Penile Spines of the Domestic Cat:

THEIR ENDOCRINE-BEHAVIOR RELATIONS [1]

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ABSTRACT The post-natal development of penile spines, their appearance in adult males, and the changes that occur in them after castration, after treatment of castrated males with testosterone propionate, and after cessation of hormone treatment were studied using both pre and postpuberal castrates. Most of the observations were made on live animals and the conditions of the spines were correlated with levels of sexual activity using data from mating tests with estrous females. In all the conditions of testing, the spines increased in size as the androgen level increased, and decreased in size as the androgen level fell. These changes correlated positively with the rise and depression of mating activity as the androgen levels increased or decreased. The relationship, however, was not always consistent in that sexual behavior declined rapidly in some castrated males before the spines started to decrease in size, and in other castrated males, sexual behavior persisted long after the spines had disappeared. While our data are not inconsistent with the hypothesis that loss of spines leads to reduced stimulation of the penis during intromission and hence to a decline in sexual arousal, it emphasizes that the great variability in sexual behavior after castration must be due to other causes.

The glans penis of the male cat is covered by relatively large, pointed, horny spines or papillae. These spines are sensitive to androgens, and they are the only known external indicators of the level of male hormone in cats. Several descriptions of the penile spines of the intact domestic cat and other felines appear in the older literature which has been summarized by Retterer and Lelièvre ('14). The spines were not present in three postpuberally castrated male cats that were examined 3 or 7 years after operation (Retterer, 1887; Retterer and Lelièvre, '12). Reisinger ('37), on the other hand reported no changes in the spines of a male one year after postpuberal castration, but two other males prepuberally castrated at the age of one and two months did not have spines when examined at 12 years and 16 months respectively.

Spines or papillae of similar nature, but much smaller and more numerous, are also found on penises of laboratory rats and other rodents. After castration these papillae disappeared at approximately the same rate as sexual behavior declined (Beach and Levinson, '50). Likewise, small doses of testosterone given to castrates, maintained a small number of papillae and low levels of mating, while larger doses of hormone maintained more papillae and higher levels of sexual behavior. Since numerous touch corpuscles are located directly beneath the base of the papillae, these investigators concluded that the effects of castration upon sexual behavior in the male rat are due in some measure to lowering of tactile sensitivity in the glans penis as a result of deterioration of the genital papillae.

During a long term study of the endocrine relationships of sexual behavior in male cats (Rosenblatt and Aronson, '58, '58a; Cooper and Aronson, '58; Rosenblatt, '65; Aronson and Cooper, '66) we examined many living cats for the appearance of the spines, recording these photographically and by verbal description. Since even brief inspection involved restraining the animal and retracting the prepuce, while careful examination and

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TABLE 1

Stages in the development and regression of spines

Stage in development (read down)	Description	Stage in regression (read up)
1 —	Glans smooth or pitted, may have minute hair-like projections (figs. 1, 2, 9, 14, 15).	— 1
2 —	Glans with low mound-like protuberances (figs. 2, 10, 16).	
	Spines on glans very small and thin; may be fewer in number (figs. 8, 13).	— 2R
3 —	Protuberances on glans higher and knobby (fig. 5).	
	Spines on glans one-fourth adult height and thin.	— 3R
4 —	Spine-like protuberances one-half adult size; proximal row usually knobby (figs. 7, 11).	— 4
5 —	Spines approximately three-fourths adult size and pointed.	— 5
6 —	Spines large and pointed; adult appearance (figs. 6, 12).	— 6

photography required an anesthetic (Surital), or more recently, a tranquilizer (Vetame), we felt that frequent and regular examination might disrupt sexual behavior. Observations were therefore scattered, were made on only a limited number of animals from the several experiments, and were so scheduled as to cause minimal interference with the mating tests. The data that have been accumulated and that have been supplemented by dissection and histology nevertheless provide an overall picture of the relationships of the spines to hormonal status and behavior.

RESULTS

Because the spines develop or regress in response to changes in androgen level, we have outlined a series of six descriptive stages that characterize the process (table 1). For the most part, regression is the reverse of development, but certain of the intermediate stages differ and are therefore designated by the letter "R" following the stage number. The observations are summarized by group and stage in table 2.

Group I. Post-natal development of the spines. For the first 5 or 6 weeks after birth the prepuce adhered completely to the glans which could not be everted. Removal of the prepuce by dissection at four weeks revealed a perfectly smooth glans — stage 1 (fig. 1). At nine weeks the prepuce still adhered tightly, but un-

Fig. 1 Glans penis of kitten four weeks old. Prepuce is dissected away. × 4.

Fig. 2 Glans (G) of nine week old kitten. With prepuce (P) removed, shallow pits are seen on glans. App. × 2.5.

Fig. 3 Glans of 12 week kitten, PL, showing small knobby spines. × 4.7.

Fig. 4 Penis of PW at 18 weeks. Prepuce was adhering tightly and could not be everted. × 4.7.

Fig. 5 Penis of AB at 22 weeks. The prepuce was partially everted revealing knobby spines. × 4.

Fig. 6 Glans of adult male. × 4.7.

Fig. 7 Glans three weeks after postpuberal castration, showing knobby spines on proximal row. × 4.7.

Fig. 8 Glans of BA six weeks after postpuberal castration. Spines are small, thin and fewer in number. × 4.7.

Fig. 9 Glans of DU 20 weeks after castration showing minute, hair-like spines. × 4.7.

Fig. 10 The glans of SI, a postpuberal castrate, 14 days after implantation of pellet of testosterone propionate. The spines appear as low, broad knobs. × 4.7.

Fig. 11 The glans of SP, a postpuberal castrate, 14 days after implantation of pellet of testosterone propionate. The rear spines are knobby but the distal ones are already pointed. 4.7.

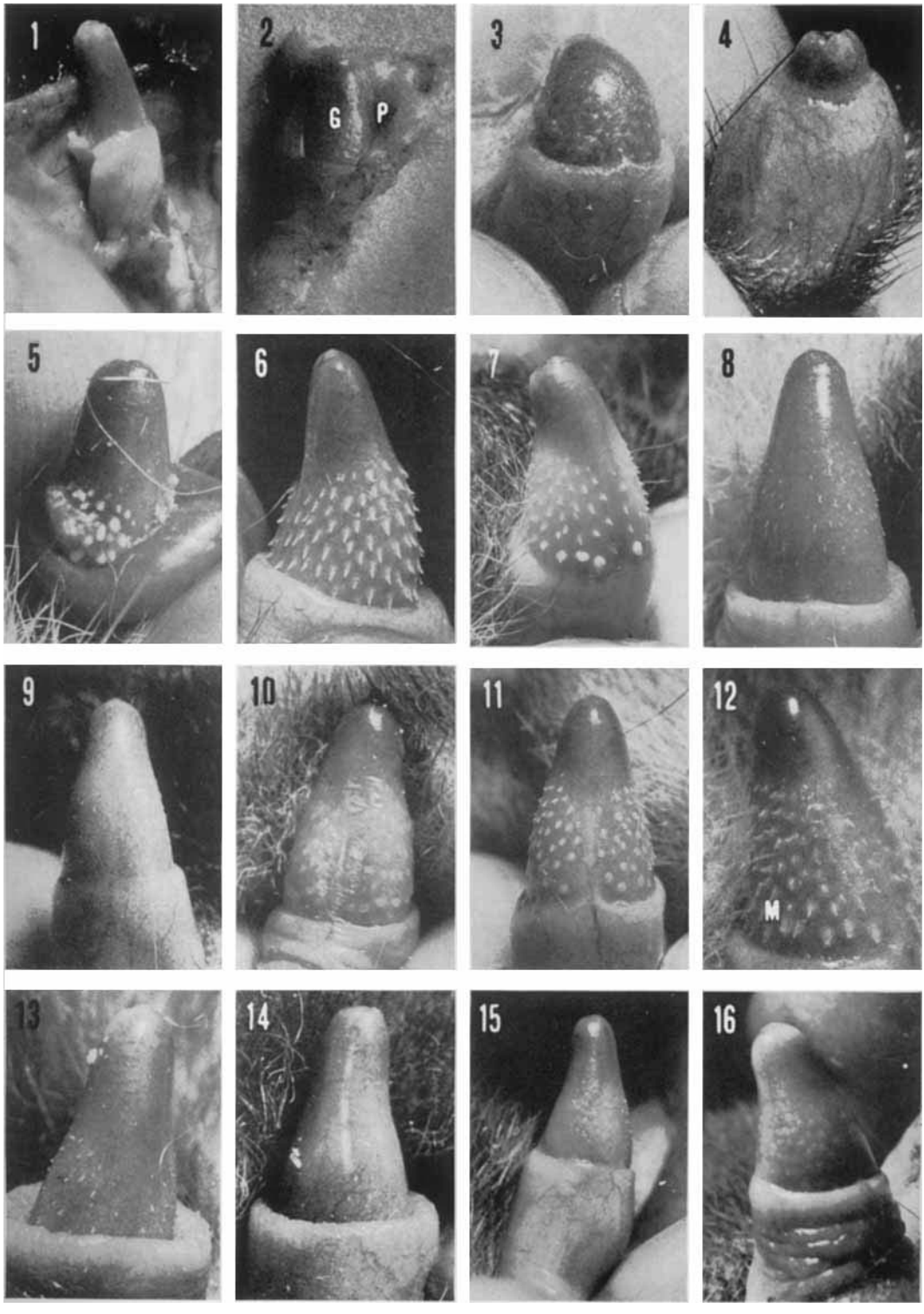
Fig. 12 The spines of SP seven weeks after start of androgen therapy have a normal adult appearance. × 4.7 (M.) multi-tipped spine.

Fig. 13 Glans of DI, a postpuberal castrate treated with testosterone propionate, six weeks after treatment stopped. The spines are small, thin a fewer in number. × 4.7.

Fig. 14 Glans of DI 16 weeks after cessation of androgen therapy. Only a few tiny spines can be seen. × 4.7.

Fig. 15 Smooth glans of a 5-year-old male prepuberally castrated when four months of age. × 4.

Fig. 16 Glans of DB, a prepuberal castrate, one week after androgen therapy started. × 4.7.



Figures 1 to 16

derneath, small, shallow pits appeared on the glans in the region where the future spines will develop — stage 1 (fig. 2). At 12 and 17 weeks respectively, the prepuce of PL and DO were partially adherent and small mound-like protuberances were observed underneath — stage 2 (fig. 3), but in males PT and PW at 18 weeks, only the blunt, smooth tips of the glans could be everted (fig. 4).

At 22 weeks the prepuce of AB could be partially everted, but where it was loose, knobby spines were revealed — stage 3 (fig. 5). At the same age the penis of UP was in stage 4 but the prepuce no longer adhered. By 25 weeks the spines of PT and PW were almost mature — stage 5. At 30 weeks, the spines of AB were mature — stage 6 (fig. 6).

When AB, PW and PT were eight months old, weekly sex tests with estrous females were started. At 25 weeks the spines of PT and PW were almost mature but the first mounts did not occur until 36 and 37 weeks respectively and the first intromissions at weeks 37 and 40. The spines of AB were matured at 30 weeks, and the first mount occurred at week 43 and the first intromission during week 45 (table 2).

The adult glans — stage 6. The prepuce is attached to the proximal end of the glans at its junction with the shaft of the penis. From here a band about 4 mm wide and consisting of approximately 120 to 150 backward pointing spines encircles the glans (fig. 6). The spines, first described in detail by Retterer and Lelièvre ('14) form 6 to 8 vaguely circular rows. Those on the proximal rows are about 0.7 mm long and many of these have broad multiple pointed tips (fig. 12, M). Those at the distal end are much smaller, some measure only 0.1 mm. The diameters at the base of the spines measure similarly from 0.7 mm proximally to 0.1 mm distally. Extending distally for another 4 mm from the first row of spines to the tip of the penis, the surface of the glans is smooth. In contrast to the blunt end and large urethral meatus in the young kitten (fig. 4), the tip of the adult penis is pointed and the urethral opening is relatively smaller.

In cross section the spines of the glans penis of the adult intact cat (fig. 17) appear as pointed projections extending from pits in the stratified squamous epithelium covering the glans. The spines consist of a connective tissue core, covered by an epithelial layer of which the outer surface is heavily cornified. This cornified layer or horny plate, which appears grossly as the actual spine, bears a striking resemblance to the spiny papillae on the cat's tongue (Retterer and Lelièvre,

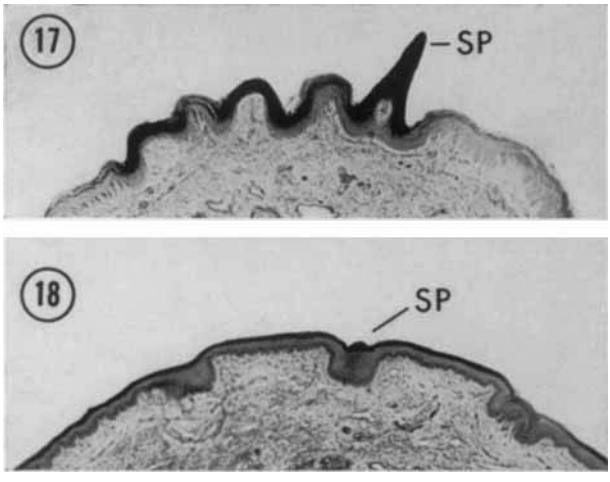


Fig. 17 Cross section through glans of intact adult male. (SP, spine) × 35.

Fig. 18 Cross section through glans of postpuberally castrated male. (SP, location of spine) × 35.

'14; Sekiguchi, '60). When the spines have completely regressed after castration, their former location is revealed by a slight depression of the horny layer of the epithelium and a considerable thickening of the stratified squamous epithelium (fig. 18). Tiny remnants of the horny spines are visible in some of the pits.

Group II. Spines after postpuberal castration. In five animals studied (table 2) the spines regressed rapidly and reached stage 3R in 5 to 6 weeks (fig. 7). Thereafter regression proceeded at a slower and more variable rate. The spines were in stage 2R (fig. 8) in 10 to 13 weeks and by 13 to 24 weeks after castration reached stage 1. These observations on the decline and disappearance of the spines after castration are not in accord with the observations of Reisinger ('37) who reported that one year after the castration of a 3-year old male there were no changes in the spines.

The two castrates, DU and BA were tested weekly after castration for sexual behavior. Both had been having one or more intromissions on every test prior to the operation. The last intromission of

TABLE 2

Summary of growth or regression of spines

Animal	Stage					
	1	2 or 2R	3 or 3R	4	5	6
		I Postnatal development [1]				
ON	4					
TW	9					
PL		12				
DO		17				
AB			22			30
UP				22		
PT					25	
PW					25	
		II Postpuberal castration [2]				
TH	15	10, 13	5	3	1	0
FO	13	10	5	3	1	0
FI	15	10, 13	5	3	1	0
BA	24	15	6			
DU	20	16				
		III Postpuberal castrates given androgen [3]				
SI	0	2				
SP	0			2		7
	IV Androgen treated postpuberal castrates — Hormone withdrawal [4]					
AP			8	4	1	0
DI	16	6			1	0
MU			8	4		0
CH		8		4		0
		V Prepuberal castrates treated with androgen [3]				
DB		1		3	5	10
TI		1		3, 5, 10		15
BI		1		3		
HR			1	3, 5	10	15
RB		1	1, 3	5		
BO			1, 3	5		
CL			1, 3	5	10	15
BL			2	5	15	
	VI Androgen treated prepuberal castrates — Hormone withdrawal [4]					
BL			8	3		0, 1

[1] Weeks after birth.
[2] Weeks after castration.
[3] Weeks after start of androgen treatment.
[4] Weeks after hormone withdrawal.

one occurred on week 24 at which time the spines were minute. On the final test, 42 weeks after castration, this male was still mounting regularly. The other cat never intromitted after castration. Sporadic mounting continued until the last test 15 weeks later.

Group III. Postpuberal castrates treated with androgen. In two males, SI and SP, 50 mg pellets of testosterone propionate were implanted subcutaneously in the shoulder region. When treatment began, the glans of SI was smooth — stage 1, while that of SP contained very tiny pits — stage 1. Fourteen days after treatment began the spines of SI were in stage 2 (fig. 10), and those of SP were in stage 4 (fig. 12).

At the time the pellets were implanted SI was mounting occasionally. He had the first intromission at five weeks. The first mount for SP occurred at three weeks at which point the spines were well along toward maturity, and at seven weeks, when the first intromission occurred, the spines were full size (fig. 12).

Group IV. Androgen-treated postpuberal castrates; effect of hormone withdrawal. At the time that the hormone treatment was stopped all five cats in this group had fully developed spines — stage 6. Regression started within a week and continued at a rate and in a manner similar to that of the postpuberal castrates (Group II). The last two stages in the disappearance of the spines are illustrated in figures 13 and 14.

Prior to the time that the hormone was withdrawn all of the males were having regular intromission in weekly tests. Three weeks after hormone withdrawal CH had his last intromission. At this time the spines were still fairly well developed (Stage 4). Male DI had his last intromission at nine weeks when the spines were small. Males AP and MU intromitted until 21 and 27 weeks respectively after hormone withdrawal. At this time the spines were very small or completely regressed. Mounting continued in all of the animals as long as testing continued (up to 34 weeks).

Group V. Treatment of prepuberal castrates with androgen when adults. Seven males of this group were taken from a current experiment in which the glans penis was partially desensitized by section of the dorsal nerves of the penis at the same time as castration (at approximately 4 months of age). Since there are no indications that desensitization of the glans affected in any way the development of the spines under the influence of male hormone, these data are included here.

When males are castrated prepuberally spines do not develop (Reisinger, '37). Actually, it is more accurate to say that the spines start to develop before castration and then regress after operation. The end result is a smooth spineless glans or one with only tiny, almost microscopic protuberances, when the males reach maturity — stage 1 (fig. 15).

One week after the males started receiving injections of 20 mg of testosterone propionate in sesame oil per day, six days per week, development of the spines was well under way. Three males, (DB, TI and BI) were in stage 2 (fig. 16), and four others, (HA, RO, BO and CL) were in stage 3; but in the first three of these subjects the prepuce was still adhering to the proximal half of the glans. At three weeks the knobs of DB, BI, HA and TI were more pointed, resembling small spines — stage 4. The glans of the other three had larger knobs than at one week — stage 3, but they were not yet pointed except for a few distal ones on CL — stage 3 to 4. The prepuce was still adherent proximally on HA, RO and BO. Subsequent development of the spines was similar to normal postnatal development but at a considerably faster rate (table 2).

One other male, BL, from an earlier experiment in which the glans was not desensitized, is included here. Two weeks after a 50 mg pellet of testosterone propionate was implanted, the glans had moderately sized knobby spines — stage 3. Further development was similar to the other animals in this group.

In a series of sex tests just prior to androgen treatment, BL was having some brief neck grips or momentary neck grips with mounts, but no intromissions. One week after hormone treatment began, the mounts were considerably longer, and at two weeks the first intromission oc-

curred. At this time the spines were less than one-half grown and knobby.

Group VI. Prepuberal castrate treated with androgen; effect of hormone withdrawal. BL, from the previous group, had been treated with testosterone propionate for eight months. At the time hormone administration was withdrawn, the spines were fully mature — stage 6. Three weeks later they were in stage 4, and at eight weeks in stage 3R.

Until the time that hormone treatment stopped, BL was having two to three intromissions per test in every semi-weekly test. Intromissions continued after hormone withdrawal but never more than one per test (and 3 tests were without intromission) until week seven at which time the spines were somewhat less than half size. Thereafter, the sex tests which were continued for 16 weeks were characterized by many brief mounts, an occasionally long mount and a few tests with no sexual activity indicating a fairly rapid decline in sexual arousal.

DISCUSSION

The penile spines increase in size as androgen level rises, and decreases in size as the hormone level falls. While there are obvious differences in rates of growth and regression, the trends are similar both within and between comparable groups. The spines begin to develop at about two months of age and reach full size at 6 to 7 months. When the male is deprived of androgen either by castration or by cessation of hormone treatment in castrates, the spines change only slightly during the first week, are reduced to half size in two months, are minute at four months, and they are gone in six months. The glans of the long-standing castrate is either smooth, contains tiny pits where spines had been, or has a small number of almost microscopic hair-like protuberances. When castrates are treated with androgen, growth of the spines is rapid during the first week or two and they are full grown in about two months. The rate of recovery seems faster than the rate of regression.

Typically, sexual behavior in male cats follows a similar trend. It increases as the androgen level rises, it is depressed when the hormone level falls, and the rise is more rapid than the decline. To this extent, our data on cats follows that of the rat and it is therefore tempting to adopt for cats the hypothesis of Beach and Levinson ('50) that the distortion of the spines during intromission contributes to genital sensitivity and helps support sexual arousal.

The situation in the cat, however, is more complicated because as Rosenblatt and Aronson ('58) have shown, the effects of castration are so highly varied. Some males show practically no sex behavior within a week or two after castration (short persisters) and at the other extreme, the long persisters have regular intromissions for months and even years after operation. Major decrements in behavior of the short persisters occur considerably before the spines recede and the long persisters are still having intromissions long after the spines are minute or completely gone. In Group II of the present series of observations, BA stopped intromitting immediately after castration before there was any change in spines while in the same group DU was still intromitting when the spines were minute. Four animals of Group IV were still having intromissions 6 or 8 weeks after cessation of hormone administration at a time when the spines were small, thin and few in number. The lack of consistent relationship between development of spines and sex behavior is also apparent when we consider that many males start sex behavior when they are around nine months old, which is 2 to 3 months after the spines are mature. Other males, however, take many months longer to start their sexual activity. Examination of five males that had not as yet started mating and were two years or older, revealed large, adult spines on all.

While our results are similar to those of Beach and Levinson, it must be remembered that our data like theirs only provide a positive correlation between size of spines and level of behavior. Causal relationships may be inferred but our observations make it clear that in some animals at least, the persistence of high levels of sexual activity is not dependent on the presence of large spines; and con-

versely, large spines do not necessarily insure high levels of sexual activity.

Thus far the spines have been considered as an adaptation to provide added sexual stimulation for the male.

Two additional functions have been proposed for these spines in felines. Nuhn (1886) and Retterer and Lelièvre ('12) suggested that they act as holdfast organs, comparable to the locking device in dogs. Since the spines are directed sharply towards the base of the penis they should not interfere with intromission but should impede withdrawal. Röder (1894) questioned this hypothesis on the basis of the normally brief duration of intromission which is in the order of a few seconds. On the other hand, Rosenblatt and Aronson ('58) found that the duration of intromission decreased after castration at a time when the spines were regressing. Since intromittive behavior of castrates is otherwise indistinguishable from that of intact males, the holdfast function of the spines cannot be easily dismissed.

A third function, namely, to provide sexual stimulation to the female was favored by Chauveau (1877), Röder (1894) and others. This hypothesis was suggested by the loud piercing cry of the female at the moment of intromission and by a sequence of events which includes, throwing off the male, pawing him, violent rolling and protracted licking of the external genitalia. Greulich ('34) demonstrated that ovulation in the cat occurs only after genital stimulation. In his experiments a glass rod was used to provide the stimulus. The smooth penis of the castrate that is still intromitting is comparable in a way to the glass rod and will most likely cause ovulation. It is still possible, however, that the spiny penis of the intact male is more effective than the glass rod or smooth penis in providing, during a typically brief intromission, the intense level of stimulation needed to initiate the ovulatory process.

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