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Robert L. Losey Ph.D.
American University

Thomas E. Lambert 1959-
University of Louisville

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Incremental Changes in Inbreeding When Comparing Stallion Pedigrees from the Years 2000 and 2020

By Robert L. Losey, PhD, and Thomas Lambert, PhD*

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Executive Summary

This paper has been written in response to the Jockey Club's proposal to limit the number of mares bred by any individual Thoroughbred stallion. The paper has three goals:

1) To provide a statistical analysis of the degree to which inbreeding in Thoroughbreds has increased over the last twenty years.

2) To review recent literature by equine geneticists who research and/or discuss inbreeding trends and genetic diversity and the advantages and drawbacks of inbreeding.

3) To discuss how the specifics of the original Jockey Club mare limit proposal could be altered to better serve the industry.

The results of our statistical analyses on inbreeding trends are consistent with those of Binn et al (2012), and McGivney et al (2020) that there has been an increase in inbreeding in Thoroughbreds in recent decades. Geneticists point out that there are drawbacks (mutational load) and advantages (the concentration of beneficial genetic characteristics) arising from inbreeding. We outline an alternative to the Jockey Club's September 2019 140-mare limit proposal that will result in a decrease in the size of large books for the majority of stallions that will provide flexibility to breeders utilizing seasons from stallions of proven quality.

Inbreeding and Thoroughbred Genetic Health

Our primary goal in developing this paper has been to inform the Thoroughbred industry (ourselves included) about inbreeding trends in the Thoroughbred breed in recent years in response to the Jockey Club's concerns as spelled out in their September 2019 announcement.[1] The Jockey Club notes that increases in inbreeding decrease genetic diversity,[2] and they fear that the loss of genetic diversity is detrimental to the genetic health of the Thoroughbred breed.

There has been an increase the inbreeding in recent years that has occurred as the number of foals have trended downward (see Figure 1 below) for more than four decades, and as fewer and fewer stallions are offered for stud services (3,098 in 2005 versus 1,136 in 2019).[3]

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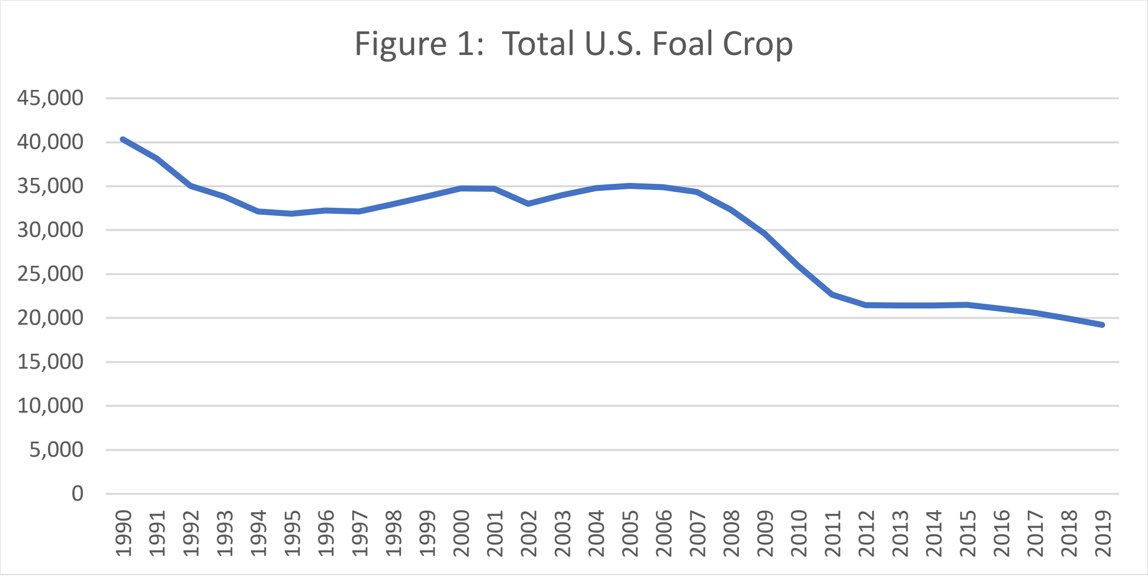
[1] Jockey Club, September 6 2019. "The Jockey Club Considers Rule Regarding Breeding Stallions", http://www.jockeyclub.com/Default.asp?section=Resources&area=10&story=1148 . Accessed on April 17, 2020.

[2] That inbreeding tends to decrease genetic diversity is generally true by definition. There are however, significant numbers of learned geneticists who come down on both sides of the question whether or not inbreeding improves of diminishes the overall well-being of the Thoroughbred.

[3] Jockey Club Fact Book. 1990 to 2019. http://www.jockeyclub.com/default.asp?section=Resources&area=11 . Accessed on April 16, 2020.



Analysis of inbreeding and its effects on our industry is best informed by rigorous scientific analysis. As later discussed when reviewing peer-reviewed publications and comments by learned geneticists, mating choices that are selected with the goal of improving the quality of future runners may or may not result in improvements in the genetic quality of foals, and especially if they entail inbreeding, they are likely to decrease genetic diversity.

Our analysis of inbreeding in Thoroughbreds had three goals:
1) To ascertain if in fact inbreeding has increased over time.[4]
2) To review recent literature by learned geneticists who research and/or discuss inbreeding trends and genetic diversity and the advantages and drawbacks of inbreeding.
3) To discuss how the specifics of the original Jockey Club mare limit proposal could be altered to better serve the industry.

To investigate changes in inbreeding in Thoroughbred pedigrees, we analyzed pedigrees of mid- and upper-tier stallions from the 2000 Bloodhorse Stallion Register and compared them with a similar cohort of stallions from the 2020 Bloodhorse Stallion Register to determine if, on the margin, inbreeding has changed over that 20-year time span.

What are Inbreeding and Line-breeding?

"Inbreeding" is the production of offspring from the mating or breeding of individuals or organisms that are closely related genetically."[5] In some animal populations, there are obviously profound risks from inbreeding. In Quarter Horses, glycogen branching enzyme deficiency (GBED) is a recessive trait carried by 8-10% of the population that results in approximately 1% of Quarter Horse foals aborting or dying at or shortly after birth.[6] Hemophilia is a life-threatening blood malady in humans that inhibits blood clotting. The condition is caused by the inheritance of one (for males) or two (females) copies of a rare recessive gene on the X chromosome.

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[4] We expected that the Jockey Club was right that inbreeding has increased in recent years, but wished to be certain that we and the Jockey Club were correct in that belief.

[5] From Wikipedia

[6] See https://ker.com/equinews/common-genetic-diseases-quarter-horses/

The prevalence of known recessive genes in the present Thoroughbred genome that can pair up to result in catastrophic consequences appears to be rarer than in other inbred populations, though the possibility that new mutations could emerge in the future always exists. But, as discussed in more detail later in this paper, all equine geneticists agree that increased inbreeding normally leads to an increase in **mutational load** that is associated with a more generalized decrease in genetic quality that can be manifested as decreased overall fitness and/or health that might not be offset by the positive effects of selective breeding. The Jockey Club proposal appears to implicitly assume that the deleterious effects of mutational load over the long run tend to be more disadvantageous to the breed than the positive effects of selective breeding.

Thoroughbred breeders sometimes purposefully choose to produce inbred foals (thus typically decreasing genetic diversity) in hopes of improving pedigrees. One such strategy involves "line-breeding," the duplication of (typically superior) individuals in a pedigree, in hopes of concentrating superior genes. Owners who choose to increase the degree of inbreeding by using line breeding are implicitly assuming that the benefits of concentrating the genes of superior individuals will exceed the detrimental effects associated with increased inbreeding depression. More on this later.

Statistical Analyses of Thoroughbred Inbreeding

We first lay out the bare bones of our own statistical analysis of inbreeding trends in Thoroughbred breeding (a detailed discussion of the approach is presented in the appendix). We then consider three research papers and a discussion piece from the University of Kentucky's Gluck Center on inbreeding and related topics that are especially germane to the Jockey Club proposal. Readers who are so inclined can access the bibliographies of these papers for more source materials.

To analyze what has happened over the last 20 years in Thoroughbred pedigrees, we used pedigree analysis to compare inbreeding in a group of comparable commercial[7] stallion pedigrees from the 2000 and 2020 Bloodhorse stallion registers. We calculated our own LLM (Losey, Lambert, Michels) index of incremental inbreeding over the 2000 to 2020 period, where an index of 32 would be the maximum value (when full-brother and full-sister are mated) and a zero value occurs when the pedigree from the Bloodhorse stallion register shows no duplicate names. We find that there has been a moderate increase in inbreeding observed in stallion pedigrees from 2000 to 2020 that is statistically significant. Our approach counts duplicate horses that appear in the 4.5-cross[8] pedigrees for stallions from the stallion registers, and calculates an inbreeding index that also weights which generations the duplicates appear in so that duplicates in more recent generations generate higher inbreeding indices.

The LLM index of incremental inbreeding averaged 5.4 for the 2000 stallions and 6.7 for the 2020 stallions that we analyzed. As an individual horse can only have an LLM index that is an integer value, it is impossible for a single individual horse to have an LLM inbreeding index of 5.4. Let's consider the

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[7] The 2000 stallion sample used all stallions with advertised stud fees of $7500 and higher. The 2020 sample used similar-priced stallions (after adjusting for inflation) from the 2020 stallion register.

[8] Pedigrees are often quoted as three or five-cross pedigrees depending on whether three or five generations of ancestors are reported for a subject foal, mare, or stallion. The Bloodhorse stallion register uses 4.5-cross rather five-cross pedigrees to save space on the stallion page. We base our analysis on the 4.5-cross pedigree to save time and expense, and because breeders are familiar with the Blood-Horse stallion register. Note though, that the values our LLM inbreeding index generates for the 4.5 generation cross will only rarely be different from that generated by a standard 5-cross pedigree. This is because the Bloodhorse stallion register omits the 5th generation of mares but retains the 5th generation of stallions. Since mares pop up as duplicates in pedigrees at approximately 2% or so as frequently as stallions, they rarely affect inbreeding calculations.

closest integer value of 5. An LLM index of exactly 5 is consistent with four possible inbreeding combinations. Two of those possible combinations of duplicate names in the pedigree are as follows:
(1) duplicate names three times in the fifth generation and one time in the fourth generation, and
(2) duplicate names once in the fifth generation and once in the third generation.[9]

An index value of 7, just over the average value of the calculated LLM index value of 6.7 for 2020 stallions, could be achieved by duplicate names in each of the 3rd, 4th and 5th generations. MacLean's Music has this profile, with Mr. Prospector in the 3rd, 4th, and 5th generations but with no other duplicate names.[10] To provide some context, consider that an individual whose only inbreeding in five generations results from having full-siblings as two of his/her eight great-grandparents would have an index value of 8, 1.3 points above the 2020 LLM inbreeding index average value of 6.7 for stallions of 2020.

We suspect that few if any geneticists or breeders would be especially concerned about inbreeding characterized by either the 5.4 or 6.7 LLM inbreeding index values respectively from our "average" commercial stallion from either 2000 or 2020. But we should also consider whether stallions that display higher degrees of inbreeding than the averages might display "worrisome" degrees of inbreeding.

Table 1: Frequency of LLM Inbreeding Scores

Class	Frequency--2000	Frequency—2020
0-2	52	19
3-5	55	19
6-8	59	22
9-11	25	26
12-14	8	7
15-17	2	3
18-21	1	0
Totals	202	96

A review of the detailed data on LLM Inbreeding scores that underlie Table 1 revealed that in the year 2000 approximately 82% of stallions from that sample had LLM scores of 8 or lower. In 2020 approximately 82% of the stallions from that sample had LLM scores of 10 or lower. The simplest example of a score of 8 is a stallion whose only duplicate names in the 5-cross pedigree are in the third

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[9] The LLM index value for duplicate names if appearing only in the 5th and 3rd generations is 5, with the 5th generation providing a value of 1.0 and the 3rd generation duplication (which on average provides four times a much genetic material to the pedigree as a 5th generation ancestor) contributing a value of 4.0. Two combinations of duplicate names not mentioned in the body of this paper that generate LLM index values of 5 are (3) the same horse once in the 5th generation and twice in the 4th generation, and (4) the same horse duplicated five times in the 5th generation.

[10] An LLM index value of 7 using only one duplicate name is rare, and MacLeans Music was the first such example we found when paging through the stallion register. The reason it's rare is that it requires that the same name appear in the 3rd, 4th, and 5th generations, and duplicate names are almost always stallions because the median stallion produces many times more foals than the median mare. Mr. Prospector appeared in three different generations of MacLeans Music's pedigree. His long career made it feasible to appear in three successive generations, which on average are ten or so years apart. His last crop of 43 live foals, only 17 foals shy of his largest crop of 60, were produced when he was 28 years old.

generation removed from the stallion (so 3 x 3). Perhaps the simplest example of a stallion with an LLM score of 10 would be a stallion with that 3 x 3 cross and also one 5 x 5 cross.[11]

Other Statistical Studies

The results of two research studies analyzing inbreeding at the gene level rather than based on pedigree analysis[12] are complementary to our study. Binns et al's 2011 "Inbreeding in the Thoroughbred Horse" [2] analyzes Thoroughbred inbreeding based on analyses of DNA from Thoroughbreds born from 1961 to 2006. They used a small sample of individual horses that had very few observations from the first decade of their data. This quote from their "Summary" section encapsulates their findings. "*The results indicate that inbreeding in Thoroughbreds has increased…demonstrating that there is a highly significant, though relatively weak correlation between the year of birth and inbreeding coefficients…(T)he majority of the increase in inbreeding is post-1996 and coincides with the introduction of stallions covering larger numbers of mares*. (Authors' note: Our [Losey/Lambert] study looks at pedigrees of stallions born on average from approximately 1990 to 2010, thus overlapping and slightly extending the Binns, et al analysis of the "larger-book" era.)[13]

McGivney, *et al's "*2020 Genomic Inbreeding Trends, Influential Sire lines and Selection in the Global Thoroughbred Horse Population" [3] is especially noteworthy for at least two reasons: 1) It is comprehensive and timely, utilizing a large international sample that draws genetic material recently obtained from all major racing regions in the world. 2) It is co-authored by Prof. Emmeline Hill (and three of the remaining six co-authors are her consulting/research firm colleagues at her PlusVital firm.) As the Jockey Club indicated that it had charged Prof. Hill with providing supporting material for their stallion limit proposal, this study is likely to be cited by the Jockey Club when they make decisions about what actions they will take regarding stallion breeding limits.

The inbreeding trends noted by McGivney, et al 's paper paint much the same picture as those from both the Losey/Lambert and Binns et al papers as seen from the following quotes from McGivney's (p. 6) "Concluding remarks" section.

"*We report here a highly significant increase*[14] *in inbreeding in the global Thoroughbred population during the last five decades…(L)imited numbers of stallions have had a disproportionate influence on the genetic composition of the Thoroughbred*." (They note that Northern Dancer appears in 97% of the horses in their sample.)

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[11] This footnote represents the opinion only of co-author Robert Losey. I know of no well-researched studies in equines that draw a line in the sand between an acceptable and an unacceptable degree of inbreeding, and of course there are always other important considerations that may cause a breeder to shade his/her opinion. My experience suggests that somewhere between an LLM inbreeding score of 8 (a 3 x 3 cross?) and 10 (a 3 x 3 cross plus a 5-5 cross in a pedigree) is the line that 50% of breeders would normally say is too high for comfort.

[12] We have no doubt but that biological research measuring inbreeding at the gene rather than the pedigree level provides a better picture of the degree of inbreeding. Pedigree-based measures of inbreeding do not account for the somewhat random transmission of genes from generation to generation while gene-based research does account for random transmission.

[13] 1990 to 2010 is approximately correct if the weighted average age of commercial stallions in the BloodHorse stallion registers of 2000 and 2020 is 10 years old.

[14] It's unclear whether the term "highly significant" is primarily associated in the authors' minds as being (1) in the statistical sense that there has been an increase in inbreeding that is consistent and/or strong enough that it is meaningful as well as not transitory, or (2) that they are referring to their belief that the increase is inbreeding is a subject of concern. In the context of this paper's analyses, we expect that both interpretations apply.

The McGivney paper appears to us to lean toward the view that there are more negative than positive effects from an increase in inbreeding. McGivney *et al* go on to provide prescriptions for actions that they feel could be taken to decrease the negative effects arising from increasing inbreeding. We return to prescriptions and proscriptions after considering two additional citations. But first a brief discussion of important terms is needed.

Genetic Terms Useful in Discussing Inbreeding Effects

The following terms are especially useful in making sense of the arguments for and against inbreeding in the from the sources we cite.

Gene Mutations – If the basic building blocks of DNA (genes) in sperm or ova mutate (perhaps as a result of radiation) this can result in an altered gene that is usually recessive and usually has a negative effect on the a future generation if it pairs up with the same recessive gene from the other parent.

Mutational Load – Over the course of the existence of a species, the species will have gradually accrued a multitude of (negative) **recessive genes** that are passed to the future generations, but are expressed only when paired up with the same recessive gene. In humans, cystic fibrosis (CF) occurs when two recessive genes for CF pair up. The sum total of all potentially negative recessive genes in an individual's DNA is called the "**mutational" load.** Breeding to a descendent of a common ancestor (inbreeding) increases the chances that two negative genes pair up and cause the expression of an unwanted trait (such as CF).

Natural Selection – Though sometimes attributed to Charles Darwin, Herbert Spencer posited that the "survival of the fittest" meant that individuals that inherited genes that contributed negatively to an individual's ability to compete would less frequently produce offspring, hence the "fittest" naturally survived over multiple generations. Part of the explanation for the survival of the fittest is that "bad" genes tend to be naturally "purged" (**gene purging**) because they decrease an individual's ability to compete.

Managed Selection – Thoroughbred reproduction is typically managed by owners who try to amplify good traits and minimize bad traits in offspring. To the extent that owners employ inbreeding to try to amplify good traits, they may choose matings that increase mutational load, thus complicating their efforts to improve the genetic makeup of a targeted mating.

The Australian Racing Paper

"Founder-specific inbreeding depression affects racing performance in Thoroughbred horses," by Evelyn T. Todd, et al [7] evidences the pull between the optimism of breeders (and some geneticists) that it is possible to improve the genetic make-up by selective breeding, and the pessimism of other geneticists that inbreeding more importantly leads to a further concentration of deleterious (and mostly recessive) genes that decrease the vigor of an inbred individual. (Authors' note: "Founder" refers to "original ancestors, not the hoof malady.)

In this paper's abstract we find the following: "*By analyzing the relationship between inbreeding and racing performance of 135,572 individuals, we found that selective breeding has not efficiently alleviated the Australian Thoroughbred population of its… (mutational) load. However, we found evidence for* *(gene) purging*[15] *in the population that might have improved racing performance over time*." The authors held out hope that savvy breeders could offset the tendency for inbreeding to decrease vigor by either "gene purging" (ridding a pedigree of one or more deleterious genes), or overcompensating for the increased mutational load associated with inbreeding by concentrating advantageous genes.

Todd et al test two similar hypotheses by looking at the correlations between racing performance (measured in five different ways) and degrees of inbreeding using two alternative measures. They seem to implicitly base at least a part of their optimism for the benefits of "managed selection" on the fact that Thoroughbreds have been highly inbred from their highly concentrated origins in the 16th century. They point out that "Over 80%[16] of inbreeding in the contemporary population is accounted for by a small number of ancestors from the foundation of the breed." Given that inherently high degree of inbreeding, they may feel that the detriments from a further small increase in inbreeding can be offset by the concentration of beneficial genes.

Analyzing a very large sample of pedigrees (from 135,752 individuals as noted above), and a very small sample (122)[17] of individuals from which they obtained genetic information, they concluded that one measure of inbreeding was positively correlated with performance. However, an alternative measure of inbreeding they chose (there are multiple indices of inbreeding devised by geneticists and authors including the authors of this paper) to correlate with racing performance generated what appears to be a stronger negative correlation than the positive correlation they generated by using their first measure of inbreeding.

Opinions by the Authors of the Binn and the McGivney papers

Neither the Binns nor the McGivney papers specifically set out to determine causality between inbreeding and racing performance, but each had something to say about their expectations. From p. 3 in Binns et al's 2011 paper: "*Whilst the loss of genetic diversity identified in this study is not excessive, the trend is worrisome*." In a Sept. 2019 interview published by the Bloodhorse discussing the Jockey Club proposal [5], Binn was quoted: "In the real world, you have recessive mutations that are deleterious and harmful and …inbreeding increases the chances of them finding one another and giving you a problem—a disease or unsoundness." In a Jan. 3, 2020 article in the *Courier Journal* [6], Binn's co-author, Ernest Bailey, a Gluck Equine Center PhD, struck a more positive note regarding inbreeding: " …(I)nbreeding is actually the process of selective breeding…for good genes…and against bad genes, and so the process results in a steady increase in inbreeding and a steady decrease in genetic diversity. That's how you end up with an improved population."

McGivney et al's longer paper is relatively expansive in both its discussion and recommendations. They note that Timeform ratings have not increased over the years but do not attempt to empirically test the hypothesis that inbreeding has contributed to this stagnation. The following are quotes from their "Concluding Remarks" section.

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[15] "Gene purging" is the phenomenon in which undesirable genes are diminished from a population either through natural or managed selection.

[16] Other authors also report high degrees of inbreeding based on the narrow original population of stallions (3) and mares (70 or so) that gave rise to the Thoroughbred breed, though 80% is at the high side of estimates we have seen for founder-based measures of inbreeding.

[17] Todd *et al* conceded in their paper that the sample of 122 was too small to allow more than minimal inferences.

“Inbreeding results in mutational load in populations that may negatively impact on population viability.”

“‘Genetic rescue’ of highly inbred populations may be possible by the introduction of genetically diverse individuals…(though it) will be challenging due to the limitations of a closed stud book.”

“(A) limited numbers of stallions have had a disproportionate influence on the genetic composition of the Thoroughbred.”

“Relying on pedigree alone for outcrossing is likely to be inefficient.”

“(G)enomics-based monitoring of inbreeding… will contribute to promoting economic gain and safeguarding the future of the breed.”

“97% of pedigrees of the horses included here feature Northern Dancer.”

Notes from the Spring 2020 edition of Equine Disease Quarterly [1] from U. of Ky’s Gluck Center

In two short pieces Geneticists Bailey (2020), then Bailey, Kalbfleisch, and Petersen (BK&P) (2020) present a relatively easily-understood overview of inbreeding and some recent scientific advances in genetics that offer hope for improving breeding practices so as to accumulate better genes in future generations. In this regard they share the views of the McGivney paper that applying knowledge gained from quantum leaps in the development of sophisticated techniques of analyzing and using genomics offer the best hope of more efficiently improving the quality of the Thoroughbred breed. BK&P and the McGivney et al paper seem to differ to some, perhaps even to a significant degree, on the usefulness of imposing a limit on mares bred by Thoroughbred stallions. BK&P seem to view it as a blunt instrument best reluctantly used or not at all used, while McGivney et al offer the following quote: “Directives to prevent over-production from popular sire lines and [*to promote*][18] the global movement of stallions that are distinct from the local population of mares may act to maintain and increase genetic diversity in the population.”

Whereto From Here on Limits on Inbreeding?

All reasonable geneticists agree that inbreeding tends to increase “mutational load” and that, other things equal, that is disadvantageous. But, a substantial number of highly-respected geneticists argue that well-designed inbreeding concentrates good genes and on net more than offsets the detrimental effects of mutational load. We suspect that the Jockey Club will prefer to emphasize the views of those who worry about mutational load, which can be at least loosely equated with the Jockey Club’s stated concern about “decreased genetic diversity.”

Note that the McGivney et al study, which, given that it is associated with Dr. Emmeline Hill, may well be cited as most authoritative by the Jockey Club, argues that “global movement of stallions ….may act to…increase genetic diversity. The McGivney study revealed that Galileo, Danehill, and Sadler’s Wells would have provided remarkably good sources of genes to increase genetic diversity in the U.S. Moreover, their absolutely stellar records as producers of runners argues for their use (or similar

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[18] The phrase “to promote” was not in the original wording from the PlusVital website. But in an e-mail exchange with Dr. Hill she advised R Losey in no uncertain terms that it belonged there to convey the intended meaning.

younger sources of diversity) to improve the quality of U.S. runners in addition to improving genetic diversity.

The only reasonable way we could ("can" in the case of Galileo) have shared the genes of these stallions (or younger stallions in the future with similar favorable genetic makeups) will be/would have been through artificial insemination (AI): these stallions were too popular where they were to be shipped to the U.S. There would be other dramatic advantages to using AI. Costs would be lower, injuries to stallions less frequent, disease less easily transmitted. For reasons that are not altogether clear, the Jockey Club appears to be unwilling to go this route.

If we accept that a breeding limit on mares bred will be instituted instead of utilizing AI for international stallions with favorable genetic profiles, a significant number of breeders will appreciate the institution of reasonable limits on mares bred for the two reasons unrelated to the Jockey Club's "genetic diversity" argument.

1) mare owners recognize that breeding to extremely busy popular stallions marginally lowers their chances of getting their mares in foal early, or at all. Though they recognize that limits will almost surely cause stud fees to rise, if breeding limits were implemented fairly, the unwelcomed higher stud fees would be an acceptable trade-off if pregnancy rates increased appreciably and the stallion breeding limit is not onerous.

2) Most mare owners realize that the popularity of first-year stallions represents a Faustian bargain. Foals by first-year stallions sell well but on average unproven stallions supply inferior sets of genes. In most cases the breed would be better off and individual mares would have a better chance of producing good runners if fewer unproven stallions were used by breeders. A rule to place breeding limits on unproven stallions would be viewed by many breeders as saving them from themselves.[19]

Two further related questions should logically be addressed if breeding limits are instituted:

A) Are there other factors that we should consider besides the genetic diversity question?
B) If there are other factors, how should they affect the implementation of a mare breeding limit?

Five Other Factors

At least five other factors should logically play a role in designing mare breeding limits.

1) Limits on proven high-quality stallions should be used sparingly. High quality proven stallions by definition are more likely to improve the gene pool through owners' managed selection. Why place onerous limits on breed-improving stallions? Proven stallions should logically face higher mare limits than unproven stallions both initially and in the future.

2) Economics should be considered. An economic analysis completed by the lead author of this paper [3] explains that mare limits will cause the prices of stallion seasons for top-tier stallions to rise dramatically, and stallions seasons for many mid-tier stallions to rise appreciably, if a 140-mare limit is placed on stallions. Rising prices and decreasing availabilities of very good stallions will tend to decrease the average quality of foals, and to a limited degree the number of foals produced, and will have adverse economic implications for sales and racetracks. For both economics and genetic considerations, if the 140 limit made sense for the standardbred breed,

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[19] Practically speaking, a limit on mares bred to 3rd and 4th-year stallions would only infrequently be binding, as breeders historically have significantly decreased their patronage of the vast majority of 3rd and 4th stallions even when they were extremely popular their first years.

which has annual production of approximately 40% as much as the Thoroughbred breed, it would seem to be too restrictive for Thoroughbreds.

3) Within reason, breeder choice should be respected. By definition a mare limit will infringe on breeder choice and will be resented by some people. If limits are arbitrary and/or unfair, their infringement on choice will be resented by many more people, and we can expect that some breeders will drop out and the industry will shrink further,

4) Regarding the Jockey Club's proposed "phase-in" requirement, it appears that in proposing the phase-in of mare limits, the Jockey Club has considered the time-honored view that sudden, dramatic changes in the rules of the game should not be made if they disadvantage game players (in this case breeders and/or stallion owners) who made business decisions in good faith the rules of the game would not be changed dramatically to their disadvantage on short notice. This viewpoint is logical from both fairness and legal perspectives.

    However, the logic of the choices of specific phase-in requirements proposed by the Jockey Club is unclear. The stallions that will be most affected by mare limits fall into two groups:
    A) Popular newly retired stallions who would normally breed well over the 140 mare limit, and
    B) High quality proven stallions who could command well over the 140 mare limit.

    The Jockey Club suggests we accommodate newly-retired stallions through phase-in but not proven stallions. For the good of the breed, and in fairness to the owners of high-quality proven stallions, just the opposite accommodation would make more sense for the following reasons.

    High-quality proven stallions provide superior genes to which a mare ban would limit access for the remainder of the high-quality stallion's breeding career. Because their foals have been observed for many years, the foals of high-quality stallions are known factors that generally do not manifest the significant deleterious recessive genes about which geneticists express concern. The financial loss to owners of high-quality proven stallions that can breed more than 140 mares will be dramatic, and in some cases will span a decade or so.

    In contrast, the unproven stallions that the Jockey Club proposes that we partially grandfather have the following characteristics. On average these stallions fail as U.S. commercial stallions at an 85-90% rate because their runners prove to be of modest (or less than modest) quality. The failure to limit mares bred to them tends to perpetuate a lower quality Thoroughbred gene pool.

    Unproven stallions are more likely to manifest significant deleterious recessive genes. Hence, on the basis of contribution to the gene pool, it makes more sense to limit breedings of newly-retired stallions immediately and to allow quality proven stallions to breed mares that might otherwise go to lower quality stallions, including relatively genetically disadvantaged newly-retired stallion.

5) Though we view newly-retired stallions as dramatically less likely to contribute to improvement in the gene pool than quality proven stallions, owners of newly-retired stallions deserve fair play. If you have a three-year-old colt on the Derby trail that you paid a pretty penny for in 2018 because his pedigree and conformation suggested to you that he was an extremely promising stallion prospect, a Jockey Club imposed mare limit imposed on your now stallion prospect will

> be similar to an imminent domain taking by the government in which the value of your investment will be diminished by a government edict unless just compensation is awarded. We would argue that a grandfather clause that protected the rights for this colt would be appropriate. A similar case can be made for any colt that was a logical stallion prospect that was purchased before the Jockey Club's announcement of impending limits on mares bred.

With respect to item 5 above, the question may be asked whether ~~or not~~ any future stallion isn't disadvantaged by a change in mare limit rules, and therefore should be compensated in some way. The answer is that some stallions will be advantaged by a change in the rules (good but not great stallion prospects who now have a better chance of breeding reasonable numbers of mares if a mare limit rule is enforced). Superstar prospects will be disadvantaged by a mare limit rule. But, if changes in rules are made and everyone knows in advance what the rules of the game are, future prices paid for stallion prospects will reflect the realities of the marketplace, and buyers will adjust prices paid ~~pay~~ so that they are realistic given future prospects, and no one can be said to have been treated unfairly.[20]

Appendix on the Particulars of A Statistical Analysis of Incremental Inbreeding in the Thoroughbred from 2000 to 2020.

The Jockey Club has stated that they are concerned about "a worrisome concentration of the gene pool" (caused by increased inbreeding). Given that the breed is descended from three original stallions and approximately 70 original mares, there has always been a concentration of the Thoroughbred gene pool. But has that concentration increased? When we initiated this study, we expected to find that inbreeding had increased over time in the Thoroughbred, but we wanted to formally test the hypothesis that inbreeding had increase over time before moving on to consideration of the implications for breeders as well as the Jockey Club proposal. When we initiated our study, we saw that a limited number of previous studies had suggested that inbreeding in the Thoroughbred has increased, but we wished to develop an analytical approach that would be easily understood and also would shed further light on the extent of incremental inbreeding in the breed. As we were finishing our analysis McGivney et al's comprehensive analysis of inbreeding [ ] was published on the PlusVital website.[21]

The Losey-Lambert Pedigree Analysis Approach

The Bloodhorse stallion register reports a "family tree" going back 4.5 generations -- 4 generations for mares, 5 generations for stallions for virtually all significant U.S. stallions. That family tree shows any inbreeding by **bold typing** duplicate names in the pedigrees. This inbreeding can be ranked and statistically analyzed. We have devised a method that "scores" stallions on the degree of their inbreeding over these 4.5 generations.

Consider Bayern's pedigree from the Bloodhorse Stallion Record. Bayern was a G1SW by Offlee Wild born in 2001. We use Bayern's pedigree to help illustrate inbreeding and our method of quantifying incremental inbreeding that has occurred in recent years.

Pedigree of Bayern (from The Bloodhorse Stallion Register)

Generations Removed from Subject Stallion

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[20] A breeder with an in utero foal might argue that it is a great stallion prospect for which the owner should be compensated by a change in rules. But, since even the foals of a blue hen mare are more likely to be mediocre stallions prospects than "great" stallion prospects, and mediocre stallion prospects will benefit from a mare limit rule, their argument would probably fall flat in a court of law.

[21] The McGiveney et al [4] study provides an exceedingly more comprehensive study than ours and finds similar conclusions. Moreover, the McGivney study is based on the more reliable genetic analysis rather than pedigree analysis. Our study of inbreeding trends may be easier to understand for students of pedigrees, but we recognize the superiority of the genetic approach to evaluating degrees of inbreeding in any population.

1 2 3 4 5
Fractional contribution to Genes in Subject Stallion (Bayern in this case)
½ ¼ 1/8 1/16 1/32
% contribution to Subject Stallion genes by individuals from each generation
50% 25% 12.5% 6.25% 3.125%
Numerical index value measuring contribution toward inbreeding by individuals from each generation
16 8 4 2 1

BAYERN DK B/, 2011 15s, G1W 130 f, 0 SWrs 1.04 AEI, 8.33 AWD	Offlee Wild DK B/, 2000 29s, G1W 458 f, 22 SWrs 1.45 AEI, 8.5 AWD	Wild Again DK B/, 1980 28s, G1W 943 f, 86 SWrs 2.23 AEI, 8.43 AWD	Icecapade	Nearctic by Nearco ← dam omitted
				Shenanigans by **Native Dancer**
			Bushel-n-Peck	Khaled by Hyperion
				Dama II by Dante
		Alvear DK B/, 1989 9s, W 8 f, 8 r 7 Wnrs, 2 SWrs	Seattle Slew	Bold Reasoning by Boldnesian
				My Charmer by Poker
			Andover Way	His Majesty by Ribot
				On the Trail by Olympia
	Alittlebitearly CH, 2002 0s, 7 f, 6 r 5 Wnrs, 1 SWrs	Thunder Gulch CH, 1992 16s, G1W 2,402 f, 88 SWrs 1.19 AEI, 9.16 AWD	Gulch	Mr. Prospector by **Raise A Native**
				Jameela by Rambunctous
			Line of Thunder	Storm Bird by Northern Dancer
				Shoot a Line (GB) by High Line
		Aquilegia CH, 1989 30s, G2W 7 f, 6 r 5 Wnrs, 3 SWrs	Alydar	**Raise a Native by Native Dancer**
				Sweet Tooth by On and ON
			Courtly Dee	Never Bend by Nasrullah
				Tulle by War Admiral

Inbreeding

Native Dancer: 5S X 5D
Raise a Native: 4D X 5D

Let's consider three ways that a stallion being analyzed (he's generation zero) could be considered highly inbred.

Example 1: His sire and dam (generation 1) were full siblings. In this extreme case, all the stallion's genes come from two original progenitors, his grandsire and granddam (generation 2), which each appeared twice as Bayern's second generation.

Example 2: In the fifth generation back (where there are 32 great-great-great-grand parents), assume that the same sire and dam each appear 16 times. Thus the 16 generation 4 individuals are all full-siblings.

In case 1, generation 2 is composed of the same two grandsires (paternal and maternal) and the same two granddams. Each grandsire produced ¼ of the stallion's genetic material twice (so 1/2 of the genetic material) that eventually resulted in the generation 0 stallion: Likewise for the granddam.

In case 2, the 32 packages of genes from the fifth generation were produced equally from two separate individuals. Each individual great-great-great grand parent provides (on average) 1/32 of the genes that eventually resulted in the foal in question (in this case a stallion) produced six generations later as generation zero. Since the great-great-great-grand**sire** was repeated 16 times in generation 5, he provided 16 x 1/32 = ½ of the genetic material for the generation 0 stallion.. Likewise the great-great-great-grand**dam** also appeared 16 times in generation 5 and provided 16 x 1/32 = ½ of the genetic material for our generation 0 stallion.

Based on the fact that each individual from a generation closer to generation 0 contributes twice as much genetic material as the previous generation, we can assign a contribution value of 1 for each time a duplicate name in a pedigree appears in the 5th generation, 2 for each duplicate name from the 4th generation, 4 for each duplicate name in the 3rd generation, 8 for each duplicate name in the 2nd generation, and 16 for a duplicate name in the 1st generation (there could not be two duplicate names both in the first generation unless parthenogenesis is possible).[22]

The LLM Index of Incremental Inbreeding

Using the scheme above, the inbreeding index value(we call it the "LLM Index" from Losey-Lambert-Michels)[23] assigned for Example 1 would be 32 because we have four duplicates names in generation 2, each being assigned a contribution value of 8, so 8 + 8+ 8 +8 = 32. Note that this value represents an extremely inbred individual.

Likewise, in case 2, we arrive at an LLM index value of 32. Recall that each duplication in the 5th generation has a contribution value of 1. Since there are two sets of 16 names duplicated twice in the 5th generation the LLM index value is 16 x 1 + 16 x 1 = 32. Both cases represent the same degrees of extreme inbreeding (based on pedigree analysis) because the genetic material for the generation 0 stallion originates from the same two duplicate names in both examples.

The LLM index of inbreeding contributed by the five generations is best characterized as an index of **incremental** inbreeding because it does not necessarily account for inbreeding contributed by generation 6 and beyond. Note that the LLM index can vary from 0 to 32, with 32 being an extreme. We've already considered two cases when the inbreeding score was 32. When would the incremental inbreeding be 0? --Yes, you've got it, when there are no duplicate names in the pedigree. Could the index value be 1? No, that would imply we counted one individual once: an index value of 1 is impossible because two names must duplicate each other.

For those who prefer an index varying from zero to one, merely divide the LLM index by 32 to arrive at values in the 0-1 range, with an index of 1 being an extreme example of inbreeding. A zero to one index would be more easily compared with some alternative measures of inbreeding.

Other LLM Index Values

If Ribot appears twice in the third generation as the only duplicate name, you would assign a value of 4 + 4 = 8 for the duplication in the third generation – you do NOT assign added points for Ribot's sire and dam from the 4th generation, as that would be double counting Ribot's genes.

If a horse name is duplicated in the 2nd and 4th generation of a subject horse, he or she would be counted as an 8 for the 2nd generation and a 2 for the fourth generation. The duplicate in the 2nd generation is one of four grandparents so accounts for ¼ of the subject horse's genes (so gets a score of 8 out of a maximum possible score of 32). The duplicate in the 4th generation is one of 16 great-great-grandparents, so accounts for 1/16 of the subject horse's genes (2 out of 32). Do not double count the

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[22] Moreover, it is unlikely that a generation 1 name will be duplicated elsewhere in a 5-cross pedigree: Having it duplicated in generation 2 or 3 (and perhaps 4) would be considered "too close" by most breeders, and duplicate names in generation 1 with generations 5 are difficult because the number of years between four generations typically exceeds the breeding career of a stallion.

[23] For the two authors of this paper and graduate assistant Sara Michels, who organized the data and provided spreadsheet assistance.

ancestors of the duplicate horses in the pedigrees, as their genes were accounted for when you considered the duplicate horse from the 2nd and 4th generations.

Other examples: **Anchor Down**: **Mr. Prospector** appears twice in the 4th generation and once in the 5th, so his contribution toward incremental inbreeding is 2 + 2 +1 (Ignore Raise a Native as the sire of Mr. Prospector because his genes are carried on through his son Mr. P.) Add 2 + 2 for **Blushing Groom** twice in the 4th generation (Ignore Blushing Groom's sire Red God). Total inbreeding score: 2 + 2 + 1 + 2 + 2 = 9.

Back to Bayern

Bayern exemplifies a slightly tricky point count situation (see pedigree above). **Raise A Native** appears in the 4th and 5th generations, so 2 + 1 for that combination. Raise a Native's sire ***Native Dancer*** *appears twice in the 5th generation. As he is the sire of Raise A Native in one of those cases, and Raise A Native is counted already (as a 2 in the 4th generation*) do not double count him in his role as sire of Raise A Native. **BUT -** In the case were Native Dancer does not have a duplicate bold-faced son or daughter (The Bloodhorse stallion register bold-faces all duplicates) see the **blue bold faced Native Dancer** above in Bayern's pedigree, and we have not counted this contribution to inbreeding, and should add a 1 for Native Dancer appearing in generation 5 to the 2 + 1 for Raise A Native to arrive at a score of 4.

What about those Missing 5th-generation Mares?

Fifth generation mares are excluded from the LLM index values because they do not appear in the Bloodhorse stallion register pedigrees. Does this diminish the usefulness of the indexs? Since only ~ 1% of male horses are typically significant DNA contributors to the breed, while more than ~50% of mares produce one or more foals, the average breeding stallion produces many more foals than the average mare and thus there are very few female duplicates in five-generation pedigrees. Thus the effects in leaving the 5th generation mares out of the calculations are *de minimus.*

A Note on Strengths (S) and Weaknesses (W) of the Losey-Lambert Study.

Our study, for which data analysis was completed before we saw the (comprehensive) PlusVital study on inbreeding, analyses a larger sample (**S**) than the Binn et al study and is based on easily understood (S by most non-geneticists) pedigree analysis that is less accurate (**W**) than genetic analysis.
Note that geneticists point out that names duplicated in a pedigree only on the top (sire) or only on the bottom (dam) side of a pedigree do not increase the risk of recessive genes becoming double copy, and some inbreeding measures do not count such duplicates for that reason. Some geneticists would argue that we should have omitted duplicate names when on only the top or bottom (**W**?) when calculating the LLM index. Given that both the 2000 and 2020 stallions we analyzed most likely were affected by approximately the same extent from this, we suspect that any errors largely offset each other, and that our conclusions would have changed very little had we adjusted.

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