A SEX RATIO BIAS DRIVEN BY DEER BROWSING IN A *LINDERA ERYTHROCARPA* POPULATION AT THE KASUGAYAMA FOREST RESERVE, NARA, JAPAN

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Abstract The sex ratio of *Lindera erythrocarpa* was studied, with reference to the spatial distribution pattern of the individuals and differences in vegetative growth and mortality rates between female and male individuals at the Kasugayama forest reserve, Nara Prefecture, western Japan. The species is dioecious and belongs to the family of Lauraceae. The study forest at Kasugayama has been suffered from severe browsing by deer, *Cervus nippon*. Although the male-biased sex ratio of *L. erythrocarpa* was recorded at Mt. Hiei without obvious vertebrate browsing, the female-biased sex ratios of 0.34 and 0.30 in 1997 and 2002, respectively, were found in our study forest. The spatial distribution patterns suggest the contagious spatial patterns for all, female, and male trees, respectively. The mean values of DBH (diameter at breast height in cm) in females and males are 16.5 and 17.7, respectively. These values are statistically indifferent between genders. The estimates of the two coefficients, intrinsic growth rate (r, 1/year) and carrying capacity (K, cm), of the logistic growth model in annual DBH increments are $r = 0.0318$ and $K = 68.9$ for females, and $r = 0.0261$ and $K = 58.5$ for males. Thus females are superior to males in vegetative growth. The mortality rate of 0.0074 per year per female is far smaller than that of 0.0428 per year per male. No successful seedling regeneration occurred during five observatory years due to severe browsing by deer. These results suggest that the female-biased sex ratio is brought by deer browsing on tree seedlings of *L. erythrocarpa* at the Kasugayama forest.
Key Words : *Cervus nippon*, deer browsing, Kasugayama forest, *Lindera erythrocarpa*, sex ratio

Introduction

The deep green of the Kasugayama forest reserve, Nara City, Kansai, west Japan seems to have still subsisted and is popular with naturalists, hikers etc, although the most of tall intact forests have been already lost from the Kansai area in the past. It represents a rare patch of remnant forests in the area and offers a background landscape for the historic monuments of ancient Nara, the World Heritage. An aerial view of its canopy also appears to be densely covered with healthy original vegetation with oak-laurel dominants (Mizuno *et al.*, 1999). However the some recent studies of the forest give warning of the depletion of the forest by the deer browsing on stem bark (Maesako & Torii, 2000), tree seedlings (Yamakura *et al.*, 2001) and original vegetation as a whole (Suganuma, 2001). The warning is the partial realization of a preceding gloomy prophecy that the Kasugayama forest will be critically affected by a set of different disturbance regimes; i.e. 1) the decease of the seedling regeneration together with a decrease of mature trees by deer

browsing on original vegetation, 2) invasion of introduced species such as *Podocarpus nagi* at Mikasayama or unpalatable plants into the forest reserve, 3) larceny of plants, animals, fungi, soil etc. by inconsiderate maniacs and hunters, 4) inadequate forest management after natural or artificial forest disturbances such as typhoons or forest fire, 5) impact of a circular road for travelers within the forest reserve on the plants, animals and fungi, and 6) unpredictable influence of economic development in the adjacent area of the reserve on the focal forest as a whole, including micro meteorological conditions (Koshimizu *et al.*, 1971; Suganuma, 1991). In these disturbance regimes, the deer browsing on vegetation results from the overcrowding of herds of deer, *Cervus nippon*, which has been recognized as a holly animal in the faith of the Kasuga Shinto through historic eras and protected either by the Kasuga Shinto shrine or Kofukuji temple, both of which belong to the aforementioned historic monuments, the World Heritage.

The number of deer around the focal forest is ca. 1300 heads at the present (Maesako, 2001; Foundation for the Protection of Deer in Nara Park, 2002). Some of them are strolling in the forest and seriously depriving the stem bark of many trees belonging to a variety of taxonomic species (Maesako, 2001). If the population density of deer may not decrease, *Zanthoxylum ailanthoides*, a Rutaceae pioneer species, is predicted to be exterminated from a forest patch with an area of 13 hectares after 185 years from now, since the seedlings of the species are vulnerable to deer browsing, which leads to the decease of seedling regeneration (Yamakura *et al.*, 2001). To avoid the predicted ruin of the forest by establishing a rational forest management plan, the further studies by different approaches to the deer's impact on plants are required within the focal forest. In conjunction with this research requirement, the present study deals with the impact of deer browsing on the sex ratio of *Lindera erythrocarpa* trees at Kasugayama forest. The study will offer a new aspect in the forest management plan, which needs to be proposed urgently, since the sex ratio of trees has been seldom studied with respect to the animal herbivory.

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Materials and Methods

Study species

Lindera erythrocarpa of Lauraceae species is a deciduous tree and occurs in Japan (Honshu, Shikoku, and Kyusyu), Korea and China (Dupont & Kato, 1999a, b). Since it is dioecious and animal pollinated, a pollinator's visit is necessary for pollination (Dupont & Kato, 1999a, b). Males and females show no obvious dimorphism in vegetative characters. The flower size of males is larger than that of females. A female flower has the same basic flower structure as the male, but its stamens are reduced and sterile (Dupont & Kato, 1999a, b). Both of the female and male flowers usually begin to bloom in April and fruit in September and October. The fruit is a drupe and matures 4 or 5 months after pollination (Dupont & Kato, 1999a, b).

With respect to a sex ratio, *L. erythrocarpa* population has a significant male-biased sex ratio at Mt. Hiei without obvious vertebrate browsing. The rather male-biased sex ratios are common in other four Japanese *Lindera* species (Dupont & Kato, 1999a), although an evolutional explanation for the sexual biases in the genus *Lindera* remains obscure.

Study forest

A series of observations and measurements were carried out in a 5.06 ha research plot demarcated in a warm-temperate evergreen forest, which covers the Kasugayama forest reserve with 243 ha in area, Nara City (34° 41′ N, 135° 51′ E), western Japan. The forest is the sacred forest of the Kasuga Shinto shrine and has been protected for 1100 years as a holy forest where religious spirits are believed to live. As already described, the forest is densely covered with original vegetation with oak-laurel dominants (Mizuno *et al.*, 1999; Wakasugi *et al.*, 2001). Koshimizu *et al.* (1971) listed 1277 vascular plants, including exogenous species, in the forest reserve and extracted a major vegetation type of the association: Symploco-Castanopsietum cuspidatae, which belongs to the class: Camellietea japonica.

The soil is clayish with an acidic pH between 3.5 and 4.6. The soil type belongs to the brown forest soil, and the large local variation reflects the complex topography (Nakane, 1975). The bedrock is Ryoke metamorphic complex that was deposited in the Cretaceous (Kokawa, 1954).

According to the Nara Meteorological Station (104m alt.) about 2.5 km northwest of the study forest, the mean annual temperature is 14.4°C with a range of mean monthly temperature of −0.7°C (January) to 22.2°C (August). The mean annual precipitation is 1355 mm, with mean monthly rainfall ranging from 40.4 mm (December) to 212.3 mm (June). Frost is common in winter, but snow over 10 cm deep is unusual (Wakasugi *et al.*, 2001).

Field observation and measurement

All of the trees larger than and equal to 1.0 cm in diameter at breast height (DBH) 1.3 m aboveground in the 5.06 ha study plot were labeled, mapped, identified to species, and measured by DBH by Fujii and his colleagues at Osaka City University in 1996 (Fujii *et al.*, unpublished). Forty-five living individuals of *L. erythrocarpa* were found in the study plot in 1997. In May 1997 and 2002, all the trees in the plot were measured by DBH.

The sex of each flowering individual of *L. erythrocarpa* in the plot was determined by checking reproductive organs in the spring of 1997 and 2002. Flowering individuals were separated into males and females, respectively. The individuals without flowers were tentatively considered to be neuter. The number of each gender was counted for calculating a sex ratio.

Data analyses

Statistical methods, such as the Chi-square test and *t*-test were utilized in the data analyses. In addition to these conventional methods, the Iwao's method for spatial pattern analysis (Iwao, 1968; Iwao & Kuno, 1971) was also used. The two coefficients of the logistic equation were adopted for discerning the differences between females and males in their vegetative growth characters. In the coefficient estimation of the logistic equation, the equation was rewritten by the following difference equation, $x(t+\Delta t)=a \cdot x(t)-b \cdot x^2(t)$, where t is a forest inventory year, Δt is a time interval between successive forest inventory years, $x(t)$ is DBH at the year t, the variables a and b are coefficients specific to a gender. From the estimated coefficients or a and b, the intrinsic growth rate $r=(a-1)/\Delta t$ and carrying capacity $K=(a-1)/b$, respectively, of the logistic equation are calculable.

Results

Clumping of individual trees of different genders

The habitats of 45 *L. erythrocarpa* trees in the plot were mapped and their flowering conditions were examined in 1997 (Fig. 1). The spatial patterns of all 45 trees, 27 female trees, and 14 male trees, respectively, appear to clump as shown in Fig. 1A. The mean crowding vs. mean density

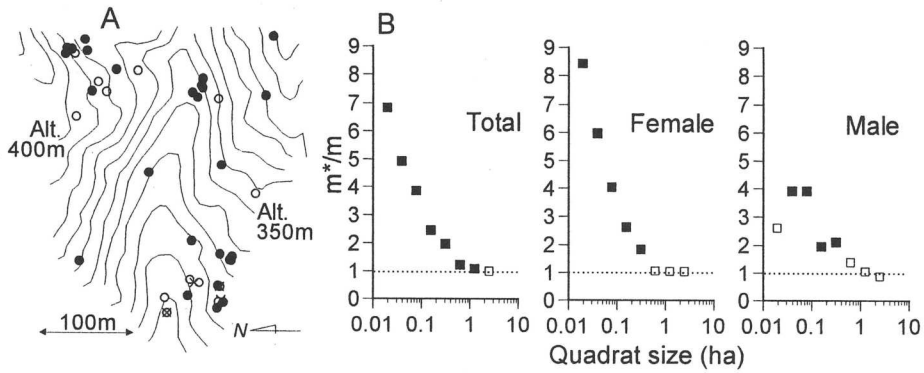


Fig.1. Spatial distribution pattern of *L. erythrocarpa* in the 5.06 ha study plot. Solid circles (●), open circles (○), and crosses (×) represent the female trees, male trees, and non-flowering trees, respectively, in 1997 (A). The m*/m values significantly different from the Poisson distribution at 5% level are expressed by the solid squares (■), while open squares (□) stand for the m*/m insignificantly different from Poisson distribution at 5% level (B). The dotted lines at m*/m=1 indicate the expected values for random distribution (B).

relationship in Fig. 1B clearly confirms the contagious spatial patterns for all, female, and male trees, respectively, although the degrees of contagion and statistical significance are different between genders.

No successful regeneration occurred during five observatory years. The new seedlings appeared in the spring but disappeared due to deer browsing within a year. Hence the general clumping pattern of the trees did not largely change with respect to observatory years, although the degree of contagions in the spatial patterns slightly decreased at the second observation.

Size structure in relation to genders

The frequency distribution of DBH of 45 individual trees is unimodal but asymmetric with respect to modal value (Fig. 2A). The largest DBH of 44.4 cm and smallest DBH of 4.23 cm were recorded from flowered females. The mean and variance of DBH are 16.5 cm and 66.74 cm^2, respectively, for females, and 17.7 cm and 74.4 cm^2, respectively, for males. These values for females and males are statistically indifferent between genders (t-test, $P>0.05$). The mean DBH of 12.5 cm and its variance of 25.5 cm^2 for four non-flowering individuals are also inseparable from those of flowered females and males (t-test, $P>0.05$).

The two coefficients, intrinsic growth rate (r, 1/yr) and carrying capacity (K, cm), of the logistic growth model in annual DBH increments were estimated from the two repeated forest inventory records in 1997 and 2002. The estimates are $r = 0.0318$ and $K = 68.9$ for females, and $r = 0.0261$ and $K = 58.5$ for males. These values clearly deny the possibility of a hypothesis of bigger males.

The sex ratios in 1997 are compared between different size classes in DBH (Fig. 2B). In the five DBH classes consisting more than four individual trees, the sex ratios are female biased and are rather indifferent between different DBH size classes, without implying the dependence of sexual bias on tree size. The female bias in sex ratios at different DBH classes seems to be interesting but difficult to explain by using the size structure of the population.

Sex ratio bias enhanced by mortality

The forty-one trees among 45 individuals flowered in the study plot in 1997. The percentage ratio of flowered trees (41) to the total individuals (45) is 91% (Table 1). The flowered trees consisted of 27 females and 14 males, suggesting a significant female bias in the sex ratio of 0.34, i.e. (males)/(males + females) (Chi-square test, $P<0.05$).

The sex reversal is not observable in 2002 as shown in Table 1 and is not influential to a

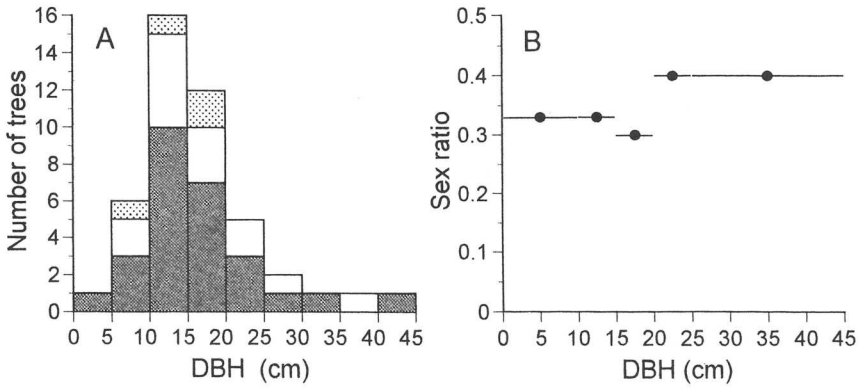


Fig.2. Size structure and sex ratio of *L. erythrocarpa* population in 1997. The dark shaded, open, and light shaded histograms represent females, males, and non-flowered trees, respectively (A). The sex ratios at different DBH classes are rather constant (B).

Table 1. Sex ratios in *Lindera* species. The sex ratio is calculated by (males)/(males+females).

Species	Locality	Year	Male	Female	Non-flowering	Sex ratio	Significance level(P)	Hamilton's x^*	Reference
L. erythrocarpa	Kasugayama	1997	14	27	4	0.34	<0.05	0.48	This study
	Kasugayama	2002	11	26	1	0.30	<0.05	0.48	This study
L. erythrocarpa	Mt. Hiei 1	1997	17	5	6	0.77	<0.05	0.40	Dupont & Kato(1999a)
L. triloba	Mt. Hira 1	1997	71	13	13	0.85	<0.01	0.46	Ibid.
	Mt. Hira 2	1997	20	12	1	0.63	N.S.	0.46	Ibid.
	Mt. Hira 3	1997	53	22	2	0.71	<0.01	0.48	Ibid.
L. umbellata	Shugakuin	1997	15	14	0	0.52	N.S.	0.46	Ibid.
	Mt. Hira 2	1997	31	31		0.50	N.S.	0.48	Ibid.
	Mt. Hiei 1	1997	35	31	0	0.53	N.S.	0.48	Ibid.
	Mt. Hiei 2	1997	18	17	0	0.51	N.S.	0.47	Ibid.
	Mt. Hiei 3	1997	15	13	0	0.54	N.S.	0.46	Ibid.
L. praecox	Mt. Hiei 3	1997	20	10		0.67	N.S.	0.45	Ibid.
L. obtusiloba	Iwakura	1997	37	27	4	0.58	N.S.	0.48	Ibid.
L. grauca	Shugakuin	1997	0	6	2	0.00	<0.05	0.42	Ibid.
	Uji	1997	0	9	1	0.00	<0.01	0.44	Ibid.

change of sex ratios in our observation, since the constancy of the sex of a given *L. erythrocarpa* individual is ubiquitous (Primack, 1985; Dupont & Kato, 1999a).

Mortality is influential in sex ratio variations, as shown in Table 1. During five observatory years from 1997 to 2002, one female out of 27 females, three of 14 males, and three of four non-flowering trees died (Table 1). The one remnant tree sexless in 1997 did not flower in 2002. Out of the seven dead trees, the two males and one non-flowering tree were killed by a strong typhoon, which haphazardly visited the study plot in September 1998. A mortality factor for four other dead trees is unknown but might die of senescence. The mortality rate of 0.0074 per year per female is far smaller than that of 0.0428 per year per male. The sex ratio in May 2002 is 0.30 representing the further female bias (Table 1). The female bias in sex ratios has never been observed in a preceding study carried out by Dupont and Kato (1999a; cf. Table 1).

Discussion

Tree clumping driven by deer

The contagious spatial patterns in Fig. 1 might result from the rarity of safe sites for seedling regeneration. Many tree species including the study species require canopy gaps in regeneration and their seedlings in gaps are severely browsed by deer *Cervus nippon* (Naka & Yoneda, 1984; Shimoda *et al.*, 1994), of which recent density is 1300 heads in a ca. 400 ha deer home range, as already described. A possible safe site in seedling regeneration is a special canopy gap enclosed by fallen big woods, which irregularly occur in the supra-annual timing of violent typhoon visits and can guard tree seedlings against deer. Another site safe for seedlings is a tree fall mound that is also rather inaccessible to deer and is produced by a strong typhoon (Naka & Yoneda, 1984). These safe sites might not be spatially uniform and each of them could guard many seedlings. Thus trees clumped in limited places in the study plot and resulted in contagious spatial patterns.

Failure of ESS model in sex ratios in our observation

The evolutionarily stable sex ratio of a species population has been clarified by Hamilton (1967). When the difference in reproductive cost between female and male individuals is negligible, the evolutionarily stable sex ratio (x^*) in a population consisting N female individuals is written in the form, $x^* = (N-1)/(2N)$ (Hamilton, 1967). The x^* is close to 0.5 as N increases. Hamilton's x^* calculated from our data of *L. erythrocarpa* is 0.48, which is in excess of the observed value, 0.34. In a *L. erythrocarpa* population studied by Dupont and Kato (1999a) at Mt. Hiei in Japan, the sex ratio of 0.77 is a significantly male-biased and represents the very large difference to our observation (Table 1). The sex ratio of 0.77 also largely differs from the corresponding x^* of 0.40 (Table 1). They also recorded the rather male-biased sex ratios in other four Japanese *Lindera* species and the homogeneity of the sex ratios among several populations of *L. umbellata*, except for a peculiar species, *L. glauca*, of which populations consist of only males in Japan (Kitamura & Murata, 1979). The most of their observed sex ratio values are different from the x^*, implying the inapplicability of Hamilton's model to *Lindera* species (Table 1). A big variation of the sex ratios between local patches of a given plant species is well known, although a plausible explanation common for any cases from a large variety of species remains unclear (Kawano, 1984).

Failure of expensive costs in female reproduction in our observation

An evolutionary explanation of the sex ratio variation is concerned with the cost of reproduction. Since the reproductive cost of female individuals is generally larger than that of male individuals, the evolution of dioecy by sexual selection predicts male-biased sex ratios (Bawa, 1980; Willson,

1983; Stephenson & Bertin, 1983). Actually, a preponderance of male individuals has been reported for populations of many dioecious species, while the female bias is less common (Lloyd & Webb, 1977; Opler & Bawa, 1978; Willson, 1983; Dupont & Kato, 1999a). The hypothesis of expensive costs in females fits to the observation by Dupont and Kato (1999a), suggesting a need of another possible explanation to our study plot.

If the males could be far bigger in their vegetative size than females, and if the trade off between vegetative growth and reproduction could occur in males, a female bias in a sex ratio might not be surprising. We tentatively designate this view in male behavior in reproduction as "big male hypothesis (or male height advantage hypothesis; Fox, 1993)". The inference appears to be worth studying in the future, although our observed results in annual DBH growth contradict the hypothesis.

Effect of deer on female biased sex ratios in our observation

As suggested by the general terminologies of primary, secondary and tertiary sex ratios, respectively, the sex ratios are determined by different but possibly mutually related mechanisms working at different timings of sexual development. Dupont and Kato (1999a) made a brief reference to the three major sources of sex ratio variations; 1) the facultative sexual expression, 2) gender specific differences in growth, reproduction and mortality, and 3) ecological niches. Out of these sources leading to different sex ratios, the second with respect to mortality is testable by using our observed mortality data (Table 1).

Figure 3 represents a rewritten expression of Table 1, postulating the mortality differences between genders. The male mortality is clearly higher than female mortality, although the ubiquity of the observed higher male mortality in *L. erythrocarpa* remains uncertain. Here we simulate the sex ratio variation with respect to time in a model population of the focal species, by assuming 1) a hypothetical seedling cohort growing in safe sites free from deer browsing and consisting of individuals simultaneously germinated in a given year, 2) the unsuccessful seedling regeneration in the cohort, 3) the male bias of the secondary sex ratio of 0.77 in the cohort (Dupont & Kato, 1999a), 4) the female mortality rate of 0.0074/yr (Fig.3), and 5) the male mortality rate of 0.0428/yr (Fig.3). The first assumption is the reflection of the aforementioned discussion about the safe sites in seedling regeneration. The second assumption describes the fate of seedlings newly born from the parental cohort, which is defined in the first assumption. It follows that all the new seedlings are eaten by deer and are impossible to grow. The third assumption gives the sex ratio at the initial growth stage of the cohort. The fourth and fifth assumptions result from our observed data. These assumptions give the limiting conditions of the population (or cohort) dynamics of plants whose regeneration is desperately driven by deer browsing.

Since no successful seedling regeneration occurs in the abovementioned model cohort, the population size of the cohort decreases with respect to time, carrying the change of sex ratios (Fig. 4). The calculated sex ratios suggest a decrease of the male bias in the sex ratio with the progress of time and the bias disappearance at ca. 33 years after the establishment of the cohort. The sex ratio of the hypothetical cohort becomes 0.34 at ca. 51 years after cohort establishment. Thus the effect of male and female mortalities on the sex ratio is conspicuous (Fig. 4).

To keep the sex ratio at a desirable level, the high male mortality should be compensated by active male natality. It follows that the rotation cycle of male individuals should be faster, suggesting the active recruitment of males, smaller threshold size for flowering in males, and earlier onset of reproduction in males. If the female superiority in vegetative growth is true, the vigorous recruitment is further required to males. Unfortunately, the seedling regeneration has

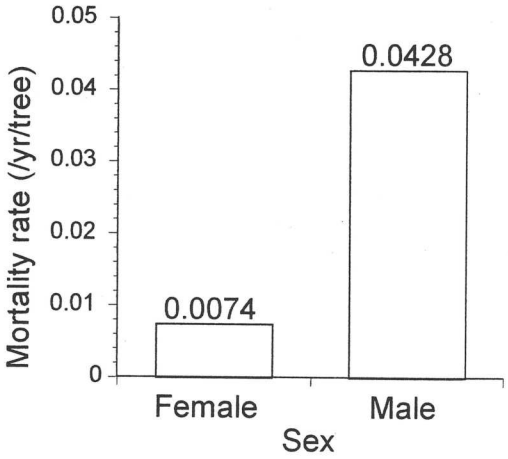


Fig.3. Mortality difference between genders in *L. erythrocarpa*. The male mortality is clearly higher than female mortality.

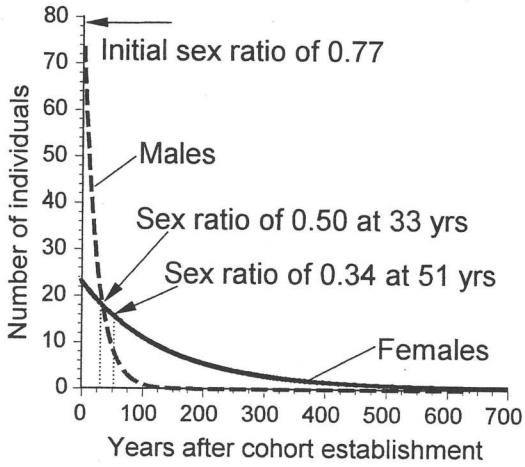


Fig.4. Simulation of the sex ratio variation in *L. erythrocarpa* without seedling regeneration. An initial seedling cohort consisting of 77 males and 23 females is assumed. Males die off with respect to the lapse of years and become smaller than 1.0 after 100 years.

been prevented due to deer in our study plot. Therefore the major cause of the highly skewed sex ratio of 0.34 results from the severe deer browsing on seedlings in the present study.

Implications for forest conservation

The sex ratio is one of the important attributes of the dioecious plants. The present study clarifies the impact of deer on the sex ratio of dioecious plants through the interference of seedling regeneration. An excessive decrease in male or female density will give rise a reduction in the effective population size. If the secondary sex ratio of a given species has a bias and if a pair to both sexes tends to easy to die, as in a case of *L. erythrocarpa*, the management of the focal species should be done separately with respect to each sex. Although a rather complicated plan might be necessary for the separated management of both sexes, the discrimination between genders appear to be of great importance in forest tree management.

The control of deer is also important in the conservation of the Kasugayama forest reserve, as already postulated by the preceding studies (Maesako, 2001; Suganuma, 2001;Yamakura *et al.*, 2001). An unconscious and dull response of forest managers to the coming prophecy of the forest depletion (Koshimizu *et al.*, 1971) will be blamed, if the predicted crisis of the Kasugayama forest reserve will be realized.

References

Bawa, K. S. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics*, 11: 15-39.

Dupont, Y. L. & Kato, M. 1999a. Sex ratio variation in dioecious plant species: a comparative

ecological study of six species of *Lindera* (Lauraceae). *Nordic Journal of Botany*, 19: 529-540.

Dupont, Y. L. & Kato, M. 1999b. Phenology and flower-visiting entomofauna of six species of *Lindera* (Lauraceae) in Japan. *Nordic Journal of Botany*, 19: 707-718.

Foundation for the Protection of Deer in Nara Park. 2002. *Population statistics of deer*. The Foundation for the Protection of Deer in Nara Park, Nara (in Japanese).

Fox, J. F. 1993. Size and sex allocation in monoecious woody plants. *Oecologia*, 94: 110-113.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science*, 156: 477-488.

Iwao, S. 1968. A new regression method for analyzing the aggregation pattern in animal populations. *Researches on Population Ecology*, 10: 1-20.

Iwao, S. & Kuno, E. 1971. An approach to the analysis of aggregation pattern in biological populations. In: *Statistical Ecology I* (eds. Patil, G. P., Pielou, E. C. & Waters, W. E.), 461-513. Pennsylvania State University Press, University Park, Pennsylvania.

Kawano, S. (ed.). 1984. *Life histories and evolution of plant species 1*.148pp. Baifukan, Tokyo (in Japanese).

Kitamura, S. & Murata, G. (eds.). 1979. *Coloured illustrations of woody plants of Japan II*. 545pp. Hoikusha, Osaka (in Japanese).

Kokawa, S. 1954. Geology of Mt. Mikasa and its environs, Nara Prefecture, with special reference to the geologic age of Mikasa-andesite. *Journal of Geological Society of Japan*, 60: 487-493 (in Japanese).

Koshimizu, T., Iwata, S., Suganuma, T., Kitagawa, N. & Hamada, M. 1971. Nature and history of Nara City. In: *Nature in Nara City* (ed. Koshimizu, T.), 109-260. Nara Municipal Office, Nara (in Japanese).

Lloyd, D. G. & Webb, C. J. 1977. Secondary sex characters in plants. *Botanical Review*, 43: 177-216.

Maesako, Y. & Torii, H. 2000. Tree barking by Shika deer *Cervus* nippon in warm temperate evergreen forest in Mt. Kasugayama, Nara Pref., Japan. *Bulletin of Kansai Organization for Nature Conservation*, 22: 3-11 (in Japanese).

Maesako, Y. 2001. Deer and plant in Mt. Kasugayama, Nara, Japan. *Bulletin of Kansai Organization for Nature Conservation*, 23: 171-177 (in Japanese).

Mizuno, T., Fujii, N., Kanzaki, M. & Yamakura, T. 1999. Fractal nature of spatial patterns in Japanese evergreen oak forest trees. *Vegetation Science*, 16: 103-113.

Naka, K. & Yoneda, T. 1984. Community dynamics of evergreen broadleaf forests in southwestern Japan. III. Regeneration in gaps in an evergreen oak forest. *Botanical Magazine, Tokyo*, 97: 275-286.

Nakane, K. 1975. Dynamics of soil organic matter in different parts on a slope under evergreen oak forest. *Japanese Journal of Ecology*, 25: 206-216 (in Japanese).

Opler, P. A. & Bawa, K. S. 1978. Sex ratios in tropical forest trees. Evolution, 32: 812-821.

Primack, R. B. 1985. Sex ratio and sexual constancy in spicebush (*Lindera benzoin*). *Rhodora*, 87: 305-308.

Shimoda, K., Kimura, K., Kanzaki, M. & Yoda, K. 1994. The regeneration of pioneer tree species under browsing pressure of Sika deer in an evergreen oak forest. *Ecological Research*, 9: 85-92.

Stephenson, A. G. & Bertin, R. I. 1983. Male competition, female choice, and sexual selection in plants. In: *Pollination biology* (ed. Real, L.), 109-149. Academic Press, New York.

Suganuma, T. 1991. *Forty-Years-Research Trajectories of Professor Takayuki Suganuma in Botany, Plant Sociology and Plant Ecology*. Vol. 2, 292pp. Editorial Board of Collected Works of Prof.

T. Suganuma, Nara (in Japanese).
Suganuma, T. 2001. Ecological status of *Podocarpus nagi* and podocarp forest in the precincts of Kasuga-Shinto Shrine. *Bulletin of Kansai Organization for Nature Conservation*. 23: 151-155 (in Japanese).
Wakasugi, M. T., Yasuda, M., Kanzaki, M. & Yamakura, T. 2001. Seed dispersal of *Sapindus mukorossi* identified by an automatic camera system at the Kasugayama forest, central Japan. *Bulletin of Kansai Organization for Nature Conservation*. 23: 3-12.
Willson, M. F. 1983. *Plant reproductive ecology*. Wiley, New York.
Yamakura, T., Kawasaki, T., Fujii, N., Mizuno, T., Hirayama, D., Noguchi, H., Nanami, S., Itoh, A., Shimoda, K. & Kanzaki, M. 2001. Predictive discussion on the fate of an evergreen broadleaf forest at Kasugayama. *Bulletin of Kansai Organization for Nature Conservation*, 23: 157-169 (in Japanese).

奈良春日山カナクギノキに歪んだ性比をもたらすシカの摂食圧

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クスノキ科の雌雄異株性落葉高木種カナクギノキ（*Lindera erythrocarpa*）の性比，個体の空間分布，および栄養成長と死亡率の性差を奈良県春日山保護林で調査した。この森林は現在鹿（*Cervus nippon*）の被食に曝されており，将来的に絶滅の危機に瀕していることが示唆されている。鹿などの大型草食動物のほとんど存在しない京都府比叡山では，カナクギノキ個体群は雄に偏った性比を持つことが知られているが，本研究の調査地春日山保護林では，1997 年と 2002 年にそれぞれ 0.34，0.30 という雌に偏った性比（雌雄個体合計数に対する雄個体数の割合）を記録した。個体の空間分布パターンは雌，雄，全個体いずれに関しても集中分布を示した。雌および雄の平均胸高直径（cm）は，それぞれ 16.5，17.7 であり，これらの値に有意な雌雄差は認められなかった。胸高直径成長に関するロジスチック成長モデルの 2 つの係数，内的自然増加率（r）と成長の上限（K）の値は，共に雌（$r=0.0318$，$K=68.9$）の方が雄（$r=0.0261$，$K=58.5$）よりも大きく，栄養成長における雌個体の優越を示唆した。個体の死亡率は，雌では 0.0074／年，雄では 0.0428／年と雄の方が遥かに高かった。調査を行なった 5 年間に，実生による更新は鹿による被食のため観察されなかった。これらの結果は，鹿による実生の被食が春日山保護林のカナクギノキ個体群の性比を大きく雌へと偏らせていることを示唆する。