KERFOOT, Eugene M., 1931-
SOME ASPECTS OF MATE SELECTION IN
DOMESTIC PIGEONS.

The University of Oklahoma, Ph.D., 1964
Psychology, general

University Microfilms, Inc., Ann Arbor, Michigan

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

SOME ASPECTS OF MATE SELECTION IN DOMESTIC PIGEONS

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

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Norman, Oklahoma

1964

SOME ASPECTS OF MATE SELECTION IN DOMESTIC PIGEONS

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ACKNOWLEDGMENTS

The author wishes to express his thanks to Dr. Theodore S. Baumberger, Dr. Arnold E. Dahlke, and Dr. William Horosz, for serving as dissertation committee members, to Dr. Clell C. Warriner, for his advice and help throughout the preparation of this work and for serving as a committee member, to the dissertation director, Dr. William B. Lemmon, without whose assistance this study could not have been carried out, to Dr. Thomas S. Ray, for his critical reading of the manuscript, to Mr. and Mrs. Paul Oakes, for their aid in rearing and maintaining the experimental subjects, and to my wife, Patricia, who helped in many ways.

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CHAPTER I

INTRODUCTION

A strictly biological or genetic view of animal behavior would imply that mate choice follows genetic lines, and that experience plays no part in the process. However, in some animals at least, mate selection is not so simply explained. In birds, for example, diverse phenomena--including territoriality, parent-young bonds, display and courtship practices, and dominance relationships--have been found to be related to this subject. The present paper is concerned with mating behavior in altricial, monogamous birds, and deals specifically with the problem of mate choice in domestic pigeons.

Historical Background

Naturalistic observations of birds have been recorded for hundreds of years. However, scientific and experimental studies of mating and other social behaviors date only from the latter years of the 19th century.

Whitman (1898) was among the first experimentalists to write about the origins of social behavior in animals, and he was almost certainly the first to study mate selection in pigeons. Whitman took the position that instinctive behavior in animals is adaptive:

> The clock-like regularity and inflexibility of instinct, like the once popular notion of the "fixity" of species, have been greatly exaggerated. They imply nothing more than a low degree of variability under normal conditions. Discrimination and choice cannot be wholly excluded in every degree, even in the most rigid uniformity of instinctive action. Close study and experiment with the most machine-like instincts always reveal some degree of adaptability to new conditions (1898, p. 331).

Sensory stimuli from the environment constitute in part the "new conditions" to which instincts adapt, and in Whitman's view, adaptability leads to intelligence by allowing experience to play a part in the organization of behavior. "Plasticity of instinct is not intelligence, but it is the open door through which the great educator, experience, comes in and works every wonder of intelligence" (1898, p. 338). These ideas led Whitman to assert that species preferences in pigeons are not automatic and inflexible, but, ". . . are to a large extent acquired and are functions of the social environment in which the birds were reared" (Whitman, 1919b, p. 98). More specifically, he suggested that birds of one species that are hatched and reared by another species are apt to mate with birds of the rearing species when grown (Whitman, 1919a).

In an early monograph, Craig extended Whitman's views by proposing that physical and behavioral attributes of rearing parents influence species preference in pigeons: "For example, the parents exhibit to the young the body-form, colors, gestures, and sounds characteristic of the species and thus the young learn to recognize their kind . . ." (1908, p. 89).

Craig also felt that mate selection is not an innate process and that it is the early exposure to salient parental characteristics that tends to direct the selection process:

> . . . 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 (1908, p. 90).

Craig (1914) later theorized that while sexual behavioral reactions in pigeons are provided by the innate nervous system, the sensory inlets that mediate the behavior are determined or supplemented by experience. This view also represented an extension of Whitman's thinking, and is an important historical link to the theory of behavior later developed by Lorenz.

Recognition in Birds

The important role ascribed to sensory process by Whitman and Craig has been validated and supplemented by subsequent literature concerned both with the determinants of recognition in birds and the part played by these processes in social behavior. For example, extensive work has established that visual acuity and sensitivity to color are faculties which are almost as well developed in birds as they are in man (Hamilton and Coleman, 1933; Lashley, 1916).

Color as a cue. Although other sensory modalities, principally audition, have been shown to be involved in recognition, color unquestionably is one of the most effective recognition cues (Collias, 1952; Craig, 1908; Levi, 1957; Lorenz, 1937; Noble, Wurm and Schmidt, 1938; Ramsay, 1951; Tinbergen, 1951). In Scott's words: "The many studies of bird behavior lead us to conclude that the world of a bird is predominantly a visual one . . . . The bright colors and conspicuous markings of . . . birds are related to their predominant response to visual stimuli" (1958, p. 147). In dimorphic birds, color also functions as a cue distinguishing sex (Marler, 1955).

Recognition and mate selection. Recognition as determined by color also has been related to mate selection. According to Nice, "The problem of pair formation is primarily that of recognition . . . specific and sexual," and she quotes Abbott (1941) as saying: "Courtship may be defined as an elaborate sexual response involving recognition, selection, and pursuit . . . . Courtship is . . . an almost exclusive visual process" (Nice, 1943, p. 192).

Cues of mate selection in pigeons. Carpenter (1929) has noted that various behaviors in pigeons are peculiar to sex, such as "charging" and "turning" in males. Based on extensive observations of differential behavior in males and females, he concluded that sex recognition can be determined by pigeons on the basis of sight alone. Noble et al. also have argued that behavior determines sex recognition. These authors assert: "Male pigeons recognize females by their behavior . . ." (1938, p. 23). It is generally agreed that such behavioral cues also are important for mate selection (Bennett, 1939; Craig, 1908; Peeters, 1962). In this connection, Carpenter cites both behavior and color: "It is suggested that coloring . . . and general demeanor have effect in the mating process of selection" (1929, p. 24).

Early Social Experience in Birds

Heinroth (1910) seems to have been the first to draw attention to the importance of the early social contacts of hatchlings and to observe that hand-reared birds direct sexual responses to humans. Craig (1914) shortly afterwards noted the same phenomenon in ring doves. It since has been recognized that hand-reared birds of many species make sexual responses to human caretakers and to a variety of other "objects" experienced early in life (Fisher and Hale, 1957; Lorenz, 1937; Schein and Hale, 1959; Thorpe, 1956; Tinbergen, 1951).

So, recognition and mateship in pigeons appear to be influenced by behavioral attributes and color cues. These factors, although biologically based, cannot be thought to operate in a purely mechanistic fashion, since experience--notably early experience--persistently has been found to influence adult sexual activity also.

Theoretical Approaches to Mateship Behavior

Several theoretical formulations appear to be capable of incorporating the kinds of observations and empirical findings thus far outlined and of generating testable propositions concerning the bases of mate selection in birds.

Imprinting. Lorenz (1937) introduced the concept of imprinting (pragung) in birds. He described imprinting as a process that involves the rapid acquisition of the characteristics of the parent or foster-parent by hatchlings. This process occurs during a definite period of time very early in life, and it is ordinarily of short duration. Lorenz suggested that its effects are durable, if not irreversible. Hess has summarized the concept and its effects in more general terms: "In a broad sense, imprinting refers to an early experience that has a profound influence on the later adult social and sexual behavior of an animal with respect to the choice of objects for these behaviors" (1962, p. 225).

Lorenz utilized a physiological model of behavior in order to explain how imprinting works. He indicated that the energy for particular actions is produced continuously within the central nervous system. This energy is held in check by inhibitory mechanisms until an appropriate stimulus appears to release it to the proper muscular system. He proposed the construct "innate perceptory pattern" as an organismic variable and suggested that in relation to this kind of pattern, instinctive behavior is evoked by certain classes of stimuli, termed "releasers." Lorenz felt that innate perceptory patterns have varying degrees of specificity:

> . . . with very many species it is practically impossible to direct experimentally the social reactions of the young to any but the normal object, because their innate perceptory patterns are so highly differentiated as to prevent the successful "faking" of the corresponding sets of stimuli (1937, p. 267).

In other species, innate perceptory patterns are rudimentary in nature.

> . . . we know of species whose innate perceptory patterns are so reduced as to form but a very rough and sketchy outline of the companion, which under the conditions of an experiment, may become filled out by a very different object (1937, p. 268).

The relationship of the releaser concept to imprinting also is fundamental. Hess, for example, has said that imprinting basically involves "selection and strengthening of one releaser out of a large range of potential releasers, with the result that only this releaser is responded to and not any of the others" (1962, p. 187). Various stimuli can function as releasers, and color has been specified as one of the most important of these: "Most of the bright colors . . . which we meet with in the bird world, actually function as releasers of social reactions" (Lorenz, 1937, p. 251).

Imprinting, then, has several important parameters which may vary among different species because of differences in the specificity of innate perceptory patterns. In general, for imprinting to occur, the size and color of the parent-object must lie within certain limits, the parent-object must engage in certain kinds of behavior, and the imprinting itself must take place within a certain time period early in the animal's life.

Psychoanalysis. Some psychoanalytic concepts are remarkably consistent with those of imprinting, although historically psychoanalysis has been directed almost exclusively to the understanding of human behavior. In 1905, Freud first pointed out that object choice in adult life is dependent upon earlier object ties: "The finding of an object is in fact a refinding of it" (Freud, 1953, p. 222). Thus, he established within psychoanalytic theory a crucial relationship between early experience and later social behavior.

In psychoanalytic writings, a genetic model of behavior, stressing the role of innate factors in the course of the developmental sequence and the formation of object relationships, has had "pervasive significance" (Rapaport, 1960, p. 22). A less mechanistic view of personality development is found in Erikson's recent contribution (1950a, 1950b). He has incorporated experiential factors more centrally within an epigenetic conception of behavior, a psychosocial view which gives systematic importance to the context within which behavior occurs. In his summarization of psychoanalytic theory, Rapaport elaborated the significance of psychosocial factors for adult sexual behavior:

> Freud considered the sexual drives and their object choices as anaclitic upon the drives of self-preservation and their object choices. This is a statement of the growing organism's first social relationships and implies the social determination of behavior . . . the budding individual's social environment provides the objects of his libidinal and aggressive drives, and the structures (identifications in ego and superego development) which the relationships between the subject and these objects give rise to, co-determine his behavior in general . . . (1960, pp. 62-63).

In other words, object finding of the anaclitic type is based upon attachment to objects experienced early in life. In Freud's words, "the first beginnings of sexual satisfaction are . . . linked with the taking of nourishment" (Freud, 1953, p. 222). Thus, the initial object choice typically is the mother or her surrogate, and this early attachment serves as the prototype of all subsequent love relationships.

A theory of instinct hierarchy. At least one theorist has given formal recognition to the congruence of imprinting and psychoanalysis. Kortlandt's (1955) contribution to behavior theory is essentially an amalgamation of these two points of view. He suggests that an animal's earliest instinctive urges, his subordinate instincts, are non-specific in nature and constitute uncanalized nervous energy. In the developmental sequence

> . . . 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 men 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 (1955, p. 159).

In Kortlandt's view, the means by which low level instincts are fulfilled determine the kinds of objects and goals to be sought out in maturity.

> In these integrative processes the object and goal towards which a higher level instinct will be directed is 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 (1955, p. 159).

Thus, for Kortlandt, the object choices of adulthood represent the integration of behaviors whose characteristics were derived from previously experienced object choices.

In all of these theoretical approaches, the early "social environment" as a determinant of object choice, first mentioned by Whitman, is a recurrent theme. The relevance of Whitman and Craig's pioneering contributions is quite apparent in later theories of animal behavior. These theoretical sources share the view that early experience with some object standing _in loco parentis_ can serve as a crucial determinant of later mate choice. In particular, it is held that the object of mate choice would possess characteristics in common with the earlier parent object.

Dominance and Social Behavior

Differential behavioral characteristics of male and female animals often have been conceptualized in terms of dominance relationships, and frequent mention has been made of the importance that dominance and related functions have in directing higher order behavior, including mateship. Dominance ties have been observed in a great many species, ranging from various mammals to amphibians, and even some reptiles (Allee, 1938; Allee, 1951; Carpenter, 1960; Collias, 1944; Scott, 1958; Scott and Fredericson, 1951; Zuckerman, 1932).

Dominance in birds. Dominance behaviors probably have been studied most extensively in birds. Schjelderup-Ebbe appears to have been the first both to theorize about dominance in birds and to present empirical evidence for his views. He suggested that dominance strivings are innate, although they are not manifest in the earlier stages of life. "The very young birds live mutually in a complete 'state of innocence,' in that they do not exercise despotism over each other. This applies to all young birds, even those which can swim or walk at once" (1935, p. 956).

The appearance of despotism is heralded by the development of secondary sexual characteristics. Once initiated, dominance strivings characterize all subsequent social relationships: "Between each full-grown bird, male and female, of the same species, there always exists a state of despotism" (1935, p. 958).

Schjelderup-Ebbe was the first to recognize the existence of dominance hierarchies in the common chicken. The social order he found in these fowl has been termed the "peck right" hierarchy. In such a dominance hierarchy, the top ranked bird pecks all other birds in the flock, receiving no pecks in return. The next highest bird pecks all but the top ranked fowl, and so forth, down to the lowest ranked bird who pecks no one and is pecked by all other members of the flock. This linear social order is ordinarily quite stable, and once established, dominance position usually does not vary within a flock. Schelderup-Ebbe (1935) did note rare instances of "triangle" formation, however, in which deviations from the direct line of pecking order occur. In such a situation, for example, bird A pecks B, B pecks C, but C pecks A. Masure and Allee (1934) repeated Schjelderup-Ebbe's work on peck right hierarchies in chickens, and reported similar findings, especially with respect to flocks of pullets. In cockerels, however, they observed a less stable hierarchy, and in such flocks noted a greater tendency for triangle relationships to occur. Triangle deviations from a linear order also have been found in other species, for example, herons (Noble et al., 1938).

Both Schjelderup-Ebbe (1935) and Allee (1938) suggested that dominance position is related to the age or maturity of individual birds. Schjelderup-Ebbe, however, felt that size, i.e., weight, also affects dominance, while Allee specifically stated that weight does not influence dominance.

Social relationships in pigeons. Male pigeons ordinarily are more aggressive than females, and male dominance in pigeons often has been demonstrated (Carpenter, 1929;

Diebschlag, 1941; Masure and Allee, 1934; Noble et al., 1938; Ritchey, 1951; Valentini, 1951). Only a few instances of female dominance have been observed (Carpenter, 1929; Masure and Allee, 1934).

The presence of a stable peck right hierarchy has not been noted in pigeons. For example, Masure and Allee (1934) found dominance ties in segregated as well as combined male and female flocks of White King pigeons, but noted nothing that approximates a peck right hierarchy in any flock observed. Dominance relationships between any given pair of birds generally were stable, although fluctuations and reversals in dominance sometimes occurred. Despite these findings, Masure and Allee felt that dominance relationships in pigeons represent a variation on the Schjelderup-Ebbe view of dominance, rather than a fundamentally different dominance principle. Allee (1938) also noted in flocks of White King pigeons that dominance position is not fixed. He remarks: "The picture that emerges is one of a flock which is organized into a social hierarchy, but one which is not so hard and fast as that found with chickens" (1938, p. 188).

In the absence of a peck right hierarchy in pigeons, a social order termed "peck dominance" has been formulated (Allee, 1938; Bennett, 1939; Masure and Allee, 1934; Ritchey, 1951). Peck dominance is a measure that differentiates individual birds on the basis of the frequency with which they administer or receive pecks. This frequency varies, unlike the peck order situation, so that one bird is not always dominant over another. In males, particularly, dominance has been found to vary with the site of encounters, since, regardless of their status elsewhere, male pigeons are dominant within their own territories (Bennett, 1939; Carpenter, 1929; Masure and Allee, 1934; Noble et al., 1938; Ritchey, 1951). On the basis of this fact, Ritchey has concluded that territorial behavior accounts for the absence of dominance hierarchies within flocks, ". . . the territorial organization in pigeons blocks a rigid dominance hierarchy, such as is found in chickens" (1951, p. 175). A similar conclusion has been stated with respect to dominance in herons (Noble et al., 1938).

Territoriality. Territories are established by a great many species of birds (Bennett, 1939; Davis, 1959; Friedmann, 1935; Howard, 1920; Masure and Allee, 1934; Noble et al., 1938; Ritchey, 1951; Taylor, 1932). Although territoriality has been defined in various ways, any consistently defended area can be regarded as the territory of the defending animal (Noble, 1939; Ritchey, 1951).

Several functions served by territorial behavior have been recognized. (1) Territories have survival value: they provide for the spacing of breeding pairs, insuring protection and food for hatchlings near the nest. (2) Sex recognition and mating are facilitated. (3) Dominance is enhanced: males compete for territories and dominant birds gain favored sites. As noted before, males tend to be dominant within their own territories. These functions of territoriality can be summarized in Howard's words: ". . . the purpose for which . . . territory has, I believe, been evolved, is the biological end of reproduction" (1920, p. 9).

Problems of dominance and territoriality. Dominance relationships in male pigeons are highly predictable in territorial encounters, but the general influence of territoriality on dominance is such that it has been said to block the establishment of stable dominance hierarchies within flocks. For this reason, the measurement of basic dominance relationships appears to constitute a practical measurement problem, and, ascertaining the significance of such relationships, a theoretical issue.

A recent discussion of dominance and territoriality (Davis, 1959) has provided a new perspective on these problems and seems to suggest a way to their resolution. Davis indicates that territoriality itself constitutes a kind of dominance hierarchy, a conclusion based on his observations of starlings. These birds form dominance ranks in captivity. In the wild no dominance ranks appear although territories are established.

> Since in nature a subordinate bird can leave the area, it does so and sets up a "rank" at another nest hole. Thus the whole breeding area is divided up into "groups" which have only one bird (the dominant one) because all others have left. In this interpretation territorialism is a special case of social rank . . . (1959, p. 217).

It is possible that dominance relationships are affected by confinement, as Davis seems to imply, and possibly are altered by domestication as well. For example, in the wild state where only territorial dominance exists, stable social ties occur. In confinement, however, the stability of territorial structuring tends to be affected by the artificially induced proximity of individual birds, territories, food supplies, etc. On the other hand, the long domestication of some species, such as chickens, may have served gradually to re-establish stability in the social order. Since territorial behavior is more pronounced in males than in females, domestication should have a less pronounced normalizing effect on dominance ties in male flocks. This situation, it is interesting to note, does seem to exist in chickens.

In any case, the formation of territories amounts to the establishment of dominance hierarchies in which dominant birds force subordinate ones to leave favored areas. Such a description seems applicable to pigeons. Accordingly, a method was devised for using territoriality to measure dominance relationships in pigeons and a pilot study was conducted to test its effectiveness. This study involved the prediction that in a small area containing only one favored territorial site, the order of its acquisition would reflect an hierarchical dominance order in flocks of male pigeons. This prediction was confirmed, a finding that would appear to have value for future studies of territorial dominance.

Studies of Mateship and Dominance

Despite experimentation, the relationship between dominance and mate selection remains unclear. For example, marked aggressiveness in chickens, particularly males, appears to lessen their chances of mating (Guhl, Collias and Allee, 1945). Also, sexual drive in male chickens has been found to be unrelated to peck order position (Wood-Gush, 1957). In line with such findings, some authors have suggested that dominance and aggression are not significant factors in the social interactions of animals (Schneirla, 1946; Scott, 1953). In pigeons, Warriner (1960) observed that aggressive males tend to mate early, but found that passive males also occasionally mate early. After reviewing studies concerned with the importance of dominance and related variables for mateship in birds, Warriner concluded: "The relationship between aggressivity and mating potential is unclear at present and deserves further study" (1960, p. 67).

Instrumental Dominance

It often has been suggested that male and female birds exert a mutual influence on mate selection. For example, in many species adult birds of both sexes display, implying that both are sexually stimulated (Huxley, 1921; Noble et al., 1938). In fact Huxley has termed the phenomenon "mutual courtship" (1921, p. 565). Many other authors also have stressed a mutual interaction between the sexes in mateship (Carpenter, 1929; Craig, 1908; Levi, 1957; Naether, 1939; Warriner et al., 1963). Although the specific nature of this interaction never has been clarified, various authors have suggested that the dominant bird of a courting pair, usually the male, controls mateship. In most species dominance is a sex-related variable, and males usually are dominant, as for example, in herons (Noble et al., 1938).

However, it has been noted that females also can control mateship (Nice, 1943; Whitman, 1919b). Schjelderup-Ebbe (1935) has indicated that, depending on species, either sex may control mating. He also observed a few species in which dominance varies with season; for example, among certain mallards the male is dominant at pairing time and the female is dominant at moulting time. Allee (1938) has reported similar findings in parakeets.

It would seem from these statements that the relative influence of male and female in the mate selection process is quite variable. However, Noble et al. (1938), discussing the impact of territorial competition on mateship in young herons, make a point that would seem to do away with much of the confusion surrounding this problem. They say, "Pairing off is not accomplished by . . . mere juxtaposition . . . . One bird must accept subordination to the other . . ." (1938, p. 13). This statement aptly summarizes an implication that is consistent with all of the views cited, namely, that for mating to occur one bird of a pair must be dominant over the other. On these grounds, it is possible to conceptualize dominance as a social process that may have little to do with mate preference *per se*, but much to do with implementing mate preferences of dominant birds, whether male or female. Viewed as an explanatory principle, then, dominance can be said to have an instrumental function in mateship.

Among pigeons it already has been noted that males usually are dominant. Applying the concept of instrumental dominance to pigeon mating behavior, it can be seen that male mateship preferences should be implemented most of the time, and female preferences much less frequently.

Studies of Mate Selection in Birds

A good deal of observational data can be cited in support of the view that early experience influences some aspects of sexual behavior in birds. For example, it has been noted that hand-reared birds frequently direct sexual responses to their caretakers, and that early object relationships of various kinds elicit courtship behavior.

Unfortunately, most of the available material concerned with early experience and mateship is anecdotal, and an extensive search of the literature has uncovered few relevant experimental studies. The earliest of these were Whitman's classic reports of mating in pigeons and doves. Craig reports that Whitman took the eggs and young of wild pigeons and fostered them under domestic ring-doves,

> . . . with the result that the young reared by the ring-doves have ever after associated with ring-doves and tried to mate with them. Passenger pigeons, for example, when reared by ring-doves refuse to mate with their own species but mate with the species of the foster parents (1908, pp. 89-90).

These findings caused Whitman to conclude that foster parent rearing in birds influences youngsters to choose mates of the species with which they were reared. Craig's contention that physical attributes of parents, including color, influence mate selection was not evaluated in a controlled way in Whitman's studies. Therefore, conclusions cannot be derived from these reports about specific cues of mate choice.

Several studies have been reported in which sexual behavior in birds has been induced precociously. For example, it was found that testosterone-injected white leghorn chicks, reared in isolation by hand, gave sexual responses to the human hand when twenty-four days old (Noble and Zitrin, 1942). In a similar study, Bambridge (1962) found that male and female imprinted chickens who were injected with testosterone from their fifth day of life, gave sexual responses to the imprinted object when tested on their nineteenth and twentieth days. In a more extensive study, Schein and Hale (1959), using androgen-injected male turkey poults, found that early social experience with various objects improved their later "releasing" value as sexual stimuli. Although all of these studies support the general thesis that early experience selectively directs later sexual behavior, the generality of their findings seems limited. It must be noted that since none of the birds in these studies were mature when the sexual behavior was induced, it cannot be said with certainty that the same objects would have been chosen at maturity. In other words, the recency of these imprinting experiences to the measures of sexual response does not permit of firm conclusions concerning the relationship between early experience and adult behavior.

In a recent and more pertinent experiment, Guiton (1961) found that courtship responses of imprinted brown leghorn males tend to decrease with age. Although most subjects gave sexual responses to imprinted objects in tests conducted early in their lives, only two of six still were making courtship responses at 24 weeks of age. These two preferred a stuffed model of their own species to the artificial imprinted model. Thus, Lorenz' contention that imprinted birds prefer imprinted objects to members of their own species was not supported, and Guiton concluded that imprinting in these birds has only a limited effect on their later sexual behavior.

Perhaps the most telling criticism that can be applied to the studies thus far cited is that, save for Whitman's experiments, none have dealt with normal mateship but have relied on hormone-induced sexual behavior and/or artificial models.

To the writer's knowledge, only one well-controlled study has appeared that deals directly with the effects of early experience on actual mate selection in birds. Warriner, Lemmon and Ray (1963) reared black pigeons and white pigeons in two ways: (1) half with parents of their own color, and (2) half with foster parents of the different color. After isolation until maturity, the birds were allowed to mate. One procedural decision may have influenced the outcome of this study. In each of its four replications, eight males and eight females were employed as subjects, and all matings of these birds were included in the results. If they were to mate, the last male and female subjects in each replication _had_ to mate with one another, since no other birds were available. These mateships were forced, regardless of the mating preferences of the birds. Subject to this criticism, the major finding of the study was that male pigeons to a significant degree (26 of 32) tended to mate with females who were the same color as the males' rearing parents. Female pigeons did not show this tendency beyond a chance level (14 of 32). The authors discussed three alternative explanations of these results:

> 1. In pigeons, the choice of mate may be primarily a male-dominate 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 addition, 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-dominate process (1963, pp. 223-224).

All of the studies cited support the conclusion that at least to some extent early experience directs sexual behavior, and one experiment revealed that actual mate selection in male pigeons was influenced by this variable (Warriner et al., 1963). The findings of this study also point to the necessity for clarification of the role of mating preferences in female pigeons.

Parental Characteristics and the Developmental Process

Although systematic evidence is lacking, there are data (Guiton, 1961) which suggest that early experience with artificial parental models has disruptive effects on adult sexual behavior. However, adaptive influences on adult sexual behavior have been reported in studies using biologically appropriate models (Craig, 1908; Warriner et al., 1963).

Guiton has argued that imprinting to abnormal parental models can alter the developmental sequence, so that appropriate social responses fail to become integrated firmly into the adult behavioral repertoire. For example, studies by Kramer (1957) and Meyer-Holzapfel (1939) indicate that infantile food-begging responses in adulthood are retained to a much greater extent by hand-reared birds, especially when reared in isolation, than by birds reared in the wild. Nicolai (1956) has reported abnormalities of mate selection in bullfinches imprinted to humans. These data are in keeping with Heinroth's observations of breeding failures in various hand-reared birds (cited in Lorenz, 1937).

Lorenz' view of these kinds of abnormal reactions seems to be grounded in his concept of the "companion" and the specific nature of reactions released by each type of companion, in accord with the innate perceptory pattern/releaser model. Aside from his recognition of an early critical period for imprinting, Lorenz does not appear to conceptualize behavioral attributes, systematically at least, within the context of the developmental process. Other approaches, such as psychoanalysis and Kortlandt's theoretical formulations, explain such behavioral anomalies more directly in terms of disruptions of the developmental sequence. In these approaches, biologically appropriate parental models can be said to facilitate the integration of "partial" instincts into higher level behaviors--such as those involved in mate selection activities in adulthood. On the other hand, abnormal or artificial models connect low level instincts to ontogenetically inappropriate objects. Since they may be unable to become integrated appropriately into higher order behavior, there is a tendency for such imprinting experiences to become fixated in infantile forms. In such a fashion the recurrence of infantile food-begging, the fixation of sexual response to inappropriate objects, and even breeding failures can be accounted for.

Pair Formation in Pigeons

Parental color as a facet of early experience has been found to influence mate choice only in male pigeons.

It is interesting to note, as did Warriner et al., that psychoanalytic theory provides a framework for the prediction of differential effects of experience on male and female behavior--at the human level (Deutsch, 1944; Freud, 1953). However, theories directly pertaining to animal behavior provide no such a priori basis from which to deduce differential effects. As suggested by Warriner et al., it is possible that in female pigeons mate choices depend on characteristics other than parental color or on determinants other than early experience. It also is possible that females do not have mate preferences or that their preferences are not effective determinants of mateship.

However, it seems possible to derive an alternative explanation by combining the concepts of instrumental dominance and early experience. Such an explanation takes account of the experimental finding that mateship in pigeons is a male dominate process (Warriner et al., 1963). Specifically, it is 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.

This position agrees with theoretical sources which assume females to have mate preferences that play a significant role in mate selection. Also, it does not require the addition of new concepts upon which female preferences might be based, such as determinants other than early experience. Thus, it has the virtue of parsimony. Most important, however, is its remarkable degree of agreement with existing experimental data. Not only is this view consistent with the major evidence presented in the Warriner study (26 of 32 mateships determined by male preference), but it concurs with residual findings of that study (5 of the remaining 6 mateships determined by female preferences), and also provides an explanatory framework for those data. In fact, in view of the high incidence of male dominance in pigeons and the low occurrence of female dominance, results such as these might well have been predicted.

This explanation of pair formation involves two major variables which comprise two separate although related problem areas. One of these problems has to do with the existence of mate preference itself in females. In order to resolve this question, female preference as a sufficient differential condition for the actual determination of mateship has to be posited and the proposition tested. The present study was designed primarily for that purpose. The other problem involves dominance. Predictions of mateship that are based on dominance would appear to depend on the feasibility of measuring and/or manipulating dominance status when mate preference is known. Since preference in females has not been established, this problem remains for the future.

CHAPTER II

PROBLEM

Male and female pigeons are commonly believed to be joint participants in the mate selection process, and theoretical grounds have been offered for the view that early experience influences mate selection in both sexes. Empirical evidence, however, has shown that early experience determines mate choice to a significant extent only in male pigeons. Dominance behaviors in pigeons also have been thought to play a part in mateship, although experimentation has failed to clarify the nature of this role.

Based on the concepts of early experience and instrumental dominance, an explanatory framework was offered which specified the role of females in the more general process of pair formation. Retaining the view that early experience determines mate preference in both sexes, the construct of instrumental dominance was introduced to describe the role of dominance in mating, *viz*., that dominance helps implement already existing mate preferences. On this basis, mate preferences could exist in female as well as male pigeons, but since male pigeons generally (although not exclusively) are dominant, their preference would tend to be implemented and female preferences masked, when differences in preference exist. This possibility was seen to be consistent both with the generally accepted view that females are involved in mate selection and with subsidiary findings of the Warriner study, in which female preferences did seem to determine a minority of mateships.

The thesis of this investigation is that early experience determines mate preference in female as well as male pigeons, and that it is a sufficient differential condition for the determination of actual mateships. In order to test this proposition, the effects of mate preference in males were controlled. Since parental color has been shown to influence mate selection in males, this variable was chosen for experimental purposes. Specifically, the study was designed to test the expected selection of mate on the basis of parental color of female subjects as a consequence of voiding differential color preferences in male subjects. The following hypothesis was derived:

> When the effects of parental color are controlled in male pigeons, mate selection will be consistent with the parental color of female pigeons under the conditions of the experiment.

A secondary aim of the study was to determine the relationship between dominance and age, size, and the temporal order of mating.

CHAPTER III

METHOD

The experiment was divided into three parts. Part one consisted of rearing the experimental subjects. In part two, the experimental hypothesis was tested. In part three, dominance ratings for male subjects were made.

Subjects. Parental breeding stock consisted of sixteen pairs of White King pigeons, eight pairs of Black King pigeons, and eight pairs of Red Carneaux pigeons. While these birds are comparable in size and configuration, they differ significantly in color (Levi, 1957). The experimental subjects were offspring of these birds.

Sexing. Three judges sexed the experimental subjects. Determination of sex was based on physical characteristics and behavior (Carpenter, 1929; Warriner, 1960). The criteria used to judge sex included relative size, secondary physical characteristics, secondary behavioral sexual characteristics, and the _gestalt_ or general impression the birds made on the judges. Decisions were based on agreement of all three judges when possible. In a few cases unanimity was not reached, and the decision was based on majority opinion. Despite careful efforts, during the course of the mating process it appeared that five birds had been incorrectly sexed. In each case the mistakenly-sexed bird was replaced immediately with an appropriate substitute. This had no discernible effect on the overall mating process.

Mating criteria. A number of signs of mating in pigeons have been established. These include frequent copulation, billing, calling to one another, occupying the same nest box, nest building, and frequent perching together (Carpenter, 1929; Warriner, 1960). These criteria were used to determine the presence of matings. Two persons observed the subjects at least once daily and kept separate records of their observations. Decisions concerning mating were based on the independent agreement of both observers that a mating had occurred.

Part one: Experimental design. In order to control for color preference in males, while utilizing color preference as an independent variable in females, pigeons of three colors--white, black, and red--were used. All female subjects were white. Half of them were reared by red foster parents and half by black foster parents. All male subjects were reared by white foster parents. Half of these males were black and half were red. These rearing conditions are outlined in Table 1.

Table 1

Rearing Conditions for Experimental Subjects

Sex	Color	
	Subjects	Foster parents
Male	Red	White
	Black	White
Female	White	Red
	White	Black

Procedure. Pigeons normally have two-egg clutches, with the second egg laid about one day after the first (Levi, 1957). It has been shown that clutches of domestic pigeons can be switched successfully if the second eggs of both clutches have been laid within two days of one another (Carpenter, 1929; Patel, 1936; Warriner et al., 1963). This method was followed in the experiment.

All clutches of black and red parents were switched with those of the white parents, insuring that all black and red hatchlings were reared by white foster parents and that half of the white hatchlings were reared by red foster parents and half by black foster parents.

The cages of parent birds were visually isolated from each other. Therefore, all hatchlings were reared under conditions which allowed them visual access only to their siblings and rearing parents. When the young birds were between 8 and 12 days old, they were banded. This variation in time of banding was due to individual differences in the hatchlings' growth rates. When the youngsters were 40 days old, they were removed from parental cages and put into individual cages, remaining there until part two of the experiment began. These individual cages also were visually isolated so that the young birds could not see one another.

Part two: _Mating replication design_. Pigeons ordinarily reach maturity and are ready to mate by the time they reach five months of age (Levi, 1957; Riddle, 1931). When enough pigeons of the appropriate color had been reared to maturity part two began.

Mateships were determined in a series of 5 consecutive replications. There were 3 matings in each replication, so that a total of 15 matings was used to test the experimental hypothesis. There were 2 pens utilized in alternating fashion during this portion of the experiment. Subjects in the mating pen at the start of each replication consisted of 8 white females, half reared by red foster parents and half by black foster parents, and 4 red and 4 black males, all reared by white foster parents. This design is outlined in Table 2.

Table 2

Subjects in the Mating Pen

Sex	N	Color	
		Subjects	Foster parents
Male	4	Red	White
	4	Black	White
Female	4	White	Red
	4	White	Black

Mated subjects were replaced by new birds at the beginning of each replication, thus assuring that every female always had at least two black and two red males available for mating. Under these circumstances, mate choice possibilities were maximized, and no forced matings could occur. Also, the possible effects of dominance relationships and establishment of territories in males were not biased by differential familiarity with the mating pens.

Procedure. At the beginning of the first replication, 16 subjects were removed from their isolation cages at the same time and were placed together in one of the mating pens. As soon as a mating occurred, the mated birds were removed from the pen and placed in an isolation cage until the beginning of part three of the experiment. When a total of 3 matings had taken place, the replication was terminated. The remaining unmated subjects then were removed from the mating pen and were placed together in the alternate pen, along with 6 new birds. The new birds corresponded in color and sex to the previously mated subjects. At this time, the total N having been re-established again at 16, a new replication was begun. This procedure was followed for all five replications.

Part three: Dominance design. Dominance ratings were obtained for male subjects according to the method devised in a pilot study conducted earlier. One dominance pen was used. It contained only one territorial site, and during the course of the dominance tests which followed, subjects competed for possession of this site.

Procedure. In order to relate dominance to mateship as directly as possible, dominance ratings were taken immediately after each mating replication. As each mating replication ended, the three males who had mated during that replication were weighed and then placed together simultaneously in the dominance pen. In this way, a series of five replications of dominance ranking was obtained, with each set of dominance ratings specifically applicable to its own mateship replication. Two separate tests of dominance were used. In each test, dominance ratings were determined by a series of trials, each trial lasting two hours. At the end of every trial, a dominance rating was assigned to the dominant bird in that trial.

The dominance measure. Dominance was based on cumulative encounters during the course of a trial. In order to meet the criterion for dominance, one bird had to win a majority of all encounters with each other bird, including at least one encounter with every other bird in the trial. It was decided to extend the time of a trial if insufficient encounters had taken place at the end of two hours. Encounters were operationally defined as: competition between two birds on the territorial site (the top of the nest box), with one bird being driven from the territory.

Test one. On trial one, all three birds were placed together in the pen at the same time. At the end of the trial, the dominant bird of the three was assigned a territorial dominance rating of 1 (t/d 1), and was removed from the pen. Trial two then began, using two birds. At its conclusion, the dominant bird of the two was rated t/d 2, and was removed from the pen. The remaining bird was rated t/d 3, and was allowed to retain the territory alone for two hours, the length of a trial. At the end of this period of time, test two began.

Test two. This test reversed the procedure of test one. On trial one, the two lowest ranked birds in test one (t/d 2 and t/d 3) competed for the territory. At the end of the trial, the dominant bird was ranked t/d 2 and the subordinate bird was ranked t/d 3. At the beginning of trial two, the bird ranked t/d 1 on test one was added, so that three birds were involved in this trial. At its conclusion, the dominant bird of the three was rated t/d 1. The method utilized in test two served two major purposes: it counterbalanced test one and it maximized opportunities for low dominance birds (as measured by test one) to possess the territorial site, by allowing them to compete in more trials than high dominance birds.

Materials. Standard NPA pigeon bands and mating bands were used throughout the course of the experiment in order to identify individual birds.

In part one of the experiment, parent birds were housed in 30" X 36" X 30" wire cages, covered on three sides by burlap sacking in order to assure visual isolation of the cages. A double nest box containing straw nesting material was placed in each parental cage, as was a 1" wide wood perch. This perch, extending the length of the cage, was placed to one side of the nest box at a height of about 20". Individual isolation cages for the experimental subjects were 20" X 20" X 20" wire cages, similarly covered on three sides by burlap for purposes of visual isolation. Water containers and standard mixtures of feed and grit in separate cans were provided for parental and isolation cages.

Two 8' X 10' X 9' wire pens were employed as mating pens in part two of the experiment. Nine double nest boxes, each containing straw nesting materials were put in each pen. Six of these boxes were placed along the walls at heights varying from one to three feet, and three were placed on the floor of the pen. Separate containers of water, food, and grit were available in each pen.

For the t/d tests in part three, a 30" X 36" X 30" wire cage was used. One double nest box was placed in the cage. Wire mesh was affixed to the front of the box so that perching in it could not occur. Since pigeons prefer elevated perches, especially when found in conjunction with nesting sites (Levi, 1957), the top of the one available nest box was the sole favored territorial site in the pen.

CHAPTER IV

RESULTS

The research hypothesis of this study involved the prediction that with male mate preferences controlled, female subjects would mate in accord with the color of their rearing parents. Table 3 presents the results of the Chi Square one sample test applied to mateship of female subjects (Siegel, 1956, p. 43). As can be seen from Table 3, the results of this test were significant and the research hypothesis was confirmed.

Table 3

Mate Selection in Female Subjects According to Color

Foster parent color	Mate color		Mateships in the predicted direction
	Black	Red	
Black	7	1	7
Red	2	5	5
			12[a]

[a] Chi Square = 5.40, 1df, p = .03.

A secondary purpose of the study was to test the reliability of dominance rankings. Table 4 presents t/d ratings obtained in two tests of dominance. In this table, rank scores on test two are presented in relation to test one ranks. It can be seen that all subjects in each replication obtained the same t/d rank on both tests.

Table 4

Rank Scores for Two Tests of Dominance in Males by Replication

Test 1 rank	Test 2 rank scores by replication					Mean rank
	I	II	III	IV	V	
1	1	1	1	1	1	1
2	2	2	2	2	2	2
3	3	3	3	3	3	3

The presumed significance of these data is affirmed in Table 5, by means of the Friedman analysis of variance test for ranked data (Winer, 1962, p. 136). Table 5 reveals that there is a significant difference between mean rank scores on test 2 for the different ranks of test 1. This indicates that the two tests are significantly related, a finding also reflected in the perfect average intercorrelation ($\bar{r}$) obtained between replications.

Table 5

Analysis of Variance Table for Ranked Data in Two Tests of Dominance

Source of variance	Sums of squares	df	$\bar{r}$	X^2	p
Dominance	10.0	2	1.0	10.0	.01
Error	0.0				
Total	10.0				

Tests also were made of the relationship between dominance and two subject variables, age and weight, and one mating variable, the temporal order of mateship. In all three of these tests, the Friedman analysis of variance for ranked data again was employed as the test of significance.

In Table 6, weight ranks (ordered 1 to 3, heaviest to lightest) of male subjects by replication are compared with dominance rank.

Table 7 presents the results of the analysis of variance for dominance and weight ranks.

Table 6

Dominance and Weight Ranks in Males by Replication

Dominance rank	Weight ranks by replication I	II	III	IV	V	Mean rank
1	2	2	1	2	1	1.6
2	3	1	2	1	2	1.8
3	1	3	3	3	3	2.6

Note.--Inspection of Table 6 reveals that mean ranks for weight occur in the same relative order as dominance ranks. The procedure of collapsing the scores into a 2 X 2 table where rank 1 and 2 scores for dominance and weight are compared with rank 3 scores would yield a significant chi square value. Since this would be an ad hoc arbitrary treatment, using a small N, it would be difficult to make a statistical statement concerning such an arrangement of the data. Repeated observations with a larger N might result in a more adequate evaluation of this proposed relationship.

Table 7

Analysis of Variance Table for Dominance and Weight Ranks in Males

Source of variance	Sums of squares	df	$\bar{r}$	X^2	p
Dominance	2.8	2	.10	2.8	NS
Error	7.2				
Total	10.0				

The statistical analysis reported in Table 7 is not significant. However, the arrangement of the data in Table 6 suggests a relationship between dominance and weight, a possibility which would bear further study.

Table 8 reports age ranks (ordered oldest to youngest, 1 to 2) in comparison with dominance rank.

Table 8

Dominance and Age Ranks in Males by Replication

Dominance rank	Age ranks by replication					Mean rank
	I	II	III	IV	V	
1	2	1	2	2	3	2.0
2	3	2	3	3	1	2.4
3	1	3	1	1	2	1.6

The analysis of variance presented in Table 9 reveals that age and dominance are not significantly related.

Table 9

Analysis of Variance Table for Dominance and Age Ranks in Males

Source of variance	Sums of squares	df	$\bar{r}$	X^2	p
Dominance	1.6	2	-.05	1.6	NS
Error	8.4				
Total	10.0				

In Table 10, the rank order in which matings occurred is compared with dominance rank.

Table 10

Dominance and Order of Mating in Males by Replication

Dominance rank	Mate order ranks by replication					Mean rank
	I	II	III	IV	V	
1	1	2	3	1	3	2.0
2	3	3	2	3	1	2.4
3	2	1	1	2	2	1.6

The analysis of variance reported in Table 11 reveals that order of mating is not significantly related to dominance.

Table 11

Analysis of Variance Table for Dominance and Mate Order Ranks in Males

Sources of variance	Sums of squares	df	$\bar{r}$	X^2	p
Dominance	1.6	2	-.05	1.6	NS
Error	8.4				
Total	10.0				

The reliability of territorial behavior as a measure of dominance relationships is reflected in more qualitative data than are revealed in Tables 4 and 5. In each trial of both tests one and two, the dominant bird of the trial lost no encounters (Tables 14 and 15). Thus, it would appear that a single encounter under these conditions serves to establish a permanent dominance relationship between any two given male pigeons.

CHAPTER V

DISCUSSION

The major purpose of this study was to test the proposition that parental color can influence mate selection in female pigeons. Female subjects did mate to a significant extent with males who were the same color as the females' rearing parents. Thus, the major hypothesis was confirmed.

Early experience with parental color again has been shown to have an important influence on the mate selection process in pigeons. In this study color was used in two ways. As an independent variable in female subjects, it influenced mate selection. As a control variable, the effects of differential color preferences were voided in male subjects. This appeared to limit sharply their capacity to determine mateships. These findings imply that color probably is the single most important cue in the mate selection process.

In a broader context, support is provided for those theories of behavior which indicate that early experience has a significant influence on adult social behavior. The present data in conjunction with the findings of the Warriner et al. (1963) study make it apparent that in pigeons this influence extends to both sexes. Specifically, it is clear now that female pigeons have preferences in mating and that these preferences can determine actual mateships. It can be concluded that parental color as an aspect of early experience is a sufficient differential condition for the determination of mating in both sexes.

The overall process of pair formation thus has been clarified to some extent. The Warriner study earlier revealed that when differential color preferences operate jointly in both sexes, mate preferences generally determine mate selection. The exceptions in the Warriner study, the five mateships consistent with female color preferences, in all probability reflect the fact that some mateships in pigeons are based on female preferences. However, since male preferences lead to mating much more frequently than do female preferences, the conclusion of Warriner et al. (1963) that mating is a male dominate process seems warranted.

Emerging from this recognition that color preferences exist in females is the problem of why mating preferences of males do predominate in the process of pair formation. It would seem that the view of pair formation proposed earlier in this paper deserves further consideration as an explanatory concept. The first premise of this explanation stated that females as well as males have mating preferences. This contention was supported by the results of the experiment. The second premise employed the concept of instrumental dominance to account for the seemingly low incidence of mateships based on female preferences. This premise is not a necessary corollary to the existence of mating preferences in females. Therefore, while the process of pair formation as conceptualized here has received partial support, the utility of instrumental dominance as an explanatory concept remains to be established.

The earlier described method of measuring dominance relationships in male pigeons also was tested and found to be reliable. The fact that competitive behavior attendant to the establishment of territories can be used to obtain rank order dominance ratings in a flock of males provides support for Davis' (1959) view that territoriality constitutes a kind of dominance hierarchy in its own right. It would seem that these results reflect the existence among pigeons of a much more consistent hierarchical dominance order than previously has been noted. Therefore, in one sense, the frequent claim that territoriality interferes with the establishment of a stable dominance hierarchy in pigeons appears questionable.

The role of dominance in mediating social behavior remains to be clarified. When dominance rankings were compared with mating order, no relationship was revealed. This finding is in keeping with Warriner's (1960) observations that dominance in males is not related systematically to mateship order. Since dominance was defined in terms of territoriality, the failure to find a relationship to mating behavior is in keeping with the view that territoriality serves a function apart from competition directly related to mateship (Ardrey, 1961; Howard, 1920).

The primary findings of this study clearly indicate that dominance in males did not detract significantly from the effective operation of female preferences based on parental coloration. However, three mateships did occur that were inconsistent with such preferences. In view of what has been said regarding instrumental dominance, it may be noted that none of the males of these mateships were low dominance (t/d 3) birds (Table 12).

Neither weight nor age ranks of males were found to be related systematically to dominance position. Therefore, Allee's conclusion that age, but not weight, influences dominance, and Schjelderup-Ebbe's view that both factors are involved, were not supported, although a possible relationship between dominance and weight cannot be discounted entirely. In general, these findings suggest that dominance is not to be explained simply on the basis of organismic variables.

Observations and Inferences

An experimental design such as the present one, where five different replications of the process of mating took place, offered unusual opportunity for repeated observations to be made of events leading to mateship. It is well known that inferences based on observational material alone are prey to various dangers, not the least of which is anthropomorphism, and so must be evaluated cautiously. In this light, observations relating to the mating process are set down here, in hopes that their heuristic value and contribution to a better understanding of mating will overshadow their liabilities.

Formation of social ties. In each mating replication, the structuring of social relationships among previously unacquainted birds in a new living space seemed to be associated with the establishment of dominance ties among flock members with specific reference to territorial behavior in males. Males spent much of their time, particularly early in each replication, gaining and defending territories--ordinarily the tops of nest boxes and close environs. As these territories became more clearly defined, the locations of birds in the pen, particularly males, became more predictable on a day to day basis. Although courting behavior and even a few mateships occurred in the early part of some replications, mating ordinarily did not take place before matters of dominance and particularly territoriality, had been settled. This temporal sequence, apart from other implications, supports the views of Ardrey (1961) and Howard (1920) regarding the role of territoriality in bird behavior.

The mating site. The initial location of the nest of mated pairs almost always was to be found within the territory previously established by the male of the pair. Since mated pairs were removed as soon as mateships were verified, the nest location over an appreciable length of time could not be ascertained. Nevertheless, this observation stands in sharp distinction to Carpenter's (1929) contention that when mateships occur in pigeons, males leave their previously established territories to settle in areas inhabited by their mates.

Inferences based on these observational data may be summarized as follows:

1. Dominance relationships among members of a flock in conjunction with territorial behavior in males greatly facilitate the structuring of social ties within the flock, and in fact seem to comprise the principal vehicle of this structuring process.

2. Mateships ordinarily take place after dominance ties and territories are relatively well established.

3. The location of nests of mated pairs tends to occur within the territory previously established by the male of the pair.

Research Implications

It has been suggested that the role of early experience in mediating adult behavior is a function of the kind of relationship that exists between parents and offspring in the developmental process. For example, in the present study it was not simply color, but parental color, that influenced mating. During the early rearing of all but one of the female subjects, siblings of a color different from that of the foster parents were present (Table 12). Yet, sibling color did not detract from the impact of parental color on mating behavior. Nor did sibling color affect the mating process in the Warriner et al. (1963) study. Thus, early experience with parental color appears to function as one of the most significant channelizing influences on the later mate selection behavior of pigeons.

Altricial and precocial birds. Birds differ in their degree of attachment to parents and have been classified as altricial or precocial as a function of maturity at hatching (Nice, 1962; Wetmore, 1951). Precocial birds, many of which are autophagous, are relatively mature and mobile at hatching, and have a limited and short dependence on parental figures. Yet, early mobility and the propensity to follow certain kinds of moving objects have made their "following" behavior an exhaustively studied imprinting response.

Imprinting responses in altricial birds are hard to identify, since they do not exhibit easily measurable responses in early development. It has been suggested that imprinting in altricial birds probably occurs while hatchlings are still in the nest (Nice, 1962). However, insofar as the present experiment could be termed an imprinting study, imprinting responses _per se_ of hatchling subjects were not observed at all but were inferred from adult mating behavior.

Altricial birds are extremely immature at hatching. Pigeons, for example, need extensive parental care, including protection, feeding and warmth. Lacking muscular development, they also are relatively immobile for some time, and early immobility in altricials has been regarded as the *sine qua non* of their developmental sequence (Nice, 1962). Pigeons also are unique among non-mammals in that they produce, not regurgitate, food (pigeon's milk) for hatchlings (Levi, 1957), and in other respects--monogamous mating habits, care of youngsters by both parents--their behavior parallels the course of some phylogenetically higher species, including man. In pigeons, then, as well as higher species, the period of primary socialization occurs over an extended length of time. In such species, Hess (1962) points out that disruptions during primary socialization profoundly alter the nature of later social behavior.

Thus, it would seem important from a comparative point of view to study further the influence of experience on the early developmental sequence in pigeons. To mention only a few possibilities--loss of a parent, parents of two different colors, vocalization, time of weaning--all hold promise in this regard.

Dominance and territoriality. A variety of problems remain to be investigated with respect to these concepts. For example, although typically they have been treated as distinct concepts, data from this study would seem to imply a close relationship between dominance and territoriality. In this regard, it would be useful to determine what correspondence exists between "peck dominance" and "territorial dominance," described in this study, as dominance measures.

In addition, the specific role of dominance in social behaviors, such as mateship, remains uncertain, and the utility of instrumental dominance as an explanatory concept needs to be explored. The determinants of dominance itself are unknown. In this regard, it would be useful to ascertain how early experience influences dominance. Utilizing Hess' (1958; 1959) law of effort as a model, Warriner (1960) presents a speculative discussion of the effects of energy expenditure by hatchling pigeons in food-getting as a possible determinant of aggressivity. One means of investigating the effects of early experience on dominance would be to compare differences in this kind of early food-getting behavior to dominance rank in adulthood.

CHAPTER VI

SUMMARY

Various theoretical sources provide a basis for the prediction that adult social behavior in birds, including mateship, is mediated to some degree by early experience variables. Observational and experimental data were found to be in general agreement with these theoretical views. In particular, it has been established by carefully controlled experimentation that early experience with parental color influences mate selection in male pigeons.

Other theoretical sources stress the importance of dominance relationships and related variables for the social organization of birds. Such variables also have been related to the mateship process.

The present study investigated the hypothesis that mate preferences exist in female as well as male pigeons, and that parental color of females constitutes a sufficient differential condition for the determination of mate selection.

This hypothesis was grounded in an explanation of pair formation which suggested that early experience influences both sexes, and that individual differences in dominance lead to the implementation of the preferences of dominant birds, whether male or female.

The first premise of this argument was tested in the present study. Specifically, it was hypothesized that when color preferences were controlled in male pigeons, mate selection would be consistent with color preferences of female pigeons. This hypothesis was confirmed.

As a secondary aim of the study, an investigation was made of dominance relationships in male pigeons, using territoriality as the dominance measure. This measure was found to be a reliable means of distinguishing hierarchical dominance relationships in males. Heretofore, the possible existence of a relatively stable peck right hierarchy in pigeons has not been explored, although the relative dominance of males within established territories is a well known fact. The territorial dominance method described in this study appears to furnish a means of demonstrating the existence of this kind of hierarchy.

Dominance rankings were compared with the organismic variables age and weight in an effort to identify determinants of dominance position, but no significant relationship was revealed between dominance and either of these variables.

Implications of all experimental findings were discussed in the light of research possibilities.

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APPENDIX

Table 12

Raw Data for Female Subjects

Replication	Female band number	Date of birth	Color	Foster parent color	Sibling in nest	Mate		Agreement with major hypothesis	T/d rating of mate
						Band	Color		
	609	2-28	White	Red	Yes	669	Black	No	1
1	618	3-10	White	Black	Yes	612	Black	Yes	3
	635	5-17	White	Black	Yes	671	Black	Yes	2
	658	6-11	White	Red	Yes	647	Red	Yes	3
2	624	4-2	White	Black	Yes	620	Black	Yes	1
	629	4-26	White	Black	Yes	627	Black	Yes	2
	632	5-9	White	Red	Yes	652	Red	Yes	3
3	623	4-2	White	Black	Yes	688	Black	Yes	2
	602	2-26	White	Black	Yes	664	Red	No	1
	638	5-23	White	Black	No	666	Black	Yes	1
4	611	2-28	White	Red	Yes	642	Red	Yes	3
	707	7-25	White	Red	Yes	679	Red	Yes	2
	633	5-9	White	Red	Yes	674	Black	No	2
5	682	7-20	White	Red	Yes	684	Red	Yes	3
	706	7-30	White	Black	Yes	699	Black	Yes	1

Table 13

Raw Data for Male Subjects

Replication	Band number	Date of birth	Sibling in nest	Date of mating	Age in days at mating	Weight in oz. at mating
1	669	6-25	No	1-1	191	29
	612	2-28	No	1-3	310	31
	671	7-6	No	1-4	183	20
2	647	6-6	Yes	1-7	216	19
	620	4-2	No	1-10	284	21
	627	4-26	No	1-16	266	24
3	652	6-9	Yes	1-19	225	18
	688	7-26	Yes	1-21	180	22
	664	6-17	Yes	1-22	220	27
4	666	6-21	No	1-24	218	21
	642	5-26	No	1-25	245	20
	679	7-21	Yes	1-26	190	23
5	674	7-7	Yes	1-28	206	21
	684	7-25	Yes	1-30	190	19
	699	7-28	Yes	2-1	189	24

Table 14

T/D Scores for Males on Test One

Replication	Trial	Trial winner	Trial rating	Other birds in trial	Encounters lost by winner	Final rating
1	1	669	1	671, 612	0	1
	2	671	1	612	0	2
					(612)	3*
2	1	620	1	627, 647	0	1
	2	627	1	647	0	2
					(647)	3*
3	1	664	1	688, 652	0	1
	2	688	1	652	0	2
					(652)	3*
4	1	666	1	679, 642	0	1
	2	679	1	642	0	2
					(642)	3*
5	1	699	1	674, 684	0	1
	2	674	1	684	0	2
					(684)	3*

*T/D ratings of 3 are obtained by those birds who failed to win either of the trials in their replication.

Table 15

T/D Scores for Males on Test Two

Replication	Trial	Trial winner	Trial rating	Other birds in trial	Encounters lost by winner	Final rating
	1	671	1	612	0	2
1	2	669	1	671, 612	0	1
						(612) 3*
	1	627	1	647	0	2
2	2	620	1	627, 647	0	1
						(647) 3*
	1	688	1	652	0	2
3	2	664	1	688, 652	0	1
						(652) 3*
	1	679	1	642	0	2
4	2	666	1	679, 642	0	1
						(642) 3*
	1	674	1	684	0	2
5	2	699	1	674, 684	0	1
						(684) 3*

*T/D ratings of 3 are obtained by those birds who failed to win either of the trials in their replication.