

**NORTHWARD EXPANSION OF
ICTINOGOMPHUS PERTINAX (SELYS) IN EASTERN
SHIKOKU AND WESTERN KINKI DISTRICTS, JAPAN
(ANISOPTERA: GOMPHIDAE)***

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The northward expansion of *I. pertinax* (Selys, 1854) in the region of eastern Shikoku and western Kinki Districts was investigated by reviewing a number of former papers. Some ecological factors enabling the species to expand northward were considered, based on observations which have been made in and near Kobe since its first discovery in 1987. This expansion started from southern Kochi about 50 years ago and the yearly mean air temperature has risen by about 1.0 to 1.7°C during the last 95 years in this region. The rise of air temperature coincides with both the temporal and spatial expansions.

INTRODUCTION

Since about the 1960s it has been said that the geographical range of *Ictinogomphus pertinax* (Selys) may expand northward in southwestern Japan (ISHIDA, 1969; HAMADA & INOUE, 1985; ISHIDA et al., 1988). In February 1992, however, overwintering larvae were found in Kobe (AOKI, 1992) and, since then, adult emergence has been observed every summer. These findings directly demonstrated that this northward expansion was attained as a result of adults dispersal and larval overwintering.

The aim of this paper is to (1) establish the routes along which the insect has passed in western Kinki and eastern Shikoku Districts, based on an intensive survey of former works; (2) discuss the ecological factors that enable it to expand northward based on observations of the species in Kobe since its first discovery.

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STUDY SITES AND METHODS

Field observations of *I. pertinax* were made from 1991 to 1994 mainly at four irrigation ponds, at Hazetani-cho, Kobe, Hyogo Pref., western Kinki District, Japan. Three of them, named Yude Pond, Maruyama Pond and Yoshigadani Pond, are topographically close to each other and located within a small valley, called Maruo Valley (34°43'N, 135°02'E), about 4.0 km N of Akashi Park, where *I. pertinax* was first found near the present study sites. The other one, named Minamidani Pond, is in an adjacent valley, 1.5 km N of them. Other sites I sometimes visited were as follows: Akashi Park and Shu Pond at Okubo in Akashi City; Otani Pond at Tamatsu; Goban Pond, Nanaban Pond and Aotani Pond in Maruo Valley; four small ponds at Teratani; and Okusuma Park at Tainohata in Kobe.

Vegetation of floating-leaved plants, such as *Trapa japonica* Flerov., *Nymphoides indica* L. or *Brasenia schreberi* J.F.Geml., extended over the water surface of all the four ponds in the main study, but did not always do so in the case of the other ponds.

The odonate fauna of the four ponds was surveyed.

Table I shows observation dates. The larvae were caught with a pond net. Their head widths were measured with slide callipers soon after collecting. Collections of exuviae and observations of adults were made on every visit during the flying season of the species.

PUBLISHED RECORDS OF *I. PERTINAX* IN THE REGION OF EASTERN SHIKOKU AND WESTERN KINKI DISTRICTS

Figure 1 shows locations and years in which *I. pertinax* was found. Before the 1950s, *I. pertinax* was distributed in southern Shikoku, e.g. at Tano in 1934 (SASAKI, 1936) or further South. In the 1950s and 1960s, the dragonfly was, however, found in and around Tokushima City (HIRAI, 1980). After then, in the 1970s, it was successively found along the Yoshino River basin at Kamojima-cho and Awa-cho in 1970, at Waki-machi in 1972 and at Ikeda-cho in 1979 (HIRAI, 1980). An adult insect which appeared in Kan'onji City in 1980 (ISHIKAWA, 1982) might have come from Ikeda-cho.

Other records followed after the occurrence of the dragonflies in and around Tokushima City; i.e. at Tomo-ga Island in 1976 (TAKEUCHI, 1976) and Kada in 1979 (MURAKI, 1980), the dragonflies probably flying across the Naruto Channel, going through the southern region of Awaji Island and flying across the Kitan Channel. From there, they appeared to expand in three directions: first, southward along the shore line of Wakayama Pref., they were found in Arida City and Yuasa-cho in 1981 (ANAZE, 1990), Gobo City in 1986 (ANAZE, 1991a) and Tanabe City in 1991 (ANAZE, 1991b); second, eastward along the Ki-no River basin, at Kokawa-cho in 1988 (ANAZE, 1990) and Gojo City in 1989 (HISAKAWA, 1991); third, northward through the Osaka Plains and then along the Yodo River basin, in Habikino City and Abeno-ku in 1987 (TSUDA & YAMAMOTO, 1988), Shirokita Park in 1989 (SHIMURA, 1989), Otsu City in 1991 (FUJIMOTO, 1991), Kusatsu City (FUJIMOTO, 1992) and Kizu-cho (Fujimoto, unpublished) in 1992.

Also there were still more successive discoveries in Awaji Island and in southern Hyogo Pref.; i.e. at Higashiura-cho in 1981 (TANAKA, 1982), Akashi Park in 1987 (NISHU, 1988b), Kobe (AOKI, 1991a) and Nishinomiya City (INOUE &

OGAWA, 1991) in 1990 and Hattori Park in 1992 (MURAKI, 1992).

On the basis of the above reviews, it is suggested that, in the region of eastern Shikoku and western Kinki Districts, the dragonflies usually move along the basins or shore lines, or through plains, and they sometimes cross over the narrow channels. There appears to be no instance of their passing over the mountains or highlands nor of their long dispersal over the ocean. The supposed routes along which the dragonfly moved are shown in Figure 1.

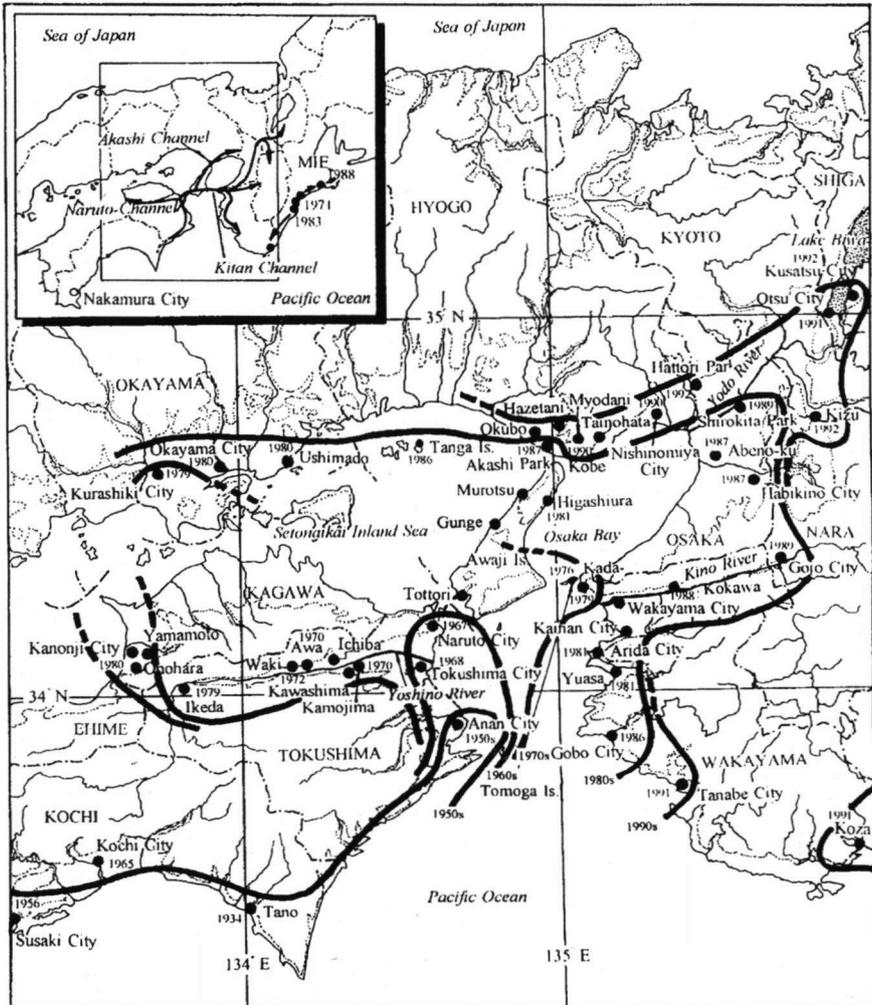


Fig. 1. The locations where *I. pertinax* occurred and the earliest year when it was recorded at/near the respective locality. - [Lines indicate expansion fronts, decade-wise, after the 1950s. Arrows in the boxed map indicate the hypothetical expansion routes].

The moving rates on land are about 8 km/year between Tokushima City and Kan'onji City, about 8 km/year between Kada and Tanabe City, about 6 km/year between Kada City and Gojo City, about 6 km/year between Kada City and Shirokita Park, about 9 km/year between Akashi Park and Hattori Park, and about 23 km/year between Shirokita Park and Otsu City. Therefore these rates are roughly constant except in the last case. The expansion rate is slower, however, in situations where channels need to be crossed; e.g. 3.5 km/year between Naruto City and Akashi Park and 4.0 km/year between Naruto City and Kada.

DISCUSSION OF THE ECOLOGICAL FACTORS WHICH MAY HAVE ALLOWED *I. PERTINAX* TO EXPAND ITS DISTRIBUTION NORTHWARD, BASED ON OBSERVATIONS MADE IN KOBE

There must be many ecological factors which allowed *I. pertinax* to expand its distribution northward. The author discusses some of them below, mainly based on observations of *I. pertinax* in Kobe, to reveal which factor(s) allowed the species to do so.

DISPERSAL HABIT

WATANABE & KOHAMA (1986) and ISHIDA et al. (1988) reported that teneral adults are sometimes found in the hills far from water. In Kobe, a teneral female was collected on 20th July 1991 about 5 km from the nearest pond which *I. pertinax* had colonized. In the present observation, moreover, teneral adults could not be seen around the emergence sites for several days after emergence, but in paddy fields in a small valley far from the emergence sites. Therefore they are certain to disperse for several kilometers from the emergence site immediately after emergence. This dispersal habit of teneral adults seems to result in colonizing of new breeding sites, or expanding their geographic distribution, and this distance of dispersal agrees with the expansion rate, i.e., 6-9 km/year on land (see above).

In *I. pertinax*, there have been no records of extremely long dispersal over the ocean, but a possibility of it still remains, since *I. pertinax* is widely distributed in most of the islands of Ryukyu, which are scattered in the East China Sea (WATANABE & KOHAMA, 1986). Ancestral populations in southern Shikoku or Mie Pref. might have come from the South in such a manner.

HABITAT SELECTION

The eggs of this species are laid on floating leaves, stems or other materials in the following manner: as soon as a female comes to the pond, she orients and hovers about 50 cm above floating materials such as leaves or stems of water plants, or pieces of wood, and then she descends and repeatedly touches the apex of her

abdomen on the material (an observation on 25th August 1993 at Teratani, Kobe). NARITA (1988) reported, however, that the eggs were laid on open water.

The larvae were usually found crawling in the sediments on the gravel or sandy bottom in shallow water, but in mid-winter they were hardly able to be caught at such sites (cf. Tab. I). Therefore they might move to the bottom of deeper water during overwintering.

The emergence takes place on floating leaves or other floating materials, or on the bank.

The adults were usually seen at ponds with rich vegetation, although they were sometimes found at ponds with poor vegetation. Several adult males were seen in 1991 at the following three ponds in Kobe: Otani Pond with poor vegetation; Maruyama Pond and Minamidani Pond, both with rich floating vegetation. In 1992, the larvae and exuviae were found, however, only at the latter two ponds. Other ponds where the larvae and exuviae were collected in the present study had rich floating vegetation, too.

Based on the above evidence, there seems to be no special habitat requirement, although the dragonflies seem to prefer ponds with rich vegetation, which may serve them for oviposition, concealment of larvae and emergence.

The larvae have been found in different-sized pools. The smallest one was an old concrete tank in Okinawa Is., 3 × 2m in size, in which there was a dense growth of submerged plants. Moreover, in Okinawa Is., they were also found in a small pool (about 10 × 20m), in a cattle field and in an abandoned paddy field filled with water. WATANABE & KOHAMA (1986) and ISHIDA et al. (1988) described, on the other hand, that the dragonflies could be seen at large reservoirs such as dams, too. Therefore this species seems to adapt itself to pools of a relatively wide size range.

There are huge numbers of irrigation ponds in the region along the Setonaikai Inland Sea; for example, there are more than 54,000 (61.4/km²) in Hyogo Pref., and more than 13,000 (78.8/km²) in Osaka Pref. (USUI, 1985). Because many of them undoubtedly have the conditions which *I. pertinax* prefers, it must be easy for adult dragonflies to find a new breeding site in this region.

INTERSPECIFIC COMPETITION

The four ponds studied have a rich odonate fauna; i.e. 45 species in Yude Pond, 30 species at Yoshigadani Pond, 23 species at Maruyama Pond and 21 species at Minamidani Pond. Therefore *I. pertinax* would face interspecific competition when colonizing a new site. In this region, there is a slightly larger congeneric species, *I. clavatus*, which may occupy a similar ecological niche. The topographical distribution of adults, however, seems to be slightly different from each other (Fig. 2). *I. clavatus* adults occur around open water, whereas *I. pertinax* keeps in and near vegetation. Moreover, at Yude Pond with rich vegetation, *I. pertinax* adults occur,

Table 1
All records of observations from 1990 to 1994 in and around Kobe

Date \ Ponds	Minamidanio-ike	Yude-ike	Yoshigadani-ike	Maruyama-ike	Other sites
1990					
22 Sep.	—	—	—	—	♂ : Sarukura Pond
1991					
20 Jul.	—	—	—	—	♀ : Teratani
10 Sep.	—	—	—	—	♂ ♀ : Akashi Park
21 Sep.	—	—	—	—	♂ : Otanio Pond
22 Sep.	♂	—	—	—	
28 Sep.	—	♂	—	—	
1992					
5 Mar.	F-4	—	—	F-4, F-2	
30 May	—	F-0	—	—	
13 Jun.	—	F-3, F-1	—	—	
15 Jun.	—	—	—	—	F-0: Shu Pond
3 Jul.	none	—	tencrals	10 exuviae	
4 Jul.	F-0, 15 exuviae	7 exuviae	—	—	
8 Jul.	F-0, 13 exuviae	—	—	7 exuviae	
13 Jul.	—	—	♂	—	
15 Jul.	—	—	♂	—	
24 Jul.	—	♂	♂	—	♂ : Goban Pond
22 Aug.	—	♂	♂	♂	
28-30 Aug.	—	♂	♂	—	♂ : Okusuma Park/Shu Pond
5 Sep.	—	♂ ♀, ovi- position	—	—	
18 Sep.	—	♂	♂	♂	
12 Oct.	—	F-0, F-1, F-2, F-3, F-4	—	—	
16 Oct	—	F-0	—	—	
29 Dec.	—	none	—	—	
1993					
13 Feb.	—	none	—	—	
25 Feb.	none	—	—	—	
18 Mar.	—	none	none	—	
27 Mar.	none	—	—	—	
12 Apr.	—	none	—	—	
1 May	—	F-6, F-4, F-3	—	—	
2 May	F-4	F-3, F-4	—	—	
17 May	—	F-0, F-6	—	—	
3 Jun.	—	F-0, F-3, F-4	—	—	
7 Jul.	none	F-0, F-2	—	none	
9 Jul.	—	1 exuviae	none	none	
14 Jul.	none	F-3	17 exuviae	1 exuviae	
16 Jul.	—	none	♂, 3 exuviae	—	
8 Aug.	—	—	—	—	1 exuviae: Teratani*
25 Aug.	—	♂ ♀	♂	—	♂ ♀ : Teratani, oviposition
29 Aug.	—	—	♂	—	
11 Sep.	—	♂ ♀, F-0**	♂	—	
1 Oct	—	♂ ♀, ovi- position	♂	—	

Table I (continued)

Date \ Ponds	Minamidaniao-ike	Yude-ike	Yoshigadani-ike	Maruyama-ike	Other sites
1994					
14 Jan.	—	none	—	—	
25 Feb.	—	none	—	—	
2 Apr.	—	none	—	—	
21 Jun.	—	—	—	—	F-0: Aotani Pond
28 Jun.	—	—	—	F-0, F-2	
2 Jul.	—	F-2	—	—	
11 Jul.	—	♂	♂, 31 exuviae	—	♂: Nanaban Pond. 2 exuviae: Aotani Pond

'♂' and '♀' indicate adult male and female respectively; 'F-0, F-1,', larvae and their instars; 'none', no finding; '—', not observed. * collected by N. Oshima. ** immediately after ecdysis.

whereas at Aotani Pond, with poor vegetation, only *I. clavatus* is present. *I. clavatus* larvae, which appear to prefer deeper parts of the ponds (cf. FUJIMOTO & YOSHIDA, 1993, 1994), rarely coexist with *I. pertinax* larvae, even though they inhabit the same pond. Moreover, the emergence of *I. clavatus* was observed earlier than that of *I. pertinax* (NARITA, 1988; HISAKAWA, 1991). Therefore the competition may not be serious between them and, if anything, *I. pertinax* may gain an advantage over *I. clavatus*. According to some reports (HIRAI, 1980; NARITA, 1988), *I. clavatus* tends to decrease in number at ponds or areas which *I. pertinax* has colonized.

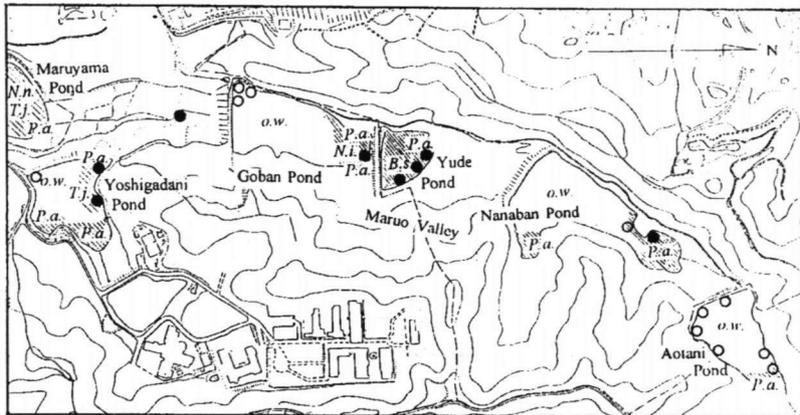


Fig. 2. The occurrence of adult *I. pertinax* (●) and *I. clavatus* (○) in Maruo Valley, Hazetani-cho, Kobe, on 11 July 1994. The shaded portions of the ponds indicate aquatic vegetation. — [*P.a.*: *Phragmites australis* Trin. ex Steud.; — *T.j.*: *Trapa japonica* Flerov.; — *N.n.*: *Nelumbo nucifera* Gaertn.; — *N.i.*: *Nymphaoides indica* (L.); — *B.s.*: *Brasenia schreberi* J.F. Gmel.; — *o.w.*: open water. — (Original)].

LIFE CYCLE

The adults were seen from early July to early October in Kobe and a peak in their number occurs from late July to early September. Oviposition usually commences about 2 weeks after emergence. The dragonflies overwinter in the larval stage in Kobe as well as in Okinawa Is. (Aoki, unpublished, for 1994).

The larvae collected during the present study could be clearly divided into six groups, based on their head width (Fig. 3). The mean head width of the groups increased in a geometric ratio (Fig. 3), and the largest one was composed of final instar larvae, so that they could be divided into groups whereby the largest one was the F-0 group, the next was F-1, and so on. Each larval instar was plotted against the time of the year collected (Fig. 4). The larval period of *I. pertinax* in Kobe appears to be more than two years. ISHIDA et al. (1988) stated that *I. pertinax* was an univoltine species. However, in Kobe, close to the northern limits of its range, the life cycle seems to change into semivoltinism at least in a part of the population. *I. pertinax* has some flexibility of voltinism, so that it can complete its growth in northern regions where total accumulative temperature is less.

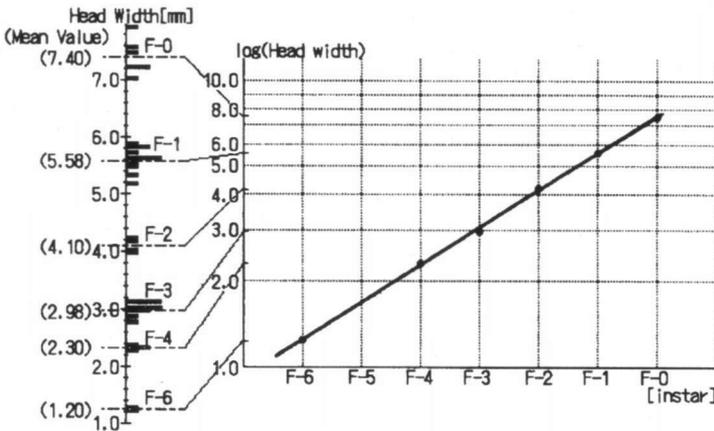


Fig. 3. Distribution of *I. pertinax* larval head width, in the Kobe population (left), and relation between head width and instar (right).

AIR TEMPERATURE

It is noted that since 1987, when a male *I. pertinax* was first found at Akashi Park (NISHU, 1988b), the mean winter air temperature (December to February) in Kobe has been higher (Fig. 5a). In 1990, two adult males were found at Sarukura Pond, Kobe (AOKI, 1991a) and in 1991, many adults, including a teneral female, were found at four sites in Hazetani-cho and one site in Akashi Park. In March 1992, three larvae (two F-4 and one F-2) were caught at two sites in Hazetani-cho, and

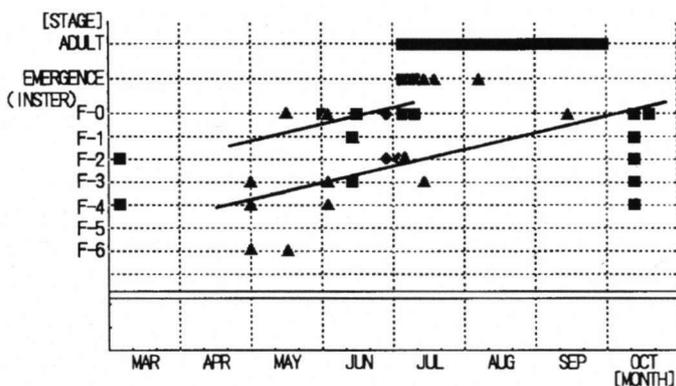


Fig. 4. Larval growth of *I. pertinax* at Hazetani-cho and Tamatsu-cho, Kobe, in 1992-1994. ■: in 1992, ▲: in 1993, ◆: in 1994. — [Lines indicate the supposed growth of two different emergence cohorts].

had obviously overwintered there. The first emergence was recorded in early July 1992 at three sites and, since then, the emergence and a number of adults have been noted every year. Also, the ponds which *I. pertinax* has colonized in and around Kobe have increased in number gradually: only six were known until 1991, but thirteen or more by 1995. The population size of *I. pertinax* in and around Kobe has also grown rapidly during the last seven years. The warm winters probably make larval overwintering easier.

Figure 6 shows that the isotherms of the mean winter air temperature shifted northward after 1987. The distributional area of *I. pertinax* has also shifted northward, depending on the shift of isotherms.

A similar rise in the mean winter air temperature occurred in Tokushima City around 1950, and then, warm winters lasted for more than 10 years (Fig. 5b). HIRAI (1980) mentioned that there were a number of individuals of *I. pertinax* in Anan City in 1965 and it was commonly seen everywhere in Tokushima City in 1968. This situation in Tokushima City in 1968 resembles that in Kobe from 1987 to 1995.

Figure 7 shows the fluctuation of mean annual air temperature since 1900 in

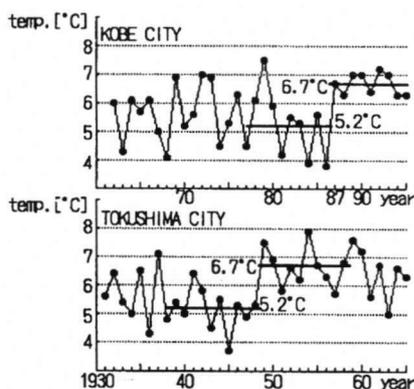


Fig. 5. Annual fluctuation of mean winter air temperature (December - February) during 1962-1995 in Kobe (at Kobe Marine Meteorological Observatory) and during 1931-1965 in Tokushima (at Tokushima Local Meteorological Observatory). — [Horizontal lines indicate the mean level for ten years before and after the beginning of warm winters, except for Kobe after 1987, which is for 9 years].

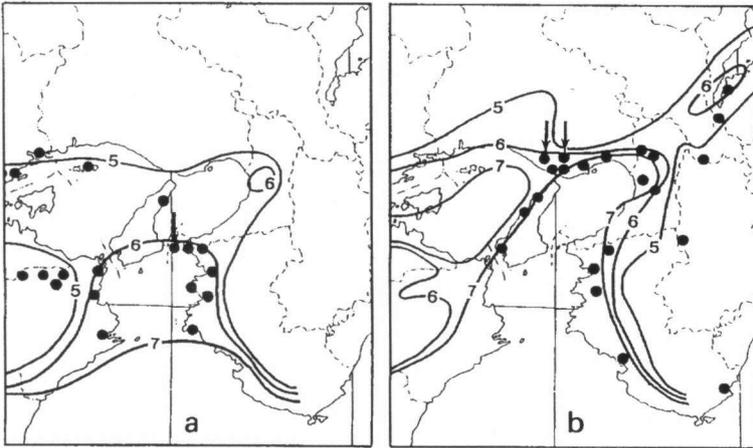


Fig. 6. The northward shift of isotherms of winter mean temperature (from December to February) after 1987: (a) isotherms of the means during 1979-1987 and distribution of *I. pertinax* before 1986; – (b) isotherms in 1991-1992 and distribution of *I. pertinax* after 1987, excluding data before 1986. – [Arrows show the localities where exuviae were collected. The isotherms are based on the data from Automated Meteorological Data Acquisition System. – Redrawn from AOKI, 1992].

Kochi, Tokushima and Kobe Cities. The equations of the regression lines indicate that rates of the rise of mean annual air temperature are about 1.0°C per 100 years in Kobe and Tokushima Cities, and about 1.7°C per 100 years in Kochi City. They also show that the present climate in Kobe corresponds to that in Kochi about 50 or more years ago, when *I. pertinax* was only distributed in Kochi City and further South.

The northward expansion of the *pertinax* range coincides with the rise of air temperature, both temporally and spatially.

CONCLUSION

It is difficult to ascertain the direct reason why *I. pertinax* has expanded its distributional area northward. However, the factors discussed above, and the ecological conditions influencing the life cycle of *I. pertinax*, enable us to make suggestions on this problem.

The northward expansion in this region commenced more than fifty years ago. The rise of air temperature is the sole factor that coincides with the temporal expansion. The other conditions have been present long before the expansion started. Therefore, it would be difficult, without considering the rise of air temperature, to explain the phenomenon.

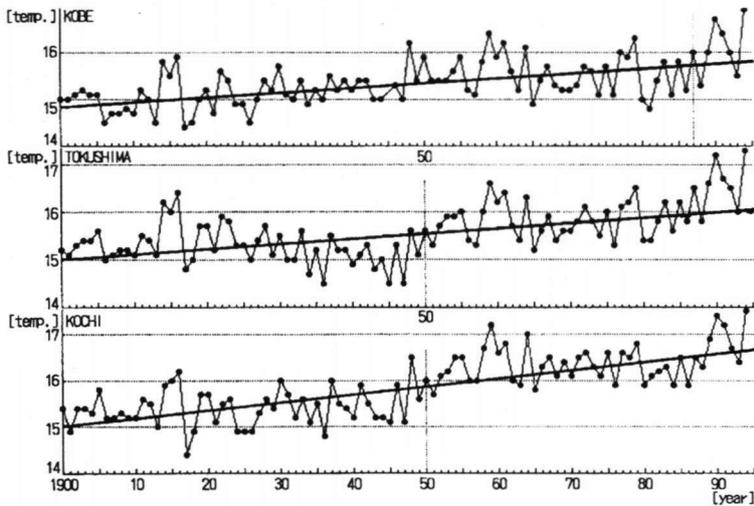


Fig. 7. Fluctuations of mean annual air temperature in Kobe (at Kobe Marine Meteorological Observatory), Tokushima (at Tokushima Local Meteorological Observatory) and Kochi (at Kochi Local Meteorological Observatory) from 1900 to 1994. – [Lines indicate regression lines and their equations as follows: Kobe: $y = 0.0102x + 14.82$, Tokushima: $y = 0.0111x + 14.98$, Kochi: $y = 0.0174x + 14.98$, (here, $x = \text{year} - 1900$ and $y = \text{temp.} [^{\circ}\text{C}]$). All the equations are significant ($P < 0.001$) from regression analysis].

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