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ABSTRACTS OF PAPERS PRESENTED AT THE MNAIS SYMPOSIUM, Kyoto, Japan, January 5-6, 1980

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Introduction

The Japanese *Mnais* damselflies (Odonata: Calopterygidae) are treated as a single species, *M. pruinosa* Selys, composed of three subspecies with eleven forms (S. ASAHINA, 1976, *Tombo* 19: 2-16; cf. Tab. I). The ranges of two subspecies, however, are largely sympatric and show a number of different features in their reproductive behaviour. Thus, studies on *Mnais* have become attractive to both academic researchers and many amateur workers. Some have worked in the field of taxonomy with reference to distribution, others in the field of ecology, with reference to behaviour. In addition, the latter workers have studied each population in each locality.

The Symposium was held at the Kyodai Kaikan (host T. UEDA) with the objective that discussions should mutually inspire the *Mnais* workers.

DISTRIBUTION AND DIFFERENTIATION OF THE JAPANSESE *MNAIS*: A WORKING HYPOTHESIS

Further distributional data were presented based on additional material taken after S. ASAHINA's 1976 (*Tombo* 19: 2-16) paper. One species is recognised, composed of three

Table 1 — The Japanese colour forms of *Mnais pruinosa* Selys, and their distribution — The names of the "forms" were introduced, for convenience, by ASAHINA (1976, cf. above), the term "typica" was used first by SUZUKI & EGUCHI (1979, *J. Coll. lib. Arts Toyama Univ.*, Nat. Sci., 12: 65-85)

	♂ forms and wing colour						*♀ forms and wing colour*			Distribution (Districts, *Prefectures* cited in the following abstracts)
Subspecies	dark brown	orange	orange opaque	pale orange	hyaline	opaque	pale orange	hyaline	opaque	
PRUINOSA Selys	*pruinosa*	*esakii*			*strigata*			typica		Central, W, SW Japan: Hokuriku, *Toyama*, *Ishikawa*; Kinki, *Kyoto*; Chugoku, *Hiroshima*; Kyushu, *Fukuoka*
					shirozui			*shirozui*		
NAWAI Yamamoto		*nawai*		*sahoi*	*kadowakii*		*nawai*	*taketoi*		Central, W Japan: Hokuriku, *Toyama*, *Ishikawa*; Kinki, *Kyoto*
COSTALIS Selys		*costalis*	*edai*		*ogumai*	*edai*		typica	*edai*	E, NE Japan: Hokkaido, Shin-etsu, *Niigata*

geographic subspecies, and represented, as well, by eleven forms; the relationship between these and the subspecies was considered. It seems advisable to assume a hypothetical stock *"protocostalis"* in North Japan from which the western subspecies *nawai*, and the eastern subspecies *costalis* originated. The subspecies *costalis* seems to be situated between *"protocostalis"* and southwestern ssp. *pruinosa*. There is also a possibility that ssp. *costalis* developed from ssp. *pruinosa*.

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THE *MNAIS* INFRASPECIFIC FORMS AND THEIR GEOGRAPHIC DISTRIBUTION IN THE HOKURIKU DISTRICT, CENTRAL HONSHU, JAPAN

The results of the field surveys in the said district were reported. Five major infraspecific forms, referable to *M. pruinosa nawai* Yamamoto and *M. p. pruinosa* Selys, have been found in the district. Several aberrant forms were also reported.

A preliminary analysis of intra- and/or interpopulational variability, particularly of body size (in several populations) and coloration of pterothoracic poststernum and pterothorax side (in one population) was reported. The body size variation shows a clear cline from southwest (large) to northeast (small) and occurs almost in parallel to both sexes; such tendencies seem to occur in parallel in the two subspecies. The colour patterns of both pterothoracic poststernum and pterothorax side vary remarkably and continuously. These two characters may not be applied as diagnostic characters, at least to the Hokuriku populations, though S. ASAHINA (1976, *Tombo* 19: 2-16) emphasized the validity of the coloration of the pterothoracic poststernum as one of the important taxonomic characters, together with that of wings.

The geographic distribution of infraspecific forms in the district was discussed. It seems that the boundary between the two Hokuriku subspecies and *M. p. costalis* Selys lies somewhere between the northeastern Toyama Prefecture and the southwestern Niigata Prefecture.

For a full account on the subject reference is made to a recent paper by K. SUZUKI & M. EGUCHI (1979, *J. Coll. lib. Arts Toyama Univ.*, Nat. Sci., 12: 65-85, 2 col. pls. excl.).

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A TENTATIVE CLUE TO POLYMORPHISM IN *MNAIS*

There are 13 elements in the haploid set of *M. pruinosa*, the male is heterogametic and sex determination is of the XO XX mode (B. KIAUTA, 1972, *Odonatologica* 1: 73-102). For convenience of printing the XO, OO geno-

type is written as OX/OO hereafter.

Let us assume that the wing colour is controlled by a gene for wing colour which is carried on the O chromosome; this gene is recessive and has a viability-diminishing factor (VDF). This O chromosome with the gene for wing colour is written as o here. oX is a coloured-winged male, but o is recessive and Oo is hyaline-winged. ♀ oo is lethal in typical populations because of the VDF. In typical populations, when ♂ OX (hyaline-winged) mates ♀ OO (h-winged), the second generation results in ♂ OX (h-w.) and ♀ OO (h-w.). ♂ OX and ♀ Oo (h-w.) result in ♂ OX (h-w.), ♂ oX (coloured-winged), ♀ OO and ♀ Oo (both h-w.). ♂ oX (c-w.) and ♀ OO (h-w.) result in ♂ OX (h-w.) and ♀ Oo (h-w.). ♂ oX (c-w.) and ♀ Oo (h-w.) result in ♂ OX (h-w.), ♂ oX (c-w.) and ♀ Oo (h-w.) with the loss of ♀ oo (lethal). Thus the population of coloured-winged ♂ — hyaline-winged ♂ — hyaline-winged ♀ are kept in the same combination; the *esakii-strigata*-typica population (e-s series) of subspecies *pruinosa* and the *costalis-ogumai*-typica population (c--o series) of subspecies *costalis* would be explained in this way.

Let us consider another possible explanation. Let VDF fluctuate in its strength in the course of some millions of years. The appearance and disappearance of the "Second Setonaikai" (inland sea) and the beginning and ending of the glacial period might have caused the variation of the strength of the VDF. If it were strengthened and ♂ oX became lethal, every ♂ would have been OX (h-w.), mating females ♀ OO (h-w.), resulting in ♂ OX (h-w.) and ♀ OO (h-w.). Such examples are known as *strigata*-typica population (s series) as well as *shirozui* population both of subspecies *pruinosa*. On the contrary, if it were weakened and ♀♀ oo lost their lethality, the possibilities become very diverse. ♂ OX (h-w.) and ♀ OO (h-w.) result in ♂ OX (h-w.) and ♀ OO (h-w.). ♂ OX (h-w.) and ♀ Oo (h-w.) result in ♂ OX (h-w.), ♂ oX (c-w., presumably ♂-f. *sahoi*), ♀ OO (h-w.) and ♀ Oo (h-w.). ♂ OX (h-w.) and ♀ oo (c -w.) result in ♂ oX (c-w., presumably ♂-f. *sahoi*) and ♀ Oo (h-w.). ♂ oX (c-w.) and ♀ OO (h-w.) result in ♂ OX (h-w.) and ♀ Oo (h-w.). ♂ oX (c-w.) and ♀ Oo (h-w.) result in ♂ OX (h-w.), ♂ oX (c-w., presumably ♂-f. *nawai*), ♀ Oo (h-w.) and ♀ oo (c-w.). ♂ oX (c-w.) and ♀ oo (c-w.) result in ♂ oX (c-w., presumably ♂-f. *nawai*) and ♀ oo (c-w.). Such combination is found in the subspecies *nawai*.

Many of the Japanese *Mnais* populations may be explained by these possibilities but of course these are only a working hypothesis, which must be investigated through breeding experiments in the future.

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STUDIES ON *MNAIS PRUINOSA* SEL. THAT HAVE BEEN CARRIED OUT BY THE MEMBERS OF THE KANSAI RESEARCH GROUP OF ODONATOLOGY

The subspecies *pruinosa* is represented by the e-s series (♂-f. *esakii*, ♂-f. *strigata* and ♀; orange- and hyaline-winged males with hyaline-winged females) in the southern part of the Kinki District with the northern limits of the valley of Kinokawa River in the west and that of Kushidagawa River in the east. The *pruinosa*, e-s series is replaced by the s series (♂-f. *strigata* and ♀; both hyaline) in the middle and northern parts where another subspecies *nawai* exists sympatrically, which is represented by the n-n series (♂-f. *nawai* and ♀-f. *nawai*; orange-winged males with pale orange-winged females). But it has been made clear through the efforts of the co-operative surveys of the members that the southern limit of the distribution of *nawai* extends as far as the valleys of the Kinokawa River and the Miyagawa River beyond the Kushidagawa River. Thus these valleys are inhabited by orange-winged males of two subspecies sympatrically. Some short observations have been made but no cross matings of these two subspecies were seen. Some significant distinguishing features between the shapes of the larvae of the two subspecies have been found.

A locality along the Amami River in the middle part of the Kinki District is inhabited by the n-n series of the subspecies *nawai* and the s series of the subspecies *pruinosa*. One hundred ultimate instar female larvae of *nawai* were collected there on March 20, 1977 and released in another locality near the top of Mt. Koya in the southern part, which was in-

habited by the e-s series, without *nawai*. They emerged, but were not mated by males of *pruinosa* and left no descendants.

Laboratory breeding of *M. pruinosa* has until recently been unsuccessful because the caught females would never oviposit. But Y. FUJIWARA (1979, *Gracile* 26: 12-14) discovered a method of getting damselflies to oviposit in 1978, and S. Obana and T. Miyazaki (unpublished) succeeded in getting oviposited eggs of *M. p. nawai* and *M. p. costalis* by this method. Thus it is expected that the *Mnais* problem might be solved through larval rearing and laboratory breeding.

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INFRASPECIFIC FORMS, HABITAT SEGREGATION AND REPRODUCTIVE ISOLATION IN *MNAIS* OF THE HOKURIKU AND HOKKAIDO DISTRICTS, JAPAN, WITH A HISTORICAL REVIEW ON THE CLASSIFICATION OF THE SPECIES

Various infraspecific forms of the Japanese *Mnais* were reported from one natural population in Sapporo City, Hokkaido District, and two from the Toyama and Ishikawa Prefectures, Hokuriku District. The Hokkaido population consists of three infraspecific forms belonging to a single subspecies, *M. pruinosa costalis* Selys (♂-f. *costalis*, ♂-f. *ogumai* and ♀-f. typica), whereas the two Hokuriku populations consist of five infraspecific forms belonging to two subspecies *M. pruinosa nawai* Yamamoto (♂-f. *nawai*, ♀-f. *nawai* and ♀-f. *taketoi*) and *M. p. pruinosa* Selys (♂-f. *strigata* and ♀-f. typica). Combination of the infraspecific forms in copulation was reported for the three populations. Mainly based on marking-reobservation experiments in the field, neither habitat segregation nor reproductive isolation has been found to occur among the three infraspecific forms of the Hokkaido population, whereas a clear habitat segregation and a complete reproductive isolation between the two subspecies, *nawai* and *pruinosa*, have been demonstrated for the two Hokuriku populations. We considered that it seemed more reasonable to treat at least each of the latter two subspecies, whose taxonomic rank was given by ASAHINA (1976, *Tombo* 19: 2-16), as an independent or good species. Our present consideration not only agrees with several former workers' opinions (e.g. Y. YAMAMOTO, 1956, *New Ent.* 5: 15-22) but also reflects the habitat segregation between the latter two taxa. Based upon a critical review of many previous studies on the recognition of infraspecific forms and subdivision of the Japanese *Mnais*, we pointed out several problems which should be resolved in the near future.

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AN ANALYTICAL STUDY OF THE TERRITORIAL BEHAVIOUR OF *MNAIS P. PRUINOSA* SEL.

The observations on territorial and breeding behaviour were carried out at a mountain stream, in the upper reaches of the Ino River, Fukuoka Prefecture, during the early summer of 1979.

Two forms of males occur in the area, orange- and hyaline-winged males (♂-f. *esakii* and ♂-f. *strigata*), and only one female form with hyaline wings. Territorial behaviour between hyaline- and orange-winged males (HW- and OW-males) is initiated only by the latter, and usually leads to displacement of HW-males (K. HIGASHI, 1976, *Physiol. Ecol. Japan* 17: 109-116). However, a HW-male will sometimes enter (in tandem with a female, without courtship) in a OW-male's territory, when the OW-male is pursuing other males, though they can neither copulate there nor make the females oviposit, since they are pursued by the OW-male (K. Higashi, unpublished).

In order to observe, therefore, the behaviour of HW-males under the conditions of the absence of OW-males, OW-males were

removed everyday from the range of 500 m along the stream (experimental area) for 15 days.

In the experimental area, HW-males established their occupied areas, and drove away the other HW-males which intruded in their areas. Also, they show the same breeding behaviour (except courtship) as OW-males when females appear in their area, i.e. they can induce the females to oviposit within their occupied area after copulation. The mean frequencies of copulations observed for HW-males under natural and experimental conditions were 1.1 ± 1.1 times and 1.0 ± 1.2 times (per 20 minutes), respectively. No significant difference between the natural and experimental conditions is observed. It is suggested, therefore, that the frequency of copulations does not increase, if HW-males establish their territory in natural conditions.

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THE RATIO OF *MNAIS P. PRUINOSA* -f. *ESAKII* TO -f. *STRIGATA* AND THE DIFFERENCES IN THEIR BEHAVIOUR OBSERVED IN HIROSHIMA PREFECTURE, JAPAN

Three populations of *M. p. pruinosa* have been studied for years at Higashi-hiroshima, Hiroshima Prefecture. Each population is limited to a water system without any interchanges though the shortest distance between populations is only about 850 m. The ratio of ♂-f. *esakii* to ♂-f. *strigata* in any population remained nearly constant from year to year, but it varied significantly from one population to another. Some differences between the two forms were observed in their habitat selection, residentiality, and interfering and reproductive behaviour.

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TERRITORIALITY AND MATING SUCCESS IN *MNAIS PRUINOSA NAWAI* YAMAMOTO

Territorial and mating behaviour were studied with reference to mating success (success in copulation and then leading females to oviposition sites within the territory) at a stream in Kyoto.

Territories of ca. 2-3 m in width were established along the river side. Territorial males had several perching sites with a good view over their territories and some oviposition sites (reeds, twigs, debris, algae etc.) in their territories. Territorial males copulated with females in their territories and the females oviposited there. Only one out of thirteen territorial males kept territory throughout the 12-day observation period. Most males often changed from territorial to non-territorial and vice-versa.

Males being highly successful in mating tended to maintain the territories for a relatively long period, but unsuccessful ones tended to abandon their territories and became non-territorial or changed territory sites. Non-territorial males were almost always unsuccessful in mating, (only one copulation was observed but did not proceed to oviposition). Territorial males were mostly successful but, in some cases, they also failed to mate. These observations seem to be explained by: (1) Males that have territories with good oviposition sites to which many females come, can easily copulate and make them oviposit; (2) Males that have territories to which a few females come, can not provide oviposition sites for females; (3) Few females come to non-territorial males.

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COMPARATIVE STUDY OF REPRODUCTIVE BEHAVIOUR OF SEVEN GENERA OF CALOPTERYGIDAE

The reproductive behaviour of seven calopterygid genera is discussed in relation to habitat utilization of each sex. (1) Both sexes prefer shady environments (e.g. *Vestalis*, *Psolodesmus* and *Echo*). These species have a narrow distribution range and have many allied species in the same genus. Male territories are situated near oviposition sites. The female spends most of her time at the forest floor, avoiding male interference. When a female is ready to oviposit she comes to a

male's territory; they copulate without courtship display. — (2) The male prefers a sunny environment, but the female prefers a shady one (e.g. *Mnais p. pruinosa*). Other details as in (1). — (3) Both sexes prefer a sunny environment (e.g. *Mnais p. nawai*, *Calopteryx*, *Neurobasis* and *Matrona*). When a female approaches a male's territory, the male gives the courtship display in order to examine whether or not the female is ready to oviposit.

According to the above observations, relations between habitat utilization of each sex and the ability to thermoregulate are discussed. In the tropics, most species prefer shady environments because of their optimum temperature range (stenothermal adaptation). Such species could not disperse beyond sunny areas (e.g. mountain, large river) and have narrow distribution ranges. But, in higher latitudes, shady areas are too cool for Calopterygidae, and most species prefer sunny environments. In a sunny environment, they must control their body temperature in accordance with the fluctuating temperature (eurythermal adaptation, cf. M.L. MAY, 1978, *Odonatologica* 7: 27-47). Such species could disperse freely and have wider distribution ranges.

It should be noted that, although *M. p. pruinosa* and *M. p. nawai* are the same species, the habitat utilizations are different.

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BREEDING BEHAVIOUR OF *MNAIS P. PRUINOSA* SEL. IN KYOTO

Observations on the mating strategy were carried out in Kyoto which is inhabited by a population consisting of hyaline-winged males (♂-f. *strigata*) and females. Relationships among each male's residentiality (R), territory size (TS) height of perching site (HP) and mating success were analysed. Generally, in the area where many females come to oviposit, R. tended to be strong, TS small and HP low. There was a positive, but not rigid, correlation between the number of females which came to oviposit and the mating success of each territory holder. This may be because the increase of male density, related to that of female numbers caused some interaction (competition for females). But most males with higher mating success were those with strong R, small TS and low HP. So it is conceivable that within a species' behaviour plasticity, males with stronger R, small TS and lower HP were selected.

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POPULATION STUDIES ON *MNAIS PRUINOSA NAWAI* YAMAMOTO AND *M. P. PRUINOSA* SEL. COEXISTING IN A CREEK

The observations were carried out at the Yu-no-kawa Creek, Kanazawa, Ishikawa Prefecture.

The main results obtained by a marking-release-recapture method from a viewpoint of population ecology were as follows: (1) *nawai* emerged at the lower reaches, whereas *pruinosa* emerged at the upper reaches of the study area; — (2) the emergence periods of the two subspecies were synchronous with each other; — (3) the peak of the emergence period in *nawai* was May 10 which was about 10 days earlier than that in *pruinosa*; — (4) the behaviour during the maturation period was different in the two subspecies — *nawai* tended to move away, whereas *pruinosa* tended to remain near their emergence sites; — (5) after 10 days of maturation, both subspecies returned to the place where they had emerged. 72.7% of *nawai* and 75.0% of *pruinosa* individuals marked during the emergence period returned and, considering the mortality during the maturation period, few adults must have emigrated to some other creeks); — (6) during the reproductive period, a clear habitat segregation was recognized between them; — (7) fluctuation of population size and survival rate were estimated by G.M. JOLLY's (1965, *Biometrika* 52: 225-247) method; — (8) the total numbers of emerging individuals in the creek in a flight season were estimated as about 250 in *nawai* and as 950 in *pruinosa*, respectively; and — (9) it was suggested that the fertility in *nawai* was higher than that in *pruinosa*.

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