

## Effects of social experience on subsequent sexual performance in naïve male Japanese quail (*Coturnix japonica*)

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### ABSTRACT

On their first sexual encounter, naïve male Japanese quail will attend to and approach a female; they sometimes mount but they do not always copulate. During the second encounter, most males successfully copulate. Although sexual experience facilitates subsequent sexual interactions, sensory cues provided by females, independent of any sexual encounter, may also enhance sexual performance. To investigate whether previous exposure to a conspecific affects subsequent sexual behavior, we allowed inexperienced males to observe an empty box, or a conspecific consisting of either an experienced female or male for 2.5 min/day on 7 days. Measures of appetitive sexual behavior were recorded during these tests. On day 8, subjects were allowed to copulate with a novel female for 5 min. On the following days, all subjects were repeatedly provided with visual access to a female and allowed to mate. In the pre-copulatory trials males initially exhibited a high frequency of appetitive responses that dissipated with repetition. Pre-copulatory experience also significantly affected motivation to mate with subjects exposed to females copulating more quickly than other subjects. Post-copulatory appetitive behavior also differed between groups: control subjects showed the highest behavioral frequency followed by males exposed to females and finally males exposed to males. These data indicate that pre-copulatory social experience profoundly influences subsequent sexual behavior and probably reproductive success. This experience effect is independent of any hormonal effect (such as one resulting from changes in secretion following different social interactions) given that the subjects were castrates chronically treated with testosterone.

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### Introduction

Sexual experience in males results in an increased efficiency in reproductive behaviors, as evidenced by improved copulatory abilities, decreased latencies to approach and mate, as well as enhanced responses to female-related stimuli (strengthened partner-preference; Domjan et al., 1992; Pfaus et al., 2001; Rosenblatt, 1965). Conditioning experiments with a variety of vertebrate species have demonstrated that pairing an arbitrary stimulus or a particular context with the opportunity to observe or to copulate with a female results in decreased latencies to copulate (Domjan et al., 1986; Zamble et al., 1985), increased semen volume and sperm release during ejaculation (Domjan et al., 1998), increased number of fertilized eggs (Adkins-Regan and Mackillop, 2003; Mahometa and Domjan, 2005) and increased number of offspring (Hollis et al., 1997; Matthews et al., 2007). Even watching conspecifics of both sexes engaging in sexual or non-sexual behaviors provides information that can affect the

occurrence of subsequent reproductive behaviors (Galef and White, 2000). Animals thus learn something from their social as well as mating environment and what is learnt may have a significant influence on their subsequent reproductive success. However, all these learning abilities that have been described in species as diverse as blue gouramis, quail and rats, and their functional consequences seem to depend on subjects being able to perform the copulatory sequence (since (1), when naïve males were used, copulation served as the unconditioned stimulus [US] and (2), in the case where the US consisted of a non-copulatory exposure to a female, males had to have had at least one previous copulatory experience). An important related question is thus whether individuals also learn something from their social environment before their first sexual encounter that can affect their future sexual behavior.

Japanese quail, like many other avian species, predominantly utilize visual and auditory cues to mediate social interactions (Balthazart and Ball, 1998; Lehrman, 1965; Mills et al., 1997). On their first encounter, naïve male quail will usually attend to and approach the female. Most are able to grab her neck but they do not always succeed in completing copulation (about 60% of naïve males do achieve a full copulatory sequence on the first copulatory opportunity; personal observation). In the second encounter, most

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males successfully perform the sequence of male-typical copulatory behaviors characteristic for the species (i.e. neck grab, mount attempts, mount and cloacal contact movements; [Hutchison, 1978](#)) suggesting that the experience occurring during the first non-copulatory sexual encounters provide some information to naïve subjects that will improve their sexual performance during subsequent opportunities for sexual interactions.

The influence of pre-copulatory environmental or social cues on sexual behavior has rarely been investigated. In the present study, we sought to determine whether exposure to a female, prior to the very first copulation, confers a behavioral advantage over males pre-exposed to a male or simply handled as controls. Sexually inexperienced males were randomly assigned to three different groups that received (1) primarily visual exposure to a sexually experienced female, (2) a sexually experienced male or (3) an empty box (controls) during 2.5 min for 7 consecutive days (phase 1). On subsequent days, all animals were tested for the appetitive and consummatory aspects of male sexual behavior (phase 2). Appetitive behavior was assessed by measuring rhythmic cloacal sphincter movements (RCSM), a response displayed by sexually motivated males when they are presented with the view of a female ([Seiwert, 1994](#); [Seiwert and Adkins-Regan, 1998](#)). Knowing that naïve male quail respond differentially to the visual presentation of males or females ([Seiwert and Adkins-Regan, 1998](#)), it is anticipated that naïve subjects will produce more cloacal contractions in response to the presentation of a female than the presentation of a male or of an empty cage in the pre-copulatory phase (phase 1). If pre-copulatory exposure provides information preparing the male for future sexual encounters, males pre-exposed to a female should subsequently copulate at a higher rate and with a shorter latency than subjects from the two other groups. Similar to what has been described in other species, social interactions influence circulating concentrations of steroid hormones in quail ([Cornil et al., 2009](#); [Delville et al., 1984](#)). To test whether the observed effects depend on gonadal steroid hormone changes following social interactions, subjects were castrated and chronically treated with testosterone capsules to restore sexual behavior.

## Methods

### Subjects

Twenty-one 8 week old adult male Japanese quail (*Coturnix japonica*) served as subjects. All subjects were experimentally and sexually naïve prior to experimental procedures. Adult and sexually experienced female ( $n=22$ ) and male ( $n=7$ ) Japanese quail served as stimuli. All animals were acquired from a local breeder. Experimental subjects were acquired at approximately 3 weeks of age and were housed as a group in large cages (91-cm long, 46-cm wide and 46-cm high), physically and visually separated from male and female stimuli. Stimulus males were housed in individual cages (25-cm long, 18-cm wide and 18-cm high), while female stimuli were housed in a single larger brooder as a group. All birds were housed in the same room and thus experienced to auditory cues produced by the other birds in the room. Throughout their life in the laboratory, birds were maintained on a photoperiod simulating long summer days (14L:10D). Food and water were available *ad libitum*. All experimental protocols were approved by and carried out under the guidelines laid down by the Johns Hopkins University Animal Care and Use Committee.

### Surgical procedures and hormonal treatments

Two or three days after their arrival, all subjects were deeply anesthetized (Secobarbital, 15 mg/kg) and both testes were removed through a unilateral incision below the last rib. Ten days later

(between 5 and 6 weeks of age), subjects were implanted subcutaneously in the neck region with one testosterone filled Silastic™ capsule (Silclear™ Tubing, Degania Silicone Ltd., Degania Bet, 15130, Israel; 1.57 mm i.d.; 2.41 mm o.d.; length = 20 mm) after topical application of Lidocaine. Immediately after the capsule implantation, subjects were isolated in individual wire-mesh cages allowing visual access to their neighbors. Subjects were thus accustomed to the view of conspecific males. Throughout the experiment, subjects were periodically weighted to the nearest gram and the size of their cloacal gland, an androgen-dependent structure ([Sachs, 1967](#)), was measured with calipers (cloacal gland area = largest length × largest width in mm<sup>2</sup>). These data confirmed the efficacy of the testosterone replacement and the general health condition of the subjects.

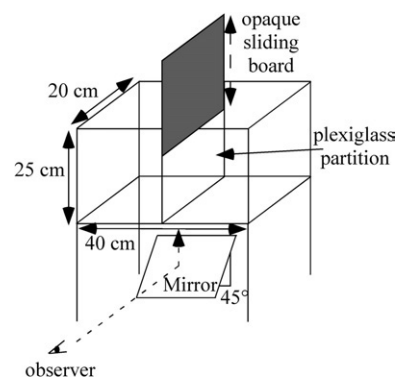
### Behavioral quantification

All behavioral manipulations were conducted in the same room. For each manipulation, subjects were transported from the aviary to the testing room in a bird carrier (box with 6 compartments designed for pigeons). They remained in the carrier until placed in the test arena.

### Appetitive sexual behavior – the rhythmic cloacal sphincter movements (RCSM)

Male quail possess a large sexually dimorphic, androgen-sensitive, external protuberance of the caudal lip of the cloaca, the cloacal or proctodeal gland ([Sachs, 1967](#)). This gland produces a stiff meringue-like foam that is transferred, along with semen, into the female's cloaca during copulation and are also deposited on top of the excreta during voiding ([Seiwert and Adkins-Regan, 1998](#)). This foam is thought to enhance the male fertilization success ([Cheng et al., 1989](#)). Rhythmic cloacal sphincter movements (RCSM) occur independently of voiding or copulation and are greatly facilitated by the view of a female. These movements whip mucoproteins secreted by the gland into the foam that will be transferred to the female's cloaca during copulation. It has been shown previously that the frequency of RCSM immediately increases in gonadally intact, sexually active males when they are provided with visual access to a female ([Absil et al., 2002](#); [Seiwert and Adkins-Regan, 1998](#)). The quantification of the RCSM frequency in reaction to the visual presentation of a female is thus considered as a reliable measure of the male's appetitive sexual behavior ([Cornil et al., 2006](#)).

The frequency of RCSM was quantified by placing subjects in an aquarium (40-cm long × 20-cm wide × 25-cm high) located on a raised platform. A mirror was located under the aquarium at a 45° angle and provided the observer with an unobstructed view of the male's cloacal area. The aquarium was divided in two equal compartments defined by a plexi-glass partition ([Fig. 1](#)). The ceiling



**Fig. 1.** Schematic representation of the aquarium used to measure the rhythmic cloacal sphincter movements (RCSM) and expose the subjects to the view of the female. See Methods for a description of the apparatus.

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