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EFFECTS OF CASTRATION AND ANDROGEN REPLACEMENT ON MATING IN MALE QUAIL*

BY FRANK A. BEACH AND NELSON G. INMAN

UNIVERSITY OF CALIFORNIA, BERKELEY

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The copulatory behavior of male mammals of several species is known to depend upon testicular hormone,[1] and although birds have been less extensively and intensively investigated, it is established that in this group also castration adversely affects copulation as well as those precopulatory responses collectively termed "courtship."[2–10] The present study was undertaken to examine the effects of androgen upon sexual behavior in an avian species which has been employed extensively in a variety of biological investigations[11] and which promises to become unusually useful for experiments on behavior.[12]

Subjects and Method.—Subjects: The birds used in this experiment belonged to the species *Coturnix coturnix japonica*, usually referred to as the Japanese quail. The birds are small (100–125 gm), easily maintained in the laboratory, and extraordinarily fecund. Both sexes reach reproductive maturity 30–40 days after hatching and will breed 12 months of the year when kept under appropriate lighting conditions. As noted earlier, the species has proved valuable for the investigation of a wide variety of biological problems, but, with a few exceptions,[13–17] its behavior has not been systematically studied.

Our animals were derived from a stock (strain 908) bred and maintained at the University of California in Davis. They were kept in individual, metal cages $9^3/_4$ in. long × 7 in. high × $7^1/_8$ in. wide, in which Purina Game Bird Chow and water were always available. The living cages and experimental apparatus were situated in a windowless room illuminated from 6:00 A.M. to 10:00 P.M. and darkened during the remaining 8 hr. All birds were adult when testing began.

Schedule of testing and treatment: The ten experimental males were observed in a series of preliminary tests with females selected for readiness to mate. During these tests, which occurred over a period of 1–3 months for different individuals, the principal elements in the mating patterns of both sexes were identified and reduced to a quantifiable scoring system. At the same time, optimal conditions for the elicitation and observation of sexual behavior were determined and a standard testing procedure was established.

Following this exploratory phase of the study, every animal was observed in three "control" tests. After the first or second of these tests, each male was unilaterally castrated. While the subject was under ether anesthesia, the testis was exposed by a lateral approach between the last two ribs. The tunica was slit and all testicular material was removed by aspiration. Behavior in tests following removal of one testis did not differ from that shown preoperatively and for this reason results obtained in these two conditions have been combined and contrasted with data collected during tests following removal of the second gonad. Lack of deleterious effects consequent to unilateral castration also serves as a partial control for temporary decline in behavior referrable to surgical shock.

The three control tests were distributed over a period of 3 weeks for half of the subjects and for 8 weeks in the case of the remaining five birds. After the last control tests, each male was reoperated and the remaining testis removed.

Regular testing for mating behavior was resumed for all birds within 8 days after complete castration, by which time copulatory responses had completely disappeared. Each animal was tested three times between the eighth and thirty-sixth postoperative days without the occurrence of any of the elements of the normal mating pattern.

Following the third negative test, each male received an intramuscular implant consisting of a small pellet of testosterone propionate.[18] This occurred from 24 to 42 days after complete castration in different individuals, the median interval being 28 days. Mating tests continued until sexual behavior had been restored to precastrational levels.

For five of the ten subjects, testing continued for 3 months after implantation of the hormone pellet. By this time they had ceased to copulate and a second pellet of testosterone propionate was implanted intramuscularly. Tests for sexual behavior were carried on for 4 weeks following the second treatment.

Test apparatus and procedure: A variety of testing procedures and observational conditions were explored during the preliminary stages of the study and it soon became evident that the amount and kinds of behavior obtained varied with methods of handling, conditions of illumination, and such seemingly irrelevant items as size of the testing cage. For example, a cage of ample size for testing copulatory behavior in rats proved too confining for quail, which are considerably smaller animals. In such a cage females that were initially receptive copulated once or twice at the beginning of a test and then became exceedingly aggressive, pecking and driving the male until his incipient courtship responses gave way to a continuous escape reaction. This type of female aggression did not occur when pairs were tested in an 8 × 12-ft room; and by a trial-and-error procedure, we eventually established the fact that mating without excessive aggression could be reliably evoked in a 4-ft-square wire screen cage 2 ft high.

This standard observation cage was illuminated from above by a fluorescent bulb which left the area outside the cage in dim light. Two bottomless release boxes constructed of transparent plastic and measuring 4 × 4 × 4 in. were suspended in diagonally opposite corners of the observation cage in such a manner that they could be raised quickly and silently when the experimenter lowered the appropriate counterweight.

Analysis of the results of preliminary observations permitted us to identify and score separately individual elements in the total mating patterns of both sexes, and during each test the frequencies of these separate acts were recorded. In addition, the use of automatic timers connected with each release box facilitated the measurement of latencies to be described later.

In preparation for a mating test, the experimental male was placed underneath one release box and a female selected for her willingness to mate was confined beneath the other. After a delay of not more than 60 sec, the male's release box was raised at a time when his head was pointed in the direction of the release box containing the female. The male was allowed 2 min to approach within one body length of the female's release box. If he remained this close for 3 sec, the female was released. If the male failed to approach the second release box within 2 min after his own liberation, the female was set free. Following the release of the female, the male was given 5 min to mount the female. If he did not do so within this time limit, the test was terminated. If mounting occurred within 5 min or less, testing continued for 10 min from the time of the female's release.

The measures recorded during each test and the behavior to which they applied were the following. Approach latency (APL), time from the raising of the male's release box until release of the female; mount latency (MTL), time from the release of the female until the male's first mount; head or neck grab, frequency with which the male seized in his beak the feathers or skin of the female's head or neck; mount (MT), frequency with which the male mounted the female, placing both feet on her back, and usually maintaining the grasp on her head or neck feathers; cloacal contact movement (CCM), frequency with which the mounted male lowered his posterior bringing his tail feathers beneath those of the female and his cloaca into a position ventral to hers. When the female is cooperative and the male's movement is accurate, the CCM results in juxtaposition of male and female cloacae and permits the passage of sperm into the female reproductive tract. The actual occurrence of cloacal contact cannot be visualized because the tail feathers of both birds obscure the view. For this reason, only the occurrence of the male's movement was recorded as definitely observable.

Another response frequently but not always executed by males is a special form of locomotion which we have termed "strutting." In performing the fully developed strut pattern the male walks slowly toward or around the female with his legs fully extended. At the same time his neck is stretched more or less horizontally and his head is slightly tilted, usually with the side nearest the female being lower than the contralateral one. Strutting was recorded when it occurred but was not frequent enough to serve as a reliable indicator of the male's sexual condition. It should be added, however, that all males exhibited the strut at some time during preliminary testing.

All of our subjects crowed at one time or another before castration and this response was always recorded when mating tests were in progress. However, crowing was infrequent or absent during many tests and seemed to bear no meaningful relation to reactions to the female; hence, it is not treated extensively in the following analysis of results.

The behavior of a female which is ready to copulate includes several characteristic elements. One of these is a rapid approach toward the male if he fails to approach her. In executing the approach response the female often crouches with her head oriented in the male's direction and then makes a brief but energetic run which brings her into close proximity to him. She may then peck her partner briskly once or twice (usually on the head), or she may pass directly in front of him rubbing briefly against his breast feathers. Sometimes the female positions herself before the male and pecks at or rubs against his anteroventral body surfaces. Another item in the repertoire of the receptive female is the spontaneous crouching response which consists of adopting the copulatory position in front of or beside the male even though he has not grabbed or attempted to mount.

When the male responds to any of these forms of solicitation by grabbing and mounting the female, she flexes her legs and lowers the anterior part of her body so that her back is approximately horizontal. As the mounted male executes the CCM, the female's tail feathers are deviated laterally facilitating the approximation of cloacae.

Results.—The effects of castration and androgen replacement upon each of the behavior measures were clear-cut and pronounced. In sum, all sexual activity disappeared within 8 days after removal of the testes and returned to normal within 8 days after the implantation of an androgen pellet.

Approach latency: In 29 of 30 control tests, the male approached the female's release cage within 10 sec or less after his own liberation. The range of the APL in individual tests was 2–12 sec and the median was 5.0 sec. In the course of 30 tests beginning 8 days after castration, eight of ten males never approached the female's cage within 2 min after their own release. The most common reaction was to wander slowly about the observation cage. One male approached in one of his three postoperative tests and the tenth animal approached in all three tests, but when the female was released, he made no further response to her.

The approach response reappeared in nine of the ten castrates within 3–7 days after implantation of the androgen pellet. In five birds the reaction was present on the third day, which was the first time these males had been tested after receiving the hormone. The median APL during the 15 tests in which it appeared within the first week of treatment was 5.0 sec. However, in other tests males failed to approach at all and, as noted later, other measures showed that the complete sexual pattern had not yet been restored to normal.

In 30 tests beginning 8 days after pellet implantation, every male consistently approached the female's release cage within the 2-min time limit. The APL in individual tests ranged from 5 to 16 sec, and the median was the same as the control median, i.e., 5.0 sec.

Mount latency: In general, mount latencies were quite brief. If a normal male approached the female's release cage within 2 min, he was practically certain to mount her within a few seconds after she became available. The MTL was not recorded consistently throughout the control period, but scores are available for 8 males in 16 tests. The range was 1–6 sec and the median 2.0 sec.

During the entire postoperative period before hormone replacement, there were no mounting responses despite the fact that, as recorded earlier, two birds did approach the female's release cage on three occasions.

All males mounted the female within 1 week after androgen replacement was initiated. The earliest MT response was shown by three individuals on the first day they were tested, which was the third day after implantation. The median MTL for the 16 tests in which mounting occurred during the first week of treatment was 2.0 sec. In other words, if mounting occurred at all, the latency was normal.

Mount latencies recorded during the 30 tests that began 1 week after placement of the androgen pellet ranged from 1 to 6 sec with a median of 2.0 sec which is precisely the same as the median for the control tests.

Mount frequency: It should be held in mind that mounts are, in a sense, incomplete copulations, i.e., when a male mounts and then executes the cloacal contact movement the reaction is scored as CCM rather than MT. For this reason a low MT score does not necessarily reflect a deficiency of sexual response.

In the control period mount frequencies ranged from 0 to 11 with a median value of 1.0, all males mounting without CCM in at least one test. During the postoperative tests preceding hormone treatment no mounting was displayed by any of the ten males. Seven birds mounted one to four times in tests conducted within 3–7 days after implantation of the androgen pellet, but if negative tests are included, the median frequency was 0. For tests occurring after 8 or more days of hormone treatment the range of mount frequencies was 0–16 and the median was 4.0. This is higher than the comparable score for control tests but the difference is not statistically significant by the two-tailed sign test corrected for continuity.[19]

Cloacal contact movement: Since the CCM represents our best criterion of a completed copulation, it stands as the most rigorous test of successful sexual performance. All males exhibited this response in all of the control tests. The frequency per test ranged from 1 to 16, excluding one score of 25 which we have reason to assign to observational error. The median CCM value before complete castration was 5.0.

No bird displayed the CCM in any test conducted more than 7 days after castration and before androgen administration.

All 10 subjects exhibited this reaction at least once within the first week after hormone treatment began but the frequency was appreciably below preoperative performance. Three males showed the CCM in their first post-treatment test on the third day after pellet placement. During the first 7 days following pellet implantation, the CCM occurred from one to eight times in a total of 15 tests at a median frequency of 3.0 per positive test. If negative tests are included, the median becomes 0.

The response in question was recorded in 29 of 30 tests conducted after 8 or more days of treatment. For all tests combined the range was 0–16 and the median was 5.0, both values being the same as those recorded in the control tests.

Strutting and crowing: As explained earlier, the strut response did not occur with sufficient regularity to serve as a reliable measure of sexual performance, and crowing appeared to bear no relation to the male-female interaction with which this study is concerned. Nevertheless, both strutting and crowing were affected by the experimental conditions and the results deserve brief mention.

Before bilateral castration, seven males displayed the strut at least once in a total of 15 tests. No bird strutted after gonadectomy without androgen treatment. This response reappeared after implantation of the hormone pellets. It was shown by seven individuals in 17 tests. Six of these seven had strutted preoperatively.

Five males crowed in at least one control test, and no bird did so after complete castration. After administration of androgen, crowing was displayed by four birds including three of the five that had crowed before removal of the testes.

Response of five males to reimplantation: Three months after implantation of the first pellet of testosterone propionate, each of five males was given three tests during which there were no approach responses and no mounting. A new pellet was implanted and three more tests were conducted beginning 8 days later. All subjects exhibited restoration of sexual behavior at preoperative levels. Median scores for the various measures during the original control tests and those conducted after the second implantation were as follows. APL, 5.0–4.0 sec; MTL, 1.0–2.0 sec; MT, 2.0–5.0; CCM, 7.0–8.0.

Summary.—Ten male quail (*Coturnix coturnix japonica*) were observed in a series of standardized mating tests and then castrated. Testing continued for approximately 1 month after operation. Each castrate was then implanted with a pellet of testosterone propionate and given additional behavior tests for several weeks.

All sexual responses, including even the tendency to approach the receptive female, were abolished within 8 days after gonadectomy and did not reappear until androgen replacement was instituted. Approach to the female and occasional mounting responses occurred in tests conducted 3 days after the implantation of the hormone pellets, and behavior shown 8 days after the initiation of androgen treatment was comparable in every respect to that displayed prior to castration.

Five castrates were tested for 3 months following placement of the original pellet, by which time all sexual responses had again been eliminated. These males were reimplanted and within 8 days had resumed mating at preoperative levels.

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SEMIFORMAL REPRESENTATION OF ORGANISMIC CONCEPTS

BY WALTER M. ELSASSER

DEPARTMENT OF GEOLOGY, PRINCETON UNIVERSITY

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Organismic biological theory assumes that there are certain principles pertaining to the abstract realm of "systems" which are acting in organisms but cannot be properly represented by standard physicochemical methods. The term "organismic" used here has been popularized by von Bertalanffy[1] but similar views are maintained under various names by many biologists; as a sample we mention a recent concise review by Paul Weiss.[2] A critical question to be answered is whether the system properties can be subsumed wholly under the type of relationship considered in the theory of automata (computers) or whether there are properties that cannot be described in terms of automata theory as known to us. The existence of properties of the latter type (coexisting with and extending those that can be represented by automata) constitutes a chief claim of the author's[3, 4] theory. This note presents the basic concepts in an outwardly novel form which brings out much better the possibilities of observational verification.

Given the tremendous structural and dynamical complexity of all living systems, we do not aim at rigorous mathematical methods but introduce what will be called a semiformal approach: We use a well-established language pertaining to physical theory but use it in a nonrigorous manner, that is, without inquiring how in each of the applications a well-defined algorithm is to be constructed. We find this method quite advantageous in the usual case where the complexity of biological systems forces one otherwise to an even more qualitative, purely conceptual description—or where the analysis is carried through in terms of partial systems in a manner that leaves their mutual interrelationships essentially obscure.