

The ram as a model for behavioral neuroendocrinology

Anne Perkins^a, Charles E. Roselli^{b,*}

^a *Psychology Department, Carroll College, Helena, MT 59625, USA*

^b *Department of Physiology and Pharmacology, Oregon Health and Sciences Univ., Portland, OR 97239, USA*

Received 26 March 2007; revised 26 March 2007; accepted 27 March 2007

Available online 31 March 2007

Abstract

The sheep offers a unique model to study male sexual behavior and sexual partner preference. Rams are seasonal breeders and show the greatest libido during short days coincident with the resumption of ovarian cyclicity in the ewe. Threshold concentrations of testosterone are required for the acquisition and display of adult sexual behavior. In addition, estrogens produced from circulating testosterone by cytochrome P450 aromatase in the preoptic area are critical for the maintenance of sexual behaviors in rams. Sex differences in adult reproductive behaviors and hormone responsiveness are the result of permanent organizational effects exerted by testosterone and its metabolites on brain development. Early exposure to ewes enhances ram sexual performance, but cannot prevent some rams from exhibiting male-oriented sexual partner preferences. Neurochemical and neuroanatomical studies suggest that male-oriented ram behavior may be a consequence of individual variations in brain sexual differentiation.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Sheep; Rams; Sexual partner preference; Aromatase; Sexually dimorphic nucleus; Preoptic area

Introduction

Scientists have used laboratory animals (primarily rats) for many years to study physiological mechanisms underlying the regulation of behavior. The information acquired from this body of work has been pivotal. The rat has been a convenient model that provides preliminary information that, at least in part, can be applicable to other species, including humans. Therefore, we have a large repository of information about the natural history and physiology of the laboratory rat. The rat, however, may not always be the best model for a particular research project. Recently the domestic sheep has become valuable as a tool for understanding sexual behavior, neural and endocrine systems related to reproduction. Although there is an abundance of information about domestic sheep, most of it is written from an animal husbandry perspective. The purpose of this article is to

review information about the natural history, behavior and physiology of the domestic ram for scientists who may be interested in using sheep as a model for their work in behavioral endocrinology and physiology. This paper will review our current understanding of the biological and social aspects of sexual behavior in domestic rams.

Domestication

Sheep were domesticated in southwest Asia around 9000 BC. There are four main breeds: the Argali (*Ovis ammon*) of central Asia, the Bighorn (*Ovis canadensis*) of North America, the Urial (*Ovis vignei*) of southwest Asia, and the Mouflon (*Ovis musimon*). Mouflon are restricted mainly to Mediterranean islands. All wild type sheep can interbreed and are considered a single species. Domestic rams can interbreed with wild type ewes if a wild ram is not present (Ryder, 1983). Scientists speculate that the Mouflon is the progenitor of all European breeds (Ryder, 1983). All domestic sheep, as well as the wild Mouflon, have 54 chromosomes (Vorontsov et al., 1972). Some modern domestic sheep could have arisen by

* Corresponding author. Fax: +1 503 494 4352.

E-mail address: rosellic@ohsu.edu (C.E. Roselli).

hybridization of other wild types such as the wild Argali ($2n=56$) followed by selection for a reduced chromosome number (Nadler et al., 1973).

Domesticating sheep did not alter their new inheritance, but rather allowed for a greater range of variation to survive. The observations of variation led to selective breeding for preferred traits such as a woolly fleece, longer tails and no horns (Ryder, 1983). Sheep breeders have used artificial selection by selective breeding over many generations. These selection criteria differ widely around the world and have resulted in numerous modern breeds.

The biological process involved in domestication probably involved “imprinting” of young lambs on a human rather than its mother. There is a critical period that lasts only for a few hours following the birth of lambs, during which lambs develop a sensory image of their mother (or substitute; for review on this topic see chapter by Nowak et al., in this issue). The ewe learns to identify her own lamb during this same critical period. It is this ability to bond to humans during a critical period along with the inherent flocking behavior of this species that contributed to the early ecological relationships between humans and sheep (Lay et al., 1971; Reed, 1977).

How to study sexual behavior in sheep

Reproductive efficiency is an important selection criterion for sheep. In a modern-day sheep operation, females that fail to become pregnant are eliminated from the flock. Rams are tested for fertility using semen evaluation and a behavioral evaluation called a “serving capacity test”. Serving capacity refers to the ability of a ram to successfully inseminate a number of ewes (preferably during the ewe’s first estrous cycle following introduction of the ram). Since the recommended stocking ratios for American sheep producers is between 1:30 and 1:50 rams to ewes, sheep producers must be certain that their rams are efficient breeders.

The serving capacity test was first developed by Mattner and colleagues in Australia (Mattner et al., 1971). These scientists defined serving capacity as “the number of matings with estrous ewes a ram achieves in a specific time period when confined to a pen of limited size.” In the basic serving capacity test, yearling rams are exposed individually to 3–4 unrestrained hormone-induced estrous ewes in 4 m × 4 m pen enclosures for a 30-min test during which the number of services (ejaculations) are recorded. Rams can be classified as either sexually active or sexually inactive after their first test with females. Sexually active rams are assigned an ejaculation score (total number of ejaculations in 30 min). Rams that are sexually active on their first test rarely become inactive. If they are tested repeatedly with females, they can be assigned a serving capacity score, which is the average number of ejaculations each ram achieves over repeated 30 min. testing periods. Rams classified as high libido show an average of 5–6 ejaculations within 30 min, whereas low libido rams perform less than 4 ejaculations. Among the sexually active rams, serving capacity scores are predictive of fertility success in pasture matings (Price, 1987). At the U.S. Sheep Experiment Station in Dubois, Idaho serving

capacity tests were routinely used to select potential sires and to identify individuals that fail to become sexually active. Hundreds of rams have been tested annually for the past 18 years. Each year approximately 20% of the rams are below optimum for selection as herd sires. There are many different reasons for poor performance during a serving capacity test.

The first major observation made during the use of the serving capacity test is the tremendous variation in sexual behavior of rams. Some rams are immediately stimulated by the ewes and begin courtship and mounting within minutes of being introduced into the testing pen. Other rams fail to even investigate the ewes and never direct courtship behaviors toward them.

Some sexually inactive rams will begin to copulate when provided with additional opportunities. These rams are typically called low sexual performers because they inseminate fewer females (Perkins et al., 1992b). Among the group of rams identified as sexually inactive, are rams that will not mount females but will mount male pen-mates. A ram that fails to become sexually active when exposed individually to at least three estrous females for 20 min on repeated occasions, and that mounts males exclusively in the presence of estrous females is classified as a male-oriented ram (see Mate preferences and sexual attraction).

A brief description of ram copulatory behavior

Sheep are polygamous breeders. Rams use olfactory cues to detect estrous ewes (Lindsay, 1965). If a receptive ewe is introduced into a pen containing a ram with prior copulatory experience, the ram will approach her within several seconds. There are several stereotyped behaviors that the ram may engage in prior to his initial mount. These include sniffing the genital region of the ewe; pawing at her flank repeatedly with his foreleg while standing behind and at a small angle to her (foreleg kick); and nuzzling, licking and nibbling at her flank and ano-genital area. Prior to copulation rams will also elevate the head and retract the upper lip in response to the odor or taste of the ewe’s urine, a behavior referred to as flehmen. The flehmen response draws non-volatile odors into the vomeronasal organ for detection by the accessory olfactory system. Some males additionally emit low-pitched ‘gargling’ vocalizations before and while pawing the ewe. The sum total of these behaviors is frequently called “courting behaviors”.

There is considerable variation among males in the frequency and duration of these precopulatory responses. It is not clear whether they play a functional role in stimulating the ewe or inducing her to stand for copulation. A fully receptive ewe stands quite still after the initial approach by the ram and will often turn her head to one side and appear to watch him. There is also a characteristic wagging of the tail (fanning) that accompanies full receptivity and which may help disperse relevant olfactory cues.

Mounting behavior in rams is accompanied by a series of shallow pelvic thrusts. Rams usually mount several times prior to vaginal penetration and ejaculation, but an experienced ram may ejaculate on the first mount. Rams are capable of multiple

Download English Version:

<https://daneshyari.com/en/article/322971>

Download Persian Version:

<https://daneshyari.com/article/322971>

[Daneshyari.com](https://daneshyari.com)