



Genetic and physiological aspects of mating behavior in Japanese quail (*Coturnix coturnix japonica*)
by Siegfried Mahn

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY in Genetics

Montana State University

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Abstract:

In a study involving 419 male and 618 female Japanese quail (*Coturnix coturnix japonica*) selection pressure was applied for five generations to increase and decrease mating activity in the males. The males only were tested and the females were drawn at random from the control group. The high and low line were clearly separated in the first generation (G-1) and remained significantly different to the end of the experiment. Though the difference between the mean scores of the high and low line remained significantly different in all generations except the G-2, no further progress was made in widening the difference. The lack of further progress was attributed to one or a combination of factors such as the use of an inadequate selection index, small number of segregating alleles, small population size, selection in one sex only and a decrease in the number of families.

The absolute difference between the mean scores of the high and low line remained about the same to the G-5 but the average scores declined in the last two generations. This decline was attributed to environmental effect, the increasing number of males not contributing to the score, and a shift in selection pressure. In the high line, a shift in selection pressure seems to have occurred with the result that greater emphasis was placed on mating behaviors with lower positive numerical values (picking, mounting, courting). In the low line, the mating score index consisted to an increasing extent of displacement activities rather than copulations.

In the fifth generation (G-5), the high and low line differed considerably in their reaction to being handled. The low group males and females were wilder and more excitable than the high group males and females. The low line males also became more "timid" as the study progressed.

Courting displays occurred predominantly after copulation. The five generations of selection for increased and decreased mating activity did not change any of the measured physiological characters (I131 uptake, BMR, hatchability, post-hatch mortality, body weights, testes weight, anesthetic out-time, hematocrit, and heart rate). The heritability estimates of the non-selected traits followed those reported in the literature when comparisons were possible. I131 uptake very probably estimated the level of endogenous PBI rather than the inverse of it.

In the fifth generation, the low line females matured later and laid at a lower rate than the high line females. Egg weight was significantly positively correlated with rate of production.

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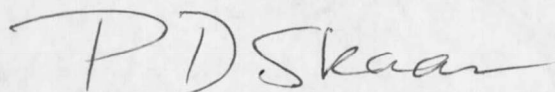
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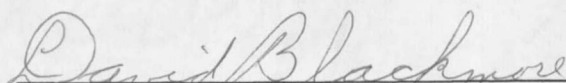
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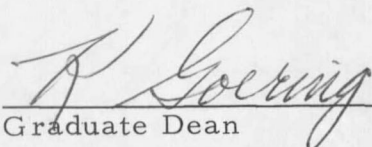
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ABSTRACT

In a study involving 419 male and 618 female Japanese quail (*Coturnix coturnix japonica*) selection pressure was applied for five generations to increase and decrease mating activity in the males. The males only were tested and the females were drawn at random from the control group. The high and low line were clearly separated in the first generation (G-1) and remained significantly different to the end of the experiment. Though the difference between the mean scores of the high and low line remained significantly different in all generations except the G-2, no further progress was made in widening the difference. The lack of further progress was attributed to one or a combination of factors such as the use of an inadequate selection index, small number of segregating alleles, small population size, selection in one sex only and a decrease in the number of families.

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INTRODUCTION

Adequate sexual behavior is very important in reproduction. It has been observed that some bulls lose their usefulness as semen donors due to their decreased response to teaser animals (Kerruish, 1955). This problem could perhaps be overcome by selection for increased sexual activity or sexual drive if a genetic difference exists. Greater sexual activity in response to selection has been observed by Rasmussen (1952), Wood-Gush and Osborne (1956), Manning (1961, 1963), Parson (1964), Fulker (1966), and others. Relatively little has been reported about changes in associated physiological parameters as selection for increased sexual activity continues. Reduction in fertility of sexually highly active males has been indicated by Parker et al (1942), Rasmussen (1952), and Fomin et al (1963).

Japanese quail (Coturnix coturnix japonica) are very suitable for selection studies and the determination of physiological characters. Findings obtained from studies of this bird may be applicable to other birds, particularly domestic fowl. Genetic correlations between selected and unselected characters may also give an indication of the responses to expect when selection for higher sexual activity is undertaken.

in larger domestic animals.

This study was undertaken to observe possible associated changes in certain physiological characters when selection pressure is applied to a behavioral character, in this case mating propensity.

REVIEW OF LITERATURE

Japanese quail (Coturnix coturnix japonica) were chosen because they are relatively small, require little space; have a short generation interval; and have enough sexual dimorphism for easy identification.

Coturnix belong to the same order (Galliformes) as chickens and turkeys. They belong in the same family (Phasianidae) with partridges (Perdix), pheasants (Phasianus), and bob white quail (Colinus). However, Colinus and Coturnix are classified in different subfamilies, Odontophorinae and Phasianinae, respectively (Storer, 1960) cited by Sachs (1966b). Mainardi (1959) has questioned the validity of this division.

The Coturnix of Europe and North Africa are classified as Coturnix Coturnix coturnix, whereas the Asian form is Coturnix coturnix japonica. There has been some question as to whether the Asian and European quail are really distinct races or belong to a Rassenkreis (Stanford,

1957). Coturnix have a long history and were esteemed as good food as early as the Merovingina times (500-750 A. D.) (Zeuner, 1963).

Japanese quail have been domesticated at least since the end of the sixteenth century. Intensive breeding for eggs and meat was started from the basis of those domesticated, and probably also wild quail at the turn of the twentieth century (Shimakura, 1940); approximately 200 generations have passed since then.

In the laboratory, under appropriate conditions, one can obtain fertile eggs all year around with some fluctuation in fertility (Beach and Inman, 1965). In the wild, the quail usually raise one brood of young, but some hens sit a second, though rarely a third time in one season (Stevens, 1961).

I. MATING BEHAVIOR OF QUAIL

Mating behavior in the wild has not been described well. Bannerman (1963) wrote that migration occurs in unisexual flocks, the males arriving first to establish territories. The females follow and without concern for the males establish nest sites. When a suitable location has been found, the female calls and usually the male in the territory closest to her will mate with her. Copulation may be preceded by short vertical flights and vocalization by both mates. Courtship, other than those flights was not indicated.

Descriptions of the courting and mating behavior of quail in the laboratory have been provided by Beach and Inman (1965) and Farris (1967). They indicated that courting may occur before and/or after copulation. Either the male or the female may take the initiative. The male will often "strut" during the approach, i. e., walk stiff-legged and up on his toes, the neck extended forward almost horizontally with the head cocked towards the female. His feathers are erect, and the wing facing the female is more or less depressed as he circles the female. The female's approach begins with picking at the male in the general forward area of the body or she may rub past under his neck and against his breast. The female may show lordosis, but the male is not deterred when this feature is absent: the male then grabs the female by the feathers or skin of the head or neck. This orientation gives the correct line-up and he will quickly mount and copulate. After cloacal contact is achieved, the male, or both birds, may fall. Dismounting is most often followed with fluffing of the feathers by the male, and shaking. Strutting may also occur after dismounting.

II. MATING BEHAVIOR OF OTHER ANIMALS

Mating behavior has been studied in many different animals. Schein and Hale (1965), Smith (1956), and Guhl (1961) indicated that every step

in the sequence of mating behavior is governed by stimuli that first serve to bring potential mates in proximity of each other (broadcast stimuli), then to establish mating pairs (identification stimuli), and then to coordinate the species-specific motor patterns of each partner so that fertilization will have a high probability of occurring (synchronization stimuli).

For mammals, Schein and Hale (1965) suggested that sequences of sexual responses over time are not based upon fluctuations in sex drive, thresholds or sexual deprivation. The entire sequence of events is based on the amount of novelty in the situation and the only ceiling on sexual responses is that established in terms of the organism's capacity to identify novelty (Goy and Jakway, 1962). But novelty is a feature which evokes avoidance in rats (Kagan and Beach, 1953). Flight from novelty is automatic and indiscriminating, and has survival value for wild rats. In the cockroach, novelty will maintain exploration: children, like monkeys, will readily learn a simple task when the only reward is the sight of something novel (c.f. Hale and Almquist, 1960; Barnett, 1967).

The sources of display or courtship movements include: 1. Intention movements, 2. Displacement activities, and 3. Redirected activities

(Hafez, 1962). Courtship patterns of birds are essentially identification stimuli. Usually receptive female turkeys solicit in the presence of a displaying male; the male responds most strongly to the female's head. Schein and Hale (1965) suggested that the difference between chickens and turkeys is due to the fact that the latter are more deliberate and the former are more agile. Roosters can see more of the hen during the copulation than the turkey tom (c.f. Carbaugh et al., 1962). Some strains of turkeys extend their sexual responses to humans and thereby show less specificity of sexual choice than other strains reared under identical conditions. Since the F_1 between such strains is intermediate in specificity, a genetic basis has to be assumed for this difference (Schein and Hale, 1959, 1965).

Form, posture and color together elicit the mating response in the Brewer's Blackbird (Icteridae), but none of the factors alone was sufficient. Howell and Bartholomew (1952) concluded from the reaction of the males to dummies from which different parts had been removed, that the tail is probably the most important feature in mating posture.

Courting with hissing is done by both male and female ruffed grouse (Bonasa umbellus L.). Allen (1934) suggested that these birds do not

recognize sex as such and that the intimidation display is a matter of relative strength. In their mating display, in contrast to many other birds, their feathers are depressed instead of ruffled and their tails drag on the ground. The male walks slowly and upon approaching another bird, gently picks at the base of the beak. Domination and fear are the important principles in the control of the mating cycle and in the development of secondary sexual characters.

Copulations without preliminaries have been observed in the Yellowhammer (Emberiza citirnella) and other Buntings. The female solicits when the male approaches. Copulation attempts may be broken off due to the increase of fear in the male as he comes closer to the female. The male either hovers above the female or lands directly on her back. After a few seconds he copulates and flies away. The males of these species sometimes mount from the ground after courtship displays and make violent attempts to copulate, during which they seize the females by the nape or back. The copulation call and accompanying postures of the Corn Bunting (Emberiza calandra) suggest that originally in this species the male had the tendency to attack as he approached to copulate (Andrew, 1956).

Zebra finches (Poephila guttata) are strongly dimorphic and yet form pair bonds (Morris, 1954). Courting does not take place without song, although there may be song without courting. In courting, the male moves as to exhibit all the markings which are particularly male. After dismounting, both birds will often preen. Raping may occur when a female comes into the territory of a mated pair and then the new female seems to be a stronger sex stimulus than the paired one.

Male and female sexual responses share certain short term causal factors (Seward, 1941). The soliciting of the male Yellowhammer is an example of compromise behavior since it expresses the sexual tendency, but, being a stationary display, permits the male to avoid the female and so is compatible with strong fear of her (Andrew, 1956).

Darwin (1874) stated that when males have harems, they are much larger than the females, but they are of about equal size when monogamous. Birds with greater color dimorphism tend to be polygamous. He quotes Audubon as writing that "when several males of the Virginian Goatsucker (Caprimulgus virginianus) court, in a highly entertaining manner, the female, and no sooner has she made her choice, than her approved gives chase to all intruders, and drives them beyond his dominions."

Darwin considered that females of the pea fowl (Pavo cristatus) and the wild turkey (Meleagris gallopavo) make the choice of a mate by fighting, or even courting the male to gain his possession.

Elaborate post-coital displays have been attributed to the European Avocet (Recurvirostra avosetta) . by Marler and Hamilton (1966) which may trigger ovulation. The male and female start copulation by picking at their feathers or the water (they usually mate in shallow water) and make similar movements when on land. Preening by the mates always precedes copulation, but not all preenings lead to copulation. Excitement seems to be important as the Avocets frequently mate after a fight or other disturbance. There is no raping. After copulation, the birds may hold each other's bill and run together for a short distance. Makking (1936) disagreed with Domm and Davis (1948) that sex recognition is by behavior only as he observed no wrong pairings.

The rear approach of the male toward the female gives the best orientation for mounting in the White Leghorn fowl (Guhl, 1961). Waltzes and wing-flutter were most common when the potential mates were unacquainted. These behaviors are associated with sex drive and should be considered displacement activities. If a White Leghorn male has a high

sex drive, he may approach a female and mount and tread before the female crouches (Guhl, 1951).

Hinde (1954), Morris (1954), Andrew (1956), Wood-Gush (1956) considered that all courtship behaviors are a result of the tendencies to attack, flee, and behave sexually towards the mate. In the Greenfinch (Chloris chloris chloris), the most frequent form of redirected activity was bill-wiping; and Hinde (1953) suggested that the male's soliciting after copulation involves the thwarted tendency to flee.

Tidbitting is done in a conflict situation by Brown Leghorn and is more frequent when the male is molting or his sexual activity is low for some other reason (Wood-Gush, 1956). He also indicated that the display of the cock includes at least two groups of behaviors, depending on the overt female reaction. First, he intimidates the female, and then he entices and pacifies her. To behave sexually, therefore, must involve first a suppression of aggressiveness and later the tendency to flee.

Greater sexual activity and courting was observed in male chickens of different breeds that had been raised in all male flocks or maintained in individual cages (Parker et al, 1940; Wood-Gush, 1956; Siegel and Siegel, 1964).

It has been proposed (Young, 1957) that patterns of sexual behavior have a somatic basis and that the character of the behavior displayed depends on the character of the soma or the substrate on which the hormones act. In guinea pigs, contact with other animals is important, if not necessary for the development or organization of the complete pattern of sexual behavior (Valenstein and Goy, 1957). The genetic background may impose limitations which neither the experiential factor, nor any action of gonadal hormones can overcome. It is rare for a male guinea pig to be interested in a female after having achieved ejaculation, and only in about one percent of the time, a second ejaculation is achieved (Young and Grunt, 1951).

Like the caged roosters of Parket et al (1940) and Guhl (1961), isolated guinea pig males engage in more sexually exploratory behavior such as sniffing and licking. It is not isolation per se that prevents a male from displaying the full sexual pattern as long as the behavioral skills had been acquired previously (Valenstein and Goy, 1957). Valenstein et al (1955) explained the sustained exploratory behavior on the basis that the sexual behavior of the isolated males had not been organized into an effective pattern, which the social animals had a chance to develop. Experience

with the broad environment is more important than with species-mates to facilitate copulation in the platyfish (Xyphophorus maculatus) (Shaw, 1962).

Visual stimuli are the most important cues influencing courtship behavior in the fruit fly, Drosophila subobscura. Mating does not take place in the dark, and in contrast to other males of the obscura group, males will attempt to mate with wax models, provided they are moved in an appropriate manner (Smith, 1956). As the male approaches, he extends his proboscis and dances. The sequence may end there if the female does not respond positively. If she does, the male then circles and mounts. The courtship may be a ritualized escape or avoidance movement. Discouragement of males may come about by inseminated females or by females kept with other males. In the latter case, the discouragement is only temporary. Males inbred for 18 generations had greater difficulty to complete courtship than outbred males. If they were thwarted a few times, they attempted to approach the female from the side or from behind to mate directly, which was never observed in the outbred males. Smith (1956) considered this as desperation rather than discouragement. The inbreds were considered physically not as fit as the outbred males.

For most classes of vertebrates, it is generally agreed that both sexes actively cooperate in courtship and that male adornment, posturing, and sounds are essential to the courtship pattern. Evans (1938) corroborated these findings in his observations on the lizards, Anolis carolinensis and A. sagrai. However, Noble and Bradley (1933) reported that female lizards never show interest in the courtship or copulation, and while they may be quieted by the actions of the courting male, they never take an active part in facilitating copulation. The latter authors considered, in contrast to Evans, that the bright colored dewlap of Anolis evolved as a frightening device, and not at all to stimulate the female to mate.

III. FACTORS AND CONDITIONS AFFECTING SEXUAL BEHAVIOR

A. GENETIC

That behavior is under genetic control has been well established from the following observations: 1. Mutations at certain loci can change behavior, 2. Different inbred strains differ in morphological and behavioral characters, 3. One can successfully select in the positive and negative direction for a behavioral trait (Caspari, 1958). But no behavior is inherited; its capacity is developed through growth and maturation and is organized by hereditary factors and learning (Hafez, 1962).

Sir Francis Galton began in 1869 to study the inheritance of mental capacities in twins (Broadhurst, 1960). Tyron called behavior genetics the basic science of individual differences. The relation between behavioral variation and relevant genetic variation is never constant. Behaviors must be measured in specific populations and under specific conditions, as they vary with both (Harch, 1965).

Rasmussen (1952), Siegel and Siegel (1964), Wood-Gush (1956), Guhl (1951), and Manning (1961, 1963) have been able to successfully select for increased and decreased sexual behavior in different organisms. However, in general, there seems to have been a lag period before the lines diverged (c. f. Mather, 1960).

Lorenz (1958) showed that hybridization of two species of ducks varying in wildness may lead to the suppression of some parental traits in courtship behavior, or to the exposure of some patterns not seen in either parent.

Genetic differences between strains of guinea pigs are responsible for differences in the age at which organization of sexual behavior may take place, and for the amount of sexual excitement exhibited during tests. These genetic differences are not overcome by the administration

of large quantities of exogenous androgen (Valenstein et al, 1955).

Inbreeding Drosophila subobscura for 18 generations resulted in a reduction of male fertility. These males were also found to be deficient in the quality and quantity of sperm produced compared to outbred males. Environmental and experiential factors seem to contribute to this difference (Smith, 1956).

Factors which are of evolutionary and reproductive significance (size, viability, fertility, etc.) are generally inherited polygenically; their final expression depends on the action and interaction of many genes on which the effects of the environment are superimposed. Since in polygenic blocks there are several or many genes, mutations affecting characters determined by these blocks will be relatively frequent; therefore, polygenic characters may be considered to be not very stable in populations (Caspari, 1958).

When searching for genetic bases of sex behavior, it is important to realize that there are individual differences, and that the performance of the individual varies from test to test. That the limits of the phenotypic expression of elements in sexual behavior are set by the genome is strongly suggested by the consistency of individual differences found in genetically heterogeneous populations (Beach, 1942). The hereditary

nature of libido has been established in female sheep (Hafez, 1951, 1952), and bulls (Frazer, 1957, 1960).

Hybrids obtained in the laboratory between two subspecies of Drosophila paulistorum possess a genetic constitution which is so discordant that the hybrid females repel the courtship of all males. The hybrid males will court but are rejected by almost all females (Ehrman, 1960). A balancing mechanism was found by Sheppard (1953). In the moth Panaxia dominula individuals carrying the gene "medionegra" mate preferentially with partners not carrying this gene. Crosses between three South American species of Drosophila paulistorum resulted in the production of fertile female and sterile male hybrids, which was found to depend on the genotype of the mother (Ehrman, 1960).

Individual genes have been shown to affect mating behavior in Drosophila melanogaster. Reed and Reed (1950) showed that the presence of the gene w (white eye) decreased mating frequency by 25%. Rendel (1951) found that the gene e (ebony) reduced the mating activity of homozygous males in the light, whereas in the dark they were equal to, or better than, the vestigial control males. Bastock (1956) found that y (yellow) reduced the effectiveness of mating in that these males are slower and less active than the controls. Females carrying the domin-

ant y became more receptive after seven generations of selection, which may have been a secondary adaptation to compensate for the deficient courtship of the males. Crawford and Smyth (1961) found that Fayoumi fowl females with columbian pattern have a higher social rank and show greater sexual response than those with barred pattern. Fuller (1967) found that C57BL/6J mice homozygous cc (albino) sired smaller litters than the pigmented (Cc or CC) males. The primary defect of the cc animals is a diminution of tyrosinase and dopa oxidase in the skin. Dopa is the precursor of norepinephrine and it is conceivable that the observed behavioral effects are due to an imbalance of catecholamines in the central nervous system, rather than due to peripheral effects of the gene.

Particular chromosome arrangements have been proposed as the basis for differences in geotaxis (Hirsch and Erlenmeyer-Kimling, 1962) and also mating behavior in Drosophila (Kaul and Parsons, 1965; Parsons and Kaul, 1966; Prakash, 1967; and Spiess and Spiess, 1967) and in the white-throated sparrow (Zonotrichia albicollis) (Thornycroft, 1966). The authors concluded that the chromosomal arrangements as found in the natural populations are best adapted for reproductive fitness, though environmental conditions (food, temperature, age at mating) will

exert a considerable influence (Spiess and Spiess, 1967).

There is strong natural selection for high mating speed in Drosophila. This was indicated by asymmetrical selection response. Much greater response was observed in the downward than in the upward direction and the high line was much closer to the controls (Manning, 1961, 1963; Prakash, 1967).

Prakash (1967) invoked the following mechanisms to explain the stability of the gene frequency, and therefore the mean mating speed in natural populations:

1. Heterozygotes for the genes which affect male mating speed exhibit overdominance which ensures both the maintenance of genetic variability and the mean mating speed at a stable value. Counterbalance in another component of fitness as mating speed increases could give an intermediate phenotype the greater overall fitness.
2. Stability of the gene frequency and the mean mating speed in a population may be maintained by recurrent mutations.
3. The stability of the genetic variability and the mean mating speed could be maintained by frequency-dependent selection of mating speed. As the frequency of high-mating speed genes increases, the mating speed decreases and vice versa. Such frequency-dependent selection for mating activity has been demonstrated in Drosophila pseudoobscura.

B. PHYSIOLOGIC

Physiological effects on mating behavior are multiple and cover any or all factors from neurophysiology to the size of the animal. Several of these factors are considered, though there are probably many which have not been identified, or their significance is unknown.

1. HORMONES

That gonadal hormones influence behavior, and particularly sexual behavior, has been known for a long time. Men were castrated as early as the beginning of the Byzantine Empire (450 A. D.) (Encyclopaedia International, 1966) and trusted as harem guards. The fact that animals become more docile after castration has been observed, and castration is widely practiced in animal production (Mumford, 1917; Aronson, 1959, 1965).

Hormones may act at the molecular level by: 1. Changing the properties of the membranes of mitochondria. 2. Inducing an allosteric change in the conformation of a protein molecule in order to alter its enzymatic activity. 3. Altering the rate of synthesis of a specific protein. 4. Serving as a co-substrate in a specific enzymatic reaction. 5. Initiating the transcription of a specific section of DNA. The last mechanism seemed to be involved in the response of blowfly larvae to

ecdysone, the effects of androgens on the ventral prostate of the rat, and the effects of estrogens on the endometrium of the rat's uterus. RNA extracted from the seminal vesicle of one rat can, after being instilled into the lumen of the seminal vesicle of another rat, lead to a response similar to that induced by testosterone. Denatured RNA did not bring about the response. Chironomus larvae injected with ecdysone show a characteristic pattern of puffing of the Balbiani rings (Karlson, 1962, a, b). Liao and Williams, and Ashman (cited by Villet, 1967) suggested that testosterone increased the synthesis of mRNA in the rat's prostate and so affected the rate of protein synthesis (c.f. Frieden, 1964; Tata, 1964).

some of the earliest work with hormone injections was done by Domm and van Dyke (1932), who used hebin on three-day old male chicks. They observed crowing six days later, and after ten days, treading. Further similar studies were done by Hamilton (1938), Allee et al (1939), Breneman (1939), Noble and Zitrin (1942), Beach (1948), Nalbandov and Baum (1948), Mason (1952), Herrick and Adams (1956), all in domestic fowl; Bennett (1940) in ring doves, and Schein and Hale (1959, 1965) in turkeys.

Females of the Wilson's Phalarope (Steganopus tricolor) resemble

in many respects (color, display, territoriality) males of other species (Dyrenfurth and Höhn, 1963; Höhn and Cheng, 1967). Qualitative analyses of the testicular and ovarian hormones of these birds showed that the ovarian testosterone content exceeded that of the testes. Domestic fowl and the Mallard (Anas platyrhynchos), which show obvious male dominance, had a higher level of testosterone on the testes than in the ovaries (c.f. Phillips and McKinney, (1962).

Dipping hatching eggs into a solution of ethyl alcohol with two per cent testosterone added affected the organization of sexual behavior in males hatched from eggs so treated. Only one of ten such males mated, but semen from three of four such males fertilized eggs. The failure to mate may have been caused by a hormonal imbalance or a defective neural mechanism (Glick, 1956). Injection of estrogen into eggs on the fourth day of incubation resulted in males with behaviors ranging from essentially normal to definitely neutral at 22-24 months of age (Domm and Davis, 1948).

Phoenix et al (1965) injected testosterone propionate into pregnant guinea pigs. The females born from such mothers showed greatly reduced capacity to display lordosis following administration of estrogen and progesterone, but male-like mounting behavior was shown by many

of them. The male siblings showed no structural abnormalities and their behavior was essentially normal (c.f. Boss, 1943; Witschi, 1959).

Goldstein (1957) suggested that gonadal hormones have a general effect on male or female sexual patterns and a specific effect acting primarily on the native pattern. Wolfson (1954) concluded that androgens play an important role in the regulation of the activity and size of the secondary sex organs.

Allatectomy, gonadectomy, and a combination of both do not influence the mating behavior of male or female wax moths (Galleria monella). Implantation of additional corpora allata in pupae or adults also had no effect (Roeller et al, 1963). However, Engelmann (1960) and Loher (1961) found that allatectomy in Madeira cockroaches (Leucophaea maderae) and Mediterranean grasshoppers (Schistocirca gregaria) respectively, reduced or eliminated mating behavior.

Removal of one testis did not change the mating behavior of male quail, but bilateral castration eliminated copulation within eight days. Replacement with an androgen pellet restored the full behavior within eight days. Crowing and strutting did not change (Beach and Inman, 1965).

In addition to the effects of gonadal hormones, the effects of thyroxine on mating behavior have been of particular interest to several inves-

tigators. Anderson and Anderson (1938) found a tendency for the thyroid secretion to be positively correlated with emotional tests of rats and negatively with tests of sexual behavior (c.f. Lashley, 1924).

Peterson et al (1952) found in guinea pigs that the sensitivity of many of the reproductive tissues to hormonal stimulation may be influenced by the level of thyroid activity. The results were equivocal (c.f. Salmon, 1936; Young et al, 1952; Valenstein, 1955), but fertility was decreased in both sexes after thyroidectomy.

For fowl, Crew (1925) reported an acceleration of gonad activity upon injection of thyroxine in physiological doses, and Benoit and Aron (1934) found that thyroidectomy had an inhibiting effect on the endocrine and gametogenic activity of the testes of White Leghorns (c.f. Greenwood and Chu, 1939). Large quantities of thyroxine caused hens to molt, but smaller doses depressed sexual activity which Collias (1946) attributed to increased nervousness and sensitivity of the skin. The thyroid appears to have a general calorigenic effect and specific action on other hormones (Blivaiss, 1947).

Other hormones, particularly those of the pituitary and adrenal glands, have not been thoroughly investigated as to their effect on sex-

ual behavior. Some work has been reported for fowl (Anderson and Anderson, 1938) and for guinea pigs (Jakway, 1959).

2. OTHER FACTORS

Some of the most important factors affecting sexual behavior in birds are the biological cycles, light and dark periods, and the conditions related to those factors, such as temperature, availability of food, etc. (Morgan, 1965; Barnett, 1967).

It is the total amount of relevant sensory stimulation rather than any particular kind of stimulation that arouses sexual behavior and allows reproduction to take place (Hinde, 1965). Photoperiodic control of reproductive cycles in various birds has been reviewed by Lehrman (1959), Marshall (1959), and Witschi (1959). Reports about particular species were presented by Farner (1964) for the white-throated sparrow; Marshall (1961) for Quelea quelea; Karapetian (1955) for the guinea fowl; Konishi (1967) for the Japanese quail; Kirkpatrick and Leopold (1952) for the bobwhite quail; Lehrman (1965) for the ring dove; Bisonette (1932) for the starling; and Dol'nik (1964) for Fringilla coelebs coelebs.

Ewing (1961) found that Drosophila melanogaster males, selected for large and small body size, differed in their courtship behavior. There was a negative correlation between body weight and vibration. But males

