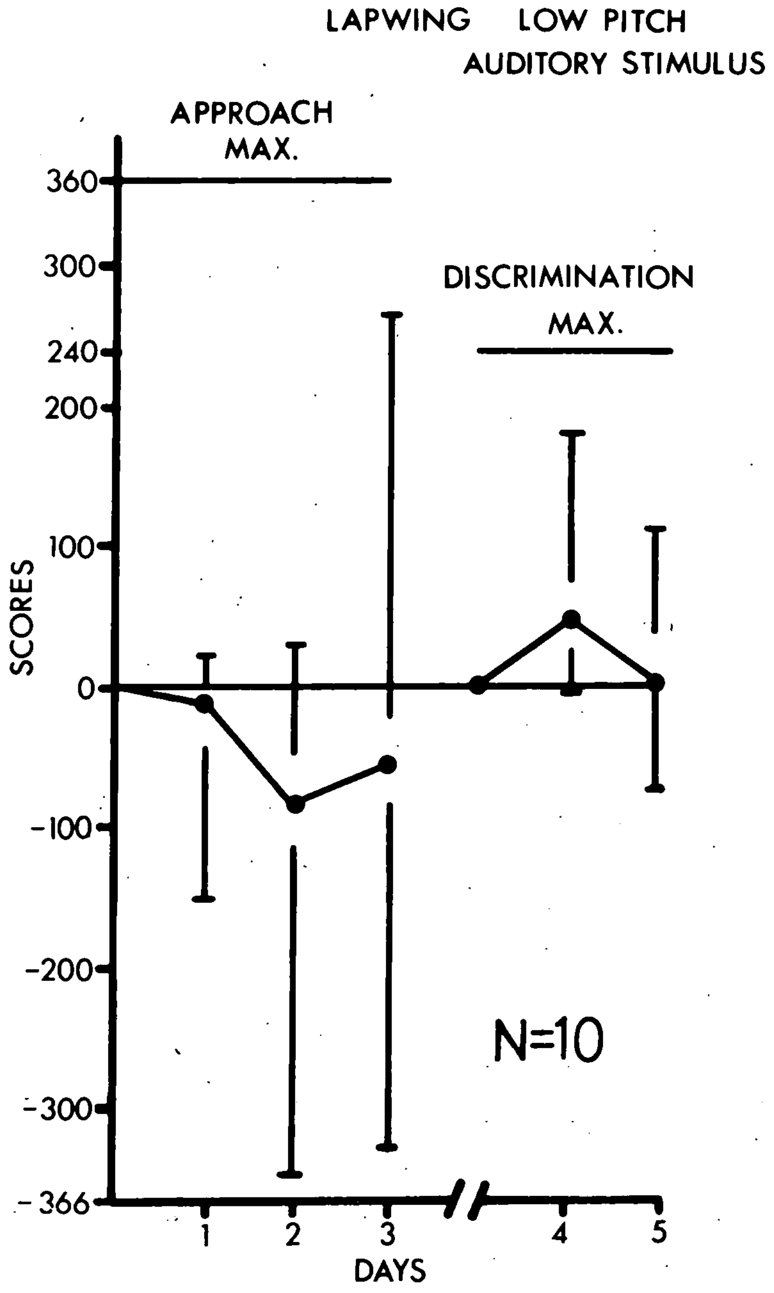


Figure 14

The performance of the lapwing subjects during exposure (or approach) and preference (or discrimination) trials in experiment 4.

In conclusion the lapwing species did not approach the stimulus to any significant extent, in either exposure or preference trials. We therefore cannot decide whether the species will or will not imprint on an inappropriate stimulus. Some subjects did approach the stimulus. In figure 15, it can be seen that bird 8 approached the stimulus irregularly during exposure trials, but during preference trials the approach distinctly improved. After five days of experimentation was completed, this subject was left in the experimental chamber. Subject 8 persisted in its approach to stimulus A. Because of this result, and those previously obtained for the curlews, it was decided to carry out a further experiment to test the hypothesis that a greater exposure time will result in greater approach to an inappropriate stimulus. This experiment is described in chapter four.

Oyster Catcher (Heamatopus ostralegus occidentalis)

Only four subjects could be obtained for this species. However their results are indicative of their imprintability and are therefore included. The behaviour of these four subjects resembled that of the other wader species. The vocalizations differed in note, but had the same pitch, when the subject was 'afraid', or 'contented'. Quivering of the wings and crouching took place in front of the stimulus, i.e. 'brooding' and 'food seeking' behaviour. Nestling and contentment calls, a low-pitched whistling, also took place in front of the stimulus.

FIG.15.

LAPWING

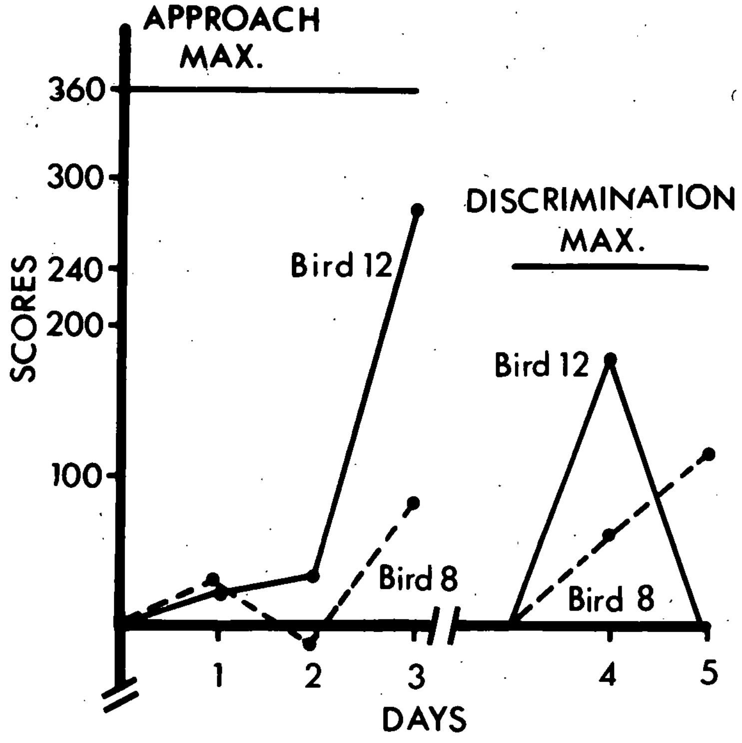


Figure 15.

The performance of the best lapwing subjects during exposure (or approach) and preference (or discrimination) trials in Experiment 4.

During the first day of exposure trials the four subjects approached the stimulus after an average of 129 seconds. Their responses increased from a mean of 30.7 on day one, to a mean of 158.5 on day three. This is quite a high degree of approach (higher than any other wader, see table 6 and figures 12, 14 and 16.) The best responses were given by two of the subjects, the first received scores of 145, 192 and 278 on each respective day of exposure trials; the second subject received scores of 32, 357 and 305 (figure 17) on each respective day of exposure trials.

The mean for all subjects during exposure trials is 105.1 with a standard deviation of 145.0. t - test analysis shows that this result is not statistically significant, ($t = 1.44$, $0.2 < P < 0.3$).

In preference trials the oyster catcher chicks approached stimulus A, none however approached stimulus B. The low scores in the trials (see tables 6 and 8), are due to a lack of responsiveness, rather than negative scores obtained. On day 4, the first day of exposure trials, approach scores were significant, $t = 1.759$, $0.1 < P < 0.2$.

In conclusion, the oyster catcher does not appear statistically to imprint on stimulus A. However, the oyster catcher subjects do approach this stimulus. Perhaps with a greater number of subjects a significant result could have been obtained.

FIG. 16

OYSTER CATCHER

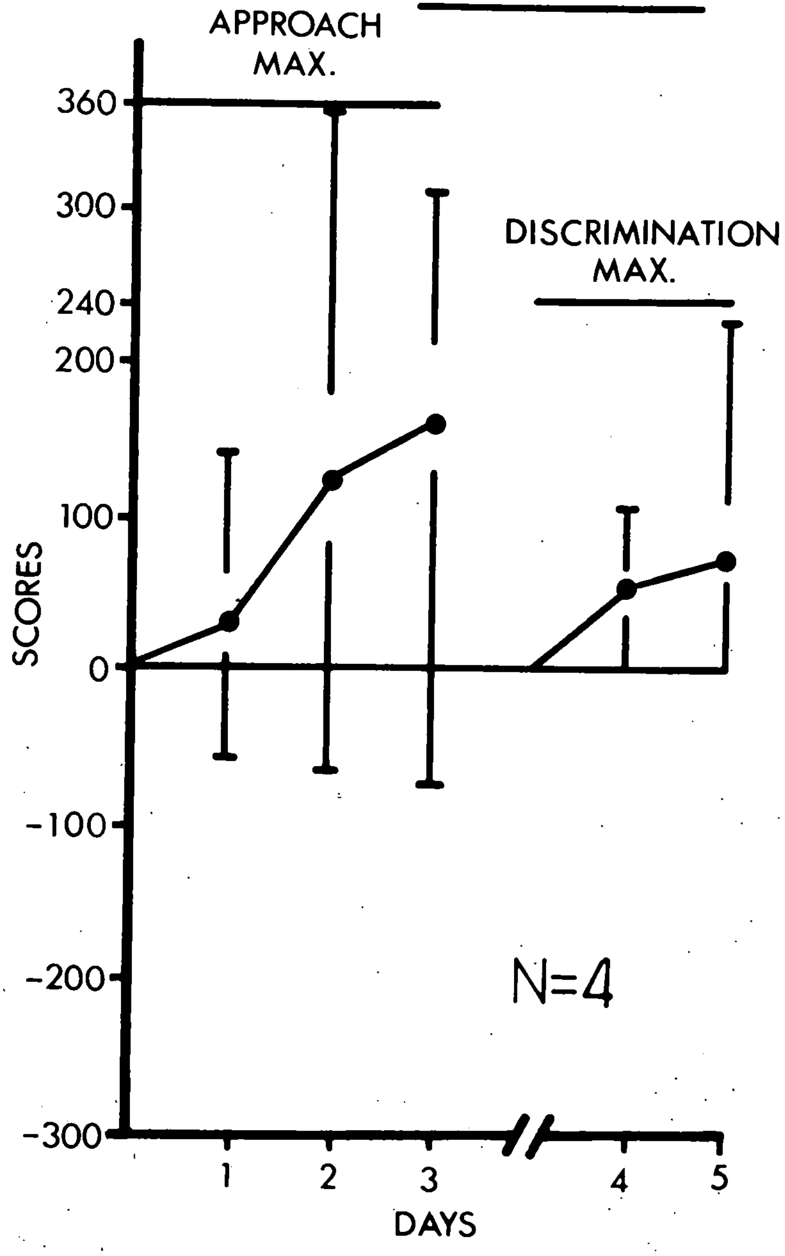


Figure 16.

The performance of the oyster catcher subjects during exposure (or approach) and preference (or discrimination) trials, in Experiment 4.

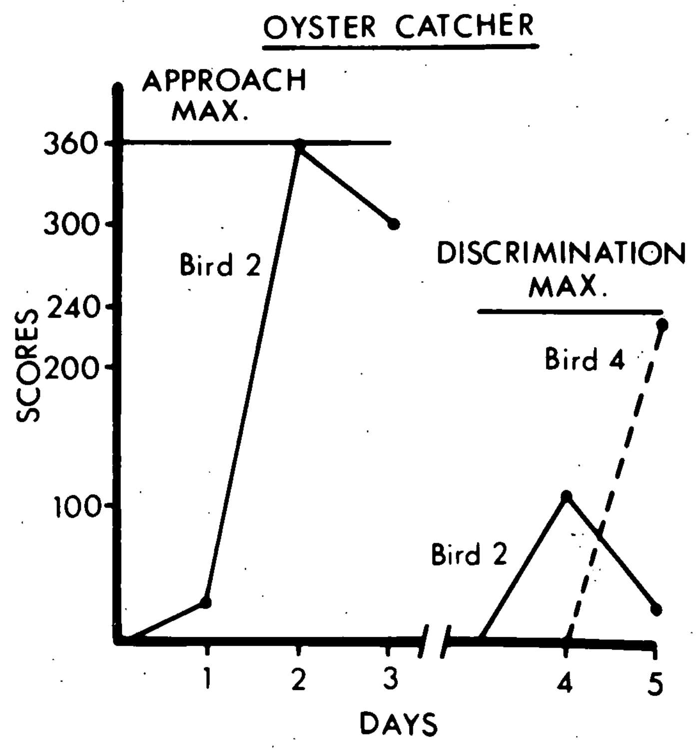


FIG. 17.

Figure 17.

The performance of the best oyster catcher subjects during exposure (or approach) and preference (or discrimination) trials, in Experiment 4.

The oyster catchers responded to stimulus A more than any other species of wader. This is probably because in the wild the oyster catcher chicks, unlike the other waders, are fed by their parents. This requires a heightening of the chick's responsiveness to an imprinting stimulus. This will be considered in greater depth in Chapter 5.

CHAPTER FOUR

Experiment 5 : An Attempt to Increase the Approach Responses in Lapwings.

In the previous experiment the waders in general, and the lapwings in particular, showed little evidence of imprinting on the stimulus used. This was manifest by, a) poor approach behaviour in the exposure trials of that experiment, and b) their apparent failure to prefer the stimulus to the competitor stimulus B in the preference trials. In the present study experimental variables were manipulated in an attempt to improve this performance. The experiment is in two parts.

In the first part of the experiment the frequency of the auditory stimulus, associated with stimulus A, was modified. This was done because some species of bird have preferred ranges of frequencies to which they will respond (Collias and Joos, 1953; Gottlieb, 1961a). The auditory stimulus was changed from a male voice repeating the words 'Kum, kum', to a female voice repeating the same words. The sound was of the same intensity but of a different frequency. If lapwings do have a preferred range of frequencies, either due to self audition, a particularly sensitivity in the inner ear, or an innate preference, then the higher frequency of the female human voice may be preferred. The procedure for the rest of this experiment remained the same as in experiment 4.

Most imprinting experiments investigate the parent - infant bond by attempting to imprint the infant on an inappropriate stimulus. One important factor of imprinting is artificially modified in these experiments i.e. the length of time the infant is left with the parent. Most imprinting experiments only have short exposure times to the imprinting stimulus. If the exposure time were increased it may be found that imprinting on inappropriate objects increases markedly. For this reason the exposure time of part two of experiment 5 was increased by 3 minutes per day. This gave a total possible score of ± 480. The preference trials remained the same as in Experiment 4.

Part One.

The effects of a High-Pitched Auditory Stimulus on Approach and Discrimination in the lapwing.

Subjects

The subjects were 9 lapwings (Vanellus vanellus).

Procedure

The subjects were exposed to stimulus A, plus a high frequency 'Kum' call for 3 x 3 minutes trials per day, lasting for 3 days. These trials took place in the rectangular run (see figure 1a). The preference trials took place in the triangular run (figure 1b) for 2 x 3 minute trials on days 4 and 5.

Results

The performance of the lapwing subjects, during exposure trials, varied tremendously. Approach to the stimulus was positive on day one, but decreased, becoming negative on days 2 and 3 (see tables 9 and 10 and figure 18). Seven of the nine subjects gave some approach to stimulus A, during exposure trials, although this was poor. For the exposure trials the mean approach was 39.92, and the standard deviation, 107.3 This result when

FIG. 18

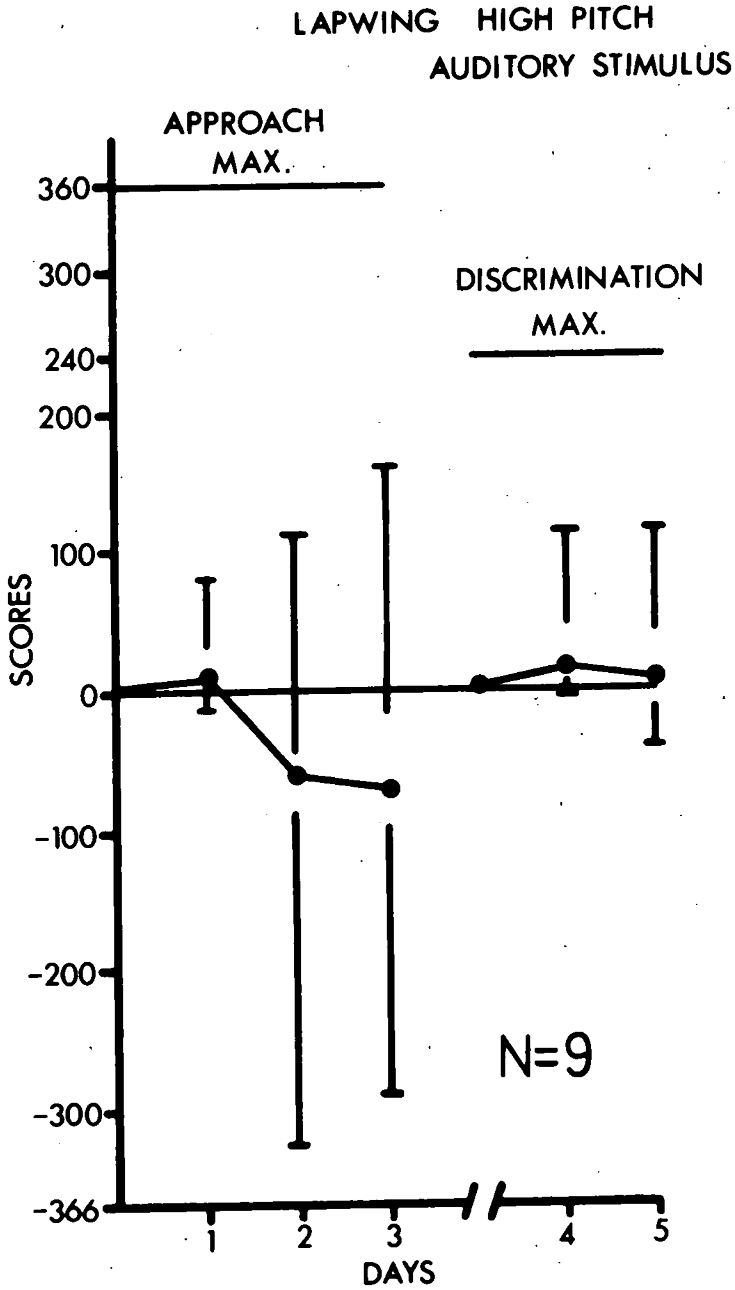


Figure 18

The performance of the lapwing subjects exposed to a high pitched auditory stimulus during exposure (or approach) or preference (or discrimination) trials in Experiment 5, part one.

analysed by the t-test, gave $t = 1.068$, $0.3 < P < 0.4$. There was therefore, not a significant level of approach to, or avoidance of, the stimulus during exposure trials.

In the preference trials there was little or no evidence of a positive response to stimulus A (figure 18). The results from this experiment showed that a higher frequency auditory stimulus, of the type used, did not cause a significant increase in approach over that shown by the lapwing subjects in experiment 4.

Part Two

The Effects of an Increase in the Time of Exposure to the Stimulus on Approach and subsequent Preferences.

In this part of the experiment the length of exposure to stimulus A was increased. This modification was an attempt to increase the approach response to stimulus A, an inappropriate stimulus.

Subjects

The subjects used were 8 lapwing chicks.

Procedure

In its natural environment a chick would be in almost constant contact with its parents. The imprinting object would not be artificially restricted to 9 minutes per day, as was the case in the earlier experiments. An increase in the length of time of exposure to the stimulus may alter the degree of responsiveness of subjects in exposure and preference trials. For this reason exposure to the familiar stimulus in exposure trials was increased by 3 minutes per day.

Table 9

Experiment 5 - Parts One and Two

EXPERIMENT	EXPOSURE TRIALS			PREFERENCE		TRIALS
	DAYS			DAYS		
	1	2	3	4	5	
Part One	96.6	-63.6	-65.7	14.0	10.2	MEAN
N = 9	25.0	122.3	123.7	35.4	42.2	St.D.
Part Two	86.0	148.6	161.2	48.0	43.2	MEAN
N = 8	193.5	208.4	277.4	64.3	73.3	St.D.

This table gives the means and standard deviation on the subject's scores in experiment 5. Scores from part two of experiment 5 are higher on the first three days, since exposure trials lasted for a longer period, per subject, than they did in other experiments.

Table 10

Experiment 5 : Parts One and Two

EXPERIMENT	EXPOSURE TRIALS DAYS 1,2,3.	PREFERENCE TRIALS DAYS 4,5.	
Part One	- 39.92	12.11	MEAN
N = 9	107.3	39.04	St.D.
	$t = 1.068$, $0.3 < P < 0.5$	$t = 0.9305$, $0.3 < P < 0.4$	t - test
Part Two	131.9	45.62	MEAN
N = 8	231.7	69.01	St.D.
	$t = 1.609$, $0.1 < P < 0.2$	$t = 1.869$, $0.1 < P < 0.2$	t test

In table 10 the mean and standard deviation are calculated for the exposure and preference trials. The t - test analysis is also shown.

After the 3 x 3 minute trials, the subject remained in the apparatus to commence a further 3 minute period. The subject was not removed from the run between the 3rd and the 4th trials. The total score possible, per day, for the exposure trials was ± 480, and the total score for the preference trials remained the same at ± 240 per day. These were the only modifications to the procedure used in experiment 4.

Results

Analysis of the results showed that all subjects approached the familiar stimulus on each day of the exposure and preference trials. This positive response was not always high. The percentages of subjects giving overall positive responses were 75%, 87.5%, 75%, 75% and 62.5%, on days 1,2, 3,4 and 5 respectively. Thus, on average, more subjects responded positively than negatively. The means were reasonably high, but the wide range of scores produced a high standard deviation (see table 9 and figure 19). Analysis of the exposure trials, indicates that the level of approach was not significant, ($t = 1.609$, $0.1<P<0.2$).

The approach scores during preference trials were lower than the scores obtained during exposure trials (see figure 19). The mean and standard deviation for each day can be seen in table 9. Analysis of the preference trials (see table 10), indicates a lack of significance in approach to stimulus A ($t = 1.869$), $0.1<P<0.2$.

FIG. 19

LAPWING EXTRA 3 MIN. EXPT.

SCALED DOWN TO SIZE.

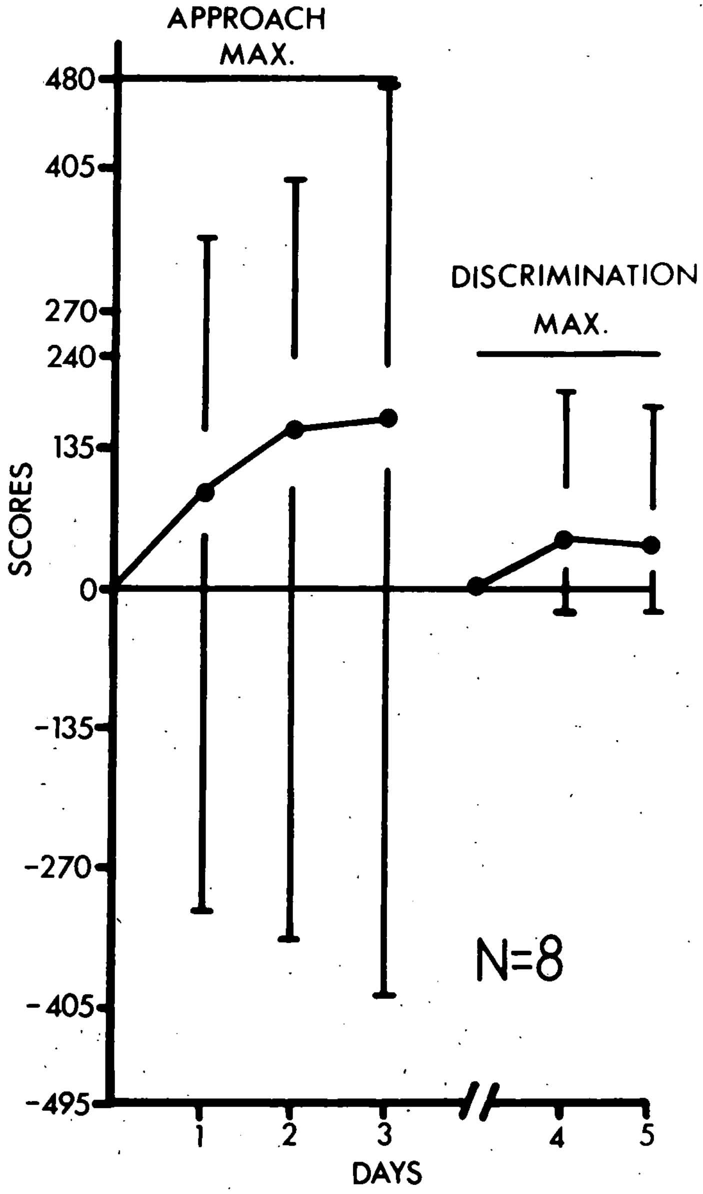


Figure 19.

The performance of the lapwing subjects given three minutes extra exposure time during exposure (or approach) or preference (or discrimination) trials in experiment 5, part 2.

One subject did exceptionally well in both presentation and discrimination trials. This subjects scores are shown below:-

Days	Scores	Maximum Possible Scores
1	333	480
2	399	480
3	474	480
4	202	240
5	184	240

Discussion

The exceptional results for this subject might indicate that imprinting, to the combined stimulus, had occurred. However, because only one subject did this well. it is difficult to know how to interpret this behaviour.

As the majority of subjects did not obtain high scores in the preference trials it cannot be said that the subjects had imprinted.

It may be noted that on average the approach to stimulus A during exposure trials and during preference trials were somewhat higher than in the other two experiments in which lapwings were used. However, statistical comparisons of the results of the preference trials between these experiments did not yield any significant differences. Whilst it is still tempting to speculate that a further increase in exposure time might lead to imprinting in this species, this must remain at a speculative level.

CHAPTER FIVE

Conclusions

In this study the importance of experimental uniformity has been stressed and a comparative study of imprinting is reported, in which the imprintability of various species of precocial, nidifugous birds was investigated. By maintaining uniformity of experimental procedure it was hoped that differences in response to the experimental stimuli would be due solely to species differences. All subjects were hatched and reared in approximately the same manner, allowing for differences in temperature and humidity of the species in incubation.

The responses of the species varied greatly. The gallinaceous birds (the domestic fowl, partridge and pheasant), responded favourably in approach during exposure and preference trials. This would indicate that they had become attached to, or imprinted on, the stimulus. In exposure trials the order of approach amongst the different species was : melanistic pheasants; partridge; domestic fowl; and ring neck pheasant. However, in preference trials this order changed, so that the domestic fowl subjects now achieved the highest approach scores. Given the variability of response of all the game birds in exposure and preference trials, they could be said to have imprinted successfully and more or less equally.

This result was expected, at least for the domestic fowl, because of Lorenz's hypothesis (1935, 1937), and the work of other experimentors on this species. The fact that other game birds also react in the same way as the domestic fowl appears to substantiate Lorenz's view.

In the anseriformes, the wild mallard (Anas platyrhynchos), was studied. This species reacted in much the same way as did the game **birds,** except that during the preference trials they made more approaches to stimulus B than the game birds.

Results obtained with the charadriiformes (waders) were variable. No significant level of approach or attachment was shown by any specie of waders. This would appear to substantiate Lorenz's hypothesis. However, the responses of individual curlews and lapwings suggests that some birds did approach and might have become attached to the stimulus. Three possible factors could account for the wader's lack of responsiveness; the length of time the subjects were exposed to the stimulus; the stimulus chosen; and the imprintability of the species to a non-natural stimulus.

The length of time that the subjects were exposed to the stimulus was manipulated in the experiments on lapwings. Those subjects exposed for the longest intervals (4 x 3 minute trials per day, experiment 5, part 2), gave positive results overall, but there was no real evidence of imprinting. It remains possible that a longer exposure time could result in the lapwing imprinting, but the author has no firm evidence to support this suggestion.

Stimulus A, used in these experiments, was found to be effective in eliciting responses from domestic fowl and mallard ducklings. It was felt that this stimulus might also have been effective for the other species. The oyster-catcher appears to have been attracted to the stimulus, but the waders did not significantly approach it. This may have been due to a lack of attractiveness of the stimulus, or a natural lack of responsiveness of curlew and lapwing chicks to a non natural imprinting object.

If the mode of life of the species were to be taken into account, this could aid interpretation of the experimental results. The oyster catchers for example, appears to do better in these experiments than other waders (a larger number of oyster-catcher subjects may have confirmed these observations). The oyster-catcher's parents feed their chicks, they do not merely 'guide' the chicks to an area where food can be found, as do the parents of lapwings and curlews. The oyster-catcher parent calls the chick and then presents food in its red bill. The chick then takes the food from the parent's bill (Tinbergen & Norton-Griffiths, 1964). This close, strong bond between chick and parent is also required because the chick must be taught the difficult task of feeding on mussels and other shell fish. If the oyster catcher chick has to imprint strongly on the parent, for its survival, then imprinting responses in this species are likely to be stronger than for others not fed by the parent, e.g. curlews and lapwings. (The moorhen (Gallinula chloropus) a gruiformid, is also fed by the parent, and it shows strong responses to the imprinting stimulus in imprinting trials, (Hinde et al, 1956). The better performance of some of the species in these experiments may be due to the closeness of the link between parent and offspring, in the natural environment. From the point of view of natural selection a 'close' attachment during the first two days of life would be essential for the survival of the chicks of these species (e.g. the domestic fowl, partridge, pheasant, mallard, moorhen and oyster catcher).

After the curlew and lapwing chicks have left the nest, the parent vaguely 'guides' them. Contact subsequently tends to occur only during brooding. The chicks become more attached to siblings than to their parents. Lind (1961), described this behaviour, amongst waders, with specific reference to the black-tailed godwit (Limosa limosa). In an experimental situation, such as described here, the curlews and lapwings may be responding positively to the non natural stimulus but because of the natural bond between parents and chicks, i.e. a loose bond, little or no approach response is given to the stimulus.

On this basis the high level of approach, and subsequent attachment of most game birds and the mallards, may be due to the very close parent-chick bond normally found with these species (Gottlieb 1963). In future experiments with waders the special nature of the parent-chick bond should be taken into account. Lorenz's postulation (1935), of the completeness of the innate schemata in the curlew may not be necessary i.e. the response of this species could be dependent on the natural responsiveness of the chick to the parent, than to the presence of an innate schemata.

A classification if imprinting behaviour, based on the type of contact between parent and offspring, may help in explaining the levels of imprintability of different species. In this way species would be classified according to the type of contact between parent and chick. The species with the closest parent-chick bond, i.e. most game birds would be placed at one extreme. Those with a 'feeding and protecting' bond, i.e. the oyster catcher and moorhen, would be located centrally. Those with the loosest bond of protecting and brooding, i.e. curlews and godwits would be at the other extreme. The ease of imprintability in the laboratory may be directly related to their position on the scale. Listing species on this scale would allow experimenters, examining imprinting, to take the 'closeness' of the response to the natural parent, into consideration. Previously when chicks, with a 'loose' parent-chick bond, showed how responses to non-natural stimuli it was assumed to be due to a'lack of imprintability'. If a scale of responsiveness, for the parent-chick bond existed, experiments for each species could be suitably devised.

Three suggestions for further experiments, which take into account the nature of the parent-chick bond, are:-

a) If, in preference trials, a stuffed, moving adult curlew or lapwing were used as an imprinting stimulus, and the chick approached this, then the curlew or lapwing chick can be said to have imprinted. However, if no significant approach was made to this stimulus, then the presence of a loose parent-chick bond would be supported.

b) A longer exposure time to the stimulus would mirror the naturally occurring situation more closely;

c) A reduction in the temperature of the experimental chamber to below 16°C, the temperature at which brooding occurs in waders (Lind 1961), may cause subjects to approach the stimulus, as they would naturally approach their parent in the brooding situation.

The variety of results found in the experiments described in this thesis indicates that species are fundamentally different in their learning and degree of responsiveness. In examining a natural phenomenon such as imprinting, the natural situation must be referred to constantly. The results in this thesis have been interpreted with reference to natural situations and phenomena.

APPENDIX

1. Appraisal

The experiments carried out in this thesis were basically exploratory in nature. Very little was or is known on the imprintability of wild species such as the curlew, lapwing and oyster catcher. In this thesis, a study was made of the comparative responsiveness of these species to a single stimulus. Difficulties arose in :
a) choosing a suitable stimulus as the limited number of subjects obtained precluded the possibility of prior testing to a range of stimuli, and b) the difficulty of finding and collecting eggs. When the eggs of the wild species of curlews, lapwings and oyster catchers were obtained the age of the embryos could not be calculated. This meant that the neonatal behaviour of some subjects may have been affected by their transportation and subsequent change of incubatory temperature, humidity and lighting conditions.

The godwit (Limosa limosa) eggs are more difficult to obtain than wader's eggs. It is for this reason that the godwit was not used in these experiments to verify the regulative/mosaic hypothesis of Lorenz. Had there been a greater number of the species used it may have been possible to verify an interesting point which emerged from a pilot study. Approach and preference for stimulus A did not reach a significant level in any of the wader species, but one or two subjects in each species did make substained approaches to the stimulus with a greater and more assured supply of eggs and with suitable modification of the experiment, these approach behaviours may well reach a more significant level in the species as a whole.

2. Mixing of a Species After Isolate Rearing

An interesting sequence of behaviours occurred when a previously isolated lapwing was placed with siblings, after experimentation. This chick was taken from the cage where it had been reared in isolation until it was five days old, and placed into a communal cage with its peers. Immediately, the chick emitted a sequence of 'fear chirps' and avoided the other nestling lapwings. This behaviour continued for a few hours. Often, the other 'socialised' chicks approached the newcomer. The chick would then avoid the approaching chicks, though sometimes avoidance would subside and it would peck at the other chicks. This pecking response may have been investigatory or aggressive in nature. Eventually, possibly due to habituation, the chick nestled with the others. Constant exposure had led to socialisation with peers. Whether this also affected its later social, sexual and parental behaviours is unknown, as these chicks were released before sexual maturity was reached.

These finding possibly indicate two factors. Firstly, that the sensitive period had terminated after 5 days, and novel stimuli caused fear and produced avoidance (Moltz 1960; Salzen, 1962). Certainly fear had developed, since the chick could no longer be induced to approach or follow novel stimuli. Secondly, the same species, i.e. lapwings, were treated as novel stimuli by the newcomer. This is very important. If an innate schema of the species existed (Lorenz 1935) then fear would not have been induced by peers. These lapwing chicks would have been the innate releasing mechanism for the innate response, and they would have been accepted by the chick. If, however, fear had reached a sufficiently high level, then the innate schema would not have been released (Dimond, 1971).

3. Statistical Tests

Three statistical tests have been used in this thesis: the Mann-Whitney U test; the sign test; and the t-test. These tests are the standard forms of the test as described in McNemar (1969) and Siegel (1956)*

1. Mann-Whitney U Test

$$U1 = N1 \quad N2 + \frac{N1 \ (N1 + 1)}{2}$$

(where both N1 and N2 are greater than 8)

(U2 = N1. N2 - U1 as a check for the lowest U). Special tables can be used when N1 or N2 is less than 8.

2. Sign Test

The null hypothesis tested by the sign test is :

$$p \ (XA \quad X^{B}) = p \ (XA \quad XB) = \tfrac{1}{2}$$

or $p = Q = \frac{1}{2}$

Where N is the number of matched pairs for a N 25.

Any pairs with the same sign or which are indistinguishable are considered as 'ties' and deducted from the N.

X is the number of fewer signs. Tables can then be used to find out the probability for a particular N value, i.e. when X deviates significantly from 50:50 chance.

3. t - test

The t-test is used for experiments in which the number of subjects used is small (N 30). The smaller the number of subjects the greater is the change from a normal distribution curve.

$$\text{Hence} \qquad t = \frac{(M - ML)}{Sm}$$

where M = mean of the sample,

ML = hypothetical population mean,

and $Sm = \frac{SD}{N}$

N = number of scores used to compute the means.

SD = the standard deviation.

To allow for the change in the distribution curve, the degrees of freedom for the N must be considered; leading to a N - 1 number of possible deviations. For a particular N - 1, the t can be checked against a probability level.

* McNemar, Q (1969) 'Psychological Statistics'
Publ. John Wiley & Sons Inc.

Siegel, S. (1956) 'Non parametric Statistics for the behavioural sciences'.
Publ. McGraw-Hill

Bibliography

Abercrombie, B. & James H. (1961).	'The Stability of the Domestic Chick's Response to Visual Stimuli', Anim. Behav. 9, 205-212.
Adam J. & Dimond, S.J. (1971a).	'The effect of Visual Stimulation at Different Stages of Embryological Development on Approach Behaviour', Anim. Behav. 19 (1), 51 - 54.
Adam J. & Dimond S.J. (1971b),	'Influence of Light on the Time of Hatching in the Domestic Chick'. Anim. Behav. 19 (2), 226-229.
Andrew R.J. (1966)	'Precocious Adult Behaviour in the Young Chick', Anim. Behav. 14 485-500.
Barrett, J.E. (1972)	'Schedules of Electric Shock Presentation in the Behaviourial Control of Imprinted Ducklings', J. Exp. Anal. Behav. 18 (2), 305-321.
Bateson P.G.G. (1964a),	'Effect of Similarity Between Rearing and Testing Conditions on Chick's Following and Avoidance Responses', J. Comp. Physiol. Psychol. 57, 100 - 103.
" " (1964b)	'An Effect of Imprinting on the Perceptual Development of Domestic Chicks', Nature, Lond. 202, 421-422.
" " (1966)	'The Characteristics and Context of Imprinting', Biol. Rev. 41, 177-220.
Brown L.T. (1964)	'A Critical Period in the Learning of Motionless Stimulus Properties in Chicks', Anim. Behav. 12, 355-361.
Campbell, B.A. & Pickleman J.R. (1961),	'The Imprinting Object as a Reinforcing Stimulus', J. Comp. Physiol, Psychol. 54, 592-596.
Cofoid, D.A. & Honig, W.K. (1961)	'Stimulus Generalization of Imprinting', Science 134, 1692 - 1964.
Collias, N. & Joos, M. (1953),	'The Spectographic Analysis of Sound Signals in the Domestic Fowl', Behaviour 5, 175-187.
Dare P. (1966).	'Oystercatcher Populations in the British Isles', Min.Agr.Fish. Ser II Freshwater Fish 25 (5) 1 - 69.

Dimond S.J. (1968) 'Effects of Photic Stimulation Before Hatching in Chicks', J. Comp. Physiol. Psychol. 65, 320 - 324.

" " (1970). 'Social Behaviour in Birds and Mammals', Ed. Crook, Academic Press.

" " (1971) 'Personal Communication'.

Fabricius, E. (1951) 'Zur Ethologie Junger Anatiden', Acta. Zool. Fen. 68, 1 - 178.

" " (1964) 'Critical Periods in the Development of the Following Response in Young Nidifugous Birds', Z. Tierpsychol 21, 326-337.

Fabricius, E. & Boyd, H. (1954) 'Experiments on the Following Response of Mallard Ducklings', Wildfowl Trust Abnu. Rep. 1952 - 55, 84 - 9.

Fabricius E. & Falt L. (1969) 'Sexuell pragling hos grasandhonor'. Zool Revy 31: 83 - 88.

Fischer G.J. (1966) 'Auditory Stimuli in Imprinting'. J. Comp. Physiol 61, 271-275.

Fischer, G.J. (1968) 'Comparison Between Chicks that Fail to Imprint and ones that imprint - Strongly'. Behaviour 29 262 - 267

Fischer, G.J. Campbell, G.L. & Davis, W.M. (1965) 'The Effect of E.C.S. on Retention of Imprinting', J. Comp. Physiol. Psychol. 9, 455 - 457.

Gottlieb, G. (1961a) 'The Following - Response and Imprinting in Wild and Domestic Ducklings of the Same Species (Anas Platyrhynchos)', Behaviour 18, 205 - 228.

Gottlieb G. (1961b), 'Developmental Age as a Baseline for Determination of the Critical Period in Imprinting', J. Comp. Physiol. Psychol. 54. 422 - 427.

" " (1963) 'Following-Response Initiation in Ducklings: Age and Sensory Stimulation', Science 140, 399-400.

" " (1965) 'The Question of Imprinting in Relation to Parental and Species Identification by Avian Neonates'. J. Comp. Physiol Psycho. 55, 821 - 826.

" " (1967) 'Species Identification by Avian Neonates: Contributory Effect of Perinatal Auditory Stimulation', Anim. Behav. 14 (314,) 282 - 290.

Gottlieb G. (1970)	'Development of Species Identification in Birds: An Inquiry into Prenatal Determinants of Perception', Univ. of Chicago Press; Chicago III U.S.A.
Gottlieb G. & Kuo Z.Y. (1965)	'Development of Behaviour in the Duck Embryo', J. Comp. Physiol. Psychol. 59 (2) 183 - 188.
Gray P.H. (1960).	'Evidence that Retinal Flicker is not a NNecessary Condition of Imprinting', Science 132, 1854 - 1835.
" " (1961)	'The Releasers of Imprinting; Differential to Colour as a Function of Maturation'. J. Comp. Physiol. Psychol. 54, 597 - 601.
" " (1962)	'Is the Imprinting Critical Period an Artifact of a Biological Clock?', Percept. Mot. Skills. 14, 70.
Guhl, A.M. & Fischer G.J. (1969)	'The Behaviour of Domestic Chickens', 'In the Behaviour of Domestic Animals', Ed. Hafes, Publ. Baillier, Tendall & Cassell.
Guiton, P. (1966)	'Early-Experience and Sexual Object-Choice in the Brown Leghorn', Anim. Behav. 14 (4) 534 - 538.
Heaton, M.B. (1975)	'Pupillary Reflex in Bird Embryos', J. Comp. Physiol. Psychol. 84 (1) 134 - 139.
Hebb, D.O. (1946)	'On the Nature of Fear', Psychol. Review 53, 259 - 276.
Heinroth, O. (1911),	'Beitrage Zur Biologie Namentlich Ethologie Und Psychologie Der Anatiden', Verh. V. Int. Orn. Kong. 589-702
Heinz G. (1973)	'Response of Ring-Necked Pheasant Chicks (Phasianus colchicus) to Conspecific Calls', Anim. Behav. 21 (1) 1 - 9.
Hess E.H. (1959)	'Imprinting', Science 130, 133 - 141.
" " (1964)	'Imprinting in Birds', Science 146, 1128 - 1139.

Hinde R.A. (1955) 'The Following Response of Moor-Hens and Coots', Brit. J. of Anim. Behav. 3. 121 - 122.

Hinde R.A., Thorpe W.H. & Vince, M.A. (1956) 'The Following of Young Coots and Moorhens', Behaviour 9, 214 - 242.

Hoffman H.S. (1968) 'The Control of Distress Vocalization by an Imprinted Stimulus', Behaviour 30, 175 - 191.

Hoffman H.S. Searle J.L. ~~Move~~ Toffey, S., & Kosma, F. (1966) 'Behavioural Control by an Imprinted Stimulus', J. Exp. Anal. Behav. 9 (3) 177 - 189.

Hoffman H.S., Stratton J.W. & Newby J. (1969) 'Punishment by Response-contingent Withdrawal of an Imprinted Stimulus', Science (Washington) 3868 702-704.

Hubel, D.H. & Wiesel, T.N. (1959) 'Receptive Fields of Single Neurons in the Cat's Striate Cortex, J. of Physiology (Lon) 148, 574.

Immelmann, K. (1964) 'Drought Adaptations in Australian Desert Birds', Proc. Internatl. Ornithol. Congr. 13, 649 - 657.

" " (1967) 'Abstr. Xth Int. Conf. Ethol. Stockholm.

Impekoven, M. (1973) 'Response-Contngent Prenatal Experience of Maternal Calls in the Pecking Duck (Anas Platyrhynchos)', Anim. Behav. 21 (1), 164 - 168.

James H. (1959) 'Flicker: An Unconditioned Stimulus for Imprinting', Canad. J. of Psychol 13, 59 - 67.

James, H. & Binks, C. (1963) 'Escape and Avoidance Learning in Newly Hatched Domestic Chicks', Science 139, 1293 - 1294.

Jaynes, J. (1956) 'Imprinting: The Interaction of Learned and Innate Behaviours. I Development and Generalization'. J. Comp. Physiol. Psychol. 49, 201 - 206.

" " (1958) 'Imprinting: The Interaction of Learned and Innate Behaviours. IV Generalization and Emergent Discrimination', J. Comp. Physiol. Psychol. 51, 238 - 242.

Kear - Matthews J. (1971) 'Personal Communication'.

Klopfer, P.H. & Gottlieb G. (1962) 'Imprinting and Behavioural Polymorphism: Auditory and Visual Imprinting in Domestic Ducks (Anas Platyrhynchos) and the involvement of the Critical Period', J. Comp. Physiol. Psychol. 55, 126 - 130.

Klopfer P.H. & Hailman J.P. (1964) 'Perceptual Preferences and Imprinting in Chicks', Science 145, 1333 - 13334.

Kovach, J.K. & Hess E.H. (1963) 'Imprinting Effects of Painful Stimulation upon the Following Response'. J. Comp. Physiol. Psychol. 56, 461 - 464.

Lind, H. (1961) 'Studies on the Behaviour of the Black Tailed Godwit (Limosa limosa), Munksgaard Copenhagen, Denmark.

Lorenz K. (1935) 'Der Dumpan Under Umwelt Des Vogels' J.F. Ornith. 83, 137 - 215. 289 - 413.

" " (1937) 'Uber Die Bildung Es Instinktbegriffes', Naturwissenschafton 25, 289 - 300, 307 - 308, 324 - 331.

Maturana, H.R. & Frenk, S. (1963) 'Directional Movement on Horizontal Edge Detectors in the Pi~~d~~geon Retina' Science 142, 977 - 979.

Meyer, M.E. Couden B.N. & Westford K.L. (1970) 'Light Increment and Decrement as Sensory Reinforcer for domestic Chicks Psychol. Rev. 26 (3) 923 - 926.

Moltz H. (1960) 'Imprinting : Emperical Basis and Theoritical Significance,'(Psychol. Bull 57, 291 - 314.

Moltz H. & Rosenblum L.A. (1958) 'The Relation Between Habituation and the Stability of the Following Response' J. Comp. Physiol. Psychol 51, 658 - 661.

Olds. J.F. & Milner P. (1954) 'Positive Reinforcement Produced by Electrical Stimulation of Septal Areas and other Regions of the Rat Brain' J. Comp. Physiol. Psychol. 47, 419 - 427.

Ozmon, K. (1975) 'The Effect of E.C.S. on Imprinting in Japanese Quail (Coturnix coturnix japonica) J. Comp. Physiol. Psychol. 82 (3), 360 - 367.

Peterson, N. (1960) 'Control of Behaviour by Presentation of an Imprinting Stimulus', Science 132, 1395 - 1396.

Pitz, G.F. & Ross, R.B. (1961)	'Imprinting as a Function of Arousal' J. Comp. Physicl. Psychol. 54, 602-604
Ramsey, A.O. & Hess, E.H. (1954)	'A Laboratory Approach to the Study of Imprinting', Wilson Bull 66, 196 - 206
Rubel, E.Q. (1970)	'Effect of Early Experience on Fear Behaviour in Common Quail', Anim. Behav. 18 (3) 427 - 433.
Sackett, G.P. (1965)	'A Neural Mechanism Underlying Unlearned Critical Periods and Development Aspects of Usually Controlled Behaviour', Psychol. Rec. 70, 40 - 50.
Salzen, E. (1962)	'Imprinting and fear' SYM. 200L Lond, 8. 199 - 217.
" " (1963)	'Imprinting and the Immobility Reactions of Domestic Fowl: Anim. Behav. 11 (1): 66 - 71.
" " (1966)	'Imprinting and Environmental Learning' In Aronson, L.R., Lehrman, D.S. Rosenblatt, J.S. & Tobach, E. (Eds). Development and Evolution of Behaviour: NY. Freeman. Vol 1.
" " (1967)	'Imprinting in Birds and Primates' Behaviour 28 (3/4) 232 - 254.
Schaefer, H.H. & Hess E.H. (1959)	Colour Preference in Imprinting Objects', Zeits. f. Tierpsychol. 16, 161-172.
Schein, M.W. (1963)	'On Irreversability of Imprinting' Zeits. f. Tierpsychol. 20, 462 - 467;
* PTO → Schulman, A.H. (197~~0~~1)	'The Effect of Imprinting Training on Hyperstriatal E.E.G. in young Domestic Chicks (Gallus Domesticus)', Dev. Psychobiol. 4 (4) 353 - 362.
Schutz F. (1965)	'Ubjektfixierung Geschlechtlicher Reaktionen Bei Anatiden Und Huhnern', Naturwiss 50, 624 - 625
" " (1964)	'Uber Geschlechtlich Unterschieldliche Objektfixierung Sexueller Reaktionen Bei Enten im Zusammenhang Mit Dem Prachtkled Des Mannchens', Zool. Anz. Suppl. 27, 282 - 287.

Schutz F. (1965) 'Sexuelle Pragung Bei Anatiden', Zeits. f. Tierpsychol. 22, 50 - 103.

" " (1971) Durham, Eng. Imprinting Conference

Schwartzkopff, J. (1965) 'On the Hearing of Birds', Auk 72, 340 - 347.

Seitz A. (1949) 'Uber Das Verhatten Sweier Isoliert Aufgezogener Brachvogel (Numenius ~~A~~arquata)', Orn. Ber. 11, 32 - 39.

* Schulman, A.H. (1970) 'Precocial Sexual Behaviour in Imprinted Male Turkeys (Meleagris ~~G~~gallopavo). Anim. Behav. 18, 758 - 759.

Shapiro, J. (1971) Durham, England. Imprinting Conference.

Sluckin, W. (1962) 'Perceptual and Associative Learning' Symp. Zool. Soc. Lond. 8. 193 - 198

Sluckin W. & Salzen E. (1961) 'Imprinting and Perceptual Learning', Q.J. Exp. Psychol. 13, 65 - 77

Smith F.V. (1960) 'Towards Definition of the Stimulus Situation for the Approach Response in the Domestic Chick', Anim. Behav. 8, 197 - 200.

" " (1962) 'Perceptual Aspects of Imprinting'. Symp. Zool. Zoc. Lond. 8, 171 - 191.

" " (1969) 'Attachment of the Young-Imprinting and Other Developments', Oliver and Boyd Ltd.

Smith F.V. & Bird M.W. (1964) 'The Approach Response of Chicks in Groups in Relation to the Strength of the Stimulus.' Anim. Behav. 12, 252 - 258.

Smith F.V. & Hoyes, P.A. (1961) 'Properties of the Visual Stimuli for the Approach Response in the Domestic Chick', Anim. Behav. 9, 159 - 168.

Smith F.V. & Nott K.H. (1970) 'The Critical Period in Relation to the Strength of the Stimulus', Zeits. f Tierpsychol. 27, 108 - 115.

Sokolov, E.N. (1960) 'Neuronal Models and the Orientating Reflex' in M.A.B. Brazler (Edt.) 'the Central Nervous System and Behaviour', Trans. Third. Conf., 187 - 276.

Spalding, D.A. (1873) 'Instinct with Original Observation on Young Animals', MacMillan's Mag. 27. 282 - 295.

Taylor, A. & Taylor, K.F. (1964) 'Imprinting to a Static Feature of the Home Environment', Nature 204, 1117 - 1118.

Taylor A. Sluckin, W., Hewitt, R. & Guiton, P. (1967) 'The formation of attachments by Domestic chicks to two textures Anim. Beh. 15, 514 - 519.

Tinbergen, N. (1959) 'Comparative Studies of the Behaviour of Gulls (Laridae) A. Progressive Report', Behaviour 15, 1 - 70.

Tinbergen, N. & Norton-Griffiths M. (1964) 'Oystercatchers and Mussels', British Birds, 64 - 70.

Vince M.A. (1966) 'Artificial Acceleration of Hatching in Quail Embryos', Anim. Behav. 14, 389 - 394.

Vince M.A. & Chinn, S. (1972) Effect of Accelerated Hatching on the Initiation of Standing and Walking in the Japanese Quail (Coturnix coturnix japonica)', Anim. Behav. 19 (1), 62 - 66.

Weidmann, U. (1958) Verhaltensstudien an Der Stockente (Anas Platyrhynchos L.)' Zeits. f. Tierpsychol. 15, 277 - 300.