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Recognising the potential role of native ponies in conservation management

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Running title: Native ponies and conservation

Abstract
Population control of feral horses has been the subject of public debate in many parts of the world in recent years due to wide-reaching ecological and societal impacts. However, the feral populations in these high-profile cases are not 'native' but are instead descended from animals which escaped from or were released by settlers. This paper considers i) the potential role of indigenous equids as conservation grazers within native ecosystems currently in poor condition, and ii) the value of supporting semi-wild native ponies specifically. We argue that the high ecological overlap between ponies and cattle reported in a range of studies means that they should be considered as alternative tools for conservation management, particularly in scenarios where there is a need to reduce the dominance of plant species avoided by more-selective small ruminants such as sheep. Semi-wild ponies could be particularly suited to conservation grazing because their genomes have been predominately shaped by natural and not artificial selection, meaning they may have adaptations no longer present in domesticated equids. With agricultural and environmental policy in the EU and UK under major review, it is anticipated that the wider delivery of public goods, rather than primary production, will be prioritised under future subsidy payment schemes. Recognising the value of native ponies as conservation grazers would broaden the range of routes by which land managers could achieve biodiversity gain, while simultaneously supporting at-risk equine genotypes.

Keywords: horses; equids; semi-wild; conservation grazing; agri-environment; genetic adaptation

1. Background

Grazing continues to be a major driver of land use change worldwide and can be both beneficial and detrimental to wildlife habitat. In recent years a link between feral horse (*Equus ferus caballus*) overpopulation and environmental damage has become a contentious issue due to public protests at proposals to cull large numbers (Driscoll, 2018; Scasta et al., 2018). However, the populations in these high-profile cases are not 'native', but are instead for the most part descended from animals which escaped from, or were released by, European settlers in the 16th century (National Research Council, 2013), and are thus categorised as 'feral' (defined as living in a wild state after escape from captivity or domestication). Ecologically, they are alien species, and there is mounting evidence that they are putting ecosystems at risk through trampling and vegetation community change (Davies et al., 2014; Nimmo, 2018; Rogers, 1991).

What, then, is the role of indigenous equids within their native ecosystems? In such situations, can targeted grazing by horses (taller than approx. 148 cm at the withers) and ponies (less than approx. 148 cm at the withers) achieve conservation gains? These primitive horses or ponies have lived as free-ranging populations for thousands of years with little human intervention. Such herds are classified by the EU as 'semi-wild' and have related derogations which exempt them from legislation relating to e.g. animal identification and treatment. Whilst overall population increase is commonly a concern with feral equids, semi-wild horse and pony populations are more generally under threat. Within the UK very few pony herds that can be designated as semi-wild remain. Two examples of semi-wild native ponies thought to have been *in situ* since the Bronze Age are Dartmoor Hill Ponies and Carneddau Mountain Ponies (Fig 1). In both cases ponies have been removed to make way for domestic livestock in response to economic pressures on farmers, and there is now a serious risk that they may die out. Census data from the 1960s onwards estimate the Dartmoor Hill Pony population has declined from a maximum of 12,250 to 1,200 (*J. Hibbs, personal communication*); while there are around 300 Carneddau Ponies found on Snowdonia's Carneddau Mountains today (*H. Kehoe, personal communication*). The UK government criterion which defines semi-wild ponies (i.e. that they remain outside of human control for their survival and reproduction) also means they are not protected by societies or registers. As a result, they fall outside of initiatives on the sustainable use of farm animal genetic resources incentivising the conservation of rare or 'at risk' breeds (including breeds of horses and ponies), and the genetic variation within them. Rather short-sightedly the conservation of animal genetic resources has been considered primarily in relation to their potential contribution to agricultural productivity and sustainability (Hall & Bradley, 1995; Rege & Gibson, 2003), with little or no regard given to ecological resilience.

Agricultural abandonment of grasslands and heathlands across the EU due to changes in farming practice has being identified as a specific threat to related habitats and species (Hermoso et al., 2018; Keenleyside & Tucker, 2010), particularly in areas that are marginal for agricultural production due to environmental challenges. Left unmanaged, many of these vegetation communities have become dominated by plant species rejected by stock (e.g. *Juncus* spp., *Molinia caerulea*, *Deschampsia cespitosa*, *Pteridium* spp, *Ulex* spp.). This degradation of native plant communities limits the value of these areas for achieving biodiversity conservation objectives. Consequently, government agencies and conservation charities are resorting to mechanical cutting of vegetation (Talle et al., 2018; Valasiuk et al., 2018), as a substitute for grazing, to ensure the long-term survival of Europe's most valuable and threatened habitats and species (as listed under both the EU Birds Directive 2009/147/EC and the EU Habitats Directive 92/43/EEC; i.e. sites with NATURA 2000 status). This is however costly, does not create the same degree of structural heterogeneity as grazing, and over time leads to nutrient depletion.

Farming systems in areas designated by the EU as less favoured have for many years been supported by specific agricultural subsidies. It is anticipated that under future support schemes the wider delivery of public goods, rather than primary production, will be prioritised. Crucially this could allow the grazing outcomes of stock types other than sheep and cattle to be eligible for support payments. The biodiversity benefits of mixed-low-intensity grazing systems have been well documented (Critchley et al., 2008; Fraser et al., 2014; Liu et al., 2015; Lopez et al., 2017b) (Table 1), yet in countries including the UK semi-natural grassland and heathland communities continue to be managed predominately under sheep-only systems. A policy change which recognised the role of native ponies could have multiple benefits; improved biodiversity, diversification of income streams, and conservation of threatened genotypes of grazer. However, to date there have been little robust data collected regarding the comparative impacts of equid grazing, largely because of proportionately low levels of research funding compared to those with domesticated stock. Unless addressed, this will continue to compromise our ability to optimise deployment of conservation grazing tools, undermining our ability to meet conservation targets.

To explore these issues further we evaluated i) the potential role of native ponies as conservation grazers, and ii) the value of supporting semi-wild ponies specifically. Firstly, we examined the comparative foraging strategies and dietary preferences of equids, and identified situations where grazing by ponies could be particularly beneficial. Secondly, we considered the behavioural ecology of ponies in the context of conservation grazing schemes and free-living populations, highlighting both the merits of using ponies as conservation grazers and behavioural factors that must be considered when using ponies in these contexts. Finally, we explored the population genetics of UK native ponies and associated evidence of adaptation.

2. Dietary preferences of equids

2*.1 Physiological factors influencing foraging*

A variety of factors influence the foraging choices and grazing behaviour exhibited by large herbivores. One of the key determinants of foraging behaviours is body size, since energy requirements scale to 0.75 rather than 1 (Demment & Van Soest, 1985). Consequently, larger animals are generally less selective grazers than their smaller counterparts (Sensenig & Demment, 2010), and tend to prioritise maintaining their intake rate rather than the nutritional value of what is consumed when resources become limited. These differences are evident when the dietary preferences of cattle and sheep are compared (Critchley et al., 2008; Cuchillo-Hilario et al., 2018; Fraser et al., 2009; Grant et al., 1985). Gut morphology and function also have a role to play in influencing diet composition. While ruminants are fore-gut fermenters (with fermentation taking place in the reticulorumen), equids are hind-gut fermenters (fermentation occurs in the caecum and colon). A mainly post-gastric site of fermentation (i.e. after the stomach) means they can digest and absorb available soluble carbohydrate and protein directly, without the potential inefficiencies associated with the synthesis of microbial protein (Santos et al., 2011). Evidence suggests that equids achieve higher nutrient extraction rates than bovids on all forages, whether housed or at pasture (Duncan et al., 1990; Illius & Gordon, 1992; Santos et al., 2011). Without selective retention of large particles in the rumen, digesta passes relatively quickly through the equine fermentation zone. This faster throughput is an advantage which outweighs their lower digestive efficiency, particularly on poor quality forages, allowing them to ingest large amounts of fibre-rich forage.

2.2 Comparative foraging strategies

Studies of natural grazing systems in Africa were among the first to identify differences in foraging strategies of large grazers, and categorised the equid present (the zebra) along with ruminants of a similar size as generalist (rather than specialist) feeders (Jarman & Sinclair, 1979). There is consensus from a range of ecosytems that equids prefer graminoids to browse species (Celaya et al., 2011; Ferreira et al., 2013; Gordon, 1989; Lopez et al., 2017a; Menard et al., 2002; Pratt et al., 1986; Scasta et al., 2016). However, as generalist feeders, they will switch to alternative plant species and plant parts when preferred items become depleted. Thus, like cattle, equids will incorporate woody vegetation into their diets as high-quality grassland availability declines (Putman et al., 1987; Scasta et al., 2016). However, equids have been found to be more reluctant to browse on *Calluna* spp. (a plant species that heathland grazing prescriptions are frequently designed to protect) than are cattle (Celaya et al., 2011; Ferreira et al., 2013) or sheep (Ferreira et al., 2013). Instead, ponies prefer to consume *Ulex* spp. (Putman et al., 1987) (a plant species that grazing prescriptions are often aiming to control), with dietary inclusion rates higher than for cattle or sheep (Ferreira et al., 2013).

Studies in areas with mixed habitats found that the summer diet of ponies, like that of cattle, consisted primarily of grasses (80-90%) (Putman et al., 1987). However, *M. caerulea*, a species scarcely eaten by cattle, contributed to 20% of their diet at this time. In the UK, increased *M. caerulea* abundance has frequently been at the expense of more diverse upland heath and mire habitats (Yeo & Blackstock, 2002); a situation exacerbated by sheep-only grazing since sheep strongly avoid consuming this species. To counteract this, agri-environment schemes have offered incentives for cattle grazing, since as less selective feeders they are more likely to switch to consumption of *M. caerulea* as preferred resources decline (Critchley et al., 2008; Fraser et al., 2011). However, loss of cattle from many less favoured areas in response to economic and social challenges (poor returns, aging farmer populations, lack of labour) has meant that there in many regions there are insufficient cattle numbers to deliver recommended grazing prescriptions. Despite the potential for targeted pony grazing to also reduce *M. caerulea* dominance through increased utilisation this has not been fully explored or exploited. Indeed, the high dietary overlap between ponies and cattle shown by a range of studies (Celaya et al., 2011; Gordon, 1989; Menard et al., 2002; Pratt et al., 1986; Scasta et al., 2016) suggests that these animals could be considered broadly as alternative tools for conservation management, eligible for similar agri-environmental scheme payments based on the outcomes of their grazing.

Given that between-species comparisons of dietary preferences and grazing behaviour involving ponies are rare, it is not surprising that there is a complete lack of evidence as to similarities and differences in the diet composition of different pony breeds or types. Studies with cattle have found few differences between the diets selected by contrasting traditional and modern breed types (Fraser et al., 2009; Fraser et al., 2013), with utilisation of *M. caerulea* similar among breeds. However, results from cattle breed comparisons also highlight that adaptations to adverse environments as well behavioural responses to topographical/climactic conditions must also to be considered. Since such factors affect energy requirements and nutrient use efficiencies they can potentially influence both grazing patterns and welfare (Fraser et al., 2009; Ricci et al., 2014).

3. Behavioural ecology

3.*1 Social organisation*

Ponies show a relatively high level of social complexity compared with grazers such as sheep or cows, which can have certain implications for conservation grazing schemes. Free-living horses live mostly in either family bands or bachelor bands. Family bands are comprised of between two and 35 mares, along with one to two stallions and all immature offspring (Boyd & Keiper, 2005). These often show patterns of fission and fusion, where groups split up and reform frequently (*CS, personal observation*). Bands also show seasonal fluctuations in the relative level of social cohesion, most likely due to a combination of food availability and stallion herding frequency (Stanley et al., 2017). Whilst foals can be nutritionally independent of their mothers at the age of around six months old, youngsters of both sexes only naturally disperse from the group in which they are born between the ages of two and five years old (Boyd & Keiper, 2005). These social factors must be taken into account, in addition to grazing capacity, when considering stocking densities and sex ratios of ponies in conservation grazing schemes; for example if there are no neighbouring groups to which youngsters can disperse, they will need to be removed from the group to avoid them being the targets of aggression (Stanley & Shultz, 2012). Strong social bonds exist between females and their band stallion, but social bonds between females are also important; mares are known to remain together after the death of their band stallion (Keiper, 1985). Existing social bonds and opportunities for their maintenance should therefore be a key consideration for both the selection of individuals and their management in both conservation grazing schemes and free-living populations.

Horses are polygynous, meaning they show high levels of reproductive skew (Rubenstein & Nunez, 2009). Since not all males can hold harems at any one time, yet the sex ratio is most commonly 1:1 in free-living populations (Ransom & Kaczensky, 2016), surplus males commonly form bachelor bands. These are known to number up to 16 individuals (McCort, 1984) and are thought to be mostly unstable in terms of membership (Boyd & Keiper, 2005). If the number of breeding stallions is controlled in feral populations, conservation grazing schemes elsewhere could provide a potential sink for these excess bachelor males.

3.2 Home ranges

Horse bands do not generally defend discrete territories (Boyd & Keiper, 2005); instead, they occupy overlapping but well-defined home ranges that can persist for a number of years (McCort, 1984) and vary significantly in size, both within and between populations (Boyd & Keiper, 2005). Such site fidelity could make ponies more suited to targeting specific locations within a larger habitat for conservation grazing. Whilst hefting (selective breeding to instil a specific home range) has traditionally been used to achieve this in sheep, reduced flock sizes in recent years has reduced the effectiveness of this strategy. A herd (a group of horse bands living in same geographical area) can show significant social structure, where bands follow similar movements and have an inter-band dominance hierarchy (Miller, 1979). Home range size can vary seasonally in feral horse populations, although there seems to be no consistent trend as local conditions seem to have a significant influence (Boyd & Keiper, 2005). Habitat utilisation does, however, appear to vary seasonally in most populations; in mountainous regions, vertical migrations may occur to benefit from changing vegetation quality and abundance (Berger, 1986; Linklater et al., 2000), whilst water availability (Berger, 1977) and tabanid fly abundance (Keiper & Berger, 1982) can also influence home range use. It is important to note that whilst the factors affecting home range use have been studied across a variety of feral populations, our understanding of the influence of herd composition on grazing behaviour is lacking.

3.3 Influence of contraception

Contraceptive vaccines are being increasingly used to control female fertility and therefore limit population sizes in feral horses. Since natural predators are frequently absent from habitats in which feral horses thrive, management interventions are often required to control population sizes (Ransom et al., 2016; Saltz, 2002). However, the use of contraception can influence both behaviour and range use (Nunez et al., 2009; Ransom et al., 2010), and this could have implications both for the welfare of free-living populations and range use in conservation grazing schemes. Gelding excess colts is another approach to population control, but again the potential impacts on subsequent resource utilisation are poorly understood. Of course, such approaches to meeting sustained external pressures to control numbers also pose additional risks to already rare populations such as the

Carneddau and Dartmoor Hill Ponies, including a reduction in genetic diversity and the introduction of artificial selection to these populations. Interventions such as removal of stallions, gelding of stallions, and mare contraception all result in management decisions being imposed upon the herds, threatening their semi-wild status and potentially impacting upon the selection of specific genes and traits correlated with adaptation to the harsh environments they have evolved in.

Males used in conservation grazing schemes are frequently castrated (gelded) to avoid breeding. Gelding is also commonly carried out to facilitate handling and management (McDonnell, 2005). However, groups of geldings likely differ in home range use to the more well-studied family bands, or even compared with non-castrated bachelor bands. This could have implications for the management of gelding groups, specifically in terms of predicting their seasonal movements.

4. Population genetics

4.1 How genetically distinct are breeds?

Science has only recently begun to address the question of how distinct free-living, unmanaged populations of horses and ponies are from their registered counterparts. Factors such as adaptation, artificial selection (in the registered breeds) and inbreeding must be considered. Genetically speaking, there is no universally accepted definition of a 'breed', which is an artificial human concept based on a closed (or restricted) breeding pool of individuals which share a common phenotype (typically purely morphological i.e. height, coat colour). In cattle, for example, the primary distinction between Red and Black Angus is due to a mutation in a single coat colour gene (Matukumalli et al., 2009). In the case of semi-wild pony populations then, the question of how distinct they are from their registered relatives is perhaps not as important as the reason for any differences (i.e. are they signatures of adaptation?).

4.2 How do native pony breeds differ?

In the first studies of their kind, several studies of population diversity and relationships in both registered and semi-wild UK pony populations were undertaken (Winton et al. 2013; McMahon et al. 2015; Hegarty et al. 2017). Genotype data of semi-wild populations were generated using 15 simple sequence repeat markers (SSR) and 162 single nucleotide polymorphism (SNP) markers on samples from 16 herds of Welsh Mountain Hill Pony (McMahon et al., 2015) and 19 herds of Dartmoor Hill Ponies (Hegarty et al., 2017). These data were compared to existing genotypes (Winton et al., 2013) of Section A Welsh Ponies and Section D Welsh Cobs (breed society registered), the Carneddau Pony (semi-wild), Connemara Ponies (breed society registered), Irish Draught horse (breed society registered) and Dartmoor Ponies (breed society registered) (Fig 2).

These analyses demonstrated that the Carneddau Pony is genetically distinct from the Section A Welsh Pony (Winton et al., 2013), despite the Carneddau Ponies generally being thought of as being either an offshoot or an ancestor of the Welsh Section A. Population structure analysis showed that the two types are related, but distinct, and mitochondrial DNA analysis identified several rare variants present at high frequency in the Carneddau Ponies but not any of the other types. High levels of deviation from Hardy-Weinberg equilibrium were detected which are indicative of selective pressure, and it was argued that conservation or further study of the Carneddau Ponies was important to avoid losing useful genetic adaptations.

Similar results were observed in studies of the Welsh Mountain Hill Pony (McMahon et al., 2015) and Dartmoor Hill Ponies (Hegarty et al., 2017). In both cases, the populations can be distinguished from their registered counterparts. Thus, whilst both semi-wild populations are related to their registered cousins, there are key genetic signatures which are common across animals from the same group and can be used to distinguish them. The largest genetic difference observed was that between the Carneddau and the Section A Welsh, with a Wright's Fst (Wright, 1965) measure of genetic distance 0.157 when all datasets were compared. This value is comparable to the difference seen between established horse breeds in studies in France (Leroy et al., 2009) and Poland (Stachurska et al., 2014). Whilst we continue to argue that genetic degrees of difference should not be a hard limit on what humans consider a 'breed', the Carneddau Pony is clearly a distinct population far older than the Welsh Section A. Interestingly, other close relationships are apparent between the 'upland' types, suggesting the possibility of a shared 'upland' signature linked to adaptation, though other factors such as common ancestry may be in play. These studies were the first in the world to explore the comparative population genetics of different breeds and types of equine, and clearly show there is much to be learned about adaptation and related environmental impacts.

5. Conclusions

At a time when the ecological role of feral horses is under considerable scrutiny this paper presents evidence that grazing by native horse and ponies could play an important role in restoring and maintaining habitats of conservation importance. Semi-wild populations could be particularly suited to conservation grazing schemes due to both physiological and behavioural adaptations to a free-roaming lifestyle. They might also have a particular genetic value; their genomes have been shaped by natural and not artificial selection, meaning these ponies may have ecological adaptations no longer present in domesticated ponies. These populations are also highly valued on a cultural basis and are an important part of their regions' heritage. Conservation grazing schemes could provide an important sink for excess individuals from these populations, allowing satellite populations to be maintained as an 'insurance policy' against catastrophic events to founder populations. Such factors should be taken into account as new policies and prescriptions are being developed to meet revised targets for biodiversity gain.

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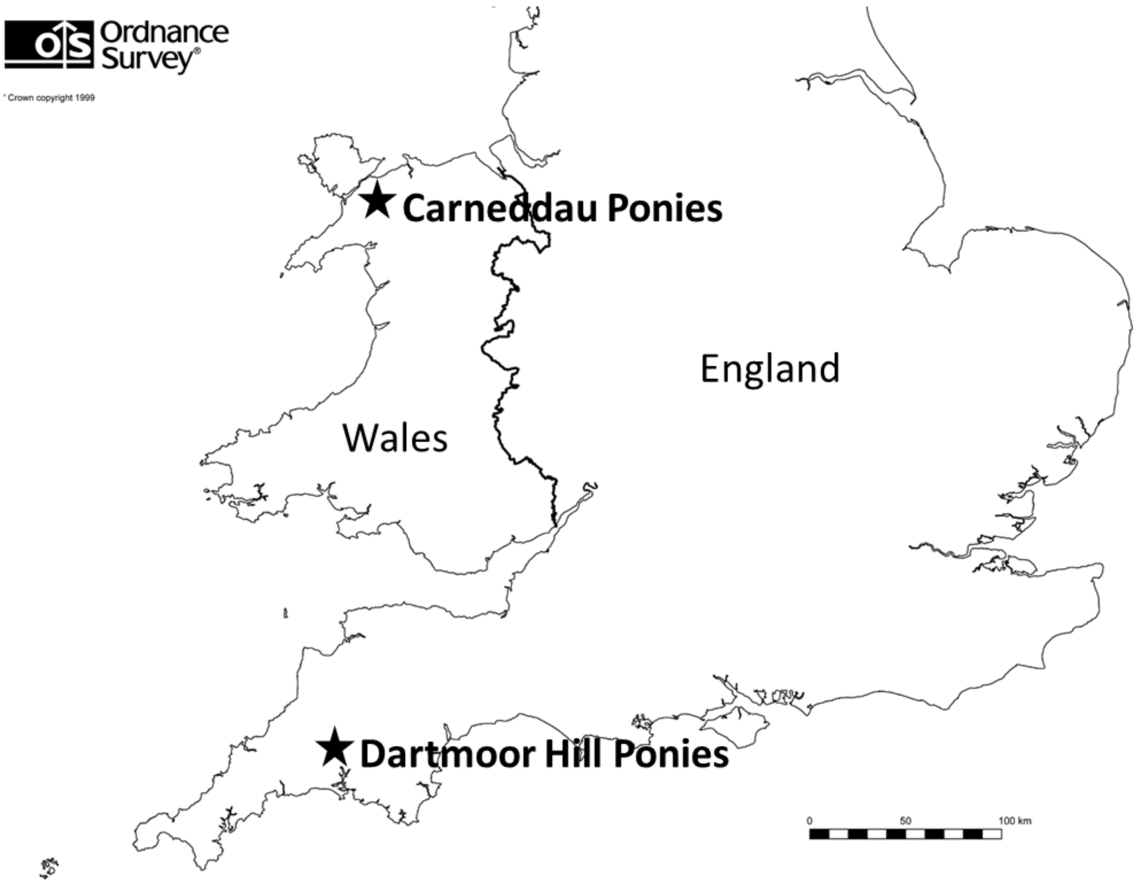
Group		Genus/species	Livestock species	Response to mixed grazing	Country	
Plants	Tracheophyta	Combined	Cattle + sheep	+	UK China	(Critchley et al., 2008; Evans et al., 2015) (Liu et al., 2015)
Mammals	Rodentia	Vole (*Microtus agrestis*)	Cattle + sheep	+	UK	(Evans et al., 2006a; Evans et al., 2015)
	Carnivora	Red fox (*Vulpes vulpes*)	Cattle + sheep	+	UK	(Evans et al., 2015)
Birds	Passeriformes	Meadow pipit (*Anthus pratensis*)	Cattle + sheep	+	UK	(Evans et al., 2006b; Evans et al., 2015)
Arthropods	Araneae	Combined	Cattle + sheep Cattle + goats	+	Spain	(Garcia et al., 2011)
	Opiliones	Combined	Cattle + sheep Cattle + goats	+/–	Spain	(Garcia et al., 2011)
	Coleoptera	Combined	Cattle + sheep	+	UK	(Dennis et al., 2008)


Ordnance Survey
Crown copyright 1999
Carneddau Ponies
Wales
England
Dartmoor Hill Ponies
0
50
100 km

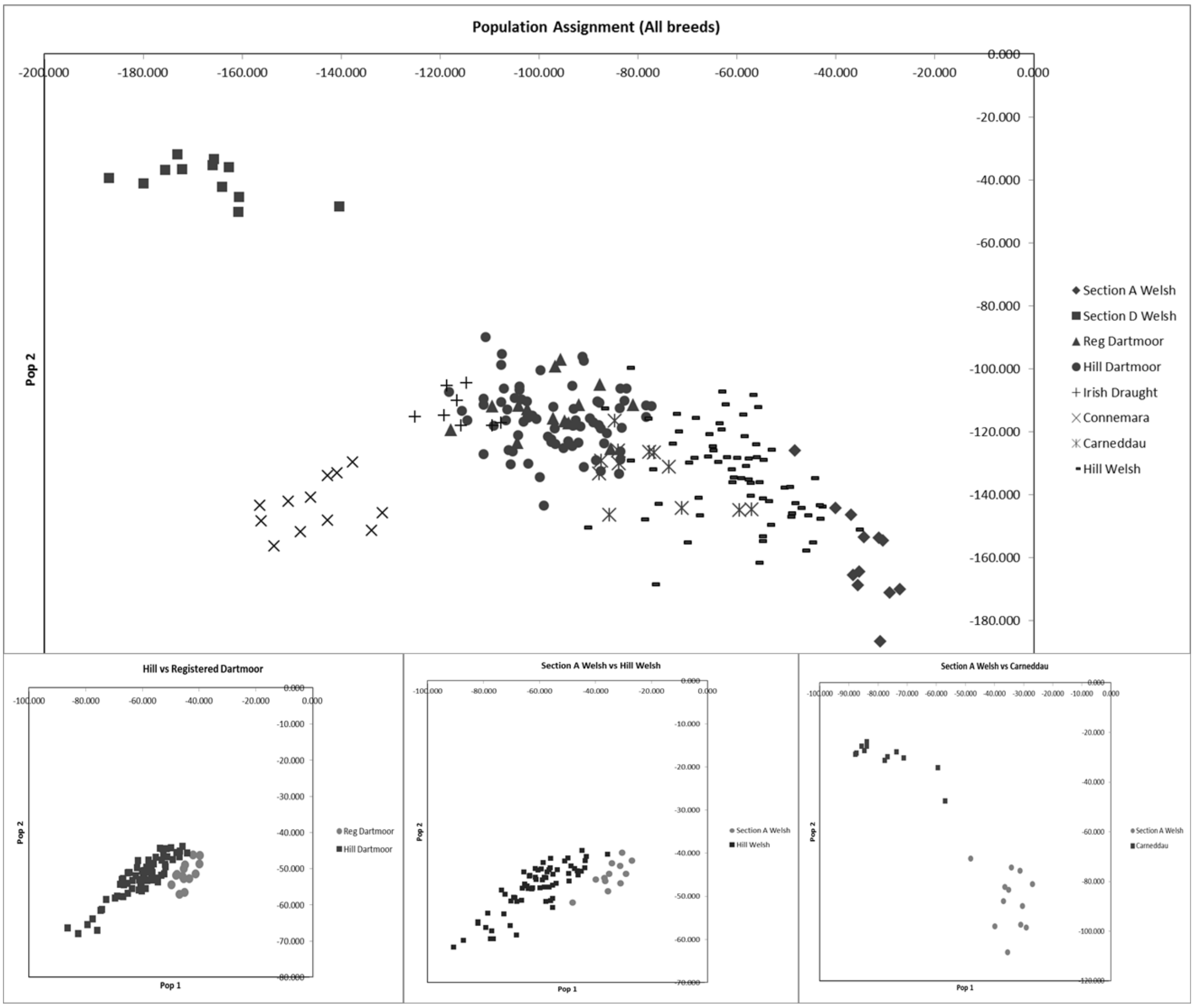

Population Assignment (All breeds)
Pop 2
-200.000
-180.000
-160.000
-140.000
-120.000
-100.000
-80.000
-60.000
-40.000
-20.000
0.000
-20.000
-40.000
-60.000
-80.000
-100.000
-120.000
-140.000
-160.000
-180.000
Section A Welsh
Section D Welsh
Reg Dartmoor
Hill Dartmoor
Irish Draught
Connemara
Carneddau
Hill Welsh
Hill vs Registered Dartmoor
Reg Dartmoor
Hill Dartmoor
Pop 1
Pop 2
Section A Welsh vs Hill Welsh
Section A Welsh
Hill Welsh
Pop 1
Pop 2
Section A Welsh vs Carneddau
Section A Welsh
Carneddau
Pop 1
Pop 2

Table 1: Examples of responses of different taxa to mixed grazing of semi-natural vegetation communities; where + = positive effects from mixed grazing, +/– = no response to mixed grazing; compared to single-species grazing treatments. Study duration ranged from 3 to 10 years.

Figure 1: The distinct geographic locations where the semi-wild Carneddau Ponies and Dartmoor Hill Ponies are found. Breeding studs and animals registered with breed societies such as the Welsh Pony and Cob Society and the Dartmoor Pony Society are found throughout the British Isles (map reproduced from Ordnance Survey map data by permission of the Ordnance Survey © Crown copyright 2001).

Figure 2: Results of population assignment clustering for all pony types based on 162 single nucleotide polymorphism markers, highlighting the close relationships of the Hill Welsh, Carneddau and Dartmoor Hill ponies. Subfigures show the results of population assignment for these three types relative to Section A Welsh (for Carneddau and Hill Welsh) and Registered Dartmoor Pony (for Dartmoor Hill Pony) in order to show that deeper levels of resolution enables separation of these types.