SPECIAL FEATURE Ecology of seed dispersal

Seed dispersal of Japanese stone pine by the Eurasian Nutcracker

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Abstract Seed dispersal of Japanese stone pine *Pinus pumila* by the Eurasian Nutcracker *Nucifraga caryocatactes* was studied at Mt. Apoi in Hokkaido, northern Japan. The seed foraging and caching behavior of diurnal birds and mammals was observed, and the relative importance of each species for pine seed dispersal was examined. All mature cones disappeared from the pine shrubs by mid-October each year regardless of the cone crop size. Eurasian Nutcrackers, Varied Tit *Parus varius*, Eurasian Nuthatch *Sitta europaea*, Red Squirrel *Sciurus vulgaris*, and Siberian Chipmunk *Tamias sibiricus* were all potential seed dispersal agents, however, observations revealed that nutcrackers carried 96% of all seeds transported from the pine trees. The nutcracker carried 142 seeds on average (max. 209) in one trip. Nutcrackers mainly carried pine seeds into their mixed coniferous forest, breeding habitat, where stone pines cannot normally become established and cached them in the soil there. Nutcracker caches averaged 12 seeds with a maximum of 51 seeds. Pine seedlings were found growing in clusters (in groups of two or more trees). The number of seedlings per cluster closely resembled the number of seeds in nutcracker caches. Results suggest that most stone pine seedlings originated from nutcracker caches. Eurasian Nutcrackers thus play an important role in the regeneration of Japanese stone pine despite their small number of caches.

Key words Caching behavior, *Nucifraga caryocatactes*, *Parus varius*, *Pinus pumila*, Scatter-hoard, *Sitta europaea*

Several members of the family Corvidae are known to store seeds and to be important seed dispersal agents (Turcek & Kelso 1968; Vander Wall & Balda 1981; Tomback & Linhart 1990; Vander Wall 1990). The interaction between Clark's Nutcracker *Nucifraga colombiana* and several pine species has been well studied in North America for *Pinus albicaulis* (Hutchins & Lanner 1982; Lanner 1982; Tomback 1982), *P. flexilis* (Lanner & Vander Wall 1980; Tomback & Kramer 1980), and *P. edulis* (Vander Wall & Balda 1977). Those studies documented the central role played by Clark's Nutcracker in the regeneration of the pines. Similar interactions were recognized between the Eurasian Nutcracker *N. caryocatactes* and *P. cembra* in Europe (Mattes 1982), *P. sibirica* in Siberia (Kondratov 1953; Reimers 1959), *P. koraiensis* in East Asia (Hutchins et al. 1996), and *P. pumila* (Saito 1983a; Hayashida 1994; Kajimoto et

al. 1998) and *P. parviflora* (Hayashida 1989a, 1994) in Japan.

Japanese stone pine *P. pumila* occurs from Siberia and Kamchatka south to Japan and Korea (Critchfield & Little 1966). A vegetation zone dominated by stone pine, known as the *P. pumila* zone, is present above the forest limit on most high mountains in northern Japan (Okitsu & Ito 1989; Yanagimachi & Ohmori 1991). The Japanese stone pine is a dwarf pine, and its thickets can regenerate vegetatively from adventitious roots (Okitsu & Ito 1984; Kajimoto 1992).

P. pumila has large wingless seeds, as do *P. albicaulis* and *P. cembra*, which belong to the Cembrae group within the genus *Pinus* (Mirov 1967). Several authors have reported that *P. pumila* seeds are cached by Eurasian Nutcrackers and germinate in their caches, as indicated by fragmentary observations of nutcracker behavior, cone and seed morphology, and seedling clumps (Saito 1983a; Hayashida 1994; Kajimoto et al. 1998). Previous studies of *P. pumila* dis-

persal have, however, lacked both quantified data of seed dispersal by animals and detailed behavioral observations of the animals dispersing the seeds.

The objective of the research described here was to determine the relative importance of the Eurasian Nutcracker and other potential dispersers for Japanese Stone Pine seed dispersal. The seed harvesting, transportation, and caching behavior of nutcrackers and other dispersal agents was studied in order to clarify the effects of animal behavior on pine seed regeneration.

STUDY AREA AND METHODS

1) Study area

The study was conducted on Mt. Apoi (811 m above sea level), which is located in south-central Hokkaido, Japan (42°06'N, 143°02'E). Mt. Apoi is composed of ultramafic rocks (dunite, lherzonite, etc.) of the Horoman peridotite complex (Niida 1984), and is covered with coniferous forests. The *P. pumila* zone extends from elevations of 500 to 800 m. Japanese white pine *Pinus parviflora* var. *pentaphylla* forest occupies the rocky slopes and ridges below 500 m, while the greater part of the mountain is covered by mixed coniferous stands dominated by *Picea glehnii*, *P. parviflora* var. *pentaphylla*, and *Abies sachalinensis* (Hayashida 1989a).

The soil (based on ultramafic rock peridotite) and meteorological conditions (frequent fog in summer and strong winds and little snow in winter), support a unique alpine flora despite the exceptionally low altitude (Tatewaki 1952). The height of the *P. pumila* scrub is dependent on the degree of wind exposure and snow depth (Okitsu & Ito 1984). Pine scrub (less than 100 cm tall) and alpine meadows predominate on wind-exposed ridges and slopes in the study area.

The native seed predators among birds are the Eurasian Nutcracker, Eurasian Jay *Garrulus glandarius*, Eurasian Nuthatch *Sitta europaea*, and several tits *Parus* spp. Nutcrackers can be observed in all seasons on Mt. Apoi, except in years when the Japanese stone pine and the Japanese white pine produce few cones. Although nesting by nutcrackers has not been confirmed in the area, there is no doubt that they do breed as they are often found in the mixed coniferous forest during the breeding season.

2) Cone fate and seed dispersal by vertebrates

Eight patches of *P. pumila* scrub (each patch had a 4 to 8 m² crown) were chosen for cone fate observa-

tion at elevations between 520 and 550 m. It takes two growing seasons for stone pine cones to mature. Immature second-year cones were mapped in each patch in June, and these cones were counted at intervals of two to four weeks until the cones were depleted. Data were collected from 1985 to 1990.

I gathered information on diurnal animal pine-seed harvesting rates, seed transportation, and seed caching behavior using 7× binoculars and a 25× telescope from an observation site at an elevation of 550 m. The observations were made within 900 m², including the eight patches for the cone fate studies. A total of 74.5 hours of observation were logged at the site from 21 August to 14 September 1985 (29.5 h), and from 12 August to 11 September 1987 (45 h). I usually observed from dawn till noon once or twice a week. Cone harvesting, cone transporting, feeding, seed harvesting, seed transporting, and seed caching were the recognized behaviors of various vertebrates. I recorded the frequency of seed transportation and the number of seeds carried each trip. These data were used to calculate the number of seeds transported per hour and to determine the relative number of seeds transported by each species.

Observations of seed storage behavior by birds and mammals at any time during the study periods were recorded. As nutcrackers flew to their caching sites after seed harvesting, it was difficult to follow them to observe caching behavior directly. Therefore I recorded the flight directions of the birds and the places where I lost sight of them, so as to be able to estimate where the caching sites were.

3) Seed caching by Eurasian Nutcrackers

Stored seeds are retrieved by nutcrackers and by other animals. Nutcrackers, however, probe into caches by thrusting their bills into the soil or forest litter, thus visible prod holes in the ground remain as signs of nutcrackers having dug up seed caches. Such excavations are easily distinguished from those of rodents. Rodent holes are three or more times larger than those made by nutcrackers, moreover, nutcrackers usually open the seeds at the recovery site, leaving behind a pile of seed coats (Tomback 1980), whereas rodents carry away seeds to consume them elsewhere. I followed such nutcracker holes on the ground and counted the number of seeds around or in caches along a 3.3 km long hiking trail (2.2 km in the mixed coniferous forest and 1.1 km in the *P. pumila* zone). This survey was conducted eight times in June and July 1986.

4) Clusters of Japanese stone pine trees

The seedlings of bird-dispersed pines have often been found in clusters consisting of several seedlings of the same age (Tomback 1982; Kajimoto et al. 1998). I counted *P. pumila* trees in two 5 m×5 m quadrats (Q1, Q2) and in a 10 m×10 m quadrat (Q3) in the *P. pumila* zone, in order to acquire information on the clumping frequency and age distribution of this species. Ages were determined by counting nodes and bud scars on trunks. I also recorded the numbers of seedlings and saplings on barren slopes along the hiking trail in the mixed coniferous forest (a 1.2 km line census, 5 m in width).

RESULTS

1) Cone fate

All second year cones of Japanese stone pine disappeared from the pine shrubs by mid-October every year, regardless of the size of the cone crop, and even though the crop size varied from year to year (Fig. 1). The cones began to disappear in early August in 1985, 1987, 1988, and 1990, and decreased rapidly from late August to mid-September. They had begun to disappear by mid-July in 1986 and 1989, and were depleted by late July. The pedicels of mature cones were loose enough to be detached easily from the branch, indicating that they might fall off under their own weight, however, I observed no intact cones falling to the ground beneath pine crowns. These findings indicate that the pine cones were harvested by animals.

2) Seed harvest and transportation by vertebrates

I observed twelve bird species and three mammal species in the study area during the study periods. These included the Eurasian Nutcracker, Eurasian Jay, Jungle Crow *Corvus macrorhynchos*, Oriental Greenfinch *Carduelis sinica*, Siberian Meadow Bunting *Emberiza cioides*, Eurasian Nuthatch *Sitta europaea*, Willow Tit *Parus montanus*, Coal Tit *P. ater*, Great Tit *P. major*, Varied Tit *P. varius*, Indian Tree Pipit *Anthus hodgsoni*, Great Spotted Woodpecker *Dendrocopos major*, Red Squirrel *Sciurus vulgaris*, Siberian Chipmunk *Tamias sibiricus*, and Snowshoe Hare *Lepus timidus*. Six species of these species (Eurasian Nutcracker, Oriental Greenfinch, Eurasian Nuthatch, Varied Tit, Red Squirrel, and Siberian Chipmunk) foraged on the pine seeds. The Oriental Greenfinch only ate pine seeds *in situ*, whereas the other five species harvested and trans-

Fig. 1. Annual cone crop size and number of cones remaining on *Pinus pumila* trees 1985–1990. Data were collected from eight patches of *P. pumila* shrubs.

ported cones or seeds.

The nutcrackers began to forage on the stone pine cones as early as mid-July in 1986 and 1989, and in early August in 1985, 1987, 1988, and 1990. These foraging times coincided with the timing of cone disappearance (Fig. 1). During these periods, the cone scales were tight and the seed coats were thin and fragile. Consequently, nutcrackers and other animals were unable to pick up whole seeds and acquired only seed kernels directly from the cones. Some cones turned brown in mid-August and their seeds matured. Nutcrackers harvested the brown cones selectively and frequently transported the seeds. Nutcrackers were usually seen in pairs, and sometimes in small flocks of up to six birds.

Observations of nutcrackers foraging for cones followed a general pattern during which a bird first selected a cone then detached it by gripping it in the bill. Brown (mature) cones were easily detached from their subtending branches, and the detached cone was then carried in the bill to a perch on a rock, on the bough of a tall tree, or on the ground, where the bird extracted seeds from the cone. Following seed extraction, some seeds were squeezed in the bill until they cracked, then they were eaten. Most seeds derived from cones, however, were stored in the sublingual pouch rather than eaten. Each seed was apparently tested for edibility by rattling between the mandibles. Forty-three (95.6%) of the 45 pine seeds discarded by Nutcrackers were aborted (empty). Forty-two (32.3%) of the 130 seeds left behind on perches by nutcrackers after harvesting cones were aborted seeds. These facts demonstrate that Nutcrackers selectively transported only edible seeds.

Nutcrackers tip their heads upwards in an easily recognised motion, when pouching seeds for trans-

Table 1. Comparative transport of *Pinus pumila* seeds by five vertebrates during August and September in 1985 and 1987.

	Number of transporting per hour*	Number of seeds per transport**	Seeds transporting per hour	Relative number of seeds transported (seeds/10,000)
Nutcracker	2.07	142	293.94	9556
Varied Tit	1.54	1	1.54	50
Nuthatch	0.12	1	0.12	4
Squirrel	0.13	43	5.59	182
Chipmunk	0.16	40	6.40	208

* Total obserbation periods were 74.5 hours.

** Refer into text.

portation. Nutcrackers extracted 9–50 seeds (mean $\pm$ SD = 29.2 ± 10.4 , N = 39) from each cone, and required 15–78 seconds (mean $\pm$ SD = 35.7 ± 22.5 , N = 7) to do so. In each session, nutcrackers harvested 2–10 cones (mean $\pm$ SD = 4.95 ± 1.88 , N = 20). Therefore, nutcrackers carried 67–209 seeds (mean $\pm$ SD = 142.2 ± 48.2 , N = 6) in their sublingual pouches when flying to caching sites.

Varied Tits and Eurasian Nuthatches visited *P. pumila* shrubs in small mixed flocks or in pairs. They were unable to open the immature cones themselves and depended primarily on nutcrackers to expose the seeds for them. They were, however, able to extract seeds from more mature cones when seeds were slightly loose. When they successfully harvested a seed, Varied Tits and nuthatches flew 5–30 m to a tree in the coniferous forest. There they either ate or cached the seed and then returned to harvest another. Both Varied Tits and Eurasian Nuthatches transported seeds singly in the bill (Varied Tit N = 115; Eurasian Nuthatch N = 9). Both species usually stored seeds in tree branches or under bark, but occasionally cached seeds in the soil on the ground.

Red Squirrels were common inhabitants of the mixed coniferous forests on Mt. Apoi, and sometimes visited pine shrubs near the forest edges. Squirrels peeled off the cone scales to extract seeds, ate some seeds and then carried other intact cones in their mouths to the coniferous forest (N = 10). As cones contained an average of 43 seeds (Hayashida 1994), Red Squirrels carried an average of 43 seeds each trip.

Siberian Chipmunks, as well as Red Squirrels, were found near the forest edges. Chipmunks harvested about 40 seeds at a time in their cheek pouches, and then returned to the forest (N = 12). No data on Red Squirrel or chipmunk caching were ob-

tained during this study.

Of the five vertebrates observed transporting seeds Eurasian Nutcrackers and Varied Tits transported seeds most frequently (see Table 1). The relative number of seeds transported by each vertebrate, was calculated by multiplying the mean number of seeds per trip by the number of trips per hour. These calculations indicated that 96% of all the seeds transported, were carried by Eurasian Nutcrackers (Table 1).

3) Seed caching behavior by Eurasian Nutcrackers

Eurasian Nutcrackers transported seeds in all directions in both 1985 and 1987 (see Fig. 2). Most of the observed transport flights ranged from 100 to 1,000 m, with a few birds transporting seeds farther than 1,000 m. Transportation could be divided into two periods. In the first (mainly in August), they flew down into the mixed coniferous forest on all trips. During the second period (in September), the nutcrackers often carried seeds into the *P. pumila* zone (53% in 1985, 60% in 1987). Thus, 83% (79% in 1985, 86% in 1987) of seed transports by nutcrackers were into the mixed coniferous forests and 17% (21% in 1985, 14% in 1987) were into the *P. pumila* zone.

Nutcrackers stored *P. pumila* seeds in many different cache sites. I directly observed and confirmed nutcrackers making two caches consisting of two and twelve pine seeds in soil at depths of 1 to 2 cm. In additional caches (N = 26) that I found near nutcracker excavations, the number of seeds per cache ranged from 1 to 51 (mean $\pm$ SD = 12.0 ± 10.1). These caches were 1 to 3 cm deep in soil. Seven (27%) of the 26 caches were found in the *P. pumila* zone, and 19 (73%) in the mixed coniferous forest. The density of caches in *P. pumila* zone and the coniferous forest were 6.36 and 8.64 per km, respectively. These densi-

Fig. 2. The direction and frequency of seed transport by Nutcrackers in 1985 and 1987. Open arrows and solid arrows show the transporting directions in the first and second half of the observation periods, respectively. Figures show the frequency of transporting seeds in each direction. Small arrows indicate one trip in each direction. The hatched area is the *Pinus pumila* zone.

ties did not differ significantly ($\chi^2=0.5$, ns). One cache was found 2.8 km from the nearest seed source of *P. pumila*. Nutcracker not only predated seeds prior to germination, but also took emergent seeds (with a germinated but not expanded cotyledon). Nutcrackers predated 34% of the germinated seeds in 26 caches.

Table 2. Frequency of stem clustering in *Pinus pumila* in three quadrats and the line census.

	No. of cluster (%)		No. of individuals per cluster	
	single	≥ 2 trees	max.	mean $\pm$ SD
Q1	29 (55)	24 (45)	16	2.5 ± 2.7
Q2	15 (34)	29 (66)	17	4.3 ± 3.8
Q3	19 (49)	20 (51)	5	1.8 ± 1.1
Line	9 (16)	47 (84)	26	5.6 ± 5.3

4) Clusters of Japanese stone pine trees

In the three quadrats studied in the *P. pumila* zone, the overall number of pine trees per cluster ranged from 1 to 17, and 53% of the clusters consisted of groups of two or more trees (Table 2). In the mixed coniferous forest, 84% of the 56 clusters of pine seedlings along the hiking trail were in groups of two or more trees. In particular, all seedlings under five years old were in groups of two or more trees. The mean number of individuals per cluster was 5.6, and the maximum number was 26 seedlings.

DISCUSSION

1) Seed dispersal agents of the Japanese stone pine

All Japanese stone pine cones in the Mt. Apoi study area were carried away by animals by late autumn, even in years with bumper crops. Five species of vertebrates (Eurasian Nutcracker, Varied Tit, Eurasian Nuthatch, Red Squirrel, and Siberian Chipmunk) were found to be potential seed dispersal agents of the Japanese stone pine, and their contributions to seed dispersal were examined.

My observations indicated that the Eurasian Nutcracker is the most frequent harvester of pine cones. Nutcrackers in this study carried up to 209 pine seeds in their sublingual pouches, close to the maximum capacity of 218 seeds recorded in previous studies (Turcek & Kelso 1968). Mattes (1982) observed that Eurasian Nutcrackers carried up to 134 Cembra pine seeds, which were estimated to be 42.4 ml in capacity, based on comparison with the similarly sized Pinon pine seed (Vander Wall & Balda 1981). The volume of 209 Japanese stone pine seeds was measured using a graduated cylinder, and found to be 42.1 ml (Hayashida, unpublished data), consistent with the capacity reported by Mattes (1982).

The mean number of *P. pumila* seeds transported

by Eurasian Nutcrackers in their sublingual pouches was 142 in the Mt. Apoi study. Bergmann et al. (2001) reported that nutcrackers in the Russian Far East carried far fewer *P. pumila* seeds (80 on average) per trip, which represented the harvestable contents of 2.8 cones. In the Mt. Apoi study, however, the mean number of seeds counted is consistent with calculations of the number of seeds carried per trip (144.5), obtained by multiplying the average number of seeds extracted from each cone (29.2) by the average number of cones harvested per trip (4.95).

Varied Tits and Eurasian Nuthatches often harvested pine seeds and transported them singly to cache them under tree bark or in the ground. The Varied Tit has long been known to cache seeds (Higuchi 1977), storing as many as 63% of cached seeds of *Taxus cuspidata* on the ground (Sakakibara 1989), and thus playing an important role in forest regeneration. Nuthatches have also been observed to cache seeds (Hendricks 1995; Hutchins et al. 1996; Hardling et al. 1997). Based on their occasional ground caching behavior, both species may potentially help Japanese stone pine seedlings become established, however, as they only carry seeds one at a time their roles are probably not as important as that of the Eurasian Nutcracker.

Red Squirrels scatter-hoard Korean pine seeds in soil and contribute to the regeneration of Korean pine forest (Miyaki 1987; Hayashida 1989b). In contrast, they store whole cones of Japanese white pine (*P. parviflora* var. *pentaphylla*, the seeds of which are smaller than those of the Korean pine) in the ground (Hayashida 1988; 1989a). Although Red Squirrels were not observed caching cones during this study, they are suspected of storing whole Japanese stone pine cones because stone pine cones and seeds are similar in size to those of the white pine. An experiment by Saito (1983b) demonstrated that Japanese stone pine seeds in a cone buried in the soil are able to germinate, but are unable to become established as seedlings. These findings indicate that Red Squirrels do not play a role in the effective dispersal of the Japanese stone pine.

Siberian Chipmunks usually scatter and larder hoard acorns (Kawamichi 1980). They also harvest stone pine seeds and carry them in their cheek pouches. Hayashida (1989a) observed a chipmunk caching 33 Japanese white pine seeds in the ground at a depth of 3 cm, confirming that chipmunks can be seed dispersal agents. The frequency and quantity of seeds that they harvest are insignificant, however, in

comparison with the Eurasian Nutcracker.

In addition to the diurnal vertebrates, two nocturnal rodents are also potential seed dispersal agents in the study area. These are both wood mice *Apodemus speciosus* and *A. argenteus*, both of which scatter-hoard seeds (Imaizumi 1979; Miyaki & Kikuzawa 1988). Although these two mice are abundant in various forest types, they are uncommon in Japanese stone pine scrub (Ota 1968), thus nocturnal rodents are unlikely to be significant seed dispersers of *P. pumila*.

In northeast Siberia, the cones of *P. pumila* are a primary food source of Brown Bears *Ursus arctos* during the fall (Krechmar 1995). Although no Brown Bears were observed foraging in the Mt. Apoi study area, recent activity was evident. The large amount of fecal material left behind contained several thousand ingested cones but no intact seeds (Hayashida, unpublished data), suggesting that the brown bear is a seed predator and not a potential seed dispersal agent.

It is clear from various aspects of this study that the Eurasian Nutcracker transports most Japanese stone pine seeds, and that the Japanese stone pine depends mostly on nutcrackers for seed dispersal.

2) The behavior of the Eurasian Nutcracker as a seed dispersal agent of *P. pumila*

Eurasian Nutcrackers usually store more than one Japanese stone pine seed in a cache, as they do with the seeds of other stone pine species (Vander Wall & Balda 1977; Hutchins & Lanner 1982; Mattes 1982; Tomback 1982; Hutchins et al. 1996; Bergmann et al. 2001). Though they sometimes cache seeds under tree bark (Hayashida 1989a), most seeds are cached at depths of 1–3 cm in soil, in a microhabitat that is favorable for germination (Saito 1983b). The number of Japanese stone pine seeds in a single cache varied more widely than for other stone pines (Hutchins & Lanner, 1982; Tomback 1982; Hutchins et al. 1996), probably because the seed of *P. pumila* is smaller than that of other stone pine species.

Some experiments suggest that nutcrackers find most of their caches by memory (Balda 1980; Vander Wall 1982; Balda & Kamil 1989; Kamil et al. 1993; Kamil & Jones 1997), however, since germinated but not expanded cotyledon seeds were eaten along with ungerminated seeds from caches, nutcrackers may also find caches by using emergent seedlings as landmarks. If so, then many emergent pine seedlings may be damaged when birds dig up their caches. Though nutcrackers are principle predators of pine seeds, the

results of this study (cf. Table 2) and Kajimoto (2002) suggest that nutcrackers also play an important role in seed regeneration of *P. pumila*.

My observations indicated that nutcrackers transported most Japanese stone pine seeds to a mixed coniferous forest beyond the stone pine habitat. It is difficult for *P. pumila* seedlings to grow and become established on the dark floors of dense coniferous forests (Kajimoto 1995) even if cached seeds survive and germinate. Nutcrackers usually store seeds in the habitat of each pine species, as with most bird-dispersed pine species (Lanner & Vander Wall 1980; Hutchins & Lanner 1982; Mattes 1982; Tomback 1982), with the exceptions of *P. edulis* (Vander Wall & Balda 1977) and *P. monophylla* (Vander Wall 1988). Stands of these two pine species and those of Japanese stone pine do not provide suitable breeding habitat for nutcrackers, thus Eurasian Nutcrackers breed in coniferous forests (Yamashina 1934; Mattes 1982), and recover cached seeds to carry to their nestlings (Swanberg 1956). Transporting seeds into mixed coniferous forest (breeding habitat) allows for more efficient exploitation of the cached food during the breeding season.

Nutcrackers cached seeds in the coniferous forest in August and often cached seeds in the *P. pumila* zone in September. The reason for this shift in caching area is not clear, but it may be due to lower levels of cache robbing by rodents (e.g. squirrels, chipmunks, mice and voles) in the *P. pumila* zone than is likely to occur in the coniferous forests. Eurasian Nutcrackers disperse small amounts of Japanese stone pine seeds in the *P. pumila* zone, but their rate of seed retrieval is low and consequently seedlings become established especially during mast crop years.

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