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The tale of two deer: management of Père David's deer and sika deer in anthropogenic landscape of eastern Asia

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Abstract. Père David's deer (*Elaphurus davidianus*) and sika deer (*Cervus nippon*) occupy two contrasting types of niches in eastern Asia: Père David's deer is a swamp deer adapted to wetlands, while the sika deer mainly live in forested areas. Both Père David's deer and sika deer have been hunted since the early days of the hunting and gathering civilisation; however, these two deer have undergone different population histories. As human society entered the era of agriculture civilisation, Père David's deer gradually lost its habitats to farmlands, and the population was greatly reduced until, finally, it became extinct in the wild in 1900. Fortunately, after 30 years of restoration and introduction, more than 4000 Père David's deer thrive in nature reserves, zoos and safari parks in China, and more than 500 Père David's deer could be found in the wild in 2014. Populations of wild sika deer were reduced as well due to hunting and deforestation, and were restricted in the forest patches in the mountains in eastern Asia. Nevertheless, the sika deer in China and Japan have different fortunes. Sika deer in China did not escape the prevalent tragedy of domestication, in that wild sika deer was endangered or extirpated in its original habitats, while the farmed sika deer thrived since late 1950s. Sika deer populations in Japan also remained at low density in the mid-1950s due to over-hunting, including poaching. After one-quarter of a century of in situ protection, sika populations are still small in China and some populations were found to leave the nature reserve to areas with high human densities, while the wild sika deer in Japan have markedly increased in numbers and extended their geographic distribution during the past few decades. Accordingly, the management strategies in China and Japan were completely different. The Chinese government is seeking all the efforts on the conservation of sika deer, while the Japanese government is revising laws to harvest and to reduce sika deer population.

Additional keywords: captive breeding, dispersal, extinction, nature reserve, population management, reintroduction, tragedy of domestication.

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Introduction

Père David's deer (*Elaphurus davidianus*) and sika deer (*Cervus nippon*) occupy two contrasting types of niches in eastern Asia; Père David's deer is a swamp deer that is adapted to wetlands, while the sika deer mainly lives in forested areas. However, these two deer experienced different population change trajectories in past centuries. In the present review, we present the origin and population history, current status and research situation of these two deer and pay special attention to the management of these two deer in the anthropogenic landscape of eastern Asia.

Through the paper, we elaborated the following questions: how did the two deer adapt to anthropogenic landscape; how should we manage the Père David's deer and sika deer, either wild, free-ranging or farmed; what should we learn from the case studies of Père David's deer and sika deer for the conservation of endangered species?

The origin and population history in China

Père David's deer

Elaphurus originated from an ancient hybridisation between a stem representative of Cervus (male) and Panolia (female) ~3.5 million years ago, and the sika deer probably originated at the same time (Groves and Grubb 2011). Père David's deer was once widely distributed throughout the wetlands in eastern and northern China. Fossils of modern species of Elaphurus, which evolved in the Pliocene period of the Tertiary era, were excavated in southern Japan (Hofmann 2007). After the last glacial period, the distribution of Père David's deer shrank and the population of Père David's deer declined due to human hunting and land reclamation in the swamp areas as human population expanded (Jiang and Li 1999). Père David's deer was restricted to swamps and wetlands in the region south of 43°N and east of 110°E in mainland China during the Holocene, and was finally extinct in

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954 Animal Production Science Z. Jiang et al.

the field in the late 19th century (Cao 1992; Cao et al. 1988; Zhou 2007).

The last herd of Père David's deer survived in the 200 km² hunting ground of the Nanyuan Royal Hunting Garden in south of Beijing during the Qing Dynasty (1616–1911), which had been sealed off as a royal garden since the Yuan Dynasty (1205–1368). The Père David's deer in the garden was 'discovered' by French missionary Père Armand David in 1864, who smuggled hinds and skeletons of an adult male, an adult female and a young male to Paris in 1866, where the deer was named Père David's deer.

At the end of 19th century, the wall of the Nanyuan Royal Hunting Garden was destroyed by a heavy flood and cannon fire of the allied foreign forces during the Second Opium War, and the Père David's deer escaped and were hunted. Fortunately, before the demise of this royal herd, Père David's deer had been introduced into the United Kingdom, France and Germany. During the last decade of the 19th century, the 11th Duke of Bedford in the United Kingdom gathered all the last 18 Père David's deer in the world to form a breeding herd at Woburn Abbey, England. Only 11 of these deer were capable of reproducing (Bedford 1951-52). Nevertheless, the heavily inbred Père David's deer safely passed through the genetic bottleneck of inbreeding and adapted to the vast open parkland of this mid-England estate (Jones and Manton 1983). At the end of WWII, the size of the Woburn Abbey herd reached 250. Since then, Père David's deer began to be shipped to other zoological gardens in England and abroad. In the 1950s, the number of Père David's deer reached several hundred, and Père David's deer was brought to Beijing Zoo and Guangzhou Zoo for exhibition (Beck and Wemmer 1983; Wang and Boyd 2007).

Sika deer

Only one sika deer species survived in eastern Asia from the early Pleistocene to the Holocene, with 13 subspecies based on morphological characteristics (Whitehead 1993; Guo and Zheng 2000). Sika deer was found only in northern China and Taiwan during the early Pleistocene, but expanded to north-eastern, central, east of the south-western and southern China, the east of Mongolia—Xinjiang region, the Qinghai—Tibet region, the north of Vietnam, Siberia, Korea and Japan in the middle Pleistocene to Holocene. Sika deer was introduced into many countries and regions of Europe, Oceania and America in the 1860s or earlier.

Sika deer was treated as game species for a very long history in China. There were records of hunting of sika deer in the Shang Dynasty (1562 BC–1066 BC). Besides that, velvet antler of sika deer began to be used in Chinese traditional medicine ~2000 years ago based on the record of *Shen Nong Materia Medica*. Until the early 19th century, six subspecies of sika deer were abundant throughout China (Sheng and Ohtaishi 1993; Guo and Zheng 1992, 2000). However, due to the human population explosion and agricultural development, the sika deer population decreased rapidly under the pressure of both human utilisation and habitat loss. Since the 1920s, three subspecies, *C. n. mandarinus*, *C. n. taiouanus* and *C. n. grassianus*, have gone extinct in the wild, and the remaining

three subspecies survived only in the forest patches in the mountains areas in China (Sheng and Ohtaishi 1993; Guo and Zheng 2000).

Current status in China

Père David's deer

Père David's deer is listed as a Category I State Key Protected Wild Animal in China. Since Père David's deer were reintroduced into China in the mid-1980s, Beijing, Dafeng, Tianezhou and Yuanyang populations had been established in 1985, 1986, 2001 and 2002, respectively. After decades of *ex situ* conservation, Père David's deer has been recovered from the brink of extinction and has become an example of rescuing an endangered species (Beck and Wemmer 1983; Ebenhard 1995; Jiang *et al.* 2015).

Twenty (5 males, 15 females) and 18 (all females) deer were introduced from the herd of Marquess of Tavistock of Woburn Abbey, England, to Beijing Milu Park in 1985 and 1987. The average annual population growth rate for Père David's deer in Beijing Milu Park in 1987–1997 was 17.3% (Jiang et al. 2000a), and the population in Beijing Milu Park reached 140 in April 2014. In addition to Beijing Milu Park, 39 deer (13 males, 26 females) were also introduced from five Zoological Gardens in England to Dafeng Milu Nature reserve in August, 1986. Since then, the population in Dafeng has increased rapidly, reaching 2818 till 2015. Moreover, the Dafeng Milu Nature Reserve released four groups of Père David's deer into the field in 1998, 2002, 2003 and 2006, respectively. In the spring of 2015, the released deer have given birth to the 5th generation, with 265 heads and 37 new-born calves as the first author inspected in the field.

Apart from the reintroduction abroad, there are also translocations of populations inside China. Thirty (8 males, 22 females) and 34 (10 males, 24 females) deer were transferred from the Beijing Milu Park to Hubei Tianezhou Milu Nature Reserve in 1993 and 1994, respectively, and 30 deer (15 males, 15 females) were released into the paddock of the Shishou Nature Reserve in 2002 (Yang et al. 2002a, 2007). By June of 2014, the population of Père David's deer in Tianezhou had reached more than 1100. Thirty deer (14 males, 16 females) were transferred from Beijing Milu Park to Henan Yuanyang Yellow River Nature Reserve in 2002. Besides these four large populations, there are more than 50 zoos, wildlife parks and nature reserves that have Père David's deer herds in China (Yang et al. 2003).

Wild sika deer

Sika deer is listed as a Category I State Key Protected Wild Animal Species in China. Sika deer in China follows the prevalent *tragedy of domestication*; the farmed sika deer populations are booming in many provinces of China, while the wild sika deer is extinct in most of its original range, with only small populations subsisting in small, fragmented and isolated habitats in north-eastern, western and southern China (Guo and Zheng 2000; McCullough *et al.* 2009). According to the national wide terrestrial vertebrate survey by the State Forestry Administration (SFA) from 1998 to 2000, there were 8427 wild sika deer in the wild in eight provinces and 287 857

sika deer in deer farms in 28 provinces, municipal regions and autonomous regions in China (Fig. 1).

The north-eastern population is considered questionable and functionally extinct by some researchers (Sheng and Ohtaishi 1993). It is the subspecies *C. n. hortulorum* that occurs in the state owned forests in the Shuiyan–Mulins area at the extreme southern tip of Heilongjiang Province that along with the Jilin Province, the Russian and North Korean borders, which might be dispersers across international borders in a source-sink system (Pulliam 1988). There are also some feral sika deer populations that are established by individuals escaped from sika deer farms in the Dongfeng and Lishui County of the Jilin Province (State Forestry Administration of PR China 2001).

In western China, wild sika deer used to distribute over most of the Sichuan Basin and its northern border to southern Gansu Province in several populations. The Sichuan population still survives in their habitat remnants, while the population in Gansu Province might be wild populations established from deer that escaped from the deer farm. The largest population in Sichuan Province occurs in Tiebu National Nature Reserve (NNR), which has received considerable attention from Chinese biologists for a long time, while the other two populations are more isolated and smaller with much less knowledge (Li and Zhao 1989; Guo 2000, 2003). More detailed information of the sika deer in Gansu Province is unknown.

In southern China, the subspecies (*C. n. kopschi*) is the most endangered subspecies of all the sika deer subspecies surviving in the world, occurring in Jingxian, Jinde, Yixian, Shexiang, Huangshan, Qimeng, Tiantai, Guichi, Qingyang,

Nanling and Ningguo Counties of Anhui Province, Pengze, Hukou, Jiujiang, Yongxiu, Boyang, Anyi, Fenxing, Leping, Fuliang County of Jiangxi Province and Lin'an County of Zhejiang Province. These sika populations live in valleys in low broken mountainous habitat at relatively low elevation of 300–600 m, with a population of ~1580.

In eastern China, there are two main feral sika deer populations in Shandong Province. In 1984, a group of sika deer introduced from Jilin Province was released into the Liugongdao Island National Forest Park, with the present population of ~200 individuals. Another feral population consists of ~100 deer in Weideshan Mountain in Rongcheng City that escaped from a deer farm.

Farmed sika deer

The domestication of sika deer started no later than 370 Common Era. However, captive sika deer were exploited on a large scale as an economic animal in the Qing dynasty since 1733 (Zhao 1990). Most of the sika deer farmed in China are the subspecies *C. n. hortulorum*. The first farm was established in Jilin province in north-eastern China and the species was then introduced to other parts of China. Currently, sika deer is farmed all over China except three Autonomous Regions or provinces, with more than 50% of the farmed sika deer being bred in Jilin Province (Fig. 1). During the breeding of sika deer, some well-bred varieties of farmed sika deer, such as Shuangyang sika deer, Changbaishan sika deer and Xifeng sika deer, were selected and introduced to many sika deer farms in China (Li and Xue 2000).

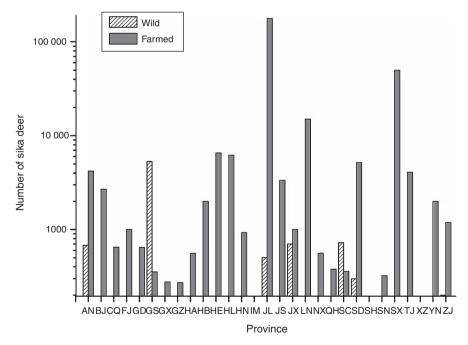


Fig. 1. Sika deer in the wild or on farms in Chinese provinces (source: State Forestry Administration of PR China 2001). Abbreviations for provinces in China: AN, Anhui; BJ, Beijing; CQ, Chongqing; FJ, Fujian; GD, Guangdong; GS, Gansu; GX, Guangxi; GZ, Guizhou; HA, Henan; HB, Hubei; HE, Hebei; HL, Heilongjiang; HN, Hunan; IM, Inner Mongolia; JL, Jilin; JS, Jiangsu; JX, Jiangxi; LN, Liaoning; NX, Ningxia; QH, Qinghai; SC, Sichuan; SD, Shandong; SH, Shanghai; SN, Shaanxi; SX, Shanxi; TJ, Tianjin; XZ, Tibet; YN, Yunnan; ZJ, Zhejiang. Number of sika deer in XZ was for the purpose of display in zoo.

956 Animal Production Science Z. Jiang et al.

Behaviour, ecology and genetics researches in China

There have been many researches on behaviour, ecology and genetics of both Père David's deer and sika deer. Due to the economic value of farmed sika deer and the long history of farming, many studies of Chinese sika deer have been focussed on physical and biochemical characters, velvet antler processing method and medical effectiveness of deer products. However, we only focussed on the recent studies on wild sika deer. The studies on Père David's deer and sika deer can be found from behaviour, habitat selection, distribution and population status, to daily rhythm and genetics (Table 1).

Management

Père David's deer

While the population of Père David's deer is expanding, the genetic makeup of the deer is homogenous; both the demographic and genetic management of Père David's deer should be treated seriously. In addition, the Père David's deer is a large mammal living in wetland; however, most of the wetlands in the lower Yangtze River watershed are reclaimed as rice paddy and aquaculture ponds. Thus, how to balance the conservation and

restoration of Père David's deer's habitat and the livelihood of people around the watershed is a big challenge.

(1) How to manage the genetic diversity in Père David's deer?

The genetic diversity in Père David's deer is extremely low: thus, special attention should be paid to the maintaining of genetic diversity in Père David's deer (Ballon and Foose 1996). Three suggestions were given for better genetic management, including the following: (i) check the genetic background of each breeding individual and establish the genetic pedigree file for them; special attention should be paid to maintain all genetic diversity in the source population while representativeness of the genetic diversity should be taken into consideration when relocated populations (Jiang et al. 2006); (ii) at least two breeding herds should be maintained at each breeding base and deer with close blood relationships should be separated when establishing breeding herds (Frankham and Briscoe 2002); (iii) in view of the harem breeding system of Père David's deer, each breeding herd should be not too large and should have approximately the same number of stags and hinds.

Table 1. The studies on Père David's deer and sika deer in China

Parameter	Père David's deer	Sika deer
Reproductive behaviour	Reproductive system (Jiang <i>et al.</i> 2000 <i>b</i> , 2004, 2006; Li <i>et al.</i> 2001; Xu <i>et al.</i> 2013); reproductive behaviour and hormones (Li <i>et al.</i> 1999, 2001, 2004)	Maternal behaviour (Lü et al. 2008a); vocalisation behaviour during rut (Ning et al. 2008); reproductive hormone variation of female (Ma et al. 2008); reproductive behaviour (Qi et al. 2014)
Anti-predator behaviour	Alert response to human disturbance (Li <i>et al.</i> 2007 <i>a</i>); long-term memories of enemies (Li <i>et al.</i> 2011); determinants of vigilance (Zheng <i>et al.</i> 2013)	Vigilance behaviour and interference competition (Ping et al. 2011a)
Daily rhythm and behaviour budget	Diurnal activity time budget (Yang et al. 2013)	Time budget and behaviour pattern (Yang et al. 1990; Liu et al. 1999, 2002, 2004; Guo 2003; Lü et al. 2008b, 2012)
Distribution and population dynamic	Population status (Jiang <i>et al.</i> 2001; Su <i>et al.</i> 2003; Yang <i>et al.</i> 2003, 2007; Bai <i>et al.</i> 2012; Ding <i>et al.</i> 2014)	Distribution and population dynamic (Sheng 1991; He 1994; Xu et al. 1998; Piao et al. 1999; Guo 2000; Huang et al. 2000; Song and Liu 2005; Yu et al. 2006; Jiang et al. 2012); population viability analysis (Li et al. 2014a)
Habitat selection	Ding et al. 2005; He et al. 2007; Liu et al. 2011; Zou et al. 2013	Yang et al. 2002b; Ma et al. 2004; Fu et al. 2006a, 2006b; Liu 2007; Li et al. 2014b, 2014c
Genetics	Genetic diversity and genetic consequences (Zeng et al. 2007); microsatellite markers (Jiao et al. 2008); fecal DNA extraction and phylogenic analysis (Sheng et al. 2009); microsatellite polymorphisms and population genetics structure (Zhang et al. 2010); protocol to isolate MHC Class II loci (Wan et al. 2011); MHC Class I genes (Zhang et al. 2012); variability of microsatellite loci and calf fitness (Zeng et al. 2013)	Genetic diversity of wild sika deer (Wilson 2000; Wu et al. 2004; Lü et al. 2006; Wang 2013); sequence variability of mtDNA and population genetic structure (Liu et al. 2003); genetic diversity of captive-bred sika deer (Wu et al. 2006); molecular mechanism of behaviour traits (Lü et al. 2009, 2011)
Diet composition	Wang and Wang 2011	Guo 2001; Liu 2007; You et al. 2007; Dong et al. 2009; Yao et al. 2010
Dispersal Other aspects	Sex-biased dispersal (Song et al. 2015b) Habitat management (Ding et al. 2005; Liu et al. 2011); animal density and hormone (Li et al. 2007b); behavioural expression and environmental factors (Li et al. 2007c); rumination behaviour (Li 2013); grooming behaviour (Li et al. 2014); host selection by cattle egrets (Fernandez et al. 2014); acoustic properties and dominance (Liu et al. 2015); zoonotic genotypes (Zhang et al. 2015)	Dispersal out of Nature Reserve (Li <i>et al.</i> 2013) Social behaviour (Guo <i>et al.</i> 1991; Yang 2014); carrying capacity analysis (Guo 2002); life table analysis (Guo and Zheng 2005); vocal behaviour (Fu <i>et al.</i> 2008; Yang <i>et al.</i> 2012 <i>a</i> , 2012 <i>b</i>); behaviour ethogram (Qi <i>et al.</i> 2010); salt lick behaviour (Ping <i>et al.</i> 2011 <i>b</i>)

(2) How to maintain the Père David's deer in a sustainable program?

The survival of Père David's deer relied on human assistance for food, health care, reproduction and relocation, to some extent, which was a kind of human-assisted survival strategy (HASS; Jiang et al. 2001). After two decades of conservation operations, Père David's deer in paddocks in Dafeng, Tianezhou and Shishou NNR all showed density- dependent declines in birth rates (Jiang et al. 2001; Song et al. 2015a). More space and funds are needed to maintain healthy reproductive herds. Sooner or later, we will have more than enough Père David's deer for further field release. Thus, we are open to explore how to maintain the Père David's deer breeding as a sustainable business.

In ancient Chinese pharmacopeia, antlers of Père David's deer are described as a traditional medicine for treating abnormal ovulation function in women (Cao 2007). Chai et al. (2007) found that antler of Père David's deer had a better effect than velvet antler of sika deer. Some researchers have suggested restoring the prescription of the antler of Père David's deer as a traditional medicine (Yang 2007). It would be an option for further conservation practice to maintain some captive-bred herds to be domesticated for production of traditional medicine, such as the sika deer, which would generate funds for Père David's deer's field conservation.

(3) How to choose suitable areas for further relocation?

Most wetlands in China, like those in the Yangtze River drainage, are heavily populated areas. Human activities, especially hunting, human settlements and land reclamations were the major causes of extinction of local mammalian fauna since the Holocene. According to Yang et al. (2005), the threats of human activities on the survival of presently endangered mammalian species are much greater than ever before. Thus, much attention should be paid to human disturbance in the reintroduction and relocation of Père David's deer in the lower Yangtze River region. A suitable habitat with enough food and space but low human disturbance, a healthy founder population under close monitoring, and active conservation measures based on the community co-management will be the prerequisites for a successful re-establishment of the extinct Père David's deer in the region.

Four groups of Père David's deer were deliberately set free on the coast of the Yellow Sea in 1998, 2002, 2003 and 2006. However, the living-space problem remains. The habitat of the re-wilded herd is engulfed by farmlands, artificial forested areas, residential areas, dikes and highways, which restrict further dispersal of the re-wilded deer (Hu and Jiang 2002). At the same time, another story happened in the Shishou NNR located in the middle Yangtze River drainage, namely, 36 Père David's deer accidentally escaped from the fenced paddock of Shishou NNR during a flood in 1998, which allowed a free run of the deer in Dongting Lake area. Now, after five generations of free-living, the runaway deer have navigated through a cluster of 'stepping stones', reached several 'refuges' and established breeding populations of more than 300 deer in the anthropogenic landscape.

As a species that was once extinct in the field, the revival of Père David's deer is an example of how to rescue endangered

species. The story of Père David's deer is a reflection of the human-wildlife relationship in the new millennium.

Sika deer in China

The management of sika deer in China is confronted with the tragedy of domestication. Although the Chinese government has adopted the in situ conservation strategy to establish nature reserves to protect the remnant sika deer populations in the wild, the subspecies (C. n. kopschi) living in south China were found to escape from the nature reserves in spite of the intense poaching outside. Whether nature reserve strategy can serve as a safe-island for endangered sika deer needs further study.

Human disturbance and habitat loss are two main factors for the conservation of sika deer. The population of sika deer in Taohongling NNR increased from 90 in 1983 to 312 in 1998, then decreased to 160 in 2005, and again increased to 275 in 2007 and 365 in 2011; however, many deer dispersed from the core area of the reserve to the surrounding areas (Jiang 2007; Jiang et al. 2012; Li et al. 2013). The initial growth of sika deer population in Taohongling NNR was due to a reduction in human disturbance after the establishment of the nature reserve; however, the following stagnation of the sika deer population inside the reserve and dispersal of sika deer from the reserve to other surrounding areas might be caused by habitat alteration and establishment of deer farms around the reserve (Li et al. 2013).

Many nature reserves have been established to protect the wild sika deer, such as those in Anhui, Zhejiang, Jiangxi, Sichuan and Jilin provinces in China. Although establishment of nature reserves has been proven to be an effective way of conservation in many cases, the simple banning of logging and human disturbance might not be the best strategy, given that sika deer prefer shrub and shrub-meadow habitats. Liu (2007) evaluated the habitat suitability of the Taohongling NNR and found that due to the succession of vegetation, the habitat in the centre of Taohongling NNR is no longer suitable for sika deer. Prescribed burning and slash logging should be carried out for the management of sika deer habitat. The same results were also found in another population of this subspecies (C. n. kopschi) in Qingliangfeng NNR (Yang et al. 2002b; Ma et al. 2004).

The growth and success of deer farms could fulfill the demand of Chinese traditional medicine; however, they might also impose big challenges on wild deer. The multitude of sika deer raised in farms in China is mainly consistent with the northern heliotypes of sika deer in China, and were derived principally from the subspecies C. n. hortulorum (Wu et al. 2006). Still, the long history of captive rearing of sika deer and the commercial trade in stock mean that high interchange of genetic stocks is possible. Deer were not only frequently captured in the wild and brought into captivity, but escaped from captivity or were released intentionally during downturns in the antler market. Given the low population density of wild sika deer, how to maintain genetic heath of the farmed sika deer and how to avoid genetic pollution from the farm-bred sika deer remain unclear (Wu and Zhang 2001; Lei 2007). The roar of the captive stags during rut was found to attract wild sika deer to the sika deer farm (Li et al. 2013). While most of these shifts of sika deer stocks were probably at a local scale, the potential to move sika deer over long distances existed for centuries. These translocations underscore the importance of establishing the natural genetic structure of sika deer over their whole range before such intermixing complicates the picture even further (Wu *et al.* 2006).

Sika deer in Japan

958

The sika deer in Japan is a completely different story. Sika deer populations in Japan also remained at low density in the mid-1950s due to overhunting, including poaching. The sika deer has markedly increased in numbers and extended its geographic distribution in Japan during the past few decades. The rapid increase in sika deer may have had multiple causes associated with changes in socioeconomic and natural environments. These include elimination of wolves, clear-cutting of forests, increased pasture acreage, increased abandonment of cultivated areas, decrease in the hunter population, and strengthening enforcement to prevent poaching. No severe winters during the past 25 years, and the decrease of human presence in mountain and rural areas have also favoured sika deer populations. The overabundant sika deer caused serious damage to crops and forests, as well as to its own habitat. To reduce the population size of sika deer, aggressive female culling has been encouraged by relaxing hunting regulation. The revised law of Wildlife Protection and Management, and Proper Hunting Act (effective as from 29 May 2015) is expected to enhance the number of sika deer harvested, and thereby reduce the population size to a half of the present size (~3.25 million deer) for the next 10 years. Hunting as resource management and culling for ecosystem management should be synergistically combined under adaptive management (Kaji et al. 2010). Detailed information on biology, population status and management of sika deer populations in Japan are reviewed in 'Sika Deer: Biology and Management of Native and Introduced Populations' edited by McCullough et al. (2009).

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960

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