Ecosystem and competition impacts of introduced deer

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Abstract.   Numerous deer species have been introduced beyond their native range into ecosystems around the world. Their economic value leads to further accidental and deliberate releases and lack of control is contributing to range expansion in Australia, South America and Europe. Despite localised or regional concern, the scale and generality of detrimental impacts have not been widely recognised. We review the direct and indirect impacts on ecosystems and evidence for interspecific effects on native deer. In New Zealand, where large herbivores were previously absent, severe and novel impacts have been found in susceptible forests. Even where ecosystems contain native deer, invasion by taxonomically exotic deer species carries the risk of cascade effects on spatial plant dynamics and forest composition. In Patagonia, introduced deer have disrupted forest composition, whereas in Europe, ecosystem impacts of introduced species can differ from those of over-abundant native deer. Introduced Chinese muntjac (*Muntiacus reevesi*) within a coniferous forestry landscape in eastern England differ from native European roe deer (*Capreolus capreolus*) in their distribution of herbivory among differing habitats, and provide much lower rates of endozoochorous seed dispersal. Frequent concern is expressed that introduced deer species may have detrimental effects on native deer and other ungulates, although potential epidemiological effects have not been investigated. Apparent competition, with introduced prey resulting in increased predation rates on native deer, may be occurring between South American huemul (*Hippocamelus bisulcus*) and southern pudu (*Pudu puda*). Habitat and dietary overlap is often substantial among native and introduced ungulates, including deer, and exploitation competition is likely. Evidence includes spatial responses of native to non-native deer and negatively correlated changes in population abundance, but demographic mechanisms have not been demonstrated previously. In a coniferous forestry landscape in eastern England, substantial habitat and dietary overlap occurs between native roe deer and high-density introduced Chinese muntjac. This roe deer population has shown a reduction in body weight and fertility following establishment and increasing abundance of non-native Chinese muntjac, compatible with interspecific competition. European roe deer also appear susceptible to competition from larger grazing deer, including native red deer (*Cervus elaphus*) and introduced fallow (*Dama dama*). The widely introduced fallow deer may be a particularly effective competitor in sympatry with intermediate or concentrate feeders. There is need for further investigation of potential interactions of introduced and native deer species, and a wider recognition of the ecological impacts of introduced deer.

Additional keywords: dietary overlap, endozoochory, habitat impacts, interspecific competition, invasive species, niche overlap, seed dispersal.

Introduction

Deliberate release of large herbivores to establish populations for game hunting, combined with escapes from enclosed populations kept for ranching or hunting, has led to the introduction of wild populations far beyond their natural range (Lever 1985; Moriarty 2004). For example, the Himalayan tahr (*Hemitragus jemlahicus*) is vulnerable in its native range (IUCN 2007), but is increasing in New Zealand (Fraser *et al.* 2000; Hughey and Hickling 2006) where it has been introduced, and other populations have established in South Africa and North America. Although other wild Caprinidae species such as chamois (*Rupicapra rupicapra*) have similarly been widely introduced, Cervidae species dominate large herbivore introductions in terms of both frequency and the variety of species involved (Lever 1985). At least thirteen species of deer have been introduced beyond their native range, involving both temperate and tropical species across multiple continents (Table 1).

Considerable deliberate releases took place during the 19th and early 20th centuries, for example by acclimatisation societies in Australia (Moriarty 2004). In addition to hunting interests, introductions within parks for amenity or landscape enhancement followed by escapes or deliberate releases have also established feral populations (Chapman *et al.* 1994; Langbein and Chapman 2002). Owing to this combination of game and aesthetic interests, most introduced deer are large or spectacular species. For example, the fallow deer (*Dama dama*), which is prized for both hunting and appearance, is one of the world's most widely naturalised animals other than domesticated or feral livestock (Lever 1985). Similarly the red deer (*Cervus elaphus*) has established extensive non-native populations, particularly in New Zealand and South America (Table 1). However, smaller species, such as Chinese muntjac (*Muntiacus reevesi*) and Chinese water deer (*Hydroptes inermis*), have also been introduced in Europe and the small

hog deer (*Axis porcinus*) has become established in Australia (Table 1).

Prospects for introduced deer

Current attitudes to introduced deer vary greatly, but their economic value as game means that introduced populations are almost invariably increasing. In New Zealand, introduced deer have long been recognised as a threat and combined control, commercial harvesting and recreational hunting have reduced most populations to 75–95% of peak levels of the mid 1900s (Nugent *et al.* 2001). However, red deer remain widespread through New Zealand. Although other deer species are currently localised, numerous new populations of red, sika (*Cervus nippon*) and fallow deer continue to establish, mainly from farm escapes and illegal release (Fraser *et al.* 2000). Introduced deer are only now emerging as an issue in Australia, with attitudes influenced by economic value for hunting and a lack of evidence of impacts on native vegetation. Consequently, populations of most introduced deer species continue to increase in Australia (Hall and Gill 2005), augmented by escapes from captive farmed populations and deliberate translocations (Fraser *et al.* 2000; Moriarty 2004). Similarly, in Britain and continental Europe, introduced deer species are often tolerated or encouraged for aesthetic and hunting interests and several introduced species are increasing in density and range (Gill and Fuller 2007). Red deer are regarded as an important economic asset in both Chile and Argentina, with no attempt to eradicate the species despite recognition that it is invasive (i.e. introduced, expanding in range and increasing to high abundance, with negative effects on native fauna or ecosystems) (Veblen *et al.* 1992; Jaksic 1998; Flueck *et al.* 2003; Iriarte *et al.* 2005). In Patagonia, the range of introduced red deer continues to expand, with further range expansion within Argentinean pampas and forests, and it has more than doubled in Chile between 1990 and 2002 (Flueck *et al.* 2003). Additional releases and escapes are anticipated within Patagonia from numerous enclosed populations established for farming and hunting (Flueck *et al.* 2003).

Purpose and scope of this review

Despite case-by-case concern over local impacts, the scale and generality of problems caused by multiple deer introductions worldwide has not been widely recognised. Meanwhile, many introduced populations continue to expand. In this paper, we first summarise the taxonomy, native distribution and ecological diversity of native deer before reviewing evidence from around the world for direct and indirect impacts of introduced deer species. We examine the evidence for impacts on ecosystem structure, composition and function and for interspecific impacts on native deer.

Natural distribution, taxonomic and ecological diversity of Cervidae

The natural distribution of deer is characterised by low species diversity in Europe, habitat-restricted distributions within South America, high diversity in Asia, contrasting with a virtual absence from Africa (where their role is fulfilled by other ruminants) and a complete absence from Australia and New Zealand (Nowak 1999). There are approximately 46 extant species of Cervidae within four subfamilies, with notable centres of species radiation in Asia and the Americas (Nowak 1999).

The Capreolinae is a diverse group comprising approximately 18 species among nine genera (Nowak 1999). In terms of the continuum of digestive physiology from grazers to concentrate selectors (Hofmann 1985; Gordon 2003), most are concentrate specialists. Several species are circum-polar or circum-boreal in distribution, including reindeer (*Rangifer tarandus*), moose (*Alces alces*) and roe deer (*Capreolus capreolus* and *C. pygargus*). A radiation of Capreolinae in the Americas includes two *Odocoileus* species of North and Central America and six or seven species of *Mazama*, small forest deer primarily distributed within South America. A further four genera are restricted to South America, including two species of *Pudu* in temperate forests of Argentina and Chile, pampas deer (*Ozotoceros bezoarticus*) in low-altitude Pampas grasslands, marsh deer (*Blastocerus dichotomus*) and two species of *Hippocamelus* deer adapted to ecotonal and forest habitats of the Andes.

The Cervinae comprises 17 species from four genera. These are large, generally herd forming, and include grassland grazers as well as browsers and forest species. Exceptionally, one genus (*Dama*) occurred in Europe earlier in the Pleistocene with refugia and extant native distribution in the Mediteranean and Persia (Ueckermann and Hansen 1994). Otherwise the Cervinae is most diverse in Asia, including four species of *Axis*, the Père David deer (*Elaphurus davidianus*) of China that is now extinct in the wild and a notable radiation of *Cervus*. With the exception of the widely distributed red deer, whose natural range includes Europe, northern Asia, North America and western North Africa (Dobson 1998), the remaining nine species of *Cervus* are restricted to Asia.

The remaining two subfamilies are entirely restricted to Asia. The Hydropotinae is represented by a single species, the Chinese water deer. The Muntiacinae comprises two genera, the monotypic genus *Elaphodus* and the diverse *Muntiacus*, with nine species of forest-dwelling concentrate specialists, many with restricted distributions within South East Asia, particularly Indochina.

Ecosystem impacts of native and introduced species

Deer are highly adapted large herbivores. As ruminants with multi-chambered stomachs and microbial digestion of cellulose they can utilise relatively low-quality forage. Consequently, deer often have a profound impact on ecosystem structure and act as keystone species in many forest systems. Deer herbivory can determine the structure and composition of forest herb layers, subcanopy and ultimately forest canopies through their impacts on regeneration, generally with an increase in unpalatable species or those resistant to browsing (Kirby 2001; Horsley *et al.* 2003; Joys *et al.* 2004; Rooney *et al.* 2004; Stone *et al.* 2004; Focardi and Tinelli 2005; Gill and Fuller 2007). In turn, this can have cascade effects on biodiversity, including songbird abundance and species composition (McShea and Rappole 2000; Berger *et al.* 2001; Fuller 2001; Allombert *et al.* 2005*a*; Gill and Fuller 2007), nest predation rates (Martin and Joron 2003), the abundance and density of invertebrates (Baines *et al.* 1994; Allombert *et al.* 2005*b*; Hegland *et al.* 2005) and the abundance and seed predation activity of small mammals (Flowerdew and Ellwood 2001; Smit *et al.* 2001).

Table 1.   A review of global introductions of deer species that have established wild populations and their ecological impacts

Species	Source	Where introduced	Ecological impacts
Temperate species Reindeer *Rangifer tarandus*	Boreal	Chile (population now failed [37, 38, 41]) Argentina (established in wild) [40] Scotland (localised)	
Red deer *Cervus elaphus*	Europe and North America	Australia [1,2] New Zealand (invasive, both European red and North American wapiti introduced, ranges 121 000 km^2 and and 2000 km^2 respectively in 2000) [3, 12] North America [4] Chile & Argentina (multiple populations, range in Patagonian steppe c50 000 km^2 in 2003, other expanding populations in Argentinian pampas and northern Tucuman forests) [5, 6, 37, 38]	*Chile and Argentina*: impacts on native forest composition and regeneration in Andean forest and Patagonian steppe including: absence of *Nothofagus dombeyi* saplings and increase in exotic understorey species in grazed treefall gaps; loss of *Aristotelia chilensis* understorey tree and decrease in other susceptible herb and shrub understorey species (e.g. *Ribes magellanicum, Chusquea culeou*) from grazed *N. dombeyi–Austocedrus chilensis* forest [6,7 38]; increase in exotic understorey species in grazed *Nothofagus antarctica* forest [7]; reduced regeneration of *Austrocedrus chilensis* in northern Patagonia [8]. *Australia*: browsing and bark stripping damage to mature trees [2]. *New Zealand*: localised failure of regeneration and replacement of subalpine scrub by tussock grassland [31]; reversible shifts in forest composition with increased dominance of browsing-tolerant species [31, 39]; altered regeneration trajectory after forest disturbance [3]; shift in tree species composition and increase in unpalatable understorey herbs in *Nothofagus* forest, north Island [9]
Sika deer *Cervus nippon*	East Asia	Britain [33] Germany [11, 19] Austria [19] Czech Republic [20] Denmark [36] New Zealand (localised populations totaling 6000 km^2 in 2000) [12, 13] North America (localised Texas, Maryland) [4, 21] Jolo Island, Sulu Archipelago, Philippines [22]	*SW England*: impact on saltmarsh vegetation composition and structure [23]
Fallow deer *Dama dama*	Near-East and some areas of Italy, Greece, Bulgaria, Turkey [10]	Britain [34]; Ireland [10]; Germany [10, 11] Netherlands, Belgium, France; Spain; Portugal; Poland; Czech Republic; Slovakia [10] Denmark, Norway, Sweden [10, 36] Finland (dependent on feeding) [36] North Africa; Republic of South Africa; Madagascar [10] Japan [10] Australia [1,2,10] New Zealand (localised populations totalling 5000 km^2 in 2000) [12] North America [13] Peru [10] Argentina (restricted to Isla Victoria and Nahuel Huapi Lake shore) [6, 7, 38] Chile (failed [37, 38] or just persisting [40])	Impacts on forest structure and composition in *Britain* [14, 15] and *Germany* [10, 35]
Roe deer *Capreolus capreolus*	Europe	Chile (localised near Osorno, >500 individuals in 2002) [40]	
White-tailed deer *Odocoileus virginianus*	North America	New Zealand (localised populations totalling 2000 km^2 in 2000) [12, 13] Southern Finland [32, 36] Czech Republic; Yugoslavia (localised) [32]	*New Zealand*: increased seedling and sapling density of unpalatable tree species in cool temperate rain forests, Stewart Island [24]

Table 1. 　(*Continued*)

Species	Source	Where introduced	Ecological impacts
Tropical and subtropical species			
Chital *Axis axis*	India and Sri Lanka	Australia (localised) [1,2] North America (abundant Texas, Florida and Hawaii) [4] Argentina (restricted to Isla Victoria [6,7] now presumed extinct [38]) Croatia, Moldava, Ukraine, Caucasus, Andaman Islands [22]	No information found
Sambar *Cervus unicolor*	India	Australia [1,2] N America (localised, California) [4] New Zealand (localised populations totalling 5400 km² in 2000) [12]	No information found
Rusa *Cervus timorensis*	Southeast Asia	Borneo, Australia [1,2] New Zealand (range just 470 km² in 2000) [12] New Caledonia [16] (abundant, ~100 000–120 000) [42] Papua New Guinea [17]	*New Caledonia*: probable impacts on sclerophyll forests [16]
Philippine brown deer *Cervus mariannus*	Philippines	Micronesia [18]	Significant changes in forest structure and species composition of native forest reported from Guam [18]
Hog deer *Axis porcinus*	India	Australia [1,2]	No information found
Chinese water deer *Hydropotes inermis*	China and Korea	France [13,25]; Britain [26]	No information found, not studied
Chinese muntjac *Muntiacus reevesi*	China and Taiwan	England [27]	*England*: major impacts on woodland herb layer composition and tree regeneration [14, 28, 29, 30]

References: 1: Moriarty (2004); 2: Hall and Gill (2005); 3: Wilson *et al.* (2006); 4: SCI (2006); 5: Flueck *et al.* (2003); 6: Veblen *et al.* (1989); 7: Veblen *et al.* (1992); 8: Relva and Veblen (1998); 9: Husheer *et al.* (2003); 10: Ueckermann and Hansen (1994); 11: Gebhardt (1996); 12: Fraser *et al.* (2000); 13: Lever (1985); 14: Joys *et al.* (2004); 15: Putman *et al.* (1989); 16: Spaggiari and De Garine-Wichatitsky (2006); 17: Osborne (1993); 18: Wiles *et al.* (1999); 19: Pitra and Lutz (2005); 20: Heroldová (1990); 21: Keiper (1985); 22: Nowak (1999); 23: Hannaford *et al.* (2006); 24: Bellingham and Allan (2003); 25: Corbet (1978); 26: Chapman (1993); 27: Chapman *et al.* (1994); 28: Cooke *et al.* (1995); 29: Cooke (1997); 30: Cooke (1998); 31: Nugent *et al.* (2001); 32: Bartos *et al.* (2002); 33: Ratcliffe (1987); 34: Chapman and Chapman (1975); 35: Zörner (1986); 36: Nummi (1996); 37: Jaksic (1998); 38: Vázquez (2002); 39: Allen *et al.* (1984); 40: Jaksic *et al.* (2002); 41: Iriarte *et al.* (2005); 42: Barré *et al.* (2002).

Where introduced species have reached high abundance, major disturbance to local ecosystems has occurred (see examples in Table 1). Where deer enter ecosystems that previously lacked ruminant herbivores, impacts may be novel to the ecosystem, and regeneration of susceptible native species may be reduced by altering forest composition (Veblen *et al.* 1989, 1992; Husheer *et al.* 2003). In New Zealand, many forest impacts have been shown to be reversible following reduction of deer density (Nugent *et al.* 2001). However, non-linear relationships between herbivore density and vegetation impacts, combined with the efficiency of ruminants as foliavores, mean some changes in the composition of susceptible forest types continue even at low deer densities (e.g. 6 per km²) (Nugent *et al.* 2001).

Where introduced species are sympatric with native deer species, herbivory impacts may be additive, though still profound (Putman *et al.* 1989; Joys *et al.* 2004; Stone *et al.* 2004). For example, Chinese muntjac have reached high densities in much of their introduced range within lowland England (Chapman *et al.* 1994; Hemami *et al.* 2005) and, in combination with locally abundant introduced fallow deer and re-established native roe deer, are having major impacts on conservation interests in ancient semi-natural deciduous woodlands (Cooke *et al.* 1995; Cooke 1997; Cooke and Farrell 2001; Joys *et al.* 2004).

The additive nature of ungulate impacts is supported by a comparison of browsing intensity on riparian willows in an area of Oregon supporting native *Cervus elaphus* and mule deer *Odocoileus hermionus* and an area with both deer species plus domestic sheep (Brookshire *et al.* 2002).

However, we urge caution in assuming that introduced and native deer species will be functionally equivalent, with the same ecological effects. In Chile and Argentina, densities of introduced red deer far exceed those of native cervids and impacts on the structure and composition of native forests are profound (Veblen *et al.* 1989, 1992; Vázquez 2002). Relative patterns of habitat use of introduced Chinese muntjac and native roe deer have been studied in a conifer-dominated afforested landscape (200 km²) in eastern England (Hemami *et al.* 2004, 2005). Much of the conservation interest in this landscape depends on open ground habitats, including a peak in plant species diversity (Eycott *et al.* 2006a), populations of scarce heathland carabids (Lin *et al.* 2007) and a population of woodlark *Lullula arborea*, a ground-nesting bird species of European Conservation Concern (Wright *et al.* 2007). In most forest growth stages, the density of muntjac exceeds that of roe (in prethicket stands, mean over-winter density is 140% that of roe; thicket 260%; pole 340%; mature 260%). However, in recently

planted stands, muntjac only attain 70% of roe density (Hemami *et al.* 2005), most likely owing to behavioural differences, because roe feed more readily in open habitats (Putman 1986*b*), whereas muntjac keep close to secure cover. Thus, in this landscape, roe deer are particularly important to maintaining open conditions in early successional habitats. Herbivory impacts in young stands benefit biodiversity, but the native and introduced species are unlikely to be equivalent in this regard.

Seed dispersal contributes to regional persistence of plant populations and generates macro-ecological abundance–occupancy relationships (Freckleton *et al.* 2005; Eycott *et al.* 2006*a*). The role of deer and other ungulates as endozoochorous seed dispersers is now increasingly recognised (Malo and Suare 1995; Pakeman *et al.* 2002; Myers *et al.* 2004), with dispersal by deer implicated in long-distance plant dispersal (Myers *et al.* 2004). Within the conifer forest landscape studied by Hemami *et al.* (2004, 2005), less than a quarter of plant species persist *in situ*; the majority recolonise stands during the management cycle (Eycott *et al.* 2006*a*), with the buried seed bank playing only a minor role (Eycott *et al.* 2006*b*). Despite the importance of spatial dispersal to regional persistence, of 101 species that colonise young stands, 27% have no dispersal mechanism. However, 34% of all vascular plant species recorded within the forest landscape were found in deer faecal material and 37% of the species germinated from dung have no other mechanism of dispersal (Eycott *et al.* 2007). Comparison of seed dispersal by muntjac and roe shows muntjac have a much lower seed density per pellet group; combined with a lower faecal pellet deposition rate per individual per day, the seed deposition rate per individual muntjac is only 15% that of roe deer (Fig. 1). Despite a population density two to three times that of the native roe and a greater total biomass (Hemami *et al.* 2005), muntjac deposit less than one-third as many seeds into restocked stands than roe deer (0.14 ± 0.06 versus 0.48 ± 0.20 seeds per m^2 per year respectively) (Eycott *et al.* 2007). Furthermore, muntjac dispersed significantly fewer species than native roe deer (Eycott *et al.* 2007). In this well studied example, the introduced muntjac is clearly not ecologically equivalent to the native roe deer. Thus, if introduced deer displace native species, important knock-on ecosystem effects may occur, with the potential to disrupt plant spatial dynamics and regional species persistence.

Impacts of introduced deer on native deer species

Genetic effects

In a few cases there is concern over introgression between native and introduced populations. For example, in Greenland localised introgression has occurred between native caribou *Rangifer tarandus groenlandicus* and introduced Norwegian semi-domestic reindeer *R. tarandus tarandus* (Jepsen *et al.* 2002), in North America between native wapiti *Cervus elaphus canadensis* and introduced European red deer (SCI 2006) and in Britain re-establishment and escape of red deer during the nineteenth century included animals interbred with wapiti. In addition, in Scotland, introgression has occurred between red deer and introduced sika (Goodman *et al.* 1999). However, despite erosion of genetic distinctiveness, such introgression among closely related congeners is unlikely to affect the ecological function of cervid populations.

Epidemiological effects

Introduced deer species may act as reservoirs and vectors for parasites and infectious disease. Although studies have examined consequences of this for humans and livestock (Barré *et al.* 2002; Frölich *et al.* 2002), we found no investigation of potential effects on native wildlife, including other cervid species. Huemul (*Hippocamelus bisulcus*) is an endangered deer species restricted to temperate southern Chile and Argentina (Wemmer 1998; Gill *et al.* 2008); total numbers are estimated at 1000–1500 following a 99% decline, and losses of subpopulations continue (Povilitis 1998; Flueck and Smith-Flueck 2006). Although it has been suggested that introduced red deer in Chile and Argentina may transmit disease or parasites to endangered native huemul (Flueck *et al.* 2003; Flueck and Smith-Flueck 2006), we are not aware of any study examining this.

Apparent competition: introduced prey adversely affecting native deer?

In Patagonia, biomass of introduced herbivores greatly exceeds that of native prey (Novaro *et al.* 2000). Introduced, non-native prey are likely to have increased densities of native predators, with potential to adversely affect native deer species including huemul and southern pudu (*Pudu puda*). Although dismissed by Smith-Flueck and Flueck (2001), their assumptions that social territoriality limits predator densities at levels too low to regulate huemul and that the long history of predator–prey dynamics means populations will be at stable equilibrium, ignore the potential for introduced alternate prey to increase effective habitat quality and carrying capacity, reduce home range size and increase predator density.

Predation by native predators is likely to be important in the demography of both pudu and huemul. In Chile, guanaco (*Lama*
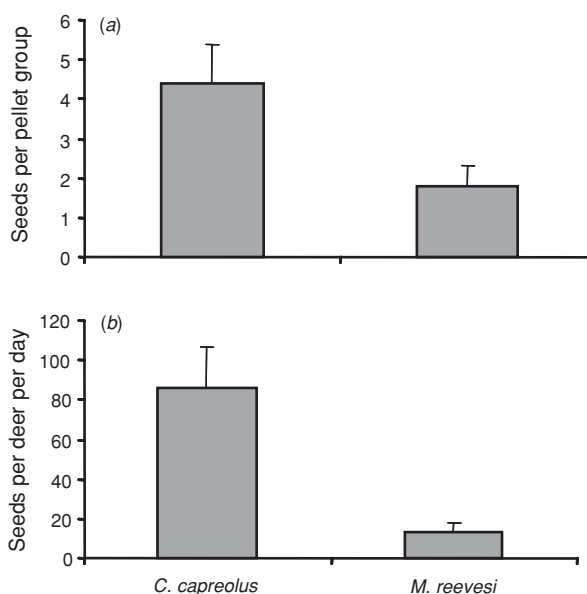
Fig. 1. Mean ($\pm$ s.e.) seed density germinated from faecal material of native roe ($n = 225$ pellet groups) and introduced Chinese muntjac ($n = 296$ pellet groups) collected from 79 stands within Thetford Forest: (*a*) seeds per pellet group; (*b*) seeds per individual per day. Data are taken from Eycott *et al.* (2007).

guanicoe) and pudu comprised 15% of puma (*Felis concolor*) diet (Rau *et al.* 1995), in subantarctic southern Argentina puma predation accounted for 37–42% of detected huemul mortality (Smith-Flueck and Flueck 2001) and in Rio Negro, Argentina, huemul hair was found in all puma scats analysed (Smith-Flueck and Flueck 1997). Native culpeo fox *Pseudalopex culpaeus* are an additional predator of huemul fawns (Povilitis 1998; Frid 1994).

There is evidence that densities of native predators of huemul and pudu are locally elevated by introduced prey. Scats of puma collected in an opportunistic study contained a very low frequency (1.7%) of introduced red deer, though this was considered to provide a large proportion of dietary mass (43%) (Novaro *et al.* 2000). However, introduced sheep are now an important prey of puma (Franklin *et al.* 1999), which also prey heavily on introduced hares (*Leupus europaeus*) and wild boar (*Sus scrofa*) (Iriarte *et al.* 1991; Rau *et al.* 1991; Branch *et al.* 1996). In southern Chile, hare formed the most frequent dietary element for puma (Franklin *et al.* 1999), whereas in huemul habitat in central Chile, the density of culpeo fox is elevated owing to abundant introduced hare (Povilitis 1998). In Argentina, ranchers and hunters locally reduce puma populations in pampas, but densities remain high in adjacent forested and mountainous areas (Franklin *et al.* 1999). In a study area with abundant hare, mean puma density was 6 per 100 km^2, reaching 30 puma per 100 km^2 during 1 month (Franklin *et al.* 1999). However, availability of livestock, wild pig and hares are more likely to affect predation pressure from puma and other smaller native predators than availability of red deer or their carrion (Novaro *et al.* 2000).

Interference competition

Apparent local decreases in native roe deer populations with the expansion of fallow deer within Britain were previously attributed to interference between fallow and the smaller roe (Carne 1955; Delap 1955). Fallow bucks at feeding stations in a deer park in Germany were observed to be aggressive to red stags and hinds (Bartos *et al.* 1996) and aggression has been reported between calving red deer and mule deer in Colorado (Stephens *et al.* 2003). However, in a behavioural study considering interactions between introduced white-tailed deer (*Odocoileus virginianus*), long-established fallow deer and native red and roe deer in the Czech Republic (Bartos *et al.* 2002), interspecific agonistic interactions were rarely observed. For the three larger species, all of which are grazers or intermediate feeders, species either grazed for longer in open pasture when joined by individuals of other species (fallow, white-tailed) or spent longer grazing when more deer were already present on entering the field (red deer), irrespective of the species identity of the other deer (Bartos *et al.* 2002). Thus for these species, it is more likely that interspecific competition will arise through habitat exploitation, than by direct interference or aggression.

Exploitation competition and potential habitat displacement

The importance of competitive exclusion and character displacement in structuring natural herbivore assemblages is shown by the regular pattern of body-mass increments among sympatric species, where each is a constant proportion larger than the next smallest (Prins and Olff 1998; Mishra *et al.* 2002). Potential for competition may be particularly high among sympatric ungulate species, which often show marked overlap of habitat and nutritional niches (Putman 1996). We review studies of overlap in diet or plant community use between native deer and introduced deer or other ungulates; it is generally high in at least part of the year (Table 2). With such diet and habitat overlap, exploitation competition may be expected, but only if depletion of forage and browse is sufficient for food resources to be limiting or regulatory. This condition is likely to be met, because density-dependent food and habitat limitation are commonly observed even in harvested deer populations (Putman *et al.* 1996; Gaillard *et al.* 2000; Gordon *et al.* 2004). For example, in roe deer, fecundity tends to be density dependent and related to maternal body mass and habitat quality (Stubbe 1984; Andersen and Linnell 2000; Nilsen *et al.* 2004; Focardi *et al.* 2006; Saïd and Servanty 2005), whereas maternal body mass and thus fecundity are also related to density at birth (Pettorelli *et al.* 2002). Density-dependent and resource- or condition-dependent effects on fecundity and juvenile first-winter mortality have also been reported in moose, red deer, reindeer, white-tailed deer and mule deer (reviewed by Putman *et al.* 1996). Although adult winter mortality tends to be triggered by stochastic weather events, when such mortality does occur its extent can be related to density and condition, as shown for red and fallow deer (Clutton-Brock *et al.* 1985; Albon *et al.* 1987; Clutton-Brock and Albon 1989; Putman and Langbein 1992). Therefore, interference competition is expected between native and introduced deer.

Most studies of competition within large herbivore assemblages describe patterns of resource use and partitioning among sympatric species, establishing the potential for competition, but rarely demonstrating its action or effect (Putman 1996; Mishra *et al.* 2004). Even changes in population sizes of two species through time (Keiper 1985), although suggestive of competition, do not conclusively demonstrate its action (Putman 1996). Although negative impacts arising through interspecific competition between sympatric deer species have frequently been suggested, they have rarely been demonstrated, with surprisingly few studies rigorously testing the evidence and mechanisms among deer. Here we review the evidence accumulated to date for competition between native and introduced deer species.

Many areas formerly occupied by huemul have been colonised by red deer (Vázquez 2002) and there is dietary overlap between the native and introduced species (Table 2). Although no hard evidence exists demonstrating negative effects through competition (Vázquez 2002), the suggestion that huemul may have been out-competed by red deer (Povilitis 1981) is frequently repeated (Flueck 1996; Jaksic *et al.* 2002; Flueck *et al.* 2003; Iriarte *et al.* 2005). The assumption that current low densities of huemul in habitats with high densities of introduced herbivores will preclude food limitation (Flueck and Smith-Flueck 2006) lacks substance. Similarly, it has been suggested that introduced red deer may be affecting the native distribution of southern pudu in Argentina (MacNamara 1981; Lever 1985; Eldridge *et al.* 1987). Occurrence of red deer is low at sites with records of southern pudu (Meier and Merino 2007), but this was attributed to differing habitat requirements with pudu occupying

Table 2. Studies of habitat and dietary overlap among introduced and native deer and other ruminants

For each study the introduced and native species, region or country, method (1, micro-histological faecal analysis; 2, rumen analysis; 3, nutritional quality of rumen contents; 4, relative use of habitat or plant community types assessed by direct observations or faecal pellet counts; 6, telemetry) and extent of dietary or habitat overlap are given. Where quantified, Pianka's index of niche overlap (from 0 no overlap, to 1 complete overlap) is given in parentheses

Introduced species	Native species	Region	Method	Extent of overlap	Source
Red deer *Cervus elaphus*	Huemul *Hippocamelus bisulcus*	Patagonia	1	92% of annual diet of huemul comprises plants consumed by both species in at least two seasons	Smith-Flueck 2003 cited in Flueck *et al.* (2003)
Red deer *Cervus elaphus*	Huemul *Hippocamelus bisulcus*	Argentina	1	High trophic overlap, *Maytenus* sp. and *Nothofagus pumilio* comprise major part of diet of both species	Galende *et al.* (2005)
Red deer *Cervus elaphus*	Guanaco *Lama guanicoe*	Argentina	1	Only red deer eat less-palatable *Stipa* grass (18% annually), but diet overlap is considerable, for red deer and guanaco respectively: palatable grasses (*Poa, Festuca, Bromus, Juncus*) comprise 10% and 20%, shrubs *Mulinum spinosum* and *Colletia spinosissima* comprise 13% and 42%; in summer, herb *Acaena* and palatable grasses combined comprise 51% and 69% of diet	Bahamonde *et al.* (1986)
Mouflon *Ovis musimon*	Roe deer *Capreolus capreolus*	Czech Republic	1	Substantial overlap (0.65)	Heroldová (1996)
Mouflon *Ovis musimon* Wild goat *Capra aegagrus*	Roe deer *Capreolus capreolus*	Czech Republic	1	Almost complete overlap (0.95) in winter diet of introduced ungulates	Heroldová (1996)
Chamois *Rupicapra rupicapra*	Red deer *Cervus elaphus*	Czech Republic	1 & 2	High dietary overlap (73% similarity in plant composition of diets)	Homolka and Heroldová (2001)
Sika deer *Cervus nippon* Mouflon *Ovis musimon*	Roe deer *Capreolus capreolus*	Czech Republic	3	Very similar nutrient composition of diet between introduced deer and introduced ungulate	Heroldová (1990)
Fallow deer *Dama dama* Mouflon *Ovis musimon*	Roe deer *Capreolus capreolus* Red deer *Cervus elaphus*	Southern Germany	3	Very similar nutrient composition of diet between native deer species and introduced deer and mouflon	Dittrich and Groppel (1980)
	Roe deer *Capreolus capreolus* Red deer *Cervus elpahus*	Germany	4	High overlap in plant community use, maximal in spring and autumn (0.88, 0.92)	Petrak (1993)
Fallow deer *Dama dama* Mouflon *Ovis musimon*	Roe deer *Capreolus capreolus*	Germany	3	High trophic overlap between native deer species and introduced deer and mouflon (rumen dry matter content ~25% raw protein 24% crude fibre for both roe deer and mouflon)	Drescher-Kaden and Seifelnasr (1976)
Fallow deer *Dama dama*	Roe deer *Capreolus capreolus*	Germany	4	High overlap in plant community use, maximal in late winter and early spring (0.70, 0.86)	Petrak *et al.* (1991)
Fallow deer *Dama dama*		Southern England	2 & 4	High overlap between two introduced deer species: in spring, summer, autumn, winter respectively (habitat: 0.61, 0.71, 0.69, 0.49; food: 0.81, 0.78, 0.79, 0.87)	Putman (1986*a*)
Sika deer *Cervus nippon*		Southern England	2 & 4		
Fallow deer *Dama dama*	Roe deer *Capreolus capreolus*	Southern England	2	Moderate food overlap in spring, summer, autumn (0.39, 0.35, 0.45), higher in winter (0.68)	Putman (1986*a*)
Sika deer *Cervus nippon*	Roe deer *Capreolus capreolus*	Southern England	1 & 2	Moderate food overlap in summer, autumn, winter: (0.32, 0.31, 0.37) higher in spring (0.53)	Putman (1986*a*)
Sika deer *Cervus nippon*	White-tailed deer *Odocoileus virginianus*	Maryland, USA	1	High forage overlap; four species (*Myrica, Rhus, Toxicodendron, Solidago*) contribute 74% of sika, 49% white-tailed diet; total shrub browse comprises 42% and 36% of diet respectively.	Keiper (1985)
Chinese muntjac *Muntiacus reevesi*	Roe deer *Capreolus capreolus*	Eastern England	6	Considerable interspecific overlap in both minimum complex polygon and core home ranges	Chapman *et al.* (1993)
Chinese muntjac *Muntiacus reevesi*	Roe deer *Capreolus capreolus*	Eastern England	4	Habitat overlap throughout year, maximal in late winter (0.7)	Hemami *et al.* (2004)
Chinese muntjac *Muntiacus reevesi*	Roe deer *Capreolus capreolus*	Eastern England	4	High habitat and spatial overlap in late winter (growth stages 0.93; stands 0.63)	Hemami *et al.* (2005)

Nothofagus dombeyi forest with dense *Chusquea coleu* bamboo understorey and red deer in more open habitats such as *Nothofagus obliqua* or *Austrocedrus chilensis* forests and Patagonian steppe. However, *Chusquea 'culeou'* is a preferred food of red deer, is highly susceptible to ungulate browsing and tends to decrease where exposed to red deer browsing within *N. dombeyi–Austrocedrus chilensis* forest (Veblen *et al.* 1992; Vázquez 2002), suggesting competition is a real possibility. For both pudu and huemul, further investigation of effects of introduced red deer and other herbivores is recommended.

Evidence of asymmetrical competition and habitat displacement between sympatric roe and native red deer is provided by work in Scotland, were their densities are inversely correlated across plantation forests (Latham *et al.* 1996). Multivariate analyses of these data, controlling for habitat and regional variation in climate, support the conclusion that roe deer density is negatively related to that of red deer (Latham *et al.* 1997). In contrast, roe deer density was not a predictor of red deer density, suggesting the previous relationship is not due to some unmeasured underlying correlate. However, the lack of consistency in habitat and climate variables between models of roe that include or exclude effects of red deer, combined with a low total sample size (with $n = 20$), mean the evidence for competitive exclusion is not robust.

Evidence for a competitive effect of fallow deer on native roe comes from an elegant study by (Focardi *et al.* 2006) in a 33 km^2 study area located in central Italy. They hypothesised that an abrupt decline in roe deer abundance, of 80% over 2 years, may have been caused by competition with increased numbers of sympatric fallow deer. To test this, they related home range size of 14 radio-tracked roe deer to both habitat composition and fallow deer density. Fallow deer density was estimated at a 50 m × 50 m resolution from detection frequencies and habitat-dependent group sizes in repeated distance transect surveys and varied spatially from 3 to 54 deer per km^2. Structural equation models that related roe deer home range directly to fallow deer density, or to a combination of fallow deer and habitat composition, received better support than the alternative fundamental niche model (that roe home range size was determined by habitat independently of fallow deer distribution) (Focardi *et al.* 2006). This provides strong support for the contention that habitat quality for roe is reduced by high local densities of fallow deer. However, statistical power is reduced by the limited sample size of home ranges ($n=14$) and pseudo-replication due to spatial autocorrelation in fallow density, whereby the landscape comprises only a few independent areas of differing density. This, and the possibility that fallow deer density may act not just as a proximal cause of roe habitat quality but also as a proxy for other aspects of habitat composition (the structural equation models considered just one of four pooled habitat classes), make further study desirable.

Further evidence that roe deer may be particularly vulnerable to asymmetrical interspecific competition comes from FORSPACE, a process-based model of plant–herbivore interactions for a multi-species ungulate assemblage in the Netherlands. The model uses species-specific parameters for foraging height, bio-energetic and population processes, overlain on a dynamic forest patch model, and assumes that ungulates select vegetation patches to maximise energy intake (Kramer *et al.* 2006). It predicts that fallow, red deer and wild boar (*Sus scrofa*) are able to coexist in a heathland and mixed forest landscape, with or without other large herbivores. When horse and cattle are also present, then roe deer persist alongside the larger deer species. However, if horse and cattle grazing is removed, red and fallow deer experience reduced competition for forage resources in open habitats, resulting in greater density and herbivory pressure inside the forest, such that roe deer are driven to local extinction (Kramer *et al.* 2003). The asymmetric competition arising in this model can be explained by a substantially greater maximum intake rate, greater maximum height to which the larger deer can browse and, to a lesser extent, lower lactation costs and slightly greater growth efficiency (Kramer *et al.* 2006). In contrast, most other energetic and demographic parameters were considered to be similar among the species (energetic cost of pregnancy, minimum maintenance costs, neonatal mortality rates), or favoured roe (maximum fertility). Interestingly, the model predicts that introduced fallow deer will attain the highest mean density in this system, 2.5 times that of the native red deer (Kramer *et al.* 2006).

The field studies in Italy (Focardi *et al.* 2006) and southern England (Putman 1986*a*) and the simulation model (Kramer *et al.* 2006) suggest fallow deer are particularly effective in interspecific competition. In contrast to the density dependence found in adult female roe and red deer, fertility of adult female fallow is remarkably resilient to high intraspecific density, with no decline found across a range from 0.5 to 8.2 per ha (Putman *et al.* 1996), although reproductive rates of yearlings and levels of winter mortality did respond to condition and resource limitation. This may relate to the park-bred, semi-domesticated status of fallow populations.

High levels of deer herbivory reduce shrub layer foliage density, deplete availability of shoots of preferred browse species, reduce the abundance of palatable herbs and increase the contribution of grass or sedge to forest understorey. Therefore, as overall density increases in multi-species deer assemblages, concentrate specialists are expected to experience stronger food limitation, whereas grazers and mixed strategists are expected to be more resilient to high total deer biomass (Latham *et al.* 1996). This prediction is supported by the apparent asymmetric competition between introduced fallow and native red and roe deer (Putman 1996; Putman *et al.* 1996; Latham *et al.* 1997; Focardi *et al.* 2006) and between introduced fallow and sika and native roe deer (Putman 1986*a*). Despite high dietary overlap between introduced fallow and sika and lower overlap of both introduced species with roe (Table 2), competitive asymmetry was much greater between the larger species and roe than between the two introduced species (Putman 1986*a*). Similarly, in North America, introduced sika, which incorporate low-quality *Spartina* forage in their diet (Keiper 1985), are reported to exert asymmetric competition on native concentrate specialist white-tailed deer (Feldhamer and Chapman 1978), whereas in Russia red, sika and introduced fallow deer are reported to compete with native roe deer (Danilkin 1996).

Potential evidence of demographic effects

Evidence of variation in population performance from interspecific competition has been demonstrated in other ungulates (Forsyth and Hickling 1998; Baldi *et al.* 2001; Mishra *et al.*

2004), but has not previously been shown for deer. In the lowland conifer forest landscape of eastern England there is evidence of habitat and dietary overlap between native and introduced deer species, but also empirical evidence of resource depletion, food limitation and potential evidence of a demographic effect on the native roe deer. In this landscape, population density of introduced muntjac (64 ± 13 per km^2) exceeds that of roe deer (28 ± 6 per km^2) (Hemami *et al.* 2005). Even considering sensitivity of these estimates to uncertainty in defaecation rate, the introduced species outnumber roe deer at least two- to three-fold (Hemami *et al.* 2005). Roe are a medium-sized deer species considerably larger than muntjac (Corbet and Harris 1991), nevertheless the biomass density of the smaller introduced species (767–988 kg per km^2) exceeds that of native roe (575–759 kg per km^2). Habitat overlap between the two species is considerable (Table 2). Local density of roe is positively associated with that of its potential competitor, in contrast to the negative association of roe with red deer in Scotland (Latham *et al.* 1996, 1997) and of roe with fallow deer in Italy (Focardi *et al.* 2006).

Bramble (*Rubus fruticosa* agg.) is a key dietary resource for both species (Hosey 1981; Hearney and Jennings 1983; Harding 1986; Forde 1989); roe deer aggregate on bramble across all habitats, whereas muntjac are positively associated with bramble in older stands (Hemami *et al.* 2004, 2005). Measurements from 24 paired exclosures and controls show substantial resource depletion, with the combined cover of bramble and other nutritious shrubs (gorse (*Ulex europaeus*) and broom (*Cytisus scoparius*)) reduced by 44% in controls exposed to deer browsing relative to that in unbrowsed exclosures (P. M. Dolman and A. E. Eycott, unpubl. data). Examination of tagged bramble stems attributed the majority (71%) of over-winter reduction in stem length to deer (Hemami 2003).

As in other roe deer populations, fertility is positively related to maternal body mass (Hemami 2003), suggesting productivity will be sensitive to reduced forage availability. Over the period of muntjac invasion and establishment, both the condition and fertility of the forest roe deer population has declined. Between 1979–83 and 2000–02, mean body weight of kids declined by 17%, that of yearlings by 22% and adults by 12% (Hemami 2003). Over the same period, fertility of yearlings declined by 66% and that of adults by 23% (Hemami 2003), suggesting roe may be experiencing detrimental interspecific competition from increasingly abundant muntjac. However, the evidence for a demographic effect is weakened by the limited number of years for which fertility has been analysed in the latter period and further study is desirable.

Conclusions

The impacts of introduced deer into forest ecosystems that have developed in the absence of mammalian herbivores in New Zealand are well known, whereas surprisingly little attention has been paid to potential impacts of introduced deer in Australia. In southern America, introduced deer have had major impacts on forest composition, despite the existence of native endemic ungulates including forest deer. In North America and Europe, the ecological impacts of increasing deer abundance are well recognised, but very little attention has been paid to subtle but potentially profound differences in the ecological function of

native and non-native introduced species. For example, grazing deer have been shown to disperse a greater number and greater species richness of plant seeds than concentrate selectors (Mouissie 2004; Eycott *et al.* 2007). Although taxonomically similar species may be expected to perform a similar ecological function, evidence for muntjac in eastern England suggests that invasion by taxonomically exotic species carries the risk of cascade effects. Thus other situations where species have been introduced beyond the natural range of their subfamily, such as introduced *Cervus* in Patagonia and *Hydroptes* in England, should receive further attention.

There is a growing body of evidence that interspecific competition may occur between introduced and native deer species. We found support for the hypothesis of asymmetrical competition among grazing deer, intermediate and concentrate feeders, with widely introduced fallow deer particularly effective as competitors. In Europe, roe deer appear particularly vulnerable to competition from introduced fallow and sika, native red deer and introduced muntjac. Evidence consistent with interspecific competition among introduced and native deer includes frequent demonstration of dietary and habitat overlap (potential niche), examples of negative association (apparent spatial or habitat exclusion, displacement of realised niche) and opposing population trends. However, other than a study suggesting introduced Chinese muntjac may have reduced condition and fertility of native roe deer in eastern England, we could find no study demonstrating a demographic response. The issue of interspecific competition with native deer and other ungulates requires further study, with experimental manipulation remaining the ultimate test of causality.

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