

Preliminary Investigation of Morphological Differences Between Ten Breeds of Horses Suggests Selection for Paedomorphosis

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Paedomorphosis is the retention of juvenile morphology at maturity and is important in generating evolutionary change in domestic species and species in the wild. When comparing dogs with the wolf, this preliminary study saw paedomorphosis in their physical and behavioral traits (Goodwin, Bradshaw, & Wickens, 1997). This preliminary study compared morphological characteristics of 10 breeds from northern regions (Shetland ponies) and southern regions (Arabians) with the Exmoor pony. Twenty-three respondents from the United Kingdom and Australia rated the breeds for 7 physical traits. As evidenced by low standard deviations, the respondents demonstrated a high degree of agreement. The study ranked breeds from the most similar (Highland pony) to the least similar (Arabian) to the Exmoor pony. The least similar breeds had physical traits suggestive of paedomorphosis: small heads, long legs, and a low head-to-body ratio. This preliminary study suggests that morphological, behavioral, and physiological differences between the breeds-plus morphometric comparisons of extant breeds and faunal remains of predomestication horses-warrant further study..

Paedomorphosis describes changes in the rate of development resulting in the retention of juvenile characteristics in adult nonhuman animals. Adults then

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resemble juvenile stages of the ancestral species (Sheldon, 1993). An extreme extant example is that of the Axolotl, a species of salamander that achieves sexual maturity while otherwise phenotypically in the juvenile stage of development (Safi et al., 2006). Paedomorphosis is considered an important mechanism for producing evolutionary change (Gould, 1977), and domestic animals have been used as models of evolutionary change since Darwin (1859/1950). Physical evidence for paedomorphism can be derived from the fossil record for dogs (Morey, 1992) and may be gleaned from fossil horses (MacFadden, 1992). However, paedomorphic effects on behavior are less easy to identify from this source.

Physical and behavioral paedomorphism has been described in domestic dogs (Goodwin et al., 1997), and there have been suggestions that they may also occur in horses (Budiansky, 1998). However, unlike the wolf, who is generally accepted as the ancestral species of the dog (Serpell, 1995), the ancestral species of the horse is extinct. This makes direct comparison impossible. It is also questionable whether extant nondomestic equids would provide reliable comparative models for such an inquiry.

In dogs, breeds showing paedomorphism are characterized by a reduction in overall body size and retention of a juvenile head:body ratio (Frank & Frank, 1982; Price, 1984). However, although the head-to-body ratio may be reduced in horses, the head-to-leg length ratio may also provide a useful indicator, as foals are generally born with smaller heads than their mother's but with limbs of similar lengths (Figure 1).

Paedomorphosis in dogs has been driven by artificial selection within closed stud books (those prohibiting breeding outside the pool of animals recognized and registered as representatives of the breed). Archaeological and genetic evidence suggest that the dog was domesticated earlier than the horse (Clutton-Brock, 1999; Jansen et al., 2002; Levine, 1999a; Vila et al., 1997), so it is perhaps to be expected that paedomorphic differences appear more extreme in dogs than in horses.

Paedomorphism in horses may influence communication, play, trainability, responsiveness, and socialization. These traits directly influence the usefulness and therefore the welfare of riding horses; therefore, by studying horses from breeds with closed stud books—the Arabian and Thoroughbred and those representing types such as warm-bloods—it may be possible to investigate whether artificial selection is producing horses who differ physically and behaviorally. Eventually we aim to make morphological comparisons with faunal remains of caballine horses from predomestication sites. For the purposes of this initial investigation, however, we selected the Exmoor pony for comparative purposes because (a) it has been claimed that 12,000-year-old horse bones found in the nearby Mendip caves resemble modern Exmoor ponies (Exmoor Pony Society, 2007) and because (b) the Exmoor has a classic pony conformation that appears similar to that of predomestic caballine equids.



FIGURE 1 Mare and foal illustrating differences in head-to-limb ratio. (Photo: P. McGreevy.)

By adapting the methods of Goodwin et al. (1997), we aim in this article to examine data that will allow us to explore evidence of paedomorphic and other heterochronic differences (Sheldon, 1993) in the morphology of 10 breeds of extant horses in comparison with each other and also with the Exmoor pony. If physical indicators of paedomorphic effects are suggested by these initial investigations, further studies of physical and behavioral paedomorphosis will be conducted in a range of contemporary domestic horse breeds from various locations around the world.

METHODS

The methods of Goodwin et al. (1997) were adapted to rate horse breeds for morphological similarity. As the ancestral species of the domestic horse

is generally considered extinct (Clutton-Brock, 1999; Jansen et al., 2002), any extant breed could be used to produce a range of physical similarities between the breeds. In this study, the Exmoor pony was selected for this purpose (Figure 2).

For comparative purposes—using supplied photographs—bay individuals (brown with a black pigmentation in the ear tips, distal limbs, mane, and tail) of 10 show breeds (Figure 2) from around the world were visually assessed for morphological similarity to the Exmoor pony. Fourteen UK and 9 Australian participants in higher education who were blind to the purpose of the study scored each breed on a scale of 1–5 for the extent to which they resembled an Exmoor pony in the following seven characteristics:

1. Shape of the head,
2. Shape of the eyes,
3. Shape of the ears,
4. Size of the head compared with the body,
5. Length of the legs in comparison with the body,
6. Coat, and
7. Tail.

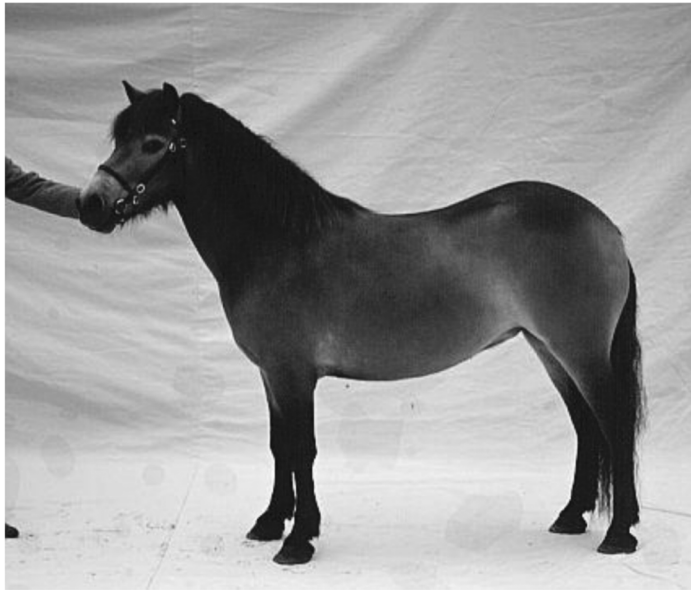


FIGURE 2 Exmoor pony. (Photo: dkimages, 2007.)

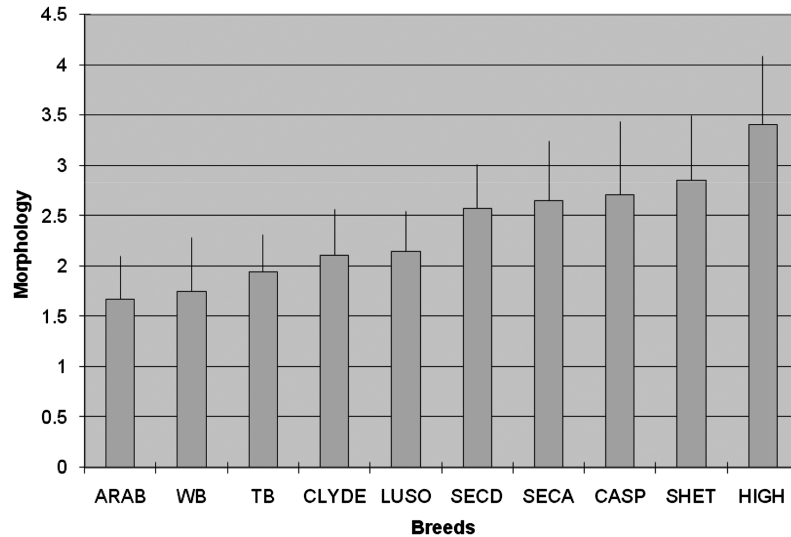


FIGURE 3 UK mean breed rankings plus standard deviation. Key: ARAB = Arabian; WB = warm-blood; TB = Thoroughbred; CLYDE = Clydesdale; LUSO = Lusitano; SECD = Welsh Section D; SECA = Welsh Section A; CASP = Caspian; SHET = Shetland; HIGH = Highland.

RESULTS

The arithmetic mean of the breeds' scores for the seven physical characteristics was used to rate the breed's overall similarity to the Exmoor pony. Breed mean scores were ranked by country (Figures 3 and 4) and overall (Figure 5) and compared.

DISCUSSION

It should be noted that "breed" can have several meanings. Breed can be used to describe a population where breeding is controlled or a geographical population with limited or no human control over breeding. Breeds can also be intentionally crossbred to create new breeds or to "improve" existing breeds. All these scenarios are likely to have associated behavioral and physical effects. Many breeds of horses and ponies now appear to have morphological differences between show and working lines (Edwards, 1992).

This study focused on breeds with closed stud books. Breed scores and ranks for the breeds were similar for UK and Australian respondents (Figures 2 and 3).

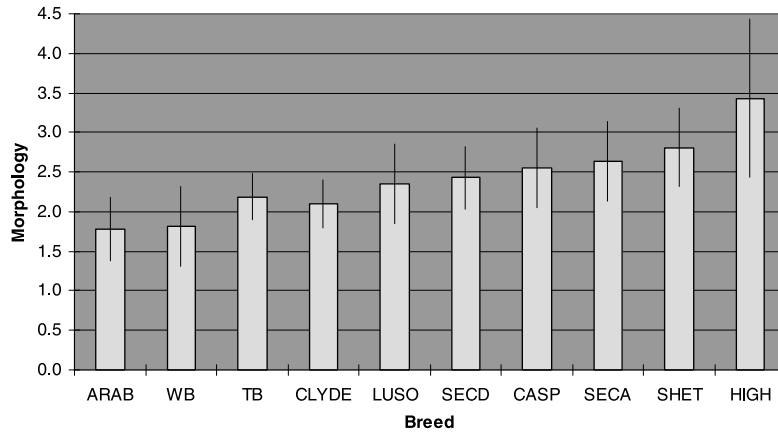


FIGURE 4 Mean breed rating for Australian respondents. Key: ARAB = Arabian; WB = warm-blood; TB = Thoroughbred; CLYDE = Clydesdale; LUSO = Lusitano; SECD = Welsh Section D; SECA = Welsh Section A; CASP = Caspian; SHET = Shetland; HIGH = Highland.

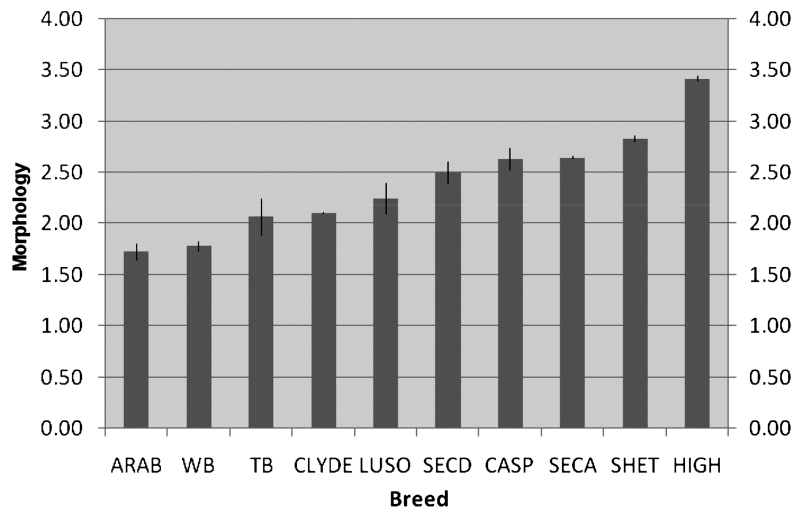


FIGURE 5 Overall mean breed rankings for combined UK and Australian data plus standard deviation for means between countries. Key: ARAB = Arabian; WB = warm-blood; TB = Thoroughbred; CLYDE = Clydesdale; LUSO = Lusitano; SECD = Welsh Section D; SECA = Welsh Section A; CASP = Caspian; SHET = Shetland; HIGH = Highland.

Standard deviations for the mean breed scores were low, indicating a high degree of agreement between respondents and resulting in similar overall ranks for the breeds (Figure 4). Overall rankings indicate a range of morphological differences across these 10 breeds in comparison with the Exmoor pony.

Before further consideration of the effects of paedomorphosis was undertaken, other potential explanations for the observed differences were considered. In many species with a large geographic distribution, including wolves and humans, it is possible to identify a geographic cline (gradual change) that affects morphology and behavior. Individuals from the northern extent of the range tend to be stockier—with adaptations for energy conservation in a cold climate—and to have a less reactive temperament (Moen, 1973). Individuals from the southern extent of the distribution tend to be more gracile in build—with adaptations to heat dissipation in a hot climate and a tendency to be more reactive. These differences are described by Bergman and Allen's rules (Goodwin, 2002; Moen, 1973). Northern equine examples would include the Icelandic and Fjord ponies whereas southern examples would include the Moroccan Barb and Indian Marwari.

When the UK and overall rankings of the 10 breeds were examined, southern and northern breeds seemed distributed throughout rankings. For example, Arabian and Caspian horses, who are classified as southern breeds, were ranked 1 and 8 (1 and 7 overall), respectively; the Welsh and Scottish breeds, classified as northern breeds, were ranked from 4 to 10 in both the UK and overall ratings. The warm-blood and Thoroughbred could be considered relatively recent types or crossbreeds—though they do have closed stud books and were ranked 2 and 3 throughout. However, Bergman and Allen's rules are dependent upon natural selection. Therefore, because these are subject to artificial selection pressures and because their locations are dependent on humans, it could be argued that they do not apply to domestic species.

The Lusitano and Clydesdale were rated closely in the United Kingdom and Australia, although their overall position varied slightly. Both breeds have convex profiles similar to the Moroccan Barb, the Kladrub (Evans & McGreevy, 2006), and the ancient ram-headed Persian Nisaeen breed (Hyland, 2003). Heterochronic and hence morphological changes in different parts of the body can occur independently, a process known as mosaic heterochrony (Sheldon, 1993). This tends to produce scatter in a linear scale of overall paedomorphic effects, as has been reported in breeds of dogs (Goodwin et al., 1997). For example, some breeds of dog—such as the English Bull dog—show overdevelopment of the skull (peramorphism) and underdevelopment of the limbs (paedomorphism) in comparison with the wolf. It is possible that effects of mosaic heterochrony are affecting the rankings of the horse breeds in this study.

Many breeds selected for showing and competition purposes—Arabians, warm-bloods, and Thoroughbreds—appear to have been selected for small heads, long legs, and reactive temperaments, all traits that could be considered paedomorphic. Arabian lines selected for the show ring are now physically

and behaviorally very different from the desert Arabians brought to the United Kingdom by the Blunts in the 1890s (Greely, 1985).

The current results raise several interesting questions regarding selection. Do modern warm-bloods and, to a lesser extent, Thoroughbreds, now resemble overgrown Arabians? The ranking of the Welsh Section D at 6 when compared with 8 for the Welsh section A (overall mean rankings) is also interesting. The Section D is a large riding cob suitable for adults to work on the hills, farm, hunt, and drive, whereas the Welsh Section A (also known as the Welsh Mountain Pony) is a small child's riding pony. Is selection producing a more paedomorphic Section D in comparison with the Section A?

Although the results of this small pilot study should be treated with caution, they seem to justify further investigation of the effects of paedomorphosis on the morphology and behavior of horse breeds. There is some evidence for this possibility in the literature on breed differences in morphology—including the Thoroughbred, Standardbred, and Arabian (Evans & McGreevy, 2006)—and the selection of small heads and long legs in warm-blood performance horses (Van Heel, Kroekenstoel, Van Dierendonck, Van Weeren, & Back, 2006). However, currently, the number of breeds studied is small.

CONCLUSION

We therefore suggest that future work should aim to collect comparative measures of skull and limb morphology from a range of breeds. In addition, we suggest that observations are recorded of the behavior of single-breed groups during social interactions under standard conditions to include the following:

1. Open field test,
2. Interactions over familiar and unfamiliar forages,
3. Interactions with familiar and unfamiliar horses, and
4. Interactions with familiar and unfamiliar people.

Comparative measures from predomestication faunal remains should be used in future studies as a more robust source of information on the morphometrics of the wild type than comparison with present-day Exmoors, who, like most modern breeds, have been subjected to selection by the breeders. This pilot study indicates some morphological evidence of paedomorphosis in horse breeds and warrants further investigation.

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