Interspecific sexual selection, a new theory for an old practice: the increase of artificial biodiversity through creation of modern, standardized breeds

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Abstract

Interspecific sexual selection, a new theory for an old practice: the increase of artificial biodiversity through creation of modern, standardized breeds. Darwin set the pillars of organismic evolution when he defined natural and sexual selection in the 19th century. Concurrently, a frenzy of selective breeding programmes, generally supported by the wealthy and aristocratic, gave rise to novel breeds of plants and animals at a rate that was previously unforeseen. Since then, breeds selected over millennia and adapted to local conditions began to disappear or were threatened with extinction, being substituted by these new, standardized breeds. It is of interest to explore how new breeds emerged and what the main criteria of the founders of these breeds were. Darwin seemed to be unaware that his contemporaries were practicing a form of interspecific sexual selection responsible for the fixation of exaggerated traits, often plainly ornamental, in the new breeds they intended to create. Parent animals were chosen by individuals who were following particular goals, often with aesthetic criteria in mind. Here we investigated who were the founders of modern breeds in five domesticated species (dogs, cats, pigs, horses and cattle), as very often a single person is credited with the creation of a breed. We found information on founders of 459 breeds, 270 of which were created after 1800. Interestingly, for these species, breed creation is overwhelmingly attributed to men. In the wild, however, the choice of mate is usually performed by the female of a species and thought to be adaptive. Breeders in the Victorian era, nevertheless, lacked such adaptive skills and had little scientific knowledge. The selection of individuals with an extreme expression of the desired traits were often close relatives, resulting in high inbreeding and a variety of genetic disorders.

Key words: Sexual selection, Artificial selection, Pleiotropic effects, Inbreeding, Domestication

Resumen

Selección sexual interespecífica, una nueva teoría para una vieja práctica: el aumento de la biodiversidad artificial a través de la creación de razas modernas estandarizadas. Darwin sentó los pilares de la evolución de los organismos cuando definió la selección natural y sexual en el siglo XIX. Al mismo tiempo, el entusiasmo por los programas de cría selectiva de plantas y animales, a menudo respaldados por familias adineradas y la aristocracia, dio lugar a la aparición de nuevas razas a un ritmo nunca visto y que aún se mantiene. Desde entonces, las razas seleccionadas durante milenios y adaptadas a las condiciones locales comenzaron a desaparecer o se vieron abocadas a la extinción al ser sustituidas por estas razas nuevas y estandarizadas. Por lo tanto, vale la pena estudiar cómo surgieron las nuevas razas y cuáles fueron los criterios de quienes las crearon. Darwin parecía no darse cuenta de que sus contemporáneos estaban practicando una forma de selección sexual interespecífica que favorecía la fijación de rasgos exagerados, a menudo claramente ornamentales, en las nuevas razas que pretendían crear. La elección de los animales progenitores fue realizada por criadores que persiguieron objetivos particulares, muy a menudo con criterios estéticos en mente. Hemos investigado quiénes fueron los fundadores de las razas modernas de cinco especies domesticadas (perros, gatos, cerdos, caballos y vacunos), ya que muy a menudo se atribuye a una sola persona la creación de la raza. Encontramos información sobre los fundadores de 459 razas, de las cuales 270 fueron creadas después del año 1800. Como curiosidad, para estas especies, la creación de razas se atribuye abrumadoramente a

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hombres, pero en la naturaleza, son las hembras quienes suelen elegir las parejas, lo que se considera un rasgo adaptativo. Sin embargo, los criadores de la época victoriana carecían de esas habilidades adaptativas y de suficientes conocimientos científicos. La selección de individuos con una expresión extrema de los rasgos deseados, que a menudo eran parientes cercanos, resultó en una alta endogamia y en trastornos genéticos.

Palabras clave: Selección sexual, Selección artificial, Efectos pleiotrópicos, Endogamia, Domesticación

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Introduction

Charles Darwin proposed the three basic modes of organismic evolution, namely natural, sexual and artificial selection by humans, and tried hard to combine these processes to explain the emergence of all variation in the living world around us (Darwin, 1859, 1871). Artificial selection (Darwin 1868), is an 'evolutionary process in its own right' (Larson and Fuller, 2014; Wilkins, 2020), conducive to the creation of domesticated varieties, and it is necessarily mediated by human intervention (Clutton–Brock, 2012). Domesticated animals, though captive of humans or precisely because of this, have thrived everywhere. Currently, the biomass of livestock is larger for both mammals (such as cattle, sheep, goats, horses and pigs) and birds (poultry) than for all wild mammals and birds combined (Bar–On et al., 2018).

However, and perhaps because artificial selection is perceived as completely conscious and goal–directed, and thus a cultural endeavor detached from nature, there has been little attempt to conceptually compare it to both natural and sexual selection. In this essay, we wish to challenge this uncritical state of affairs, and posit that selection of modern animal breeds (generally speaking, those with standard morphotypes and studbooks) may still be influenced in subtle and yet unexplored ways by our own biological and cultural inheritances, even with the possibility of a gender bias (Lindsey, 2015). This hypothesis may also partially explain why older local breeds, considered as valuable genetic resources, are globally disregarded in favor of less healthy and often highly inbred, standardized breeds (Mendelsohn, 2003; FAO, 2013). Our main goal was to explore how breeds are generated and to highlight that one of the foremost management goals for wild populations today (i.e., conservation of genetic diversity) was overlooked or disregarded in the selection process of most modern breeds (Sánchez et al., 1999). Some may argue that the genetic status is of little practical consequence in the case of breeds in which most individuals are destined for early sacrifice, such as chicken or pigs, but it should make us think twice before acquiring individuals of, for instance, dog breeds that have a lower than average life span or are prone to diseases which make them less healthy (Lampi et al., 2020).

The points we want to stress are the following: 1) breeders have been practicing a surrogate form of sexual selection; 2) It is paradoxical that selective breeding has been mainly attributed to men, as we are a primate species, and thus we belong to a group in which females tend to be the selective sex; 3) Breeders may have done a good job in quickly standardizing breeds by practicing line breeding, truncation selection and genetic isolation, but modern breeds often present a high incidence of serious genetic disorders due to inbreeding and pleiotropic effects. Natural populations of wild animals have mechanisms in place, such as stabilizing selection, to avoid these problems.

Artificial selection as a model for sexual selection

We will argue here that artificial selection is not just a mere model for natural selection (Clutton–Brock, 1999; Larson and Fuller, 2014), with humans acting as the surrogate of a filtering 'environment', selecting against individuals that are less productive or too aggressive (i.e., the less fit for living with and for humans). It has generally been overlooked that artificial selection is a good model for sexual selection. It is the mode of selection to which Darwin resorted when he realized natural selection did not easily explain the evolution of seemingly ornamental traits (Darwin, 1871), such as the peacock tail or the huge antlers of the extinct Irish Elk.

Artificial selection follows the principles of sexual selection because human breeders base their selection on trait expression and only allow some individuals to pass genes to the next generation, thus acting as the selective sex and selecting the fertilizing males. Captive male animals do not have to fight for access to females (for instance, by securing and defending a territory and/or providing food resources), and, in many instances, the sex–ratio is skewed by the human breeder so that there are fewer males than in natural populations. Breeders put themselves in the place of the female in choosing a male. We have termed this process 'interspecific' sexual selection, a novel concept limited to the realm of artificial selection mediated by humans, with no parallels known in the animal kingdom.

The selection of modern breeds in the last two centuries, for which there are often written records and studbooks, have been attributed to male breeders in the most cases. It was a favourite pastime of gentlemen, and even the aristocracy, during the Enlightenment and also later in the 19th and early 20th centuries (e.g., Montague et al., 2014; Wallner et al., 2017; Whitaker and Ostrander, 2019) when societies were still markedly patriarchal. Potentially male–biased selection would mainly concern standardized modern breeds, and not necessarily traditional breeds, as these slowly evolved from the first domesticated animals, and breed founders were many over the different generations.

Gender bias in the attribution of breed selection

In our primate evolutionary lineage, the female is the selective sex, as in most mammals (Darwin, 1871). Mate choice in modern humans is highly influenced by culture, and it is sometimes initiated by the male, or it is bidirectional (see, e.g., Brown, et al., 2009). Male humans (today and almost certainly in prehistoric times, as we are a highly size–dimorphic species) often display their physical and material power so as to be chosen by prospecting females (i.e., they play the game of intersexual selection), but sometimes they may even try to eliminate rival males or to downplay their displays engaging in what is known

Table 1. Number of domestic breeds reviewed in this study, including those originated after 1800, with an indication of the number created by women (last column to the right). The attribution of founding events to female breeders is minimal, making statistical analysis unnecessary (see table 1s in supplementay material). Sources include the Canadian Kennel Club (online information) for dogs. For cats, we used The International Cat Association (TICA: https://tica.org), The Cat Fancier's Association (http://cfa.org) and The Governing Council of the Cat Fancy (https://gccfcats.org).

Tabla 1. Número de razas domésticas revisadas en este estudio, incluidas las originadas después del año 1800, con una indicación del número de ellas que fueron creadas por mujeres (última columna a la derecha). La atribución de casos de creación de razas a criadoras es mínima, lo que conlleva que los análisis estadísticos sean innecesarios (véase tabla 1s en material suplementario). Las fuentes utilizadas son el Canadian Kennel Club (información en línea) para perros. Para los gatos utilizamos "The International Cat Association" (TICA: https://tica.org); "The Cat Fancier's Association" (http://cfa.org), y "The Governing Council of the Cat Fancy" (https://gccfcats.org).

Domestic species	Scientific name	No. breeds reviewed	No. breeds modified/created after 1800	Women involved
Dog	*Canis lupus familiaris*	209	90	4
Cattle	*Bos taurus*	58	36	0
Pig	*Sus scrofa*	75	60	0
Horse	*Equus caballus*	33	23	1
Cat	*Felis catus*	62	44	27
Total		459	270	32

as intrasexual selection (Puts, 2015). In this respect, our ancestral courtship behavior may be analogous to that of deer, sea lions, or many other mammalian species (Morina et al., 2018).

If there was a gender bias among breed founders, as suggested in table 1, this may have had consequences on how artificial selection for the creation of new breeds has been practiced. In fact, gender differences in general farm management in highly developed countries such as the USA were still significant at the end of the 20th century, with very few women –only 4 %– declaring to be farm owners and operators (Zeuly and King, 1998).

Even today, and particularly in non–western rural households in Africa, Asia and Central and South America, attitudes and values concerning livestock management are highly polarized between men and women (Kristjanson et al., 2010). Women tend to be the owners of small livestock including chicken, goats and sheep, while men are typically the owners of larger livestock, such as cattle, horses or camels (Njuki and Sanginga, 2013). In most cultures, even if women tend all kind of animals, most decisions on breeding, health practices and marketing rest on men (Kristjanson et al., 2010).

We obtained the names and gender of the breeders of a wide selection of breeds of five common domestic animals, to assess whether there could be a gender bias in the creation of standardized breeds. We based our choice of domesticated species on population numbers, current cosmopolitan distribution, and their split in numerous breeds, and we also tried to include different uses by people. We therefore considered two species mainly selected as pets (the dog, of which there are indeed working lines and breeds, and the cat), two species used for consumption (cattle and pigs), and lastly the horse, used mainly for transport and recreation.

According to our breed survey (table 1), male breeders have been credited as founders in most cases, particularly in the case of modern breeds in the last two centuries. Assuming that men have been the overwhelming force behind the domesticated animal breeds we see today, we must also assume the paradox that males, the sex which is chosen by females in the primate lineage, are acting as the selective sex on behalf of the animals they keep captive. If the attribution to men was however wrong in some cases, it is time to recognize the role of uncredited women and revise breed history records.

Mechanisms to avoid genetic problems in natural populations

It has been hypothesized that female animals in wild populations adaptively select males as fathers for their progeny based on 'good genes' (Andersson, 1994). They try to get the best possible genetic makeup to produce healthy descendants, which in turn will be preferred by future selecting females (the 'sexy–son hypothesis', Weatherhead and Robertson, 1979).

Fig. 1. Modern breeds are plagued with genetic disorders, such as the propensity to melanoma in grey horses. However, they are none–the–less highly appreciated in numerous horse breeds, such as the Spanish Purebred in the picture, due to their aesthetic appeal and symbolic value. The wild ancestors of horses were all melanized, excepting rare color mutants.

Fig. 1. Las razas modernas están plagadas de trastornos genéticos, como la propensión al melanoma en los caballos tordos, que, sin embargo, son muy apreciados en numerosas razas de caballos, como la raza pura española que se muestra en la imagen, debido a su atractivo estético y su valor simbólico. Los ancestros salvajes de los caballos estaban todos melanizados, excepto unos pocos mutantes de color.

Females, alternatively, may try to maximize genetic diversity in their progeny by selecting genetically compatible males (Mays and Hill, 2004). In addition, in natural populations, sexual selection, through male–male competition, female choice, or an interaction of both selective processes, may result in stabilizing selection on quantitative morphological traits (Kodric–Brown and Hohmann, 1990).

But how can human breeders (whether men or women) put themselves in the skin of discerning females to select the best stallion, or the best bull? Particularly men, with their engagement in intrasexual competition with other men, may prefer the larger, the faster, and generally the fancier, when practicing artificial selection, perhaps ignoring or downplaying potential 'side–effects' (including pleiotropic effects, Reissmann and Ludwig, 2013). As we said above, animal breeders often cherry–pick individuals sporting rare attributes, such as blue eyes (Negro et al., 2017), that may be associated with impairments such as deafness. In horses, grays (fig. 1) are known to have a higher propensity to develop melanoma than horses with other coat colors (Pielberg et al., 2008), but they were selectively bred, nonetheless, by Carthusian monks in Spain, for instance. And there are almost entirely gray breeds due to deliberate coat selection, such as the Lippizaner, the Camargue horse and the Kladruber. Among dogs, the Rhodesian Ridgeback has a high incidence of a serious disease called dermoid sinus (Salmon Hillbertz et al., 2007), associated with the 'ridge' along the spine. Rhodesians are traced back to a big game hunter and dog breeder named Cornelius Van Rooyen (Mann and Stratton, 1966). Brachycephalic dogs, such us pugs, boxers and bulldogs, have a ten–fold increase in the prevalence of corneal ulcerative disease (O'Neill et al., 2017) compared to crossbred dogs. In fact, almost all individuals in brachycephalic breeds are homozygous for a DVL2 mutation, reducing their quality of life (Mansour et al., 2018). Artificial selection for extremely high growth rates in giant dog breeds has seemingly led to developmental diseases that significantly shorten their life expectancy (Galis et al., 2007). Entirely white animals exist for every domesticated species. These white individuals, whether leucistics or true albinos, are extremely rare among wild species as they are possibly the focus of predation –or easily detected by prey.

Examples of pleiotropic detrimental effects abound (Reissman and Ludwig, 2013), but they have not deterred breeders from producing 'defective' animals that would not survive well in nature, and whose wellness is compromised through their lifetime. In the wild, animals have evolved numerous mechanisms to avoid inbreeding, such as kin–recognition, sex–biased dispersal and extra–pair copulations (Pusey and Wolf, 1996), mechanisms that are overridden in captivity. Modern breeders, contrary to the developers of traditional breeds of the past, are typically more interested in breed uniformity, with the consequence that domestic animals often present a high incidence of genetic disorders due to inbreeding and pleiotropic effects. This may also affect animal welfare and even increase susceptibility to infectious diseases (Luong et al., 2007). It remains to be seen, however, whether female breeders would have different selection goals, perhaps less prone to extreme trait selection, as too few women seem to have participated (or at too few have been given credit; a limitation inherent to our study) in the creation of modern breeds.

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Supplementary material

Table 1s. Breeds of dogs (A), cattle (B), pigs (C), horses (D) and cats (E) reviewed in this study. We include date and country of origin, as well as the putative founders (individual ot collective).

Tabla 1s. Razas de perros (A), ganado vacuno (B), cerdos (C), caballos (D) y gatos (E) revisadas en este estudio. Se incluyen fecha y país de origen, así como los presuntos fundadores (individuos o colectividades).

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