Pattern of Twig Cutting by Introduced Rats in Insular Cloud Forests[1]

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Abstract: We examined seasonal patterns of twig cutting by the introduced black rat, *Rattus rattus*, on Haha-jima Island, an island in the Ogasawara (Bonin) group of Japan. Censuses were conducted along seven routes to count the number of trees damaged by twig cutting in each month. Overall, 42.6% (23/54 species) of woody species were damaged. Twig cutting was greatest in spring (March–May). Probability of damage by twig cutting was not correlated with species frequency in the vegetation. This suggests that twig cutting is associated with particular characteristics of target species. Endemic plants experienced a significantly higher probability of twig cutting than alien plants. This may be due to an evolutionary loss of plant defense mechanisms in the absence of herbivorous mammals. Because the overall proportion of individuals damaged by twig cutting was not high, the behavior is unlikely to influence the population dynamics of trees and cause vegetation change. But intense twig cutting was also found on critically endangered plants, so twig cutting by black rats could be a threat to those species.

Invasive species on islands disrupt plant-animal relations, alter environmental conditions, and cause the extinction of many indigenous species (Whittaker and Fernández-Palacios 2007, Davis 2009). The black rat, *Rattus rattus* (L.), has successfully invaded islands around the world, reducing seabird nesting (Martin et al. 2000, Jones et al. 2006), changing population structure of endemic reptiles (Towns et al. 2006), and eating seeds (Shaw et al. 2005, Abe 2007). It can eat such a wide range of foods (Case and Bolger 1991) that it could affect insular ecosystems in yet unknown ways. As we report here, twig cutting by rats is one such behavior with potential ecological consequences.

Rattus rattus, *Rattus norvegicus*, and *Mus musculus* have all successfully invaded the Ogasawara Islands (Yabe and Matsumoto 1982). Ecological impacts of *R. rattus* have been reported from islands worldwide (Clark 1981, 1982, Newman 1994, Robinet et al. 1998, Campbell and Atkinson 2002, Thibault et al. 2002, Vanderwerf and Smith 2002, Courchamp et al. 2003, McConkey et al. 2003, Towns et al. 2006). The rats usually eat plant materials such as seeds, fruits, and branches (Best 1969, Norman 1970, Fall et al. 1971, Clark 1981, García 2002), and seed predation constitutes their major form of ecological damage on plants (Shaw et al. 2005, Salvande et al. 2006, Abe 2007). Recently, Abe (2007) reported seed predation by *R. rattus* on Nishi-jima Island, one of the Ogasawara Islands. Twig cutting by *R. rattus* has been reported on several plant species (Kitahara and Sato 2000, Nobushima 2003, Watanabe et al. 2003, Abe 2005), but information about its ecological effects is limited (Vestal 1938, Baxter and Hansson 2001).

This report is the first to show the quantitative seasonal pattern of twig cutting by rats. We addressed the following three questions: (1) How frequent is twig cutting? (2) Do rats

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prefer particular species for twig cutting? (3) When is twig-cutting behavior most prevalent?

MATERIALS AND METHODS

Study Site

The Ogasawara Islands lie about 1,000 km south of the Japanese mainland and consist of about 50 islands. The islands have a subtropical climate with a mean annual temperature of 23°C and mean annual precipitation of 1,200–1,300 mm at the local meteorological station in Chichi-jima. These conditions are drier than those of Okinawa, which lies at a similar latitude in southwestern Japan, and thus most of the Ogasawara Islands are covered in dry forest or grassland. Human settlement of the Ogasawara Islands started in 1830. By the end of the nineteenth century, agriculture and forestry had disturbed the islands, and many alien species had been introduced. *Rattus rattus* was introduced to the islands before 1874 (Obana 1878). The biota of the islands has a high endemic rate (44.6% in flowering plants [Abe 2006]) and many endangered species on the Japanese Red List (Ministry of the Environment 2007).

Haha-jima (26° 36′–42′ N, 142° 07′–11′ E, 462 m alt.) is located 40 km south of Chichi-jima. Subtropical cloud forest dominates the central mountains of this island, and several plants are endemic to this region. Climate conditions in the central mountains are wetter than those at the local meteorological station in Chichi-jima. Our census routes were set in this mountainous area (Figure 1).

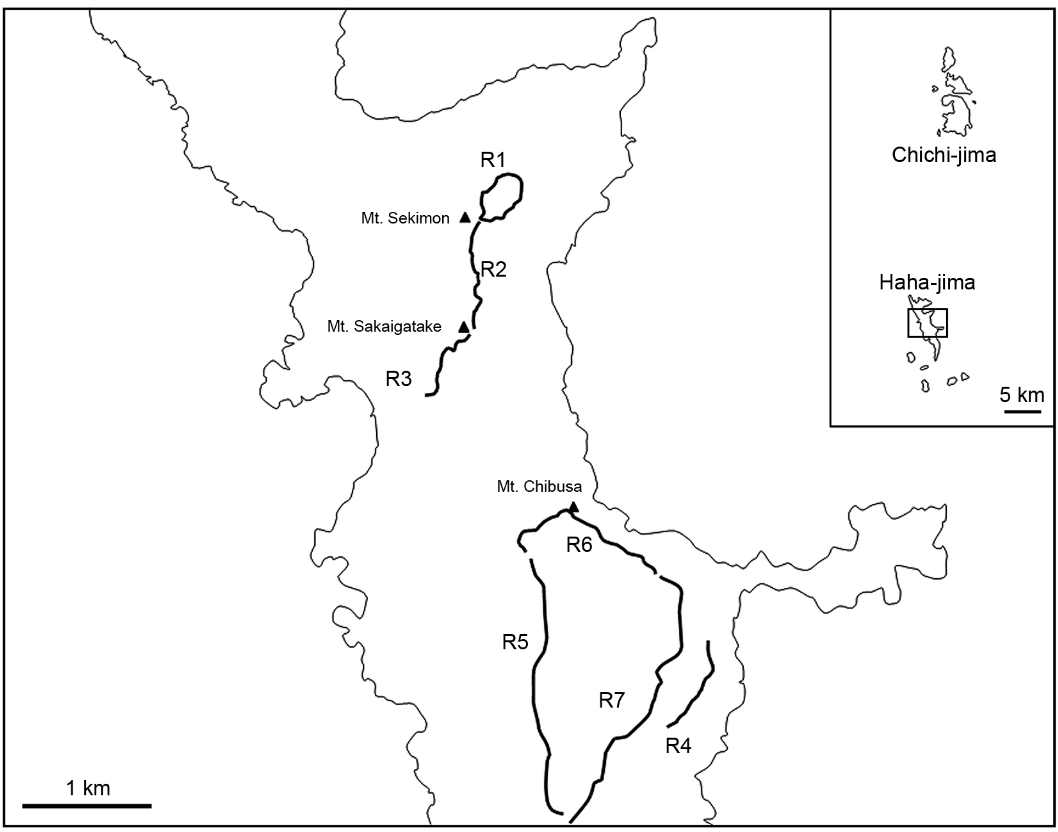

FIGURE 1. Census routes on Haha-jima.

Field Survey

We censused instances of twig cutting along mountain trails on Haha-jima (Figure 1, Table 1). Width of census routes was 1.0–1.5 m. Routes 1, 2, and 6 were covered by primary cloud forest (Ono and Okutomi 1985, Mueller-Dombois and Fosberg 1998). Route 3 traversed secondary forest dominated by an invasive alien tree, *Bischofia javanica* ("alien forest"). Routes 4, 5, and 7 were covered by mixed secondary forest dominated by *Schima mertensiana* and *Calophyllum inophyllum*. The Sekimon and Tamagawa Dam routes (1–4) were censused in May 2005; May, August, and November 2006; February, June, and October 2007; and February, June, September, and October 2008. The Mt. Chibusa routes (5–7) were censused in March, July, September, October, November, and December 2006; January, February, March, and April 2007; and March, April, May, June, August, and October 2008. While walking the routes, we looked for twigs dropped on the ground (Figure 2*a*,*b*) and recorded the number of trees damaged by twig cutting. To avoid double counting from the last census, only fresh cuttings that had green leaves were counted, and census intervals were at least 3 weeks.

To compare the species composition of damaged trees, we counted all trees whose crown covered each route. Because there was little likelihood of our finding twigs dropped from small shrubs, we omitted plants with a crown diameter of <1 m.

Statistical Analysis

Seasons were defined conventionally: spring (March–May), summer (June–August), autumn (September–November), winter (December–February). Because the number of trees and census times were different among routes, frequency of twig cutting was converted to the probability of twig cutting per individual. To clarify the pattern of twig cutting, effects of seasons and forest types (primary forest, secondary forest, and alien forest) were analyzed. To clarify the preference of *R. rattus*, the effects of plant origin ("endemic" to Ogasawara, "indigenous" to wider region, and "alien") as well as plant species were analyzed. In addition, the effect of reproductive season was tested to determine potential association between twig cutting and plant reproduction. All effects on twig cutting were analyzed using generalized linear models (GLM) with binomial error

TABLE 1

Summary of Census Routes

Route No.	Trails	Distance (km)	Elevation (m)	Forest Types	Census Periods
1	Trail around the Sekimon Doline	1.3	250–340	Primary cloud forest	May 2005–Oct. 2008
2	From Mt. Sakaigatake to the junction of the Sekimon trail	1.2	330–410	Primary cloud forest	May 2005–Oct. 2008
3	From the start of Mt. Sakaigatake trail to near the top of Mt. Sakaigatake	1.0	250–410	Alien forest	May 2005–Oct. 2008
4	From the Tamagawa Dam to a ridge on the eastern coast	1.0	190–270	Secondary forest	May 2005–Oct. 2008
5	From the start of Mt. Chibusa trail to the observatory west of the top of Mt. Chibusa	2.4	20–370	Secondary forest	July 2006–Oct. 2008
6	From western observatory via top of Mt. Chibusa to the eastern observatory	1.5	360–462	Primary cloud forest	July 2006–Oct. 2008
7	From eastern observatory to the end of Mt. Chibusa trail	2.7	20–360	Secondary forest	July 2006–Oct. 2008

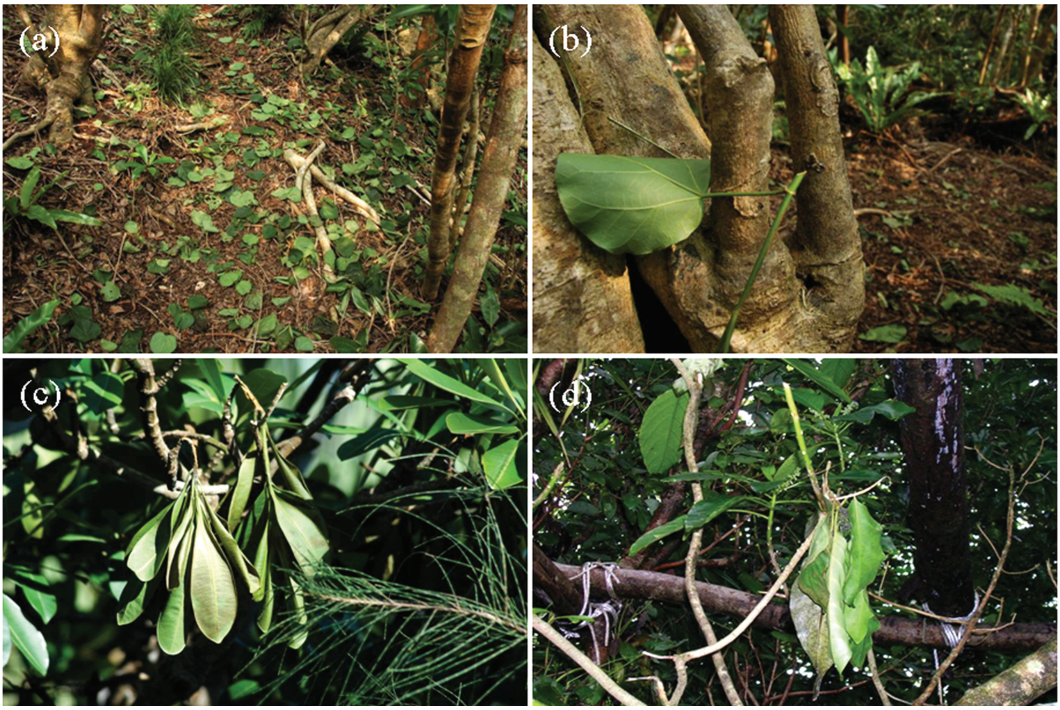

Figure 2. (*a*) Fresh twigs of *Hibiscus glaber* dropped by black rat after gnawing. (*b*) Cut end of dropped *H. glaber* twig. (*c*) Twig cutting on *Ochrosia nakaiana*. The pith was grazed, leaving the twig hanging by the bark. (*d*) Twig cutting on the highly endangered endemic tree *Claoxylon centinarium*. Note the many small flower buds behind the leaves.

distribution because data type of twig cutting was binomial (damaged or not). These analyses were performed using JMP software (Sall et al. 2004).

RESULTS

Among 54 woody species observed by route census, 23 species (42.6%) were damaged by twig cutting (Table 2). Several dropped twigs had been robbed of pith (Figure 2*c*). Twig cutting was most frequent in spring ($G = 33.6$, df $= 3$, $P < .001$ for all routes [Figure 3, Table 3]) and in primary forest ($G = 127.4$, df $= 2$, $P < .001$ [Figure 4, Table 3]). The interaction of forest type × season was also significant ($G = 21.2$, df $= 6$, $P = .002$). Twig cutting of *Hibiscus glaber* was observed throughout the year, but other species tended to be damaged in particular seasons. Damaged twigs of *Planchonella obovata*, *Tarenna subsessilis*, *Boninia grisea*, and *Ilex beechyi* frequently bore flower buds or flowers. In total, 41.8% (46/110) of twig-cutting events occurred during the reproductive season. The probability of twig cutting in the reproductive season was significantly higher than that in nonreproductive season (GLM, $G = 125.9$, df $= 1$, $P < .001$). The probability of twig cutting was high in *H. glaber*, *P. obovata*, and *Fatsia oligocarpela*. The relationship between the probability of twig cutting and species composition suggests that *R. rattus* additionally preferred *Trema orientalis*, *Dendrocacalia crepididifolia*, and *T. subsessilis*, yet the four most common species along the routes (*Ardisia sieboldii*, *Schima mertensiana*, *Bischofia javanica*, and *Rhaphiolepis umbellata*) were not damaged or only rarely damaged despite their high frequency. In total, 13 woody species had higher probabilities of twig cutting at the 1% significance level (Figures 5,

TABLE 2

List of Woody Species along Census Routes and Probability of Twig Cutting

Family	Species	Origin	Probability of Twig Cutting	No. of Individuals
Cyatheaceae	*Cyathea mertensiana*	Endemic	.000	66
	C. spinulosa	Indigenous	.000	6
Pinaceae	*Pinus luchuensis*	Alien	.000	22
Ulmaceae	*Celtis boninensis*	Endemic	.130	33
	Trema orientalis	Indigenous	.513	22
Moraceae	*Ficus boninsimae*	Endemic	.226	45
	F. elastica	Alien	.000	6
	F. iidaiana	Endemic	.000	1
	F. microcarpa	Alien	.000	5
	F. nishimurae	Endemic	.000	1
	Morus australis	Alien	.037	94
Urticaceae	*Boehmeria boninensis*	Endemic	.000	4
Nyctaginaceae	*Pisonia umbellifera*	Indigenous	.027	44
Lauraceae	*Cinnamomum pseudopedunculatum*	Endemic	.000	67
	Machilus boninensis	Endemic	.000	128
	M. kobu	Endemic	.000	10
	Neolitsea boninensis	Endemic	.000	2
Theaceae	*Schima mertensiana*	Endemic	.000	391
Guttiferae	*Calophyllum inophyllum*	Indigenous	.000	90
Pittosporaceae	*Pittosporum boninense*	Endemic	.000	4
Rosaceae	*Rhaphiolepis umbellate*	Indigenous	.000	197
Leguminosae	*Acacia confusa*	Alien	.000	6
	Leucaena leucocephala	Alien	.000	66
Euphorbiaceae	*Bischofia javanica*	Alien	.013	317
	Drypetes integerrima	Endemic	.067	17
Rutaceae	*Boninia grisea*	Endemic	.014	56
	Zanthoxylum boninsimae	Endemic	.000	5
Meliaceae	*Melia azedarach*	Indigenous	.000	10
Aquifoliaceae	*Ilex beechyi*	Endemic	.124	36
	I. mertensii	Endemic	.000	3
Celastraceae	*Euonymus japonicus* var. *boninensis*	Endemic	.000	7
Elaeocarpaceae	*Elaeocarpus photiniaefolius*	Endemic	.066	98
Malvaceae	*Hibiscus glaber*	Endemic	.843	134
Elaeagnaceae	*Elaeagnus rotundata*	Endemic	.150	10
Stachyuraceae	*Stachyurus macrocarpus* var. *prunifolius*	Endemic	.000	1
Myrtaceae	*Psidium cattleianum* f. *lucidum*	Alien	.000	19
	Syzygium cleyeraefolium var. *microphyllum*	Endemic	.035	100
Melastomataceae	*Melastoma tetramerum* var. *pentapetalum*	Endemic	.000	1
Combretaceae	*Terminalia catappa*	Indigenous	.000	12
Araliaceae	*Fatsia oligocarpela*	Endemic	.646	29
Myrsinaceae	*Ardisia sieboldii*	Indigenous	.007	1,189
Sapotaceae	*Planchonella obovata*	Indigenous	.347	108
Oleaceae	*Ligustrum micranthum*	Endemic	.000	81
Loganiaceae	*Geniostoma glabrum*	Endemic	.000	3
Apocynaceae	*Ochrosia nakaiana*	Endemic	.030	80
	Trachelospermum asiaticum f. *intermedium*	Indigenous	.198	35
Rubiaceae	*Morinda boninensis* var. *hahajimensis*	Endemic	.063	8
	Psychotria homalosperma	Endemic	.086	17
	Tarenna subsessilis	Endemic	.429	8
Verbenaceae	*Callicarpa subpubescens*	Endemic	.100	11
Compositae	*Dendrocacalia crepididifolia*	Endemic	.400	13
Palmae	*Satakentia liukiuensis*	Endemic	.000	1
	Livistona chinensis var. *boninensis*	Endemic	.000	74
Pandanaceae	*Pandanus boninensis*	Endemic	.000	35

Note: Family order was based on Melchior (1964), and species order within family was alphabetical.

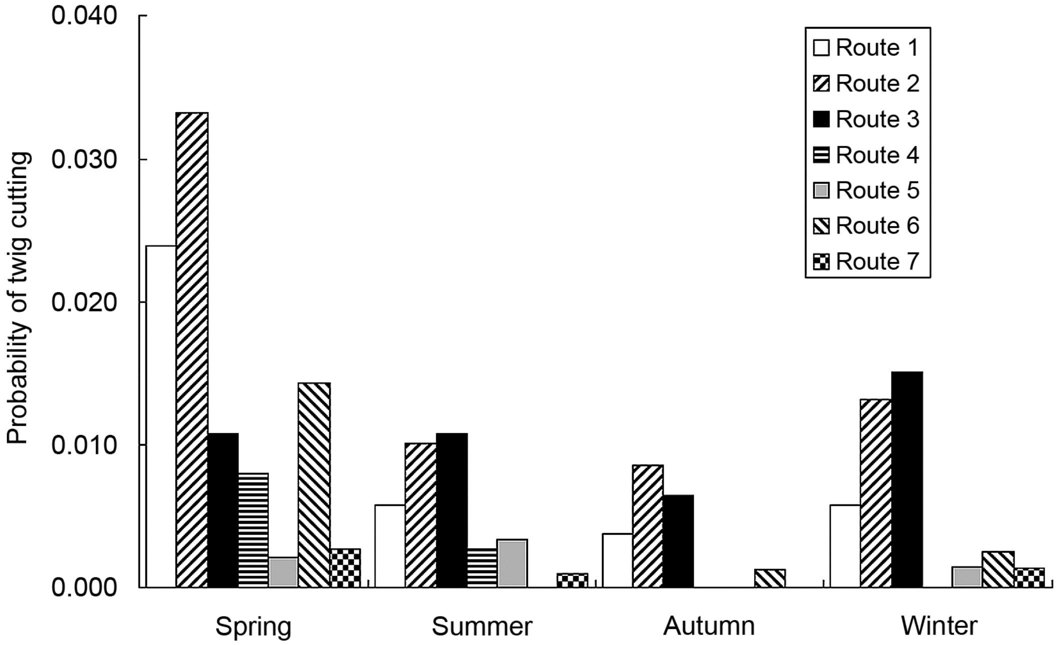

FIGURE 3. Seasonal change in the occurrence of twig cutting along each route.

TABLE 3

Results of *G*-Test on the Probability of Damaged Individuals

Factors	df	*G*	*P*
Forest	2	127.4	<.001
Season	3	33.6	<.001
Forest × Season	6	21.2	.002

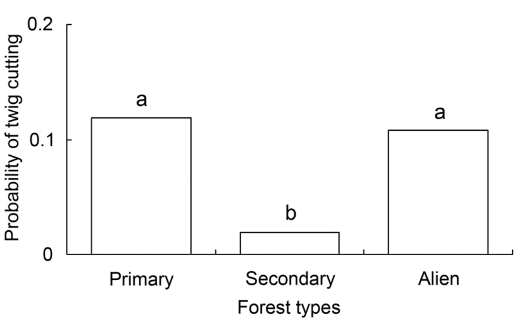

FIGURE 4. Comparison of the probabilities of twig cutting among forest types. Columns with different letters indicate significant differences ($P < .001$).

6). However, the overall probability of twig cutting per individual per year was low (.082). There was no significant difference between the number of individuals observed along routes and the probability of twig cutting ($r^2 = 0.002$, $P = .761$ [Figure 5]). Among routes, the probability of twig cutting by origin were .112 among endemic species, .035 among indigenous species, and .015 among alien species ($G = 100.2$, df $= 2$, $P < .001$).

Using a literature survey and personal observations, we recorded twig cutting in 37 species, including 14 endangered species (Appendix). The highly endangered *Claoxylon centinarium* suffered twig cutting during its flowering stage (Figure 2*d*).

DISCUSSION

Twig cutting was concentrated in particular woody species, mainly in spring. Its occurrence did not depend on the frequency of a species in any route. These results suggest that black rats have species preferences, and

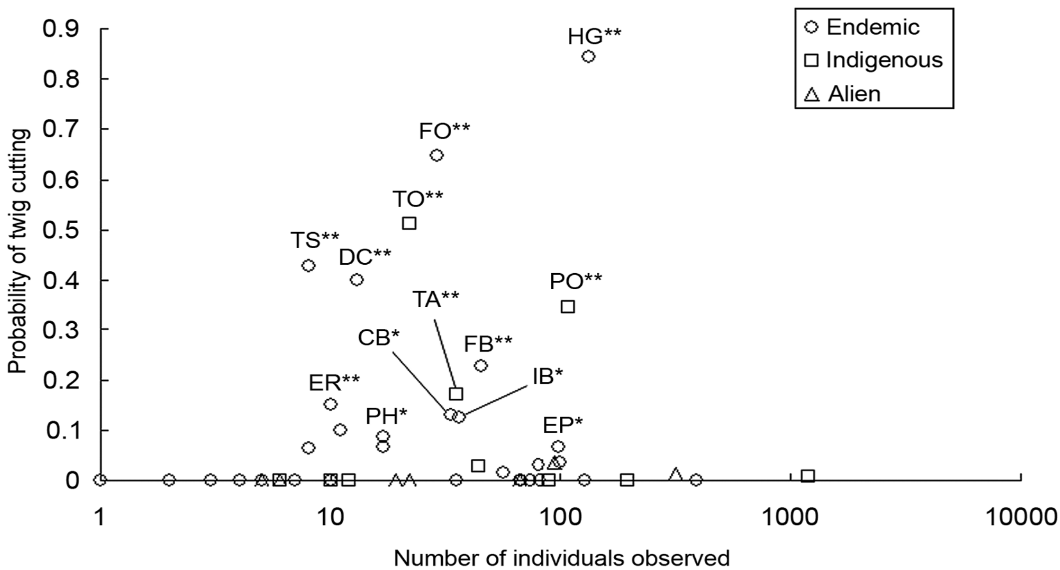

FIGURE 5. Relationship between total number of individuals along all routes and total number of individuals that suffered twig cutting. Each symbol represents a species. CB, *Celtis boninensis;* DC, *Dendrocacalia crepididifolia;* EP, *Elaeocarpus photiniaefolius;* ER, *Elaeagnus rotundata;* FB, *Ficus boninsimae;* FO, *Fatsia oligocarpela;* HG, *Hibiscus glaber;* IB, *Ilex beechyi;* PO, *Planchonella obovata;* PH, *Psychotria homalosperma;* TA, *Trachelospermum asiaticum* f. *intermedium;* TO, *Trema orientalis;* TS, *Tarenna subsessilis*. Asterisks indicate significantly preferred species (*, $P < .01$; **, $P < .001$).

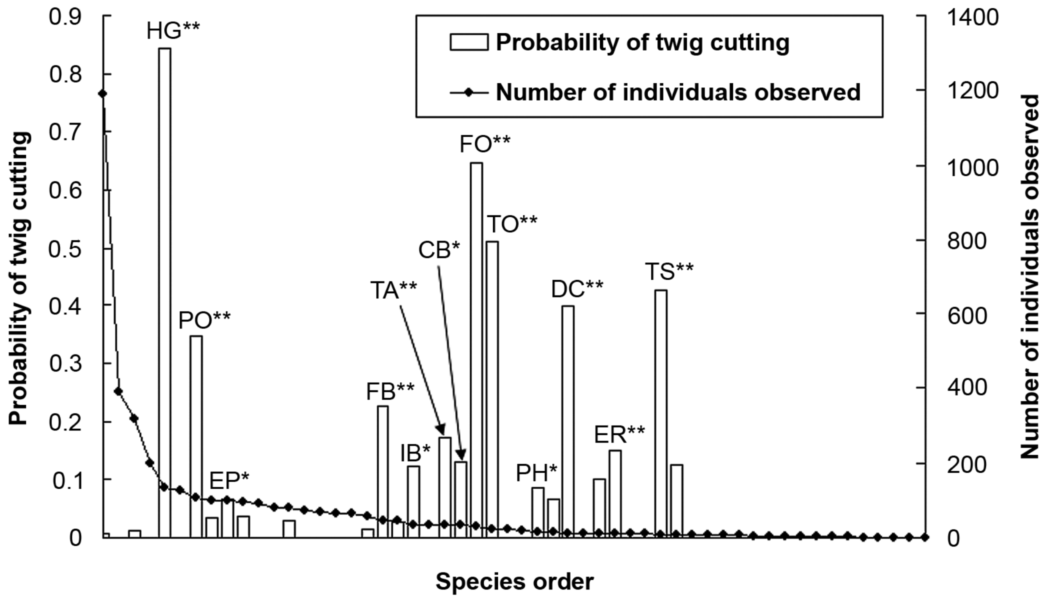

FIGURE 6. Species order curve ranking frequency along all routes (line and right ordinate) and the probability of twig cutting (bars and left ordinate). Species abbreviations and asterisks are as in Figure 5.

twig cutting may be influenced by certain seasonal plant phenomena such as events related to resource allocation for reproduction.

Previous studies reported similar frequent damages to woody species. Nobushima (2003) reported frequent damage to *H. glaber*, *Trachelospermum asiaticum* f. *intermedium*, and *Trema orientalis* on Haha-jima. Damage was most frequent in spring (April and May [Nobushima 2003]; April [Watanabe et al. 2003]). Twig cutting was most common just before or during the peak reproductive season for plants. *Hibiscus glaber*, which was damaged most often, blooms throughout the year. In general, fruits are primary food items of rats (Clark 1981, Grant-Hoffman and Barboza 2010), and fruit production is uncommon in spring in Ogasawara (Shimizu 1983). So the

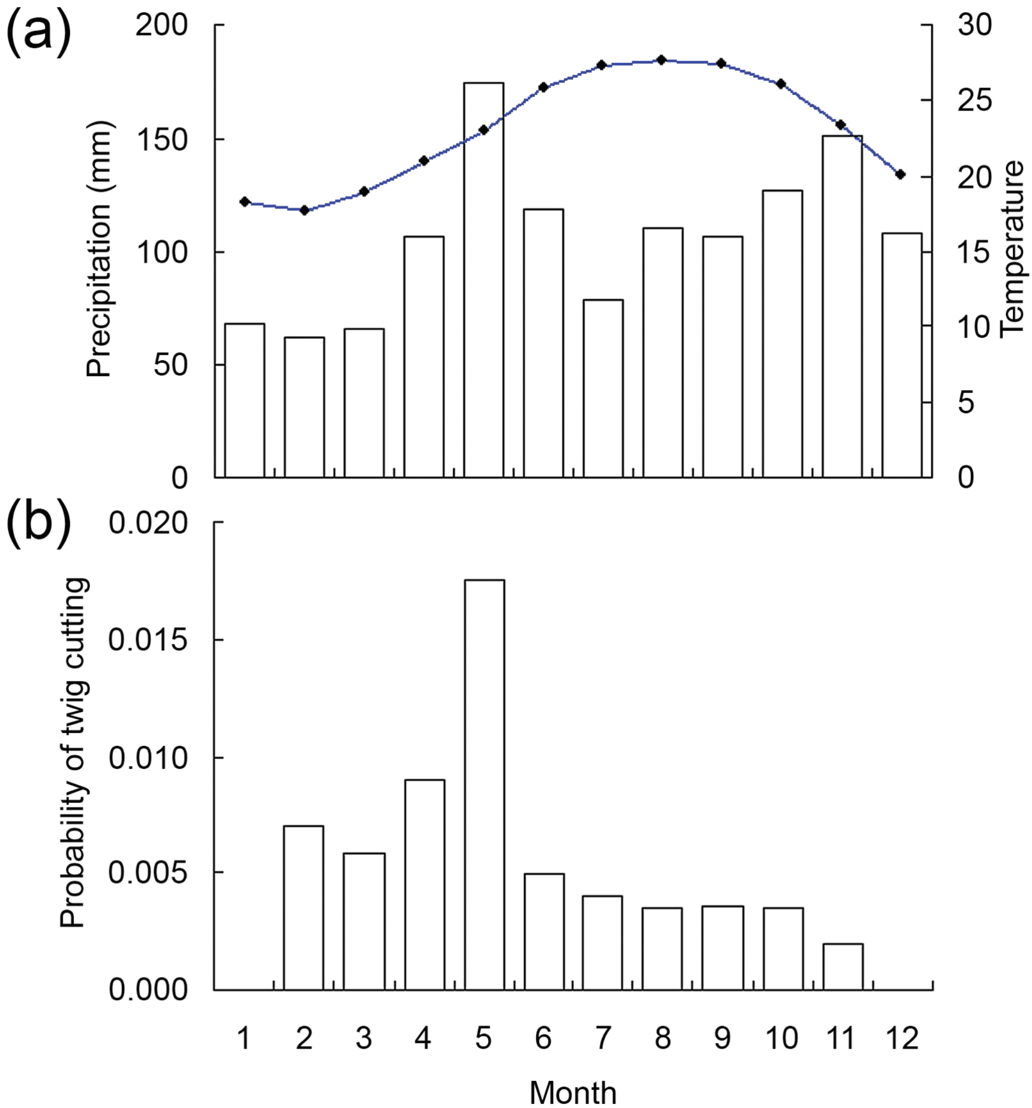

FIGURE 7. (*a*) Mean annual temperature (line) and precipitation (bars) in Ogasawara (1970–2000). Data were provided by the Japan Meteorological Agency (2009). (*b*) Annual variation in the probability of twig cutting along all routes.

lack of the rats' primary food items could explain the frequent twig cutting in spring. Yabe et al. (2010) also supposed that twigs would be supplemental foods in spring due to food shortage.

The aim of the twig-cutting behavior is not clear, but it could supply nutrients (Hansson 1991, Yabe 1998, 1999, Yabe et al. 2010) or water (Taylor 1970) in tree sap. The water-intake hypothesis was proposed on the grounds that the behavior occurred in the dry season, but this did not apply in Ogasawara (Figure 7). So water intake is an unlikely explanation of the reason for twig cutting. Escape from chemical defense could be another explanation, because higher twigs contain less chemical defense than lower ones (Danell et al. 1985, 1987). Rats also tend to strip bark from slender stems (Scowcroft and Sakai 1984, Yabe 1998). In addition, a focus on certain tree species may allow rats to escape toxic components: the higher rate of twig cutting in endemic species may arise from the lack of chemical defenses against herbivorous mammals (Bowen and Van Vuren 1997). The fact that the number of damaged trees was highest in primary forest can be associated with the preference for endemic species. However, the overall proportion of damaged individuals was so low that the impacts of twig cutting on plant populations would be mild. Although we did not monitor individual trees, damage was generally not sufficiently severe to be lethal. But the loss of current-year shoots changes the following growth (Roundy and Ruyle 1989, Bergström et al. 2000) and reduces the probability of reproduction (Roundy and Ruyle 1989). If these costs apply to plants in Ogasawara, then twig cutting could be serious for endangered plants, even if it is not lethal (Scowcroft and Sakai 1984). In Ogasawara, *Claoxylon centinarium* and *Piper postelsianum*, which are narrowly endemic to the Sekimon region of Haha-jima and are highly endangered (probably <100 individuals), were damaged by twig cutting. Because of the extremely small population size, the effects of individual decline on population maintenance would be larger than that among common species and could be the final stroke of extinction (Meyer and Butaud 2009). We also observed serious damage to herbaceous endangered plants such as *Lobelia boninensis* and *Cirsium boninense*. We observed twig cutting in 14 endangered species listed on the Japanese Red List (Ministry of the Environment 2007). Satellite islands around Chichi-jima and Haha-jima are uninhabited, and some of them retain rich native biota. However, rats have spread to all islands, and their impacts on native flora need to be clarified on those islands.

Although further study is required to clarify the effects of twig cutting on tree survival and fitness (infection by pathogens, reduction of reproductive rate, branch mortality), this quantitative field study helps us understand the general background of twig cutting.

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Appendix

List of Plant Species Damaged by Twig (or Shoot) Cutting on the Ogasawara Islands

Family	Species	Type	RL[a]	Month Damaged	References
Ulmaceae	*Celtis boninensis*	Endemic		May	Abe (2005)
				Feb., July	This study
	Trema orientalis	Indigenous			Nobushima (2003)
				Feb., Apr., May, Aug.	This study
Moraceae	*Ficus boninsimae*	Endemic			Nobushima (2003)
				Apr., Oct.	Watanabe et al. (2003)
				Apr., May	This study
	Morus australis	Alien			Nobushima (2003)
				Apr.	Watanabe et al. (2003)
				May	Abe (2005)
				Feb., Mar.	This study
Nyctaginaceae	*Pisonia umbellifera*	Indigenous			Nobushima (2003)
				May	Abe (2005)
Lauraceae	*Neolitsea sericea* var. *aurata*	Indigenous		Apr.	Watanabe et al. (2003)
Piperaceae	*Piper postelsianum*	Endemic	CR		Y. Hoshi, pers. obs.
Theaceae	*Schima mertensiana*	Endemic		Apr., autumn	Watanabe et al. (2003)
Rosaceae	*Photinia wrightiana*	Endemic	VU	Apr.	Watanabe et al. (2003)
Leguminosae	*Leucaena leucocephala*	Alien		Winter	Kitahara and Sato (2000)
				Apr.	Watanabe et al. (2003)
Euphorbiaceae	*Bischofia javanica*	Alien		Apr., May, Nov.	This study
	Claoxylon centinarium	Endemic	CR		Nobushima (2003)
				Feb.	This study
	Drypetes integerrima	Endemic	VU	May	Abe (2005)
Rutaceae	*Boninia grisea*	Endemic		May	Abe (2005)
	Zanthoxylum boninsimae	Endemic		Apr.	Watanabe et al. (2003)
Aquifoliaceae	*Ilex beechyi*	Endemic	EN		Nobushima (2003)
				May, July	This study
	Ilex mertensii	Endemic	VU	Apr.	Watanabe et al. (2003)
Elaeocarpaceae	*Elaeocarpus photiniaefolius*	Endemic			Nobushima (2003)
				Apr.	Watanabe et al. (2003)
				May	Abe (2005)
				Aug.	This study
Malvaceae	*Hibiscus glaber*	Endemic		Apr., autumn	Watanabe et al. (2003)
					Nobushima (2003)
				May	Abe (2005)
				Apr.	Yabe et al. (2010)
				Feb., Mar., Apr., May, June, Aug., Sept., Oct., Nov.	This study
	Hibiscus tiliaceus	Indigenous		Autumn	Watanabe et al. (2003)
Elaeagnaceae	*Elaeagnus rotundata*	Endemic		Mar.	This study
Stachyuraceae	*Stachyurus macrocarpus* var. *prunifolius*	Endemic	CR	Nov.	T.A., pers. obs.
Myrtaceae	*Syzygium cleyeraefolium* var. *microphyllum*	Endemic		Nov.	This study
Araliaceae	*Fatsia oligocarpela*	Endemic	VU	Apr.	Watanabe et al. (2003)
				Jan., Feb., Mar., Apr., Oct., Nov.	This study
Myrsinaceae	*Ardisia sieboldii*	Indigenous			Nobushima (2003)
				Apr., autumn	Watanabe et al. (2003)
				Feb., Mar., May, July, Aug., Nov.	This study

Appendix (continued)

Family	Species	Type	RL[a]	Month Damaged	References
Sapotaceae	*Planchonella obovata*	Indigenous			Nobushima (2003)
				Apr., Oct.	Watanabe et al. (2003)
				May	Abe (2005)
				May, June, July	This study
Loganiaceae	*Geniostoma glabrum*	Endemic	VU	Apr., autumn	Watanabe et al. (2003)
Apocynaceae	*Ochrosia nakaiana*	Endemic			Nobushima (2003)
				Apr., autumn	Watanabe et al. (2003)
				Mar., Apr.	Yabe et al. (2010)
				Apr., June	This study
	Trachelospermum asiaticum f. *intermedium*	Indigenous			Nobushima (2003)
				Apr.	Watanabe et al. (2003)
				Feb., Apr., May	This study
Rubiaceae	*Morinda boninensis* var. *hahajimensis*	Endemic	EN	July	Nobushima (2003)
					This study
	Psychotria boninensis	Endemic		Apr.	Watanabe et al. (2003)
	Psychotria homalosperma	Endemic	VU	Apr.	Watanabe et al. (2003)
				Aug., Nov.	This study
	Tarenna subsessilis	Endemic	VU		Nobushima (2003)
				May	Abe (2005)
Verbenaceae	*Callicarpa subpubescens*	Endemic		May, June	This study
Campanulaceae	*Lobelia boninensis*	Endemic		July	N. Kachi, pers. obs.
Compositae	*Crisium boninense*	Endemic	EN	June	This study
	Dendrocacalia crepididifolia	Endemic	VU	Feb., Mar., Apr.	This study

Note: Dataset includes preliminary studies of Kitahara and Sato (2000), Watanabe et al. (2003), Nobushima (2003), and Abe (2005). In Watanabe et al. (2003), records labeled as October or November were categorized as autumn. Family order is based on Melchior (1964), and species order within family is alphabetical.

[a] Category in revised Japanese Red List (Ministry of the Environment 2007): CR, critically endangered; EN, endangered; VU, vulnerable.