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Variation in stable isotope ratios of carbon and nitrogen in Hokkaido sika deer *Cervus nippon* during 1990-2000: possible causes and implications for management

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Sika deer *Cervus nippon* populations in eastern Hokkaido, Japan, increased rapidly during 1990-1998. This increase appeared to have halted in 1999-2000, probably due to increased hunting and nuisance control. The period of rapid increase was associated with a disproportionately rapid increase in compensation paid for deer damage to crops. We studied changes in diet during 1990-2000, as reflected by stable isotope ratios of C and N in tooth collagen. We hypothesised that isotope ratios would demonstrate dietary shifts related to population levels and/or time, and that shifts in isotope ratios would be consistent with increasing individual consumption of pasture grasses at higher population levels. $\delta^{13}\text{C}$ isotope ratios of tooth collagen in 3-year-old sika indicated a diet dominated by C3 plants throughout the period, and that forage species other than pasture grasses and dwarf bamboo *Sasa nipponica* (the main crop and woodland understory plants, respectively) were important elements. There was a significant decline in the $\delta^{13}\text{C}$ isotope ratio during 1990-2000 in both males and females. $\delta^{15}\text{N}$ values showed no trend with time for males, but increased over time in females. Indices of population (Sightings per Unit Effort, SPUE) were negatively correlated with female $\delta^{13}\text{C}$, and positively correlated with female $\delta^{15}\text{N}$, values, indicating a shift in diet over the period, especially among females. This shift may be related to population and/or offtake levels, in particular the rapid increase in female offtake for nuisance control and hunting during the period. The data are consistent with a relative increase in pasture grass consumption per individual at higher population levels; however, other explanations of the data are equally plausible. Possible dietary changes, and other factors, influencing the observed shift in isotope ratios are discussed. Although statistically significant, the magnitude of dietary shifts nevertheless appeared small, and did not provide evidence which would justify modifying the current policy, of limiting crop damage through managed population reduction to about 25% of peak levels.

Key words: *Cervus nippon*, diet, management, populations, sika deer, stable isotope

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The sika deer *Cervus nippon* is the only wild large herbivore on the island of Hokkaido, Japan. Abundant prior to colonisation of the island by the Japanese in the later 19th century, commercial hunting had reduced the species to very low levels in isolated refuges by the 1920s, after which the species was totally protected. Numbers and range then increased (Kaji et al. 2000). By the 1990s the species had become a major crop predator, causing damage estimated at US\$ 15 million in 1990, and > US\$ 30 million in 1996. Levels of crop damage were closely correlated with numbers shot for hunting and nuisance control (Matsuda et al. 1999, Kaji 2000), but increased considerably faster than population indices.

Hunting of males recommenced in 1953, culling of female crop predators in the later 1980s, and regular hunting for females in 1994 (Matsuda et al. 1999). Since 1997 a feedback management programme has been instituted with the intention of stabilising populations at ca 25% of the 1993 level through aggressive female culling (Matsuda et al. 1999, Kaji 2000). The primary aim of the programme is to reduce crop predation by deer. Harvesting levels for Hokkaido rose sharply from 13,000 to 46,000 during 1990-1996, roughly stabilising thereafter and representing an annual offtake of about 25% of the estimated population (Matsuda et al. 1999).

It was not clear whether the increase in crop damage could be attributed entirely to scalar effects of the increase in deer numbers, or whether a shift in diet with increasing populations was also responsible. Compensation payments suggested this may have been the case, and population-related shifts in diet have been found in isolate populations of sika on small islands (Kaji et al. 1988, 1991, Takahashi & Kaji 2001). If diet shifts do occur, they may magnify or dilute any effect of population reduction, relative to crop damage, and so affect the assessment of optimal population to be aimed for under the feedback management programme. Assessing diets in deer is difficult as both observational evidence and analysis of stomach contents contain biases towards, respectively, easily observed habitats and relatively indigestible foods. These methods are also incapable of retrospective analysis.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of collagen in animal tissues reflect a weighted lifetime average of the value of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the diet, allowing for a small fractionation in the uptake of each isotope due to digestive processes (see 'Methods'). Different dietary sources vary in their

'isotopic signatures', and the signature of the consumer reflects the proportional intake of various dietary sources (DeNiro & Epstein 1978, 1981), so that, for example, an increasing proportion of pasture grasses in sika diet would produce an isotope profile in sika tissue increasingly close to the isotope profile of pasture grasses, allowing for digestive fractionation. Further, as collagen is a very stable molecule, analyses can be made of tissue samples collected many years in the past (Koch et al. 1994). Therefore, values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been widely used as a tool in the reconstruction of diet, and in investigating geographical and/or temporal dietary variation. Previous stable isotope work on the Hokkaido sika population has demonstrated regional variation in diet (Imada 2001).

We analysed carbon and nitrogen isotope ratios from samples of deer tooth collagen collected during 1990-2000. We hypothesised that diet, as reflected in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, would be correlated with population measures. We also predicted that observed shifts in isotope ratios would be consistent with increased relative consumption of pasture grasses at higher populations.

Methods

Our study was conducted in the eastern part of the township of Ashoro in east-central Hokkaido, Japan (42°20'N, 143°50'E). Mean annual temperature is 6°C, with monthly averages ranging from 19°C in August to -8°C in February. Snow cover is typically ca 50 cm from late December to late March/early April and annual precipitation ca 600 mm. The area is hilly, ranging within 100-1,500 m a.s.l. and heavily wooded (84%) with croplands (13%), largely dairy cattle pasture, restricted almost entirely to narrow valley bottoms. The cultivated strip is typically less than 750 m wide. Forest cover is a mix of native self-sown deciduous and mixed woodland, and planted native and exotic conifers. Pasture grasses, mainly orchard grass *Dactylis glomerata*, dominate the cultivated area, and dwarf bamboo *Sasa nipponica* the woodland understory.

The two lower front teeth of sika deer shot during the hunting/culling season (autumn) were collected in 1990, and during 1992-2000 inclusive, by hunters. Date, location, sex and age of each animal shot was recorded. In addition we collected measures of population for each

year, using census data (Sightings per Unit Effort, or SPUE; number of sika counted per hunter/day). We also compiled data on Catch per Unit Effort (CPUE; number of sika shot per hunter-day). Data on the carbon and nitrogen isotope composition of pasture grasses and of dwarf bamboo, respectively the dominant food sources on agricultural land and in the forest understory in the study area (Yokoyama et al. 2000), were collected by Imada (2001) in a parallel study.

From the tooth sample obtained we selected for analysis five male and five female 3-year-old sika deer killed in the eastern part of Ashoro, east-central Hokkaido, each year. Tooth collagen isotope ratios represent an average, weighted toward later intake, over the lifetime of the animal, i.e. about three and a half years in the case of the deer studied here (which were born in spring, and killed in the autumn of the third calendar year after birth).

The surface of each tooth was cleaned using a dental sanding tool, and washed in distilled water and acetone. The sample was then crushed lightly and larger fragments of tooth apatite (which is harder, and does not contain collagen) removed by sieving through a 425 μm sieve. The resulting powder was crushed further to a particle diameter of < 250 μm . Ca 1 g (range: 0.88-1.14 g) of the powder was further processed to chemically separate collagen following the methods described by DeNiro & Epstein (1978).

Two subsamples of 0.4-0.8 mg of collagen from each sample were loaded into standard tin cups and pelletised. Pellets were placed in a Finnigan MAT 252 gas injection mass spectrometer apparatus housed at the Graduate School of Environmental Earth Sciences at the University of Hokkaido, for analysis of carbon and nitrogen isotopic ratios. When subsamples differed in isotope ratios, or the ratio of carbon to nitrogen deviated from the known ratio for collagen, we assumed that sample to be contaminated, and the data were discarded.

Results are expressed as parts per thousand (‰) relative to the standards, PDB limestone for $\delta^{13}\text{C}$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Ehrlinger & Rundel 1989), respectively.

Tooth collagen in sika shows the same fractionation as bone collagen relative to diet for $\delta^{13}\text{C}$, $\sim +3.5\text{‰}$ (Lee-Thorp et al. 1989; D. Halley & M. Minagawa, unpubl. data); while $\delta^{15}\text{N}$ tooth collagen is enriched relative to diet by $\sim +4.35\text{‰}$ (bone collagen $\sim +3\text{‰}$; DeNiro & Epstein 1981;

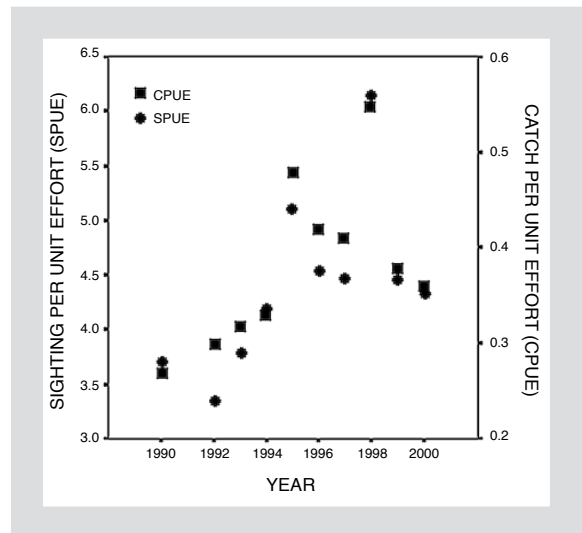


Figure 1. Sightings per unit effort (SPUE; deer/day) and catch per unit effort (CPUE; deer/day) by hunters in the township of Ashoro during 1990-2000. SPUE and CPUE were highly significantly correlated (see text).

D. Halley & M. Minagawa, unpubl. data). Therefore, we have applied correction factors for dietary carbon and nitrogen values of -3.5‰ and -4.35‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, to all values for sika tooth collagen reported below (see also 'Discussion').

Results

Populations

CPUE and SPUE were very strongly correlated ($r_{sp} = 0.988$, $N = 10$, $P < 0.001$; Fig. 1), suggesting that both

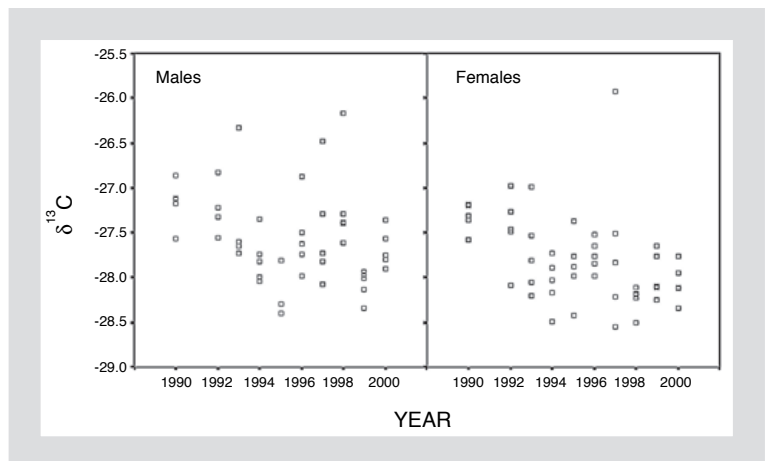


Figure 2. $\delta^{13}\text{C}$ isotope values (in ‰) for sika deer tooth collagen for 3-year-old deer shot between 1990 and 2000, corrected for trophic enrichment. There was a significant decline in $\delta^{13}\text{C}$ values for both males and females over the period (see text).

were similar as measures of population trends. We therefore analysed tooth collagen isotope ratios with respect to SPUE only. Both measures indicated rising populations to 1998. Population indices were sharply lower in 1999, and a slight further reduction was found in 2000.

Isotope ratios

One sample, from a male shot in 1992, showed elemental ratios inconsistent with collagen, indicating that the sample was contaminated. The sample was excluded from further analysis. All other samples showed expected elemental ratios, and consistent isotope ratios between subsamples from the same individual.

Both the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ values for males and females differed slightly, but significantly ($\delta^{13}\text{C}$: male = $-27.56 \pm 0.5\%$; female $-27.8 \pm 0.5\%$; Mann-Whitney $U = 833$, $N_{\text{male}} = 49$, $N_{\text{female}} = 50$, $P = 0.006$; $\delta^{15}\text{N}$ male = $-0.35 \pm 9\%$; female $-0.65 \pm 0.8\%$; $U = 929$, $N_{\text{male}} = 49$, $N_{\text{female}} = 50$, $P = 0.038$ (error terms SD)). This indicates systematic, albeit small, differences between sexes in isotopic ratios in the diet, and by extension suggests differences in their diets. We have therefore analysed data for males and females separately.

$\delta^{13}\text{C}$

Overall values (see above) are, as expected for the region, within the central isotopic range of C3 plants. Nevertheless, $\delta^{13}\text{C}$ values varied significantly with year both for males (Kruskal-Wallis: $\chi^2 = 28.0$, $df = 9$, $P < 0.001$), and females (Kruskal-Wallis: $\chi^2 = 21.6$, $df = 9$, $P < 0.01$). Overall, there was a strong tendency for $\delta^{13}\text{C}$ values to decline over time (Fig. 2), and the trend was significant for both females ($r_{\text{Sp}} = -0.517$, $N = 50$, $P < 0.001$), and males ($r_{\text{Sp}} = -0.354$, $N = 49$, $P = 0.013$).

The $\delta^{13}\text{C}$ values for females were highly significantly negatively correlated with SPUE (Fig. 3). That is, the number of deer sighted (SPUE) per hunter per day, in the year the sika were shot, was higher when female $\delta^{13}\text{C}$ values were lower ($r_{\text{Sp}} = -0.439$, $N = 50$, $P = 0.001$). However, there was no similar effect detectable for males (see Fig. 2; $r_{\text{Sp}} = -0.265$, $N = 49$, $P = 0.066$, n.s.).

$\delta^{15}\text{N}$

The $\delta^{15}\text{N}$ values did not vary significantly between years for males (Kruskal-Wallis: $\chi^2 = 5.1$, $df = 9$, $P = 0.83$, n.s.), but were highly significantly different for females (Kruskal-Wallis:

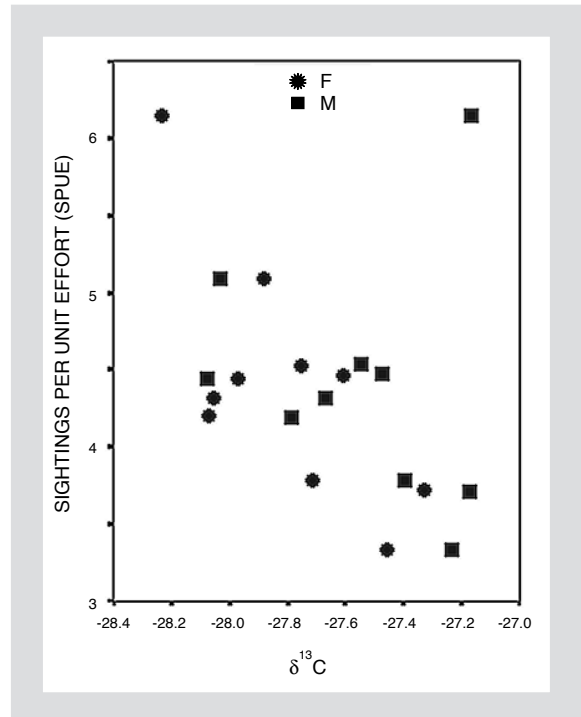


Figure 3. Scatterplot of correlation between annual mean tooth collagen $\delta^{13}\text{C}$ isotope values and sightings per unit effort (SPUE) of sika deer in that year. Female $\delta^{13}\text{C}$ values were significantly negatively correlated with SPUE, whereas male $\delta^{13}\text{C}$ values showed no significant association (see text).

$\chi^2 = 21.9$, $df = 9$, $P < 0.01$). Similarly, while there was no trend in $\delta^{15}\text{N}$ values over time in males ($r_{\text{Sp}} = 0.079$, $N = 49$, $P = 0.59$, n.s.), a highly significant positive tendency over time was found among females ($r_{\text{Sp}} = 0.436$, $N = 50$, $P = 0.002$; Fig. 4).

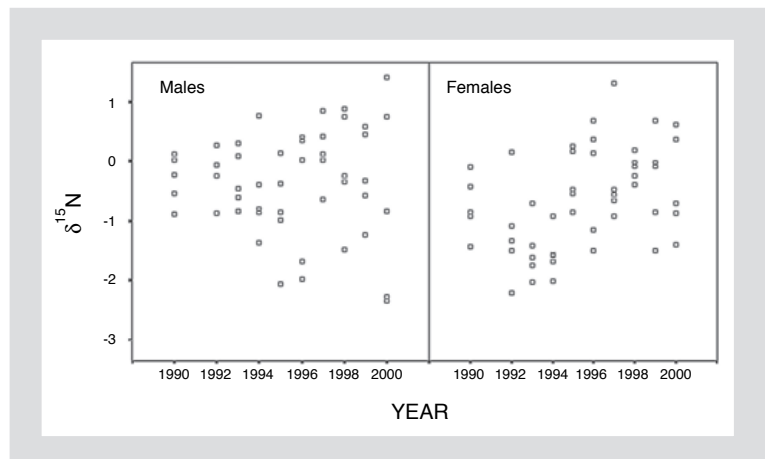


Figure 4. $\delta^{15}\text{N}$ isotope values (in ‰) for sika deer tooth collagen for 3-year-old deer shot between 1990 and 2000, corrected for trophic enrichment. Males showed no trend, but there was a significant increase in $\delta^{15}\text{N}$ values for females over the period (see text).

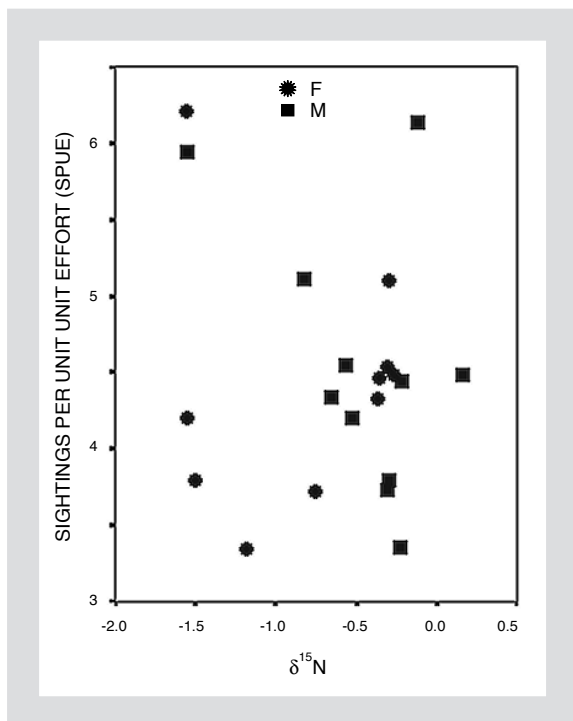


Figure 5. Scatterplot of correlation between annual mean tooth collagen $\delta^{15}\text{N}$ isotope values and sightings per unit effort (SPUE) of sika deer in that year. Female $\delta^{15}\text{N}$ values were significantly positively correlated with SPUE, whereas male $\delta^{15}\text{N}$ values showed no significant association (see text).

The $\delta^{15}\text{N}$ values for females were also highly significantly positively correlated with SPUE ($r_{\text{sp}} = 0.511$, $N = 50$, $P < 0.001$), but values for males were not ($r_{\text{sp}} = 0.27$, $N = 49$, $P = 0.85$, n.s.; Fig. 5).

Discussion

Our results demonstrate small, but significant, changes in the isotope ratios of food consumed by females, and by extension in the diets of the harvested animals, in the period 1990-2000. A smaller, and more equivocal, change was observed for males, suggesting that the introduction of female offtake just before the data collection period, and rapid increase in harvest levels during the period, may have been an important driver of the observed effect.

Almost all plants in the region use the C3 photosynthetic pathway to extract carbon from the atmosphere, and as a result show a relatively narrow range of $\delta^{13}\text{C}$ values, which nevertheless vary consistently between species, the major exception is maize *Zea mays*, a C4 plant, but the crop is not widely grown locally and insignificant in sika diet (Yokoyama et al. 2000, Imada 2001).

Pasture grass is dominated by *Dactylis glomerata*, however, other species are present; the value of pasture is therefore best measured directly from random sward samples. Samples collected in the study area have an average $\delta^{13}\text{C}$ value of $-29.7 \pm 1.20\text{‰}$. Dwarf bamboo has a slightly, but significantly, more negative value averaging $-30.8 \pm 0.40\text{‰}$ (Imada 2001). $\delta^{15}\text{N}$ in plants is mainly derived from the soil, and so varies more widely, e.g. as to whether the soil is fertilised (fertiliser nitrogen is extracted from the atmosphere and so has a $\delta^{15}\text{N}$ value near zero; Ehlinger & Rundel 1989). As a result there is a more pronounced difference in $\delta^{15}\text{N}$ values between pasture grasses ($+2.7 \pm 2.90\text{‰}$) and dwarf bamboo ($-2.1 \pm 1.4\text{‰}$).

Adjusted for fractionation (see 'Methods'), the $\delta^{15}\text{N}$ values of sika tooth collagen lie mainly between -2 and $+1\text{‰}$, i.e. between the values for dwarf bamboo and pasture grasses, and in principle consistent with a diet wholly dominated by bamboo grass and pasture grasses (while not excluding other possible dietary combinations). However, this finding is somewhat sensitive to possible errors in adjustment for trophic fractionation. Further, the $\delta^{13}\text{C}$ values for sika tooth collagen are less negative than for both dwarf bamboo and for pasture grasses. This finding is robust with regard to uncertainties in fractionation values (Post 2002, Olive et al. 2003), as $\delta^{13}\text{C}$ trophic enrichment would have to be much higher ($\approx 5.6\text{‰}$) than any previously reported values (Lee-Thorp et al. 1989, Post 2002) for a pure dwarf bamboo and pasture grass diet to be consistent with the isotope values we found.

This indicates that other food sources were important in the diet, and that changes in their relative consumption were implicated in the observed isotopic changes in sika tissue. As cultivated areas are heavily dominated by pasture grass, these other species seem likely to have been forest plants. Evidence from studies of rumen content tends to corroborate this conclusion. While pasture grasses dominated the portion of sika diet originating from agricultural habitats in the district, seasonally ranging within 71-100% of crops consumed, and dwarf bamboo (the main understory plant in woodland) dominated (45-86%) the woodland-derived graminoid portion of the diet, browsing is important in terms of mass (but less so in terms of nutrient content), during the winter months, and forbs are important in summer and autumn (Yokoyama et al. 2000).

While the combination of declining $\delta^{13}\text{C}$ values and (in females) increasing $\delta^{15}\text{N}$ values is consistent with our hypothesis of increasing relative consumption of pasture grasses over the period/at higher population levels, other interpretations of the data are equally plausi-

ble. For example, changes within the portion of the diet composed of species other than pasture grasses and dwarf bamboo could potentially explain the entire shift in isotope ratios observed. Further, the isotopic shifts observed may have been in part due to grazing-driven changes in the composition of the sward plant community (see e.g. Cohen et al. 2000, Pastor et al. 1997). In the absence of information on the isotopic values of other plants, on potential changes caused by population-related changes in plant community structure, and on the rate and pattern of nutrient cycling in the ecosystem, no real conclusion can be reached beyond the fact that diet did shift slightly, and progressively, over the period.

A caveat is that it is possible that the isotopic ratios of the digestible portions of individual plant species change as a result of grazing pressure. As far as we are aware, no work has been done on this subject, but increased cycling of N in the ecosystem consequent on increased grazing and regrowth (e.g. Cohen et al. 2000) allows the possibility of changes in isotopic fractionation levels at various stages within the nutrient cycle (C in plants is extracted from the atmosphere and so will be little affected by local changes). While there is no evidence that digestive pathways within plants themselves are affected by changes in predation pressure, the possibility of differential isotope ratios occurring within plants at differing grazing pressures, perhaps with a time lag as changes work through the nutrient cycle, cannot therefore be excluded (and would be an interesting subject for research). It would perhaps be expected, however, that in such a case isotopic changes would be more even between the sexes than we observed, and the effect stronger for nitrogen than for carbon, both contrary to our observations.

The strongest changes were observed in females, with only a relatively weak overall decline in the $\delta^{13}\text{C}$ values among males over the period. Females showed directional changes in both the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ values with time and/or population. This indicates that most of the dietary change in the period was occurring in females. This is perhaps surprising, as most previous studies have suggested that female deer exercise a despotic relationship over males in terms of diet selection (Clutton-Brock et al. 1982, 1987, Main & Coblentz 1990). Thus, one would expect shifts in female diet to drive, and so be accompanied by, shifts in male diet. However, experimental culling of females of the closely related red deer *Cervus elaphus* led to no change in male behaviour and diet (Conradt et al. 1999), and recent reviews have suggested that male ungulates select food based primarily on the energetic requirements of their larger bodies, rather than on the intensity of competitive exclusion by

females (Ruckstuhl & Neuhaus 2000, 2002). Our results are consistent with this view.

A caveat here is that it is possible that hunting, the source of our samples and a recent innovation for females, was biased towards females disproportionately using, e.g. more open habitats (in which it is easier to hunt) earlier in the period compared to later. This could lead to a systematic bias, reducing over time due to differential mortality, towards sika which used such habitats more often. If such habitat use was reflected in diet, this might lead to a systematic bias in isotope ratios.

Time and population indices are quite strongly auto-correlated for our sample. As shown above, carbon and nitrogen isotope ratios of female sika collagen were correlated both with population changes as measured by SPUE, and also directly with time. As a result, it is unclear whether the observed effect was directly related to time (e.g. through progressive depletion of some food source), to increased competition at higher populations, or to some combination of the two. Significance was stronger for SPUE than for time for $\delta^{13}\text{C}$, and stronger for time than for SPUE for $\delta^{15}\text{N}$.

However, the shifts involved are small. By far the majority of the effect of sika deer on agricultural crops can be explained by simple scalar effects of population (i.e. more deer eat absolutely more agricultural crops). The shifts in diet we document, however caused, are negligible in comparison with the increased absolute foraging impact of extra sika. We conclude that our data do not provide evidence which would justify modifying the current management strategy of reducing crop and forestry damage through a reduction in sika numbers to ca 25% of the peak population (Matsuda et al. 1999, Kaji 2000).

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