FURTHER NOTES ON THE NORTHERN DISTRIBUTION OF AEDES (STEGOMYIA) RIVERSI (DIPTERA: CULICIDAE)

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ABSTRACT. Additional records of *Aedes riversi* Bohart and Ingram from temperate Japan are presented. All new records are from islands north or west of Kyushu except one from the southeast coast of the Kyushu main island. *Aedes riversi* is widely distributed on the satellite islands of north Kyushu, though its known habitats are confined to lowland-type natural forests of evergreen broad-leaf trees (lowland-type lucidophyllous forests). The origin and present status of *Ae. riversi* populations on the satellite islands of north Kyushu are discussed in the context of habitat characteristics, human activities and interaction with *Ae. albopictus* (Skuse) and *Ae. flavopictus* Yamada.

INTRODUCTION

Aedes (Stegomyia) riversi Bohart and Ingram is a scutellaris subgroup species (Huang 1972). Initially it was regarded as endemic to the Ryukyu Islands, but later recorded from Yakushima, an island just south of Kyushu (Kamimura 1968), the southern extremity of Kyushu (Tanaka et al. 1975; Eshita and Kurihara 1979), and a few satellite islands of north Kyushu (Mogi 1976, Mori 1989). According to the definition of the subtropical zone by Kira (1949), all the Ryukyu Islands (including the Tokara Islands) belong to the subtropical zone and Yakushima lies on the southern periphery of the temperate zone.

Aedes riversi is a forest species utilizing tree holes as a primary larval habitat. The known distribution is continuous from the Ryukyus through the southern extremity of Kyushu with the exception of few highly deforested or unsurveyed islands (Toma and Miyagi 1986). A large gap in its distribution occurs between the southern extremity of Kyushu and the satellite islands of north Kyushu. Mogi (1976) inferred that populations on the islands off north Kyushu are relics, having been isolated from the southern population through extinction in the lowlands of central and north Kyushu. This report offers additional records of Ae. riversi from temperate Japan and discusses the origin and present status of the temperate populations in the context of habitat characteristics, human activities and interaction with Ae. (Stg.) albopictus (Skuse) and Ae. (Stg.) flavopictus Yamada, both of the albopictus subgroup.

RECORDS

- 1. 3 9, Hatsuse, Iki Island, 13 VII 1976, human bait, M. Mogi.
- 2. 2 ♀ and 1 ♂, Koh-zaki, Shimo-agata, Tsushima Islands, 15 VII 1976, human bait, M. Mogi.
- 1 9, Kisaka , Kami-agata, Tsushima Islands, 17 VII 1976, human bait, M. Mogi.

- 4. 14 ♀ and 4 ♂, Chikuzen-Okinoshima Island, 23 VII 1977, human bait, M. Mogi.
- 5. 1 2, Shiratori, Tamanoura, Fukue-Jima Island, Goto Islands, 8 VIII 1977, human bait, M. Mogi.
- 6. 65 ♀ and 67 ♂, Toki, Fukue-Jima Island, Goto Islands, 10 VII 1978, human bait, M. Mogi.
- 7. 12 ♀ and 6 ♂, Tajima, Kabeshima Island, 19 V 1980, human bait, M. Mogi.
- 4 9, Meotogaura, Nichinan, Miyazaki Prefecture, Kyushu, 11 X 1982, human bait, M. Mogi.
- 9. 3 ♀ and 25 ♂, Miyanoura, Hirado Island, 4 VI 1985, human bait, M. Mogi.

DISCUSSION

New records of *Ae. riversi* are all from the satellite islands of north Kyushu except one (No. 8) from the southeast coast of Kyushu. No specimens were obtained from the southwest part of Nagasaki Prefecture, northeast Kyushu despite intensive surveys by the author during 1975-1979 (Fig. 1). A relatively large gap still exists between the southernmost part of Kyushu and the satellite islands of north Kyushu.

All the known habitats of *Ae. riversi* on the satellite islands of north Kyushu are natural forests of evergreen broad-leaf trees including *Machilus thunbergii* Siebold and Zuccarini (Lauraceae) and *Castanopsis cuspidata* Schottky (Fagaceae) (lowland-type lucidophyllous forest) (Table 1). This type of forest was formerly the major vegetation of the lowlands of the western part of the main Japanese islands. Such forest now occurs in small patches due to clearing for industrial, business, residential, or agricultural use (Miyawaki 1977). Of 12 habitats, 3 are uninhabited islets and 2 are points of small peninsulas a few kilometers apart from the nearest village. The remaining 7 sites are compounds of Shinto shrines within 1 km of the nearest village. Shinto shrines have often kept forests intact because of deification of big trees. Known habitats in



Fig. 1. Geographical distribution of *Aedes riversi*. Numbers 1-9 correspond to collection site numbers in this paper. Numbers 10-17 indicate collection sites as follows: 10 from Mori (1989), 11-15 from Mogi (1976), 16 from Tanaka et al. (1975), and 17 from Eshita and Kurihara (1979). Right side of map: The islands darkened in have *Ae. riversi* (based on Toma and Miyagi 1986, Sasa et al. 1977). Left side of map: The area west of the broken line is in Nagasaki Prefecture. Triangles indicate locations where *Ae. riversi* was not found. Numerous smaller islands are omitted from both maps.

Island	Locality ^a	Geography	Altitude (m)	Vegetation	Shrine	Distance from the nearest village (km)
Tsushima	Nishidomari	Seaside	20-40	N	+	0.1
	Sao-zaki	Point	20-80	N	-	1.5
	Kisaka	Seaside	100-140	Ν	+	0.5
	Koh-zaki	Point	20-230	Ν	-	2.5
Chikuzen-Okinoshima		Islet	50-200	Ν	+	45 ^b
Iki	Hatsuse	Seaside	40-70	Ν	+	0.3
Kabe-shima	Tajima	Seaside	10-50	Ν	+	0.3
Hirado	Mivanoura	Seaside	20-60	Ν	+	0.3
Fukue-jima	Toki	Seaside	20-140	Ν	+	0.2
j	Shiratori	Seaside	10-80	N	+	0.5 ^b
Danjo	Oshima	Islet	40-220	Ν	-	60 ^b
5	Meshima	Islet	40-280	Ν	-	60 ^b

Table 1. Habitats of Aedes riversi on the satellite islands of north Kyushu.

^aAt Nishidomari (11 in Fig. 1) and Oshima (15) *Ae. riversi* was first collected by Omori and Suenaga in 1950's (Mogi 1976) and collected again by the author in 1975 (Mogi 1976) and 1978 (Mogi et al. unpublished), respectively. Minato (12) and Arakawa (14) are excluded since the collection sites were not specified.

^bOver the sea.

N = Lowland-type natural forests of evergreen broad-leaf trees.

north Kyushu are thus confined to lowland-type natural forests on uninhabited islets, or to those at unfrequented points or sacred areas on larger inhabited islands.

From where did Ae. riversi populations on the satellite islands of north Kyushu come? Invasion from the Asian continent appears unlikely, since no scutellaris subgroup species have been recorded from Korea (Tanaka et al. 1979) or temperate China (Lu et al. 1988). Lucidophyllous forests on the southern periphery of the Korean Peninsula (Yim 1977) are isolated far from those of the mountain regions in south China (Fang and Yoda 1989). Direct invasion from the Ryukyu Islands or from the southern extremity of Kyushu appears also unlikely, since, as other Stegomyia species, Ae. riversi has limited flight ability. The common occurrence of Ae. riversi on several continental islands from Danjo through Tsushima strongly suggests the continuous distribution of Ae. riversi when these islands and the Kyushu main island formed a part of the Asian continent. Most probably, Ae. riversi was once distributed throughout Kyushu and its satellite islands (possibly including the southern periphery of the Korean Peninsula), but has become extinct from most of Kyushu, leaving relic populations on the satellite islands.

Colonization of temperate Japan by Ae. riversi could not have occurred later than Interglacial II (ca. 0.3-0.4 million years ago) when all the satellite islands (except Danjo Islands) and Kyushu are thought to have formed a narrow peninsula projecting from the Asian continent (Ichikawa et al. 1970). At that time, the climate was warm and humid enough to allow the establishment of lucidophyllous forests (Ichikawa et al. 1970, Tsukada 1974). This suggestion does not conflict with the inference that the ancestor of *Ae*. *riversi* split from the ancestor of southeast Asian *Ae*. *alcasidi* Huang and *Ae*. *malayensis* Colless in mid-Pliocene (ca. 3 million years ago) (Pashley et al. 1985). *Aedes riversi* populations of Ryukyus and Tsushima are genetically compatible (Toma and Miyagi 1989), though minor morphological differences may exist between the Ryukyu populations and those of Kyushu (Tanaka et al. 1979).

Why has Ae. riversi disappeared from most of Kyushu? One explanation is that lowland natural forests have been reduced by man's activities more rapidly and extensively on Kyushu than on its satellite islands. These islands have been less strongly influenced by the industrialization and urbanization of Japan. A simple index of exploitation (the reciprocal of the number of natural forests per square kilometer) in Nagasaki Prefecture is clearly smaller for these islands, where Ae. riversi is common, than for the main island (Table 2). This exploitation index assumes the same area of all the forests. Natural forests on less exploited islands are generally larger than those on the main island. With progressive deforestation, natural forests have been fragmented and isolated. This implies an increased probability of extinction of Ae. riversi from each patch (e.g., due to unusual drought) and a decreased probability of reinvasion from other patches. The absence of Ae. riversi from remnants of natural forests on Kyushu may be a result of a low probability of reestablishment after accidental extinction rather than the lack of essential conditions for its colonization.

Reg	ion	Area in km ² (A)	No. natural forests (B)	Exploitation index (A/B)	Ae. riversi
Island	Danjo	5	2	2.5	+
	Iki	139	3	46.3	+
	Tsushima	709	9	78.8	+
H F	Hirado	165	2	82.5	+
	Fukue-jima	327	3	109.0	+
Mainland S	Southwest	771	3	257.0	-
	Central	569	2	284.5	-
	Southeast	486	1	486.0	-
	North	705	0	nc	-

Table 2. Distribution of lowland-type natural forests and Aedes riversi in Nagasaki Prefecture.^a

^a Mainly based on Culture Bureau (1974) and Nagasaki Prefecture (1980).

nc = Not calculated.

Table 3. General patterns of ecological distribution of Stegomyia species in the lowland of north Kyushu.

	Natural forest ^a		Secondary forest ^b		Developed area ^c		
	riv	flavo	albo	flavo	albo	albo	
Main island Kyushu	-	+	+	+	+	+	
Satellite islands							
Tsushima	+	+	+	+	+	+	
Iki ^d	+	+	+	+	+	+	
Kabe-shima	+	-	+	-	+	+	
Hirado ^d	+	-	+	-	+	+	
Fukue-jima	+	-	+	-	+	+	
Chikuzen-Okinoshima ^e	+	-	-				
Danjo ^e	+	-	-				

^a Lowland-type lucidophyllous (evergreen broad-leaf) forest.

^b Lowland-type lucidophyllous forest subject to periodic lumbering or bamboos cultivated at the mountain foot.

^c Industrial, business, residential areas or agricultural lands.

^d Insufficient observations.

^e Uninhabited islets without secondary forests and developed areas.

+ = Present.

- = Has not been found.

Is there any possibility that interspecific interaction has been involved in the disappearance of *Ae. riversi* from Kyushu? Table 3 shows general patterns of ecological distribution of 3 *Stegomyia* species in the lowland of north Kyushu. Observations are not sufficient for Iki and Hirado. The absence of *Ae. flavopictus* from Hirado needs confirmation. Nonetheless, the following patterns may be seen: (1) *Ae. riversi* is confined to natural forests and the only *Stegomyia* species on uninhabited islets, (2) *Ae. flavopictus* is present in natural and secondary forests on Kyushu and Tsushima but has not been found on some islands, and (3) *Ae. albopictus* is found in most habitats and is the only *Stegomyia* species in developed areas but appears not to have settled on uninhabited islets wholly covered with natural vegetation. Some habitat differentiation exists between *Ae. albopictus* and the 2 other, primarily forest species, but *Ae. riversi* coexists with *Ae. flavopictus* and/or *Ae. albopictus* in some natural forests.

Little is known of experimental interaction between Ae. riversi and Ae. albopictus or Ae. flavopictus. In laboratory cages, interspecific insemination may occur at a low rate between Ae. riversi and the other 2 species but no fertile eggs are produced (Miyagi and Toma 1989). Significance of this phenomenon in the field is unknown. Experimental studies on larval competition are needed also, since Ae. albopictus is superior to Ae. polynesiensis Marks, a South Pacific member of the scutellaris subgroup, in mixed larval rearing (Lowrie 1973a, b). Field observations, however, suggest that Ae. riversi might be less competitive compared to the albopictus subgroup species, since (1) Ae. riversi is rather rare in Tsushima's natural forests where Ae. flavopictus is abundant, and (2) Ae. riversi attains a high density on uninhabited islets having neither Ae. flavopictus nor Ae. albopictus.

Even though Ae. riversi is comparable to the other species in its competitive ability, coexistence of Stegomyia species in the same habitat may have been most detrimental to Ae. riversi. With fragmentation and isolation of natural forests, Ae. albopictus habitats have enlarged and become continuous. This could have accelerated the extinction of Ae. riversi by continuous and intensifying invasion of Ae. albopictus from the surrounding areas. The outcome of competition may depend on initial numbers of interacting species in mathematical models (Begon et al. 1986, Ribeiro 1988) and laboratory studies (Park et al. 1941, Sasaba 1964). Habitat loss of Ae. flavopictus by deforestation was partly compensated by bamboo cultivation along the foothills and mountains. Therefore, this species may have been more tolerant of deforestation than Ae. riversi.

In conclusion, the available information reinforces the hypothesis that populations of Ae. riversi on the satellite islands of north Kyushu are relict. Colonization of temperate Japan by Ae. riversi probably occurred not later than Interglacial II when Kyushu and its satellite islands (as a part of the Asian continent) were covered by the lowlandtype lucidophyllous forests. Postglacial deforestation by man has caused its extinction from most parts of Kyushu, leaving relict populations on the undeveloped satellite islands, especially those lacking other Stegomyia species. This hypothesis leads to 2 predictions. First, Ae. riversi will be found on more islands with natural forests and, by extensive surveys, in north Kyushu, Shikoku, west Honshu and the southern periphery of the Korean Peninsula. Second, it will eventually disappear from some islands once the environment around its habitats is subjected to extensive local development, even if the natural forests themselves are preserved.

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REFERENCES CITED

- Begon, M., J.L. Harper and C.R. Townsend. 1986. Ecology. Blackwell Scientific Publ., Oxford.
- Culture Bureau (Japanese Government). (ed.) 1974. Vegetation maps. Distribution maps of important animals and plants 42. Nagasaki Prefecture. Kokudo-chiri Kyokai (National Geographic Society), Tokyo (in Japanese).
- Eshita, Y. and T. Kurihara. 1979. Studies on the habitats of *Aedes albopictus* and *Ae. riversi* in the southwestern part of Japan. Jpn. J. Sanit. Zool. 30:181-185.
- Fang, J.Y. and K. Yoda. 1989. Climate and vegetation in China II. Distribution of main vegetation types and thermal climate. Ecol. Res. 4:71-83.
- Huang, Y.-M. 1972. Contributions to the mosquito fauna of Southeast Asia. XIV. The subgenus Stegomyia of Aedes in Southeast Asia. I. The scutellaris group of species. Contrib. Am. Entomol. Inst. (Ann Arbor) 9:1-109.
- Ichikawa, K., Y. Fujita and M. Shimazu. 1970. The geologic development of the Japanese Islands. Tsukiji Shokan Inc., Tokyo (in Japanese).
- Kamimura, K. 1968. The distribution and habit of medically important mosquitoes of Japan. Jpn. J. Sanit. Zool. 19:15-34 (in Japanese with English summary).
- Kira, T. 1949. Forest zones of Japan. Nihon Ringyogijutsu Kyokai (Japanese Society of Forestry Technology), Tokyo (in Japanese).
- Lowrie, R.C. 1973a. The effect of competition between larvae of *Aedes (Stegomyia) albopictus* (Skuse) and *A.* (S.) polynesiensis Marks. J. Med. Entomol. 10:23-30.
- Lowrie, R.C. 1973b. Displacement of Aedes (Stegomyia) polynesiensis Marks by A. (S.) albopictus (Skuse) through competition in the larval stage under laboratory conditions. J. Med. Entomol. 10:131-136.
- Lu, B., H. Chen, R. Xu and S, Ji. 1988. A checklist of Chinese mosquitoes (Diptera: Culicidae). Guizhou People's Publ. House, Kweiyang, Kweichow (in Chinese with English summary).
- Miyagi, I. and T. Toma. 1989. Experimental crossing of Aedes albopictus, Aedes flavopictus downsi and Aedes riversi (Diptera: Culicidae) occurring in Okinawajima, Ryukyu Islands, Japan. Jpn. J. Sanit. Zool. 40:87-95.
- Miyawaki, A. (ed.) 1977. Vegetation of Japan. Gakken Inc., Tokyo (in Japanese).
- Mogi, M. 1976. Notes on the northern records of *Aedes* (*Stegomyia*) riversi Bohart and Ingram. Mosq. Syst. 8:347-352.
- Mori, A. 1989. The distribution of *Stegomyia* mosquitoes in Kyushu and Okinawa. p. 45-53. *In:* S. Itow and K. Matsuoka (eds.). Biogeographical studies of the Tsu-

shima Current regions: Prompt report No. 1. Nagasaki University, Nagasaki (in Japanese).

- Nagasaki Prefecture. 1980. Report of the survey on plant associations. p. 1-288. In: Environmental Bureau (Japanese Government) (ed.). Important plant communities in Japan. North Kyushu. Finance Ministry Press, Tokyo (in Japanese).
- Park, T., E.V. Gregg and C.Z. Lutherman. 1941. Studies in population physiology. X. Inter-specific competition in populations of granary beetles. Physiol. Zool. 14:395-430.
- Pashley, D.P., K.S. Rai and D.N. Pashley. 1985. Patterns of allozyme relationships compared with morphology, hybridization, and geologic history in allopatric islanddwelling mosquitoes. Evolution 39:985-997.
- Ribeiro, J.M.C. 1988. Can satyrs control pests and vectors? J. Med. Entomol. 25:431-440.
- Sasa, M., K. Kamimura and I. Miyagi. 1977. Mosquitoes. p. 137-175. In: M. Sasa, H. Takahasi, R. Kano and H. Tanaka (eds.). Animals of medical importance in the Nansei Islands in Japan. Shinjuku Shobo Inc., Tokyo.
- Sasaba, T. 1964. Interspecific competition between two species of Trichogrammatidae. Jpn. J. Ecol. 14:200-207

(in Japanese with English synopsis).

- Tanaka, K., E.S. Saugstad and K. Mizusawa. 1975. Mosquitoes of the Ryukyu Archipelago (Diptera: Culicidae). Mosq. Syst. 7:207-233.
- Tanaka, K., K. Mizusawa and E.S. Saugstad. 1979. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Contrib. Am. Entomol. Inst. (Ann Arbor) 16:1-987.
- Toma, T. and I. Miyagi. 1986. The mosquito fauna of the Ryukyu Archipelago with identification keys, pupal descriptions and notes on biology, medical importance and distribution. Mosq. Syst. 18:1-109.
- Toma, T. and I. Miyagi. 1989. Reproductive isolation among *Ae. riversi, Ae. alcasidi* and *Ae. scutellaris* of the *Aedes (Stegomyia) scutellaris* subgroup (Diptera: Culicidae). Jpn. J. Sanit. Zool. 40:323-332.
- Tsukada, M. 1974. Paleoecology II. Synthesis. Kyoritsu Shuppan Inc., Tokyo (in Japanese).
- Yim, Y.J. 1977. Distribution of forest vegetation and climate in the Korean peninsula IV. Zonal distribution of forest vegetation in relation to thermal climate. Jpn. J. Ecol. 27:269-278.