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THE EFFECT OF DIMORPHIC PARENTS ON

MATE SELECTION IN PIGEONS

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THE EFFECT OF DIMORPHIC PARENTS ON MATE SELECTION IN PIGEONS

CHAPTER I

INTRODUCTION

Investigators in the field of animal behavior appear to have accumulated a great deal of evidence indicating that early experience is an important variable in determining various kinds of later social behavior (Craig, 1914; Hess, 1958; Lorenz, 1957; Scott, 1958; Tinbergen, 1953; Whitman, 1898). Within this field a considerable amount of attention has been directed toward the investigation of social behavior in birds. Zoologists, ornithologists, psychologists, naturalists and those scientists who have come to be known as ethologists have concerned themselves with bird behavior. Evidently, as Burton (1953) has pointed out, the fact that the bird is primarily a visually oriented animal (as are those who study them) has played an important part in the development of this interest.

The present study is directed toward furthering knowledge in this area, and more specifically, has to do

with the effects of early experience on mate selection in the domestic pigeon.

Antecedent Observations on Experience and Animal Behavior

Whitman (1898; 1919a; 1919b) and Craig (1908; 1914) appear to be two of the earliest and most significant contributors to the study of social behavior in birds. Both reported important aspects of social behavior in the pigeon, aspects which are particularly relevant to the understanding of mating behavior.

As a result of his careful observations of the pigeon's behavior, Whitman felt that the once widely held opinion that instincts were "fixed" in terms of the regularity and inflexibility of their operations was greatly exaggerated. He stated that "Close study and experiment with the most machine-like instincts always reveal some degree of adaptability to new conditions" (1898, p. 331). This ability to adapt to environmental stimuli led, he felt, to intelligent (as opposed to simply instinctive) behavior via the effect of experience. From this point of view he deduced that such important social behavior as sexual activity and pair formation must, in part, be determined by the early experience of the animal. In summarizing Whitman's works, Riddle (1919) stated that the early environment is an extremely important factor in determining what objects arouse and provoke sexual activities. "As a matter of fact," he notes,

> . . . pigeons normally pair with members of their own species, and this preference has generally been regarded as instinctive in character. But the data of this volume show rather conclusively that species preferences exhibited by birds at maturity are to a large extent acquired and are functions of the social environment in which the birds were reared (Riddle, 1919, p. 98).

In further discussion of this point Riddle laid the groundwork for the more current instinctual theories involving imprinting and hierarchical organization of instincts when he stated:

> The range of stimuli to which an instinctive tendency will respond may be modified by habits acquired long before the first expression of the instinct. The first expression of a delayed instinctive tendency may thus be previously acquired (Riddle, 1919, p. 28).

> The fact that the range of stimuli to which an instinctive act is susceptible may be modified by experience previous to the first expression of the act develops a novel and important principle of instinctive modification for the more prevalent doctrine assumes that instincts become modified only through the influence of simultaneous activities (Riddle, 1919, p. 98).

The effect of experience on the mating behavior of his pigeons so impressed Whitman that he concluded that their preference for a particular kind of mate was a function of what species of parents reared the bird. That is, if a particular set of parents hatched and reared the young of another species these young would prefer to mate with the birds of their parent's species when they reached maturity (Whitman, 1919a).

Craig followed up Whitman's interest in mating behavior, stating that the parent birds appeared to educate their young toward species recognition "unconsciously".

> For example, the parents exhibit to the young the body-form, colors, gestures, and sound characteristics of the species and thus the young learn to recognize their kind. Professor Whitman has proved this again and again by taking the eggs or young of wild species and giving them to the domestic ring-dove to foster, with the result that the young ever after associated with the ring-dove and tried to mate with them (1909, pp. 89-90).

Craig later reared male ring-doves in isolation himself and found that, apparently because their early experience had been limited to humans, they displayed all their instinctual courting reactions toward these "inappropriate" objects. As a result he specified the instinct-experience interaction with this statement:

> The sexual reaction of the male is, in its motor aspect, very completely and definitely provided in the innate nervous organization. But the innate sensory inlet to this reaction is not a complete sensory inlet; it is supplemented by experience (Craig, 1914, p. 132).

This extension of Whitman's views, where the environmental object becomes the key to the behavior resulting from the instinctual-experience interaction, is the precurser to the imprinting theories of contemporary ethologists. Before considering these more theoretical notions, however, some comment on the bird's ability to recognize individuals of its own species seems warranted.

Recognition in Mate Selection

The observations of Whitman and Craig, by implication, assert that birds have the capacity to recognize members of their own (or foster) species. Although audition certainly plays a role in this process, most investigators feel that

the visual apparatus is the bird's most important sensory tool. Hamilton and Coleman (1933) and Lashley (1916), for instance, have demonstrated that the bird's vision is almost as well developed as is man's, both in terms of color discrimination and visual acuity.

By and large, students of animal behavior have concluded that the differences in morphism (body-form and coloration) between the sexes in various species are the primary recognition cues (Carpenter, 1929; Collias, 1952; Craig, 1908; Levi, 1957; Lorenz, 1937; Ramsey, 1951; Tinbergen, 1951). In conjunction with this, however, behavior must be considered an important variable. Otherwise, in species where the male and female are not maximally differentiated by color, sexual recognition would be very difficult. In fact, Carpenter (1929), Bennett (1949), and Nice (1943) concluded that courting behavior in particular helps the male and female recognize each other. Nice (1943), moreover, believes that pair formation is partly determined by this capacity for individual recognition. She writes:

> The problem of pair formation is primarily that of recognition--specific and sexual. "Courtship may be defined as an elaborate sexual response involving recognition, selection, and pursuit" writes Abbott (1941). "Courtship is, in fact, an almost exclusive visual process; courting animals (not insects exclusively) depend almost entirely upon visual impressions that they receive." This is doubtless true of many fish, and partially true of birds, but with birds voice also plays an important role (Nice, 1943, p. 192).

Thus color and behavior appear to provide the necessary

recognition cues in mating, though color appears to be the more important variable in mate selection (Kerfoot, 1964).

It also seems apparent from the work of Hess (1962), Jaynes (1956; 1957), Lorenz (1937; 1957), and Tinbergen (1953) that the ability to recognize others of its species begins early in the bird's life. These authors would undoubtedly agree with Craig who, prior to their own work, stated:

> Hence we must believe that the young doves have no inherited tendency to mate with birds of a particular kind; they learn to associate with a particular kind during the period when they are being fed, when the characteristics of their nursing parents are vividly impressed upon their young minds (Craig, 1908, p. 90).

In summarizing, it would appear that observational evidence leads to the following conclusions regarding recognition and mating behavior:

1. Most birds are not innately "attached" to those of their own species. Rather this preference is acquired sometime early in their lives.

2. As a result of their visual abilities they are able to differentiate not only among different species but individually among their own kind.

3. As a result they appear to exhibit preferential mating behavior which is dependent, in large part, upon their early experience.

Theoretical Formulations Regarding Mating Behavior

There are at least three theoretical formulations which seem to be capable of accounting for the apparent re-

lationship between early experience and later mating behavior in birds. All involve the concept of instinct and are in agreement in their predictions regarding the direction mate choice will follow.

Ethology and imprinting. The general field of ethology with its specific concept of imprinting has, more than any theoretical system, emphasized the importance of early experience in the understanding of animal behavior. This discipline, which began in an unofficial sense with the work of Whitman (1898; 1919), Craig (1908; 1914), and Heinroth (1910), began as a purely phylogenetic and comparative investigation of behavior and until recently was carried on primarily by zoologists who were interested in behavior rather than anatomical and physiological taxonomy. Through the more recent works of such investigators as Lorenz (1957), Tinbergen (1951; 1953), and Hess (1958; 1962), however, it has moved from description to causal analysis. Currently, according to Hess (1962), the underlying physiological mechanisms are beginning to receive attention.

As a result of exhaustive observations, workers in this area became interested in instinctual behavior and Lorenz (1957), among others, has stated that instinctual behavior may even be used as a means of classifying animals. More pertinent to the present investigation, however, are the theoretical notions about the operations of the instinctual reactions themselves. In essence the ethologists hold that the animal

possesses innate, "fixed action patterns." Such patterns are defined as a "sequence of coordinated motor actions that appear without the animal having to learn it by the usual learning processes" (Hess, 1962, p. 173). These instinctive behaviors are set in motion only by specific stimuli which are termed "releasers." According to Lorenz (1937) and Tinbergen (1951) these reactions or fixed action patterns are held in check by an inhibitory block until an "innate releasing mechanism" (IRM) removes this block as a result of receiving sensory impulses from a releaser stimulus. In birds especially, the releaser for social behaviors may be a certain shape, color, or contrast in colors, or a behavioral sequence exhibited by another animal. Thus objects in the environment play a vital role in determining which pattern of behavior will be set in motion.

The concept of "imprinting" is crucial in explaining why certain environmental objects serve as releasers for instinctual behaviors which are directed toward fellow members of the species. This phenomenon, which was first observed by Heinroth (1910) and named by Lorenz (1937), has been most carefully studied in birds, although it does exist in many other species, including some mammals (Hess, 1962). In a broad sense it refers to

> . . . an early experience that has a profound influence on later adult social and sexual behavior of an animal with respect to the choice of objects for these behaviors (Hess, 1962, p. 225).

In order for imprinting to take place the young animal

must be exposed to an object which possesses certain size, color, or behavioral characteristics during a critical period early in its life. This critical period is of short duration in birds who are motile immediately after hatching. In several species its duration has been established (Hess, 1962). In other species, however, where the parents must care for the young over an extended period of time, the length of the period has not been specifically determined. Lorenz was the first to point out the importance of this critical period and he postulated that the first object which elicited a social response from the young animal later released not only that response but also related responses such as are found in sexual or mating behavior.

During the critical period the young bird becomes more or less irreversibly conditioned or imprinted to its parents and for the rest of its life directs its social and sexual behavior towards parent-like objects, thus ensuring the propogation of the species. If, moreover, the early experience is manipulated through the use of foster parents who possess the characteristics necessary to set off the innate releasing mechanism, the bird will direct its social and sexual behavior toward this kind of object, be it biologically appropriate or not. It should also be noted that if the "right" parental object is not available the appropriate behavior patterns involved in social and mating reactions may become confused and/or inchoate (Thorpe, 1951).

Barring the use of an inappropriate early object, then, the theory of imprinting would predict that birds tend to select mates who possess characteristics similar to the species or breed which reared them.

Kortlandt's theory of instinct hierarchy. A somewhat more elaborate instinctual theory has been proposed by Kortlandt (1955), a European ethologist who recognized the congruence existing between the ethological study of animals and psychoanalysis and drew on the latter in his theoretical formulations.

Essentially, the predictions from Kortlandt's theory that involve most sexual and mating behavior are consistent with those derived from imprinting formulations. That is, he postulates that the bird's instinctual reactions are more or less irreversibly conditioned or attached to objects early in their life and that the nature of these objects determine where and when the instinctual behavior manifests itself later. His main contribution to this more general theory is his notion of a hierarchy in the instinctual development. He believes that the animal's earliest instinctual urges are non-specific and uncanalized in nature and that only through the maturation and experience of the animal do they become more specific. As the animal develops, more or less discrete, lower order motor mechanisms appear and are released in association with environmental objects. As maturation increases these mechanisms become linked or integrated with each other to produce higher order instincts. Throughout this ascending integration,

the environmental situation or class of objects which served to set off the lower order instincts continue to be the objects capable of releasing the higher order instinctual behavior. Further, the effectiveness of the instinctual act, in terms of fulfilling the animal's biological potential, is dependent on the animal passing through the preceding hierarchical levels successfully; that is, having appropriate objects toward which the lower level instinct can be directed. It is because of this process, he believes, that we see similar objects releasing both lower and higher order instincts and lower order behaviors exhibited within the context of higher order behaviors. For example, in pigeons "billing" transpires between two adult birds who are courting as well as between the parent and its offspring during the feeding of the latter (Carpenter, 1929).

While Kortlandt conceptualizes many other aspects of behavior ascribed to instinctual motivation such as displacement, priming, etc., the importance of his theory for this paper centers on his postulation that most birds will direct their higher order instincts (such as their instinct to mate) toward objects which were used to satisfy or release lower order instincts. Thus, he would predict that the early experience of the bird would tend to set up preferences for adult mate choices.

Psychoanalysis. Although psychoanalytic theory (Fenichel, 1945; Freud, 1953) has been directed almost ex-

clusively toward explaining human behavior, its basic tenets are remarkably similar to those proposed by ethologists and by Kortlandt in particular. Thus, it would appear to offer principles worthy of consideration in the understanding of animal behavior and its development.

Psychoanalysis is a theory of hierarchical instinctual development within which partial instincts mature and function more or less independently of each other until they are integrated into larger units as a result of further maturation and experience. This process, which begins with innate, diffuse energy states, precedes in an ascending development with the result that higher order social behavior is dependent on the interaction of the organism with early environmental objects. For Freud, as for the imprinting theorists, "The finding of an object is in fact a refinding of it" (Freud, 1953, p. 222).

Kortlandt had summarized six major points of Freud's theory which are particularly applicable to the ethological approach of instinctual development. Two of the more important points are that following the maturation of lower order or subordinate instincts

> (1) . . . all these subordinate instincts become more or less irreversibly conditioned to an object ("object-finding" or "object-choosing," a process identical to "imprinting" in ethological terminology) and they find a motor outlet or goal by way of a satisfying activity. . . . Object finding in man can be paralleled to imprinting in animals. . . . Hence, the mother represents the first sexual object for the child in the same way as the parent (or foster parent) of a newly hatched gosling serves as its first sexual object (Kortlandt, 1955, p. 159).

> (2) In later phases of development (initiated by further maturation, arousal and conditioning processes) low-level instincts unite into larger wholes under the giverance (Primat) of higher level instincts. In these integrative processes the object and goal towards which a higher level instinct will be directedis for a large part built up by the characteristics of the objects and goals towards which the participating lower level instincts are directed owing to their previous development. In other words, translated into ethological terminology, the releasing sign stimulus and the consummatory act of a higher level instinct is for the most part built up by the adoption of the releasing stimuli and consummatory acts of the lower level instincts which compose them, or by a recombination of elements derived from them. The organization of behavior is so to speak built up from the bottom step by step (Kortlandt, 1955, p. 159).

Thus, psychoanalytic theory predicts that the objects (or fellow species members) through which the organism satisfies his early instinctual drives will determine its later social and sexual behavior. From this theory too, then, it may be predicted that, when grown, an animal will tend to direct his sexual or mating behavior toward objects which possess characteristics similar to those possessed by its parents.

Experimental Investigations of Sexual and Mating Behavior

While the earlier works of Whitman (1898) and Craig (1908; 1914) are consistent with the more recent theoretical approaches just discussed, they may not be considered as actual experimental investigations of sexual and mating behavior. Controlled investigations began to appear when psychologists and others began using experimental methods rather

than naturalistic observations in the study of early experience and its relationship with later behavior. Unfortunately, however, many of the experiments in this area appear to have fallen prey to just what the early ethologists cautioned against; ignoring the native aspects of the animal's world. In the words of Verplanck:

> More than once . . . a psychologist has controlled literally out of existence the necessary environmental conditions for, or necessary behavioral correlates of, behavior that he wished to experiment upon (1958, p. 102).

For the most part this criticism was directed toward such practices as prematurely inducing sexual and mating responses through the use of chemical injections. Bambridge (1962), Noble and Zitrin (1942), and Schein and Hale (1959) have all demonstrated that birds will exhibit sexual responses to "imprinted" objects prior to sexual maturity. In another type of study Guiton (1961) found that courtship responses of brown leghorn male chicks which had been imprinted tended to decrease as they grew older and concluded that imprinting, at least in this species, had only a limited effect on their later sexual behavior. In this study, however, artificial models were used as objects, a condition which certainly reduces confidence in generalizing from the results.

To the writer's knowledge the first controlled experimental study involving the effects of early experience on actual mate selection in birds was that reported by Warriner, Lemmon and Ray (1963). In this investigation pigeons were

reared under parents of their own species and color and under foster parents of a different color; that is, under the following conditions:

A. White King parents reared their own young.

B. Black King parents reared their own young.

C. and D. White King clutches were exchanged with those of the Black King pigeons so that these groups of young would have their early experience with parents who possessed characteristics different (primarily in coloration) from their own breed.

When the young birds were old enough to leave the nest they were housed in separate, isolated cages until they reached sexual maturity, at which point their mating preferences were determined. As a result of this procedure it was found that male pigeons tended, to a significant degree, to mate with females who possessed characteristics similar to their (the male's) rearing parents, whether these parents were natural or foster parents. The female birds, however, did not exhibit a similar preference. In discussing these results the following alternative explanations were offered:

> 1. In pigeons, the choice of mate may be primarily a male-dominant process or
> 2. Mate choice in female pigeons may not be a function of early experience, or
> 3. Mate choice in female pigeons may be based on early experience with parental characteristics other than colour.
>
> Direct observations of courtship and mating behaviour do not lead to an easy acceptance of the hypothesis that mate selection is exclusively a male prerogative. On more than one occasion females were noted to act in a soliciting manner toward particular males. In a number of these cases the two birds eventually mated. In addi-

> tion, in five of the six instances which did not fit the male parent-colour data, the male colour was that of the parents of the female with whom the male mated. These instances are compatible with the notion that the females of some pairs make choices and that these choices are based on parental colour. Nevertheless, the data is overwhelmingly favourable to the hypothesis that mate choice in pigeons is largely a male-dominant process (Warriner et al., 1963, pp. 223-224).

There is one methodological aspect of this study that should be mentioned, since the outcome may have been influenced by it. The mating phase of the study was carried out in four separate, successive replications. In each replication eight males and eight females were placed together in a mating pen until all had been mated. This kind of situation could have forced certain matings to occur. For instance, the first matings, either according to or contrary to the hypothesis would possibly have biased the remaining choices by altering the balance of available choices. This could have wholly determined one of the later matings, since only one male and one female would be left unmated at the end of the replication. It is possible, then, that at least four out of the total of thirty-two mateships were not determined by the rearing conditions alone.

Subsequent to the Warriner et al. (1963) study, the question regarding female mating preferences was investigated by Kerfoot (1964) who conducted another of the very few well controlled experiments which have been reported. He proposed that:

> . . . (1) Preferences for particular types of mates based

> on early experience exist in males and females, and that actual mateship may be based on the preferences of either sex, as well as on the mutual preferences of both. (2) Dominance does not determine preferences in mating, but helps to implement them, so that dominant birds of either sex are more likely to implement their preferences (Kerfoot, 1964, pp. 29-30).

He reasoned that since male pigeons are generally more dominant their preferences would tend to mask female choices whenever differences in preferences existed. This explanation of the mating process was consistent with the Warriner et al. (1963) data as well as with their finding that some females were apparently demonstrating preferences in their mating behavior.

As a way of testing this notion Kerfoot followed the general procedure employed by Warriner, et al. (1963) but controlled for male preferences by using only one female color. He reared white female pigeons under red or black foster parents to provide differential early experiences for them, but reared red and black male pigeons all under white foster parents. Thus, during the mating situation the female birds could exercise preferences by choosing males who possessed color characteristics similar to or different from their parents. Since the males in this situation only had birds to choose from which resembled their parents, male preferences did not conflict with and thereby obscure choices based on preference by females. Kerfoot also met the earlier mentioned criticism of the Warriner, et al. design by using an open ended mating situation wherein each mated pair was

replaced by appropriate subjects as soon as three mateships had been completed. Thus, his replications were continuous rather than successive, a procedure which eliminated "forced" choices.

The results of this study clearly indicated that females tended to mate with males who were the same color as the female's parents. The secondary proposition, that dominance helps implement preferences, however, was only partially supported by the data.

In summary, then, there is now experimental evidence indicating that both male and female pigeons tend to mate with birds who possess characteristics similar to those of their rearing parents, with parental color appearing to be the primary determining factor. It would also seem apparent that mating is a male dominant process.

Differential Parental Effects on Mate Choice

In both the Warriner, Lemmon and Ray (1963) and Kerfoot (1964) studies, the male and female young were exposed to only one parental color in their respective rearing conditions. Thus, it could not be determined whether one sexed parent rather than the other exerted a more important effect on later mate choice of the offspring. Since many investigators (Bennett, 1939; Carpenter, 1929; Craig, 1908; Nice, 1943; Tinbergen, 1953) report that birds are capable of individual and sexual recognition, and since such recognition has been

linked with sexual behavior (Nice, 1943), the question of differential influences (between parents) on mating behavior seems worthy of consideration.

Of the three theories discussed in this paper only psychoanalysis (Freud, 1953) considers principles concerning differential influences by mother and father. Unfortunately, the psychoanalytic principles underlying sexual identification and differential effects of parental behavior on the young do not seem applicable to the study of birds for a number of reasons; one being that developmental studies in this specific area are lacking. In addition, the human's capacity for symbolization and conceptualization so far surpasses the bird's that generalization from one species to the other in such a specific area does not seem warranted considering our present state of knowledge.

The ethological theories do not contain principles which would lead to any specific predictions, although observational data do lead to the speculation that differential effects might exist.

Sexual recognition. In many animals the male of the species possesses more elaborate and colorful plumage than the female (Burton, 1953; Scott, 1958) and this difference in color is thought to play a part in individual and sexual recognition. Carpenter (1929) and Abbott (1941) have suggested that birds are capable of sexual recognition at a distance and by sight alone. This position would seem to imply that sexual

recognition is acquired during the early experience of the animal, perhaps through the differential general or rearing behavior of the parents. Carpenter (1929) has reported, for instance, the male pigeon is more easily driven off the nest but that, as the brooding cycle progresses, he becomes more "fatherly," and that after hatching he carries most of the rearing burden. Craig reported similar observations, noting that the " . . . mother becomes unwilling to feed long before the father . . . this difference in behavior leads the young to distinguish between the two parents and thus adds to their knowledge of individuality" (Craig, 1908, p. 90).

On the other hand, such investigators as Whitman (1898), Craig (1908), Tinbergen (1953), and Allen (1954) have concluded that sexual recognition is dependent on each bird's behavioral response to the other's sexual or aggressive advances, especially when the male and female of the species are alike in appearance. If this is true then it would seem less likely that sexual recognition as such is acquired early in the bird's experience, i.e., before the maturation of the more specific sexual instincts. Thus, prediction of differential effects on the young could not plausibly be based on the idea that the young could distinguish between sexes as such or that differential response to parents would be based on instinctual sexual drives not yet matured.

Purpose of the Present Investigation

The present study was designed to investigate whether one sexed parent is more influential in determining the later mate choice of the offspring. Since it has been reported that parental color seems to be the single, most important factor determining mate choice (Kerfoot, 1964), color was used as the independent variable. Following the general procedure utilized by Warriner et al. (1963) and Kerfoot (1964) domestic pigeons were used as subjects. By cross-fostering eggs, the male young were hatched and reared by foster parents who had been previously mated so that their own coloration was dissimilar, but who were similar in other important characteristics such as size and general configuration. It was concluded that such rearing conditions would produce one of three outcomes in later mating behavior of the offspring: 1) the first possibility was that the young might be equally influenced by each parent and thus tend to mate with birds possessing either the mother's or father's color characteristic. 2) One sexed parent might influence the young to mate with birds possessing its particular color. Or, 3) in breeds such as the ones used in this experiment, the male and female parents normally show the same color. It is possible that rearing them under the experimental conditions when parental colors differ would produce an "unnatural" situation which would

disrupt and disorganize the normal imprinting process and thus void any demonstrable preferences in mate selection.

Since both Kerfoot (1964) and Warriner et al. (1963) appear to agree that mate selection in domestic pigeons is largely a male dominant process, males will serve as primary experimental subjects with the coloration of their potential mates being varied to provide a test of mate preference.

CHAPTER II

PROBLEM

A review of the literature has revealed observational evidence that much of the social and sexual behavior of birds is determined by the early experience of these animals. In the two experimental investigations of this problem (Warriner, Lemmon & Ray, 1963; Kerfoot, 1964) it was found that both male and female pigeons respectively tended to mate with birds whose physical characteristics resembled those of their rearing parents.

In the Warriner, et al. (1963) and Kerfoot (1964) studies, the fact that both parents in a pair were of the same color prevented a determination as to whether one or the other parent was a more important influence in determining their offspring's choice of a mate. The purpose of the present investigation was to determine whether parents function as a unit or individually in their influence on the later mate choice of their young. This goal was accomplished by rearing male pigeons under conditions where the male and female parents differed in coloration. Briefly, red male birds

were reared under one black and one white parent (color and sex being counterbalanced) and then allowed to choose mates from a group of females who resembled either their father or mother or neither of these (i.e., birds of a third color).

These conditions permitted one of three alternative outcomes:

(1) The experimental birds could avoid mating with birds of the third color and choose mates of colors like either parent but not exclusively that of the parent of one sex. This finding would be consistent with the theory that while neither the male nor the female parent plays a more significant role, the presence of these two colors opens up both of these possibilities as alternate mate choices.

If the parents have equal influence there would be no significant difference in matings with birds whose color is like either parent, but there would be significantly fewer matings with birds whose color was different from either parent.

(2) On the other hand, it was possible that one parent or the other would be dominant as an influence on later mate choice of the young. That is, the male parent might play a more significant role in determining the offspring's choice than does the female parent--or vice versa. While there is no theory of animal behavior which would specifically predict this outcome, observational evidence regarding the bird's capacity for sexual and individual recognition generally tends

to support such a possibility.

For this hypothesis to be supported the data would have to show a significantly greater number of matings with females whose color was like that of the parents of a particular sex.

(3) Finally, it was possible that birds reared by parents who differ in color might not select mates in any systematic fashion but rather would tend to select mates indiscriminately. This prediction would be consistent with Thorpe's hypothesis that mating and social reaction patterns may be disrupted under circumstances where the usual, consistent imprinting objects are not available (Thorpe, 1951). Since the pigeons imprinting reaction patterns are normally with similar colored parents or "imprinting objects," it was possible that sexually dimorphic (i.e., dissimilar colored) parents used in the present study might bring about such disrupted orientation. Thus, the young bird, in attempting to attend to two different simulus objects, could not establish a sufficiently stable imprinting "image" to use either of them as a model object for their later mating choice. Thus, during a mating situation, any colored pigeon might suffice as an object.

With this hypothesis matings would not be expected to be greater with females of colors like either parent and thus would be distributed in all three categories to an extent not significantly different from chance.

CHAPTER III

METHOD

The objective of this study was to examine the influence of parental color characteristics on the mating behavior of male pigeons reared under parents who differed in color. In order to meet the aims of this experiment, three breeds of pigeons with different coloration were employed. Red Carneaux, Black King and White King pigeons were used. These birds are essentially of the same body configuration and size, but are different in coloration.

In order to control for the possibility of a genetically based mate choice on the part of the young, a design was employed wherein the male subjects were cross-fostered and reared under male and female parents of a different breed and color. That is, Red Carneaux young were reared by parents made up of White King males paired with Black King females and Black King males paired with White King females. By rearing half of these subjects under each combination of parents any innate color or breed preferences the subjects might have as a group could be determined in-

dependently of the "imprinting" effects by sex of parent.

Finally, it seemed possible that the choices of the subjects might be masked if, during the mating or test condition, one or more females was individually unacceptable as a mate. That is, her color might be suitable as far as any male subject was concerned, while other characteristics were not and as a result she would not be selected. In order to control for such a possible contamination of the data, it was decided that any female who had not been selected as a mate after being in the mating pen for two weeks would be replaced by another female of the appropriate type.

Experimental design. The male experimental birds in this investigation were all Red Carneaux pigeons. The rearing conditions of these birds were varied by fostering them under parent birds of White King and Black King breeds. Half of the male birds were hatched and reared by White King male - Black King female parents (Condition Wb) and half by Black King male - White King female parents (Condition Bw).

At maturity the males reared under each of these conditions were placed in a mating cage in which an equal number of White King, Black King and Red Carneaux females were available.

The data of the experiment are the frequency with which the male birds mated with females of a particular color characteristic (i.e., like father, like mother, or like neither).

Subjects and rearing conditions. Fourteen pair of Red

Carneaux were used to provide eggs to obtain the 12 male offsprings, who served as the experimental birds. The female offspring from this stock, along with 25 other females, the offspring of 10 pair of Black King and 20 pair of White King pigeons, constituted the potential mates for the experimental males in the test condition.

The foster parents used to rear the experimental males were 16 pair of mixed Black King and White King pigeons. These mixed pairs were obtained, in part, as a by-product of a previous experiment wherein the individual bird's early experience facilitated such pairings.

The Black and White King females were reared by their natural parents, while the Red Carneaux females were reared in the same manner as the experimental males, since sex could not be determined until maturity. That is, they were reared by the mixed parents. Since the eggs of these parents were not used in the experiment, they were discarded.

In order to avoid bias which might be due to female preferences, all female birds were reared by Black, White, or mixed Black and White parents, irrespective of their own color, so that none were reared by Red parents. Thus, parent coloration was never like that of their prospective mates. The rearing or parental conditions of the males consisted of the following:

Condition Wb: Ten Red Carneaux males reared by White male and Black female parents.

Condition Bw: Ten Red Carneaux males reared by Black male and White female parents.

Procedure. Each pair of the previously mated (mixed King) parents were placed in individual 30" X 36" X 30" wire cages which were constructed so that their adopted young did not have visual contact with any but the appropriately colored parental birds (in addition, of course, to their siblings). Each of these cages contained a double nest box containing straw nesting material, along with water containers and standard mixtures of feed and grit.

It has been demonstrated that efficient rearing of adopted eggs and young is contingent on the adopted eggs (usually two per clutch) being approximately the same age as the foster parent's own clutch (Levi, 1957; Warriner, 1960). Thus, the switching of the clutches of eggs was accomplished during that period when eggs of the two sets of parents did not differ more than two or three days in age. At the appropriate time the eggs of the Red Carneaux parents were switched to the nests of the foster parents so that half would be reared under Condition Wb and half under Condition Bw. These eggs were allowed to hatch and the squabs were reared by foster parents until they were mature enough to be separated from them (approximately 30 to 40 days). Warriner, et al. (1963) and Kerfoot (1964) found this to be sufficient exposure to the foster parents for the later mate choices to be influenced by them. During this time these

birds were banded for later identification of the condition under which they were reared.

When the birds were taken from the nests they were placed in isolation cages in order to eliminate visual experiences with other birds. These cages were 20" X 20" X 20" in size and were equipped with two one-pound coffee cans for feed and water and a smaller container which held grit. The young were kept in these cages until they reached sexual maturity at four to six months (Levi, 1957). As soon as possible during this time an attempt was made to determine the sex of the birds, following the procedure outlined by Warriner (1960). When a sufficient number of males from each condition were mature they were placed in a mating pen with equal numbers of Red Carneaux, White King and Black King females for the test condition.

As previously stated, Black King and White King parents reared their own young. These young were placed in the individual wire cages described above sometime between the ages of 40 and 60 days in order to prevent the females, which were to be used, from having mating experiences prior to the test condition.

Test condition. As has been described, the investigation of mate selections was begun when enough birds or each type were available. While it was originally felt that the ideal male-female ratio in this situation would be two males from each condition and three females of each color, pre-

liminary work suggested that mating behavior proceeded very slowly under this kind of condition. Mating activity appeared to increase when a smaller number of birds were used. Thus, while it was not possible to have an equal number of males from each of the rearing conditions in the mating pen at the same time, a balanced number of males from each condition was used over successive replications.

The replications were begun when ten males reared under Condition Bw, eight males reared under Condition Wb, thirteen White females, twenty Red females and five Black females had reached sexual maturity. At this time three Red males (2 from Condition Bw and 1 from Wb) and two each of the White, Black and Red females were placed in a mating pen where their pairings were observed and recorded.

Mating criteria have been established through earlier studies (Carpenter, 1929; Kerfoot, 1964; Warriner, 1963). These include billing, calling to one another, frequent copulation, occupying the same nest box or territory and nest building. A mating was considered established in the present study when at least three of these signs were observed.

The mating pen measured 8' X 10' X 9'. It was equipped with feed, water, grit, and four wooden nest boxes and nesting material. Two of the nest boxes were placed three feet off the ground and two were left on the ground.

When it was established that one of the males had mated, he and his mate were removed from the pen and replaced by a

male and female of the appropriate types. This procedure allowed each of the males to have access to a balanced sample of females with whom to mate.

Although the original plan of the investigation had called for 20 subjects (10 males reared under each Condition), after the ninth mating it was evident that there were too few Black females generally and too few Red males from Condition Wb to meet this requirement, that is, unless another period of months were to be spent in rearing young. Thus, it was decided to analyze the available data after the twelfth mating and to determine how many more subjects would be needed in order to more firmly substantiate these results. Since the results of this analysis suggested that almost five years would have to be spent in order to rear enough pigeons at the existing rate to alter the significance levels, it seemed justifiable to terminate the experiment after 12 matings.

CHAPTER IV

RESULTS

An analysis of the data accumulated via the procedure described in the last Chapter was carried out when the twelfth mating had been established.

The results of the twelve pairings are presented in Table 1 below:

Table 1

Mates Selected

Color of female mated		
Like male parent	Like female parent	Other (Red)
7	5	0

It can be seen that all the subjects chose mates whose color characteristics were like those of one or the other of their parents. Since no bird selected a Red Carneaux for a mate, and the choices between parent color were about even, Hypothesis I is supported: Under the conditions of the experiment male pigeons tend to choose mates whose color characteristics resemble those of either of their parents.

In order to examine Hypothesis II, wherein it was predicted that one parent or the other would play a dominant role in influencing the offspring's choice of mate, the totals under each parental color were examined. The results of such a comparison indicates that 5 or 42% of the subjects chose mates whose color characteristics resembled those of their female parent while 7 or 58% selected mates whose coloring resembled their male parent. By consulting the Table of Cumulative Binomial Probabilities (Walker & Lev, 1953, p. 458) it can be seen that, under the hypothesis P = .5, the probability that p = .42 is well within the region of acceptance. Thus, with 12 subjects there is no evidence to suggest that either parent exerts a significantly dominant influence on the choice of mate of their young.

In order to estimate how many subjects would be needed to attain statistical significance if the proportions already accumulated were maintained an approximation of the normal to the binomial distribution was used, solving for N rather than z. Formula (3.1) as presented by Walker and Lev (1953, p. 67) with $z = 1.06$ $p = .42$ and $P = .50$ was utilized. This formula yields an N of 152.63. Thus, the proportions obtained with 12 pairings suggests that it would require 153 subjects to establish a statistically significant differential parental effect. Since it would require approximately five years to rear this many subjects and since the data accumulated through 10 pairings indicated that the proportion actually

might tend to stabilize around a p of .50 (with an N of 10 p was equal to .50), it was judged to be not worthy of expending more time and subjects. Therefore, the existing proportions were taken at face value, as indicating no statistically significant differential parental effects.

Secondary Findings

Although it was not expected, another trend is apparent in the data. It appears that White King females were mated more frequently than the other two breeds.

Table 2 presents the frequencies with which male subjects from the two rearing conditions mated with females of the two colors.

Table 2

Mating Patterns

Rearing Condition of Males	Color of Female	
	White	Black
Wb	5	2
Bw	4	1
Totals	9	3

It may be noted that the frequencies in cells are not significantly disproportionate, thus, there is no interaction between rearing condition of males and color of females, per se. However, the marginal totals reveal that 9 White females

were mated while only 3 Black females were mated. The Cumulative Probabilities Table (Walker & Lev, 1953, p. 458) indicates that these values may be expected to occur with a probability of .146. While this difference is thereby not significant, with a slightly greater number of subjects it could readily become significant. Therefore, it may be of practical importance in planning future experiments with these breeds. These particular results appear to be related to the already noted finding regarding the lack of availability of Black female subjects and will be discussed in the following section.

In summary then, with a limited, but apparently sufficient number of subjects, the Red Carneaux males consistently selected mates whose coloration was similar to those of their parents, though neither the male nor female parent color was preferred. In addition, the subjects tended to select White females as mates more often than any other color.

CHAPTER V

DISCUSSION

The results of this investigation lead to several conclusions. Consistent with the earlier studies reported by Warriner, et al. (1963) and Kerfoot (1964), the present data support the hypothesis that the domestic male pigeon tends to mate with females who possess color characteristics similar to those of his rearing parents. In addition, the present study shows that neither sexed parent exerts a differential effect on the mate choices of the offspring. It also seems clear, as it was in the earlier studies, that there is no significant influence exerted on these choices by early experience with the siblings in the nest.

The findings suggest that the mate choice is not genetically determined but rather that early experience with parents, or foster parents, may serve the function of providing the first object for instinctual drives and thus largely determine the direction toward which drives will be expressed when the birds are mature. It appears, then, that the young pigeon can use either or perhaps even both parents

as a model for later mate choice, and that, having parents of differing coloration does not tend to disrupt the imprinting process as Thorpe's hypothesis (1951) suggests it might.

It should be noted, of course, that this conclusion is based on the conditions of this experiment and on the data of the subjects as a group. It is possible that both the male and female parent served as model objects. That is, the subjects were imprinted to Black and White colors so that, during the mating trials, birds of either color were "appropriate" objects for the mating instinct.

There is an alternative possibility, however. The results do not indicate whether the choice of a mate of any particular bird was, in fact, equally influenced by both parents. Thus, the data is also consistent with the interpretation that the young selected one or the other parent as his particular model. That is, individual birds might have been imprinted to one parent or the other, but not both. The data of the present study does not provide evidence supporting one or the other of these alternatives. Further research is needed to determine which of these alternatives is true, or whether both might obtain.

In addition, the original attachment may have been on some basis other than color or sex. If this were the case the subjects would still select mates who were Black or White because color was a readily identifiable associated characteristic. That is, characteristics of rearing parents other than

color and sex such as feeding and care (functions not provided by siblings) could have been the original basis for attachment in the nest, while color was an identifiable secondary characteristic of parents which influenced the later mating choice of the subject.

Sexual Recognition vs. Mate Choice

Since coloration was used as the independent variable which has been shown to be important in mate selection, it might seem that physical appearance alone is involved in sexual identification and recognition. However, Whitman (1898), Craig (1908), Allen (1934), Tinbergen (1953), and Nice (1943) hold that sexual recognition is highly dependent on behavioral cues arising within the context of courting behavior. This is especially true in species such as were used in the present investigation, where the male and female do not differ in plumage.

Observations made during the mating trials of this study do not appear to contradict such a position. It was during this time, it may be recalled, that the sexually mature pigeons had their first opportunity to interact with each other. When the first birds were placed in the mating pen, their exploratory and other activities could be observed with relative clarity. Initially, their activity seemed to be directed toward certain goals: Particularly the male birds appeared to spend much of their time establishing a territory

and, in conjunction with this, made aggressive advances toward most of the other birds. Those birds which the author knew to be male characteristically responded aggressively to these gestures while the females either took flight or, less often, presented themselves for copulation. That is, the female birds reacted either with receptiveness or flight. It appeared quite possible that this enabled each bird to determine the sex of each of the birds with which they came into contact and that this identification and recognition process was dependent on behavior cues. Thus, while sexual discrimination may have been based on behavioral cues the actual selection of a particular mate can still be regarded as a function of early experience.

Secondary Results

As was mentioned in the preceding chapter, the fact that males from both rearing conditions demonstrated a trend toward mating with White female birds was an unexpected finding. Two explanations for this phenomenon seem plausible. First, despite attempts to prevent it, some non-experimental White King pigeons managed to enter the isolation area and thus may have been seen by some of the experimental birds prior to their maturity. It is possible that these experiences had some enhancing effect on the squabs relationship with White coloration. That is, it may have briefly presented the young with another White object model, reinforc-

ing the effect of the original White parent.

Secondly, observations of the females in the mating situation strongly suggested that Black females were more elusive than their White King counterparts. The behavior of the Red females is difficult to characterize in this respect, since they were largely ignored by the males in the mating situation. In response to aggressive male gestures, the Black females most often "scattered," flying to and perching on the wire enclosing the pen or on beams near the ceiling. This left them less available as potential mates. The White females, on the other hand, spent more time on the ground where most courting took place. In addition, the White females were sometimes observed soliciting the attention of the males while the Blacks were not.

These observations appeared consistent with those of Warriner, et al. who stated that: "On more than one occasion females were noted to act in a soliciting manner toward particular males. In a number of these cases the two birds eventually mated" (1963, p. 224). In the present study such was the case on at least two occasions. In addition, it was observed that other females were occasionally found on or in a nest box in an apparent attempt to share a territory with a male or otherwise provoke a mateship. It is possible, therefore, that White females were mated more frequently than Blacks due to their greater accessibility during the mating trials.

It is possible, of course, that both of these factors contributed to the prevalence of White matings. In any case, this prevalence does not appear to be due to a breed preference on the part of the male subjects. This possibility had been considered in planning the study and as a result a counterbalancing of parental color characteristics through the Wb and Bw rearing conditions was employed.

Observations Regarding Black King Females

As mentioned earlier, this study had to be terminated after 12 matings, in part because an insufficient number of Black females were available. This was due to the fact that the Black King parents produced proportionately fewer offspring than either the White King or Red Carneaux stock. Further, the lack of Black females seemed to be a result, in part, of an unexpected male-female ratio among the birds produced by the Black King parents. The Black King parents appeared to produce fewer eggs and more infertile eggs and possibly the young that did hatch did not survive as well in the nest, perhaps due to inadequate care. Any or all of these factors may have contributed to the lack of Black females. They all, of course, appear to be related to the reproductive-parental functions of the Black King breed.

In this connection,it is interesting to note that a paucity of males reared under Condition Wb (White King males and Black King females) was the next most critical factor in

terminating the experiment after 12 pairings. Any or all of the factors mentioned as possibly contributing to the lack of Black females may have also functioned to reduce the number of male subjects reared under Condition Wb. It was also clear throughout the rearing period that Wb parents consistently produced fewer eggs than their Bw counterparts. Since it was necessary for own eggs to be present before other eggs could be cross-fostered, this fact limited cross-fostering under Wb parents which, in turn, limited the number of Wb cross-fostered males available to fulfill the needs of the experimental design.

It would appear, then, that the lack of Black females in this investigation may have been a result of some kind of factor in the Black King constitutional make-up which affects their egg laying potential. This explanation is consistent with the results of an earlier study by Oakes (1964), who, while replicating portions of the study reported by Warriner, et al. (1963), found it necessary to change her procedure during the latter part of her investigation because of an unexpected lack of Black King females. As a matter of fact, some of the Black King - White King mateships produced in her study served as Condition Wb parents for the present investigation.

It is possible that the "elusiveness" of the Black King females during mating trials, the relatively reduced egg laying, and the greater infertility of eggs, are sub-

components of a more general constitutional factor affecting the entire reproductive cycle in the Black King female. The observations of this investigation suggest that this aspect of this breed should be taken into consideration in future research.

Conclusions

(1) The findings of this investigation are consistent with the results reported by Warriner, et al. (1963) and Kerfoot (1964) who found that pigeons of both sexes tend to establish mateships with pigeons who possess color characteristics resembling those of their rearing parents and that the choice of mate appears to be a male dominant process. The results of the present study suggest that, in males, this phenomenon also obtains when the rearing parents differ in coloration, and that either or both parents appear to have equal influence on the choice of mates by their offspring.

(2) Observational evidence in this study does not appear to contradict the work of Whitman (1898), Craig (1908) and others who have theorized that sexual recognition is primarily based on behavioral responses and reactions to these responses rather than on non-behaviorally based cues.

(3) The prevalence of White matings in this study appeared to be due to the fact that the White King females were more accessible during the mating trials.

(4) Finally, the observational data of this study

suggest the possibility that there was some kind of constitutional factor present in the Black King females used which limited their reproductive-parental functions, compared with the other breeds used. Thus, it would perhaps behoove researchers to consider these factors before using this breed in experimental work similar to the one reported here.

CHAPTER VI

SUMMARY

A review of the literature reporting observations concerning the social behavior of birds has indicated that a great deal of the social and sexual behavior of these animals is contingent upon critical events occuring during their early experience. Various theoretical systems, most notably those of Ethology and Psychoanalysis, provide a basis for interpreting this behavior via the animal's instinctual drives and the early stimulus objects with which they interact. In particular, experimentation has established that parental color plays a significant role in determining mate choices in domestic pigeons.

In previous studies all of the parental birds utilized were of the same color so that no determination could be made regarding a possible differential parental effect on mating choices of offspring. The present experiment was designed to investigate the differential effect of parents which were dimorphic in coloration on their male offspring's selection of a mate. This was accomplished by rearing Red Carneaux

male pigeons under mixed Black and White King parents and then providing a situation wherein they would select a mate from a group of Red Carneaux, Black King and White King females.

With a limited, but apparently sufficient, number of subjects, the results of the study confirmed earlier findings in that these subjects tended, to a significant degree, to select mates whose coloration resembled either their male or female parent's color. Neither sexed parent appeared to play a significantly dominant role in this phenomenon.

Secondary findings of this study tended to suggest that the subjects, more often than not, mated with White birds. This result appeared to be influenced by the fact that White birds were more accessible during the mating trials.

Finally, observational data was discussed in terms of its consistency with earlier works regarding sexual recognition, and the inadequacy of the reproductive-parental functions of the Black females utilized in this investigation were noted.

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Table 3

Raw Data for Red Carneaux Males

Band Number	Date of Birth	Date of Mating	Rearing Condition	Color of Mate Selected
R2	3-30-64	12-4-64	Bw	White
R10	5-30-64	1-16-65	Bw	White
7	7-14-64	1-19-65	Bw	White
27	5-31-64	1-23-65	Bw	Black
731	3-30-64	1-26-65	Wb	White
11	8-2-64	1-28-65	Wb	Black
743	5-5-64	1-31-65	Wb	White
35	8-8-64	2-7-65	Wb	White
735	4-12-64	2-13-65	Wb	White
729	3-30-64	2-16-65	Bw	White
762	6-4-64	2-17-65	Bw	Black
748	5-5-64	3-6-65	Wb	White

THE UNIVERSITY OF OKLAHOMA

The Graduate College

Final Examination

of

JAMES A. MOORE

B.A., Butler University, 1955

M.S., University of Oklahoma, 1963

For the Degree of

DOCTOR OF PHILOSOPHY

Wednesday, July 7, 1965, 2:30 p.m.

Room 108, Psychological Clinic

Committee in Charge:

Adjunct Assistant Professor Thomas S. Ray, Chairman
Professor William B. Lemmon
Assistant Professor Arnold E. Dahlke
Assistant Professor William W. Trousdale
Assistant Professor Kenneth R. Merrill

OUTLINE OF STUDIES

Major Subject: Psychology

Adult Test; Child Testing; Clinical Diagnosis; History of Psychology; Systematic Psychology; Projective Techniques, Seminar in Abnormal Psychology; Intermediate Statistics; Social Psychology; Perception and Thinking; Research Methods in Psychology; Learning; Diagnostic Practicum; Therapeutic Practicum; Energetics; Psychotherapeutic Methods; Modern Learning Theory; Advanced Psychological Statistics; Experimental Psychodynamics; Experimental Psychopathology; Seminar in Social Psychology; Selected Problems in Motivation; Contemporary Problems in Psychology; Seminar in Psychoanalytic Theory; Clinical Internship

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DISSERTATION

THE EFFECT OF DIMORPHIC PARENTS ON MATE SELECTION IN PIGEONS

A review of the literature reporting observations concerning the social behavior of birds has indicated that a great deal of the direction of social and sexual behavior of these animals is contingent upon critical events occuring during their early experience. Various theoretical systems, most notably those of Ethology and Psychoanalysis, provide a basis for interpreting this behavior via the animal's instinctual drives and the early stimulus objects with which they interact. In particular, it has been established that both male and female pigeons tend to mate with birds whose coloration resembles that of their parents.

In previous studies, the parent birds utilized were of the same color so that no determination could be made regarding a possible differential parental effect on mating choices of offspring. The present experiment was designed to investigate the differential effect of parents which were dimorphic in coloration on their male offspring's selection of a mate.

This was accomplished by rearing male Red Carneaux pigeons under mixed Black and White King foster parents. Six males were reared, from birth, under parents consisting of White King males and Black King females (condition Wb). Six other males were reared by Black King males and White King females (condition Bw). Between 30 and 40 days of age the subjects were removed from the parents and placed in isolation cages until they reached sexual maturity. At maturity the subjects were placed in a mating cage where Red Carneaux, White King, and Black King females, who had had no previous sexual or significant visual experience with Red birds, were available.

All male subjects selected mates whose coloration resembled that of one of his foster parents, i.e., either white or black. Five subjects mated with birds whose color resembled that of their female parent while seven mated with birds whose coloration resembled that of their male parent. None mated with own or sibling color, i.e., red. Thus, while either or both parents appear to influence mating choices of their foster young, neither appears to have a greater influence.

Secondary findings were that White King females were mated most often. This result appeared to be influenced by the behavior of the White females which made them more accessible during the mating trials. Further, it was noted that the Black King pigeons, females in particular, may have been less adequate in their reproductive-parental functions compared to the Red Carneaux and White King breeds.

Finally, the behavior of the birds during the mating trials seemed congruent with the conclusions of Whitman in 1898 and Craig in 1908 that sexual recognition in birds is highly dependent on behavioral cues.