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在人工授精中如何最大限度地利用遗传上优良的公畜

约翰·〇·阿姆奎斯特

（美国宾夕法尼亚州州立大学）

编者按 为了庆祝三十周年校庆，我们特别邀请和我院有校际联系的美国宾州州立大学最近（1981）获得沃尔夫奖金的乳牛生理学教授阿姆奎斯特博士为我院《学报》写一篇有关家畜人工授精的论文。

从1944年起阿姆奎斯特博士在宾大任职，他早期的工作就为现已大大扩展了的育种研究中心奠下了基础。二十多年前他已认识到人工授精对乳牛业的巨大潜力，并且倡导广泛应用冷冻精液，抑制排卵及改善饲养和管理方法。他发明在公牛精液里加抗生素的方法，这就可以广泛利用优良公牛的精液来迅速增加牛奶和牛肉的产量，特别对小农家有利，因为他们买不起这种优良公牛。据估计，仅仅在美国宾州就有四分之三的奶牛是用人工授精繁殖的，这个方法目前已为世界各国普遍采用。阿姆奎斯特博士在牛人工授精的开拓工作中，为提高肉类和乳品的产量做出了贡献。

提　　要

正常公牛形成和排出巨大数目的精子。大多数公牛具备足够的性活动水平，但在一定性刺激条件下将出现无反应的饱和状态。只要频频变换刺激条件，每周经常采精四至六次是可行的。如果每次射精前加强性准备（假爬跨和限制性保定）的话，这种采精频率将能够使每周精子产量达到最高水平，而不会损害公牛和其繁殖力。没有证据说明长期高频率的采精（每周采精六次，长达7年之久）对于畜体生长、睾丸发育、精液的质和量，精子产量或受胎率有不利影响。大多数年青公牛在到达14月龄时，每周所射出的精子量（80到160亿）足以完成后裔测定计划中抽样的需要量。成年公畜每周应该能排出400至600亿精子，如果种用公牛群内大多数公牛未能达到这些标准，那么应该对管理措施作仔细的审查。

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MAXIMIZING THE USEFULNESS OF GENETICALLY SUPERIOR SIRES IN ARTIFICIAL INSEMINATION

John O. Almquist

Dairy Breeding Research Center
Department of Dairy and Animal Science
The Pennsylvania State University
University Park, PA 16802 USA

Research on the potentials and limitations of sexual activity and seminal production of bulls was initiated at this Center in 1951. Early experiments conducted in collaboration with professors E. B. Hale and R.P. Amann concerned development of quantitative techniques for measuring sexual behavior and spermatozoal production (Almquist and Hale, 1956; Hale and Almquist, 1960) and methods for increasing output of spermatozoa (Almquist *et al*.,1958) .In 1961, a series of three long term experiments was undertaken with Holstein-Friesian(Almquist and Amann, 1976; Almquist and Thomson, 1973; Almquist, 1982), Angus and Hereford (Almquist and Cunningham,1967; Almquist and Thomson, 1973; Martig and Almquist, 1969) , and Charolais (Almquist *et al*., 1976) bull calves to enhance the efficient exploitation of artificial insemination with genetically superior sires.Two broad goals were:(1)to complete progeny testing of young bulls at the earliest possible age and (2) to maximize the breeding usefulness, i.e., number of females mated per bull per year, of those bulls proved desirable. At puberty, experimental bulls were ejaculated three or six times weekly (3X or 6X) and control bulls once weekly(1X).Continuous collection of semen as frequently as 6X weekly, starting at puberty,had no harmful effect on body growth,testis growth, seminal quality, spermatozoal output, ability of spermatozoa to withstand freezing and thawing, or fertility when compared to control pairmates collected 1X weekly.

This report concerns primarily our studies on methods by which the

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sexual activity of bulls can be manipulated to maximize the output of spermatozoa for artificial insemination. No attempt will be made to summarize all published literature. However, no published report states that collection of semen from bulls at a high frequency of ejaculation has a deleterious effect on fertility.

SEXUAL BEHAVIOR. The importance of novel (new) stimuli in eliciting the sexual responses of bulls has been discussed extensively (Almquist and Hale, 1956; Hale and Almquist, 1960). Novelty can be achieved by three approaches; presentation of the same stimulus animal (teaser) in a new location, presentation of a new stimulus animal or combination of animals in the original location or presentation of a new stimulus animal(s) in a new location (Hale and Almquist, 1960). Only the bull, however, can decide what is a desirable stimulus situation.

The interval between presentation of the stimulus animal to the bull and his initial mount is termed reaction time (Almquist and Hale, 1956). Reaction time to the first mount is the most objective measure of the intensity of a bull's sexual stimulation in a specific situation. The interval between the presentation of the stimulus animal to the bull and his ejaculation is the reaction time to ejaculation. It serves to indicate the level of sexual activity. Other publications (Almquist and Hale, 1956; Hale, 1966; Hale and Almquist, 1960) fully consider methods for reducing reaction time and evaluating the effectiveness of changes in stimulus situations.

A second useful term in managing bull behavior is stimulus pressure. The number of combinations of stimulus animals and/or locations necessary to obtain mounting and ejaculation has been defined as stimulus pressure (Almquist and Hale, 1956). To a large extent the stimulus pressure required to maintain a reasonably short reaction time is dependent upon the frequency of semen collection. If semen is collected frequently from a bull, stimulus pressure should be increased and by this technique a short reaction time can be maintained. The gradual lengthening of reaction time which accompanies repeated presentation of the same stimulus situation to the bull has been termed satiation and this satiation is specific for that stimulus situation and does not represent generalized fatigue (Hale and Almquist, 1960). Consequently, if we expect to collect semen from a bull several days each week for a long period of time, more stimulus animals must be available for making changes in the

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stimulus situation than are necessary for a bull collected infrequently (one or two ejaculates every 7 days or longer) . The sex of the stimulus animal is not important for most bulls, although some bulls prefer male teasers and use of male teasers is advantageous for controlling spread of reproductive diseases.

Behavioral characteristics of beef bulls are very different from those of dairy (Holstein-Friesian) bulls and recent research at this center (Almquist, 1973; Almquist and Amann, 1976; Almquist and Cunningham, 1967; Almquist *et al.*, 1976) has documented certain of these differences. When two successive ejaculates are collected on one day each week, the reaction times of Holstein-Friesian bulls remain very short for both the first and second ejaculates(Table 1).For Angus and Hereford bulls,however,the interval between initial presentation of the stimulus animal and the first false mount is typically much longer than the interval required for subsequent mounts. Consequently, reaction time to first ejaculation is long even when using our management procedure in which the stimulus situation is altered ***every*** 10 ***minutes*** if there has been no response.

TABLE 1. Differences in mean reaction times between beef and dairy bulls when collected twice on one day weekly. From Almquist (1973).

	Beef bulls		Dairy bulls	
Reaction time (min)	1st ejac	2d ejac	1st ejac	2d ejac
To first false moumt	13.2	6.0	1.2	3.5
To ejaculation	20.3	12.3	2.7[a]	5.9[a]

[a]Excludes 2.0 min of planned restraint between first and second false mounts for 6 Holstein-Friesian bulls. No restraint was used for 7 Angus and Hereford bulls.

Once the initial mount has been obtained with dairy bulls, subsequent mounts usually occur in rapid succession.With many beef bulls, however, the reaction time for each and every mount may be rather long. For both beef and dairy bulls, however, immediately after ejaculation there will be a brief refractory period during which the bull will not mount regardless of the stimulus situation. The techniques of false mounting and restraint are termed sexual preparation and they have been conclusively demonstrated by us (Almquist, 1973; Almquist *et al.*, 1958; Foster *et al.*, 1970; Hale and Almquist, 1960) and many others to increase the number of spermatozoa obtained per ejaculation from dairy bulls. ***Sexual***

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preparation has been defined (Hale and Almquist,1960) as prolonging the period of stimulation beyond that adequate for mounting and ejaculation. *Sexual stimulation*, on the other hand, is the presentation of a stimulus situation adequate to elicit mounting and ejaculation. Thus, sexual preparation and sexual stimulation are not synonymous. The function of optimal stimulation is to obtain an ejaculation in the shortest possible time while the function of sexual preparation is to provide high-quality semen containing the greatest possible number of spermatozoa per ejaculate (Hale and Almquist, 1960).

Given a demand for a certain number of inseminating units from a particular sire, this demand can best be met by judicious use of sexual preparation to maximize output of spermatozoa. Surprisingly, the best sexual preparation procedure when two successive ejaculates are to be obtained on a collection day is different for Angus and Hereford bulls than for Holstein-Friesian bulls (Almquist, 1973). With Holstein-Friesian bulls, utilization of three false mounts prior to ejaculation increases the number of spermatozoa in both first and second ejaculates. With Angus bulls, however, the increased spermatozoal output when utilizing three false mounts prior to the second ejaculate is minimal (Table 2). The few additional spermatozoa obtained (15.1 vs 13.4×10^9; $p>0.05$) do not justify the 50% increase in the time required for ejaculation (30 min vs 46 min).

TABLE 2. Effects of sexual preparation level on the reaction time to ejaculation (min) and the number of spermatozoa (10^9) collected from eight 1.5-to 6.5-yr-old Angus bulls. Adapted from Almquist (1973).

Sexual preparation		Reaction time to ejac			No. spermatozoa/ ejac		
1st ejac	2d ejac	1st ejac	2d ejac	Total	1st ejac	2d ejac	Total
0 FM -	0 FM	4.9	5.1	10.0	4.9	4.6	9.5
0 FM -	3 FM	8.7	21.9	30.6	4.9	7.5	12.4
3 FM -	0 FM	21.8	8.0	29.8	9.1	4.3	13.4
3 FM -	3 FM	27.4	18.6	46.0	8.7	6.5	15.1

Restraining a bull in a sexually stimulating situation can increase spermatozoal output as does false mounting. However, for physically sound bulls the use of false mounts is preferred since the initial false mount by the bull is a crucial check to insure that the bull is receiving

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adequate sexual stimulation.

REPRODUCTIVE PHYSIOLOGY. To evaluate the effectiveness of semen collection procedures for maximizing spermatozoal output, knowledge of daily production of spermatozoa is essential. ***Daily spermatozoal production*** represents the total number of spermatozoa produced per day by the testes (Amann, 1970). It is impractical to directly measure daily spermatozoal production of living animals, but accurate estimates of its magnitude have been verified by quantifying the spermatozoa recovered after direct cannulation of the rete testis (Amann *et al*., 1974). ***Daily spermatozoal output*** represents the total number of ejaculated spermatozoa collected over a period of time expressed on a per day basis (Amann, 1970). When an animal is routinely ejaculated at a high frequency, daily spermatozoal output is not significantly different from daily spermatozoal production (Table 3). Under these conditions almost all spermatozoa may be recovered for use in commercial artificial insemination.

TABLE 3. Within bull comparisons of testicular spermatozoal production and spermatozoal output from the vas deferens or in semen ejaculated during daily ejaculation (10^9 spermatozoa/day). From Amann *et al*. (1974).

Source of samples	Means-10 bulls	Means-11 bulls
Rete testis cannula	2.96	-
Testicular homogenates[a]	-	3.42
Output of sperm from vas deferens cannula	3.59	3.81
Output of sperm in ejaculated semen (1/2)[b]	3.24	3.17

[a]Calculated from spermatid reserves using a time divisor of 5.32 days.

[b]Daily spermatozoal output in ejaculated semen collected just prior to surgery was divided by two to equate it with the other values.

Since testicular growth continues for at least 5 years after puberty (Coulter *et al*., 1975), it is not surprising that daily spermatozoal production also increases with age (Table 4). Although 40 to 60×10^9 spermatozoa per week should be collected from an adult Holstein-Friesian bull (production of 6.0 to 8.0×10^9/day), a reasonable goal for an 11-to 15-mo-old bull being sampled for progeny testing is 8.0 to 16.0×10^9 spermatozoa per week. Testicular size is a heritable trait and bulls with small testes should be considered for elimination.

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TABLE 4. Development of spermatozoal production in Holstein-Friesian bulls. Compiled from the literature (Almquist and Amann, 1961; Killian and Amann, 1972; Macmillan and Hafs, 1968) and unpublished data.

Age	No. bulls	Gross weight paired testes (g)	Daily spermatozoal production[a]	
			10^6/bull	10^6/g testis parenchyma
0 - 4 mo	25	20	0	0
5 - 7 mo	15	97	104[b]	1[b]
8 - 10 mo	20	284	1750	7
11 - 12 mo	15	370	3300	10
17 mo	13	480	4480	10
3 yr	10	586	6040	11
4 - 5 yr	11	647	6530	11
> 7 yr	11	806	8000	11

[a]Calculated from testicular homogenate counts using a time divisor of 5.32 days.

[b]Mean for six bulls producing spermatids or spermatozoa.

When establishing goals for the total number of spermatozoa to be collected per week from bulls, differences among breeds must be considered. Although the data shown in Table 5 are confounded by differences in season of birth and possibly nutritive plane, postpuberal increase of weekly output of spermatozoa is much slower for Angus and Hereford than for Holstein-Friesian and Charolais bulls.

TABLE 5. Mean weekly output of spermatozoa (10^9) for bulls collected twice a day on three days each week(6X) with three false mounts before each ejaculation. Adapted from Almquist *et al.* (1976) and unpublished data.

Age (yr)	5 Angus & Hereford	10 Holstein-Friesian	10 Charolais
1	7	10	14
1.5	13	22	26
2	18	25	34
3	24	28	44

In addition to the testicular rate of spermatozoal production, the storage capacity of the epididymis (extra-gonadal spermatozoal reserves) also should be considered for a sound plan of bull management(Almquist

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and Amann, 1961). The extra-gonadal spermatozoal reserves of young bulls are rather small (Killian and Amann, 1972; Macmillan and Hafs, 1968; Macmillan *et al.*, 1972) when compared to mature bulls (Almquist and Amann, 1961). Ejaculation does not hasten the transport of spermatozoa through the caput and corpus epididymidis where they become mature and acquire fertilizing capacity (Amann *et al.*, 1974). However, the interval spent by mature, fertile spermatozoa in the cauda epididymidis differs between young and mature bulls (Table 6).

TABLE 6. Age associated differences in daily spermatozoal production, epididymal spermatozoal reserves and the time required for spermatozoa to pass through the epididymis of Holstein-Friesian bulls.[a]

	Young bulls (15-17 mo)	Mature bulls (2-12 yr)
Daily spermatozoal production (10^9)	3.1	7.2
Caput-corpus reserves (10^9)	11.2	24.2
Cauda reserves (10^9)	7.6	37.6
Transit in caput-corpus (days)	3.6	3.4
Transit in cauda (days)	2.4[b]	5.2[b]

[a]Calculated from data in the literature (Almquist and Amann, 1961; Macmillan *et al.*, 1972). Daily spermatozoal production was calculated from counts of testicular spermatids; transit time of spermatozoa through the epididymis was estimated by dividing spermatozoal reserves by daily spermatozoal production.

[b]Estimate of the number of days' production of spermatozoa stored in the cauda epididymidis and potentially available for ejaculation.

The different relationship between daily spermatozoal production and cauda epididymal spermatozoal reserves for young and mature bulls (Table 6) means that different management practices may be necessary to obtain the maximum number of spermatozoa. In the young bull, the cauda epididymidis can accommodate no more than 2 or 3 days' production of spermatozoa. Consequently, every-other-day collection of two successive ejaculates probably is necessary to obtain the maximum number of spermatozoa and collection more frequently probably will be counter productive. For the mature bull, however, the cauda epididymidis can accommodate 5 to 6 days' production of spermatozoa. This increase in the relative size of the cauda epididymidis occurs relatively late as compared

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with testicular growth. For mature dairy bulls, maximum spermatozoal output is achieved with collection of one ejaculate daily but similar results probably can be obtained by collection of two or three ejaculates every 3 to 4 days. As stressed above, effective sexual preparation also is essential for maximizing spermatozoal output.

Breed differences in testes weight, daily spermatozoal production, extra-gonadal spermatozoal reserves and transit time of spermatozoa through the epididymis of mature dairy and beef bulls have been summarized (Weisgold and Almquist, 1979). Angus, Hereford and Charolais breeds differed widely in testicular weight, efficiency of spermatozoal production and spermatozoal storage capacity.

Finally, the most important physiological question is whether ejaculation of bulls at high frequency for prolonged periods of time affects fertility. This information was lacking until a recent report (Almquist, 1982) in which it was shown that ejaculation of dairy bulls at high frequency (6X/wk) continuously for 7 years did not harm either spermatozoal motility after freezing and thawing or fertility of spermatozoa (Table 7). Fertility at 4, 6 or 8 yr of age did not differ significantly between one and six time bulls.

TABLE 7. Post-thaw motility and fertility of spermatozoa from Holstein-Friesian bulls ejaculated weekly at high (6X) or low (1X) frequency continuously from 1 through 8 yr of age[a]. From Almquist (1982).

Age[b]	Percent post-thaw motility[c]		No. first services		percent 60- to 90-day nonreturns[d]	
	1X	6X	1X	6X	1X	6X
4	34	38	1881	1933	76	77
6	32	34	343	379	76	76
8	42	42	361	383	77	80

[a]Means for motility and nonreturn rate at each ejaculation frequency.

[b]For six 1X and six 6X bulls at 4 and 6 yr and five 1X and five 6X bulls at 8 yr of age.

[c]After storage at -196°C for 3 wk.

[d]Bulls weighted equally.

BULL MANAGEMENT. There is no physiological reason why semen should not be collected from a young sire starting at the attainment of

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puberty. Although the fertility of early postpuberal ejaculates from some bulls may not be quite as high as for those collected subsequently, economically satisfactory conception rates usually result if the seminal characteristics and postthaw spermatozoal motility are adequate (Martig and Almquist, 1969; Thibier and Colchen-Bourlaud, 1972). Since early determination of the genetic value of a sire is important, we recommend collection of two successive ejaculates every 2 or 3 days starting shortly after puberty. This recommendation is based on the limited storage capacity of the caudae epididymides, relative to testicular spermatozoal production, in the young bull (Table 6).

Age at puberty for our Holstein-Friesian and Charolais bulls averaged 39 and 41 weeks(Almquist and Amann, 1976; Almquist *et al*., 1976), while the mean puberal age for Angus and Hereford bulls was 45 weeks (Wolf *et al*., 1965). The latter agrees with age at collection of first viable spermatozoa from Sychevka and Brown swiss bulls (Meljnikov, 1967). Age at puberty for Charolais collected by artificial vagina is the same as that reported (Bellows *et al*., 1964) for collection by electroejaculation of the first motile sperm from beef breeds. By 1 yr of age, the typical Holstein-Friesian bull should ejaculate 10×10^9 spermatozoa weekly; norms for beef breeds are given in Table 5. The reproductive development of Black Pied and Normandy bulls (Thibier and Colchen-Bourlaud, 1972; Thibier *et al*.,1972)follows patterns similar to those shown for Holstein-Friesian and Charolais bulls in Table 5. For each of the five breeds studied (Almquist and Amann, 1976; Almquist and Cunningham, 1967; Almquist *et al*., 1976; Thibier and Colchen-Bourlaud, 1972; Thibier *et al*., 1972), the output of spermatozoa with adequate fertilizing ability is such that most bulls should have ejaculated sufficient spermatozoa to complete progeny testing by 14 months of age.

Not all young bulls will have satisfactory sexual behavior or seminal characteristics. Bulls with deficiencies in either area can be detected quickly by the frequency of ejaculation regime proposed and should be eliminated from the bull stud. Measurements of testicular size are helpful in making decisions concerning elimination of bulls with low spermatozoal output associated with severe testicular hypoplasia. However, such measurements on a young bull probably do not enable precise prediction of his spermatozoal output as a mature sire (Almquist *et al*., 1976).

Production of spermatozoa by the testes will continue at the same

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abundant rate whether the cells are collected and used for artificial insemination or voided and lost by masturbation and micturition. Although collection of semen at high frequency may reveal existing defects in seminal characteristics (Hale and Almquist, 1960), this procedure is not harmful to bulls. The severity of vertebral body osteophytes in Holstein-Friesian bulls was not related to ejaculation frequency (Almquist and Thomson, 1973).

Assuming that the semen is to be frozen, we recommend collection of two or three successive ejaculates every 3 or 4 days from a sire of known genetic superiority. The same ejaculation frequency should be useful when it is desired to bank frozen semen from a bull awaiting proof (Coulter and Foote, 1974; Allen and Almquist, 1981). Each ejaculation should be preceded by intensive sexual preparation. Except for bulls which have developed severe physical problems, use of one false mount, 2 min of restraint, and two additional false mounts should maximize spermatozoal output per ejaculation for most bulls. However, as discussed above, for beef breeds false mounting prior to a second ejaculate probably is a waste of time. Active restraint rather than false mounting should be used to provide sexual preparation for bulls with physical limitations (e.g., foot, leg or back problems).

APPLICATION. Breeding potential for top bulls is tremendous. Mature bulls can be mated by artificial insemination to from 50,000 to 100,000 cows per year compared to the 1950 USA average of only 1,250 cows inseminated annually per sire. However, such extensive use of sires of known genetic superiority only can be achieved by maximizing the harvest of spermatozoa. The bulls must be ejaculated at high frequency (at least four and preferably six ejaculates weekly). Further, intensive sexual preparation (false mounting and restraint) must precede ejaculation. Recently, a Pennsylvania artificial insemination cooperative using these recommended procedures was able to obtain a yield of 150,000 units of frozen semen in one year from a dairy sire of outstanding genetic merit.

FUTURE. Artificial insemination organizations might consider a program combining (a) early liberal energy allowance (Almquist, 1982), preferably one providing maximum energy intake from birth to about 18 mo of age, (b) bulk freezing of semen (Allen and Almquist, 1981), and (c) ejaculation at a high rate starting at puberty. This program supports

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efficient establishment of a large bank of frozen spermatozoa for a bull before his proof becomes available. Someday a bull might be killed after his bank of spermatozoa has been completed to reduce the high cost of feeding and housing a mature bull. One obvious disadvantage of banking spermatozoa is that the bank would have to be discarded for a bull proved to be undesirable.

SUMMARY. Normal bulls produce and ejaculate spermatozoa in enormous numbers. Most bulls have an adequate level of sexual activity, but will become satiated to a specific stimulus situation. Provided frequent changes of the stimulus situation are made, routine collection of four to six ejaculates weekly is feasible. This collection frequency will maximize weekly spermatozoal output if each ejaculation is preceded by intensive sexual preparation (false mounting and restraint) and will not harm the bull or his fertility. There is no evidence that long term ejaculation at high frequency (six ejaculates per week for as long as 7 years) has a detrimental effect on body growth, testicular development, quality and quantity of semen, output of sperm or fertility. Most young bulls can ejaculate sufficient spermatozoa weekly (8 to 16 billion) to complete sampling in a progeny testing program by 14 months of age. Mature sires should ejaculate 40 to 60 billion spermatozoa weekly. If most of the bulls in a stud do not meet these standards the management procedures should be carefully scrutinized.

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