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DISTRIBUTION, NATURAL HISTORY AND RELATIONSHIPS OF *ISCHNURA ERRATICA* CALVERT (ZYGOPTERA: COENAGRIONIDAE)

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I. erratica, previously poorly known, has been found to be locally common between southwestern British Columbia and the San Francisco Bay region of California. It is an early spring species, flying progressively later toward the north; extreme dates are 23 March and 8 August. Adults typically occur at beaver ponds but inhabit other fresh-water habitats as well. Behavior is atypical for *Ischnura* but rather similar to many species of *Enallagma* and *Coenagrion*. Other attributes of the species indicate it may occupy a primitive position within the genus.

INTRODUCTION

Ischnura erratica was described by CALVERT (1895) from a male and a female from Mendocino County, California, and a male and female from Olympia, Thurston County, Washington. It was again briefly mentioned by KENNEDY (1917) as occasional about ponds at Palo Alto, Santa Clara County, California. Since that time, the species has been cited from the three Pacific states only once, in the description of its larva (CANNINGS & DOERKSEN, 1979). It is a testimony to the much greater knowledge of the Odonata of British Columbia compared to that of the Pacific coast of the United States that the species is much better known at the northern end of its range than through all the rest of it. Beginning with OSBURN (1905) and extending through a series of reports (WALKER, 1927, 1953; WALKER & RICKER, 1938; WHITEHOUSE, 1941), the presence of *I. erratica* in

southern British Columbia has become increasingly well documented, culminating in the surveys of SCUDDER et al. (1976) and CANNINGS & STUART (1977) that gave 15 localities for the species. At present there are 19 known localities in British Columbia, 13 in Washington, 5 in Oregon and 7 in California.

DISTRIBUTION

Ischnura erratica is still not well known, but a rough sketch of its distribution is now possible (Fig. 1). The picture presented is basically one of distribution through the coastal lowlands of southwestern British Columbia, western Washington and Oregon and northwestern California. The British Columbia records are from the Fraser valley west of Hope, southern Vancouver Island and the Gulf Islands, and the west coast of Vancouver Island north to Tahsis. Despite the lack of records, it is probable the species also occurs north along the Strait of Georgia to at least Quadra Island. The northern limit of the range of *I. erratica* may be considerably farther up the coast than the records indicate; there have been very few insect collections between Campbell River and Kitimat.

The southernmost record to date is that of KENNEDY (1917) at Palo Alto, California, and we would not be surprised to find it farther south, perhaps to the Santa Barbara region, as the coastal areas between the San Francisco and Los Angeles re-

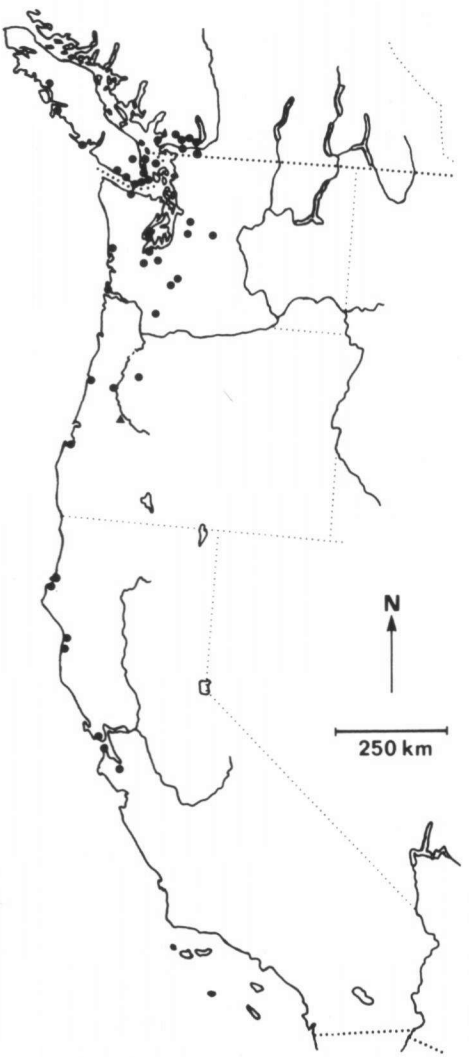

Fig. 1. Distribution of specimen records of *Ischnura erratica* on the Pacific coast of North America. Triangle in Oregon represents a county record with no exact locality specified.

gions are poorly sampled for Odonata. Although *I. erratica* is listed from Baja California (WALKER, 1953), we know of no such record. This anomaly may stem from the fact that the original description of *I. erratica* is in a paper about that region (CALVERT, 1895). The California records are all coastal or near-coastal, but in Washington the species has been taken as far inland as the 2200' (670m) contour west of Stevens Pass, King County, and in Oregon it occurs up the Willamette River as far south as Corvallis, Linn County. Probably it is distributed throughout the Puget Sound Lowland and at least the lower Willamette and Fraser valleys as well as along the coast.

PHENOLOGY

Little-known species are often eventually found to be common at some time and/or place, and *I. erratica* is no exception. On several occasions DRP has seen young or teneral individuals in great numbers, for example in late April of two different years at Ocean City State Park, Grays Harbor County, Washington, and at Shore Acres State Park, Coos County, Oregon. At the latter locality about 160 individuals emerged from a patch of *Myriophyllum* sp. 4m in diameter in an ornamental pond during one hour (10:30-11:30h) on 23 April 1978. At Pitt Meadows, British Columbia, on 28 April 1976, G.P. Doerksen found numbers of *I. erratica* emerging from a small pond inside the dyke of the Alouette River. On 2 May 1976, 30 exuviae and 10 teneral adults were observed at the same locality. Details of emergence are documented by CANNINGS & DOERKSEN (1979).

On only one occasion were mature adults seen in large numbers in Washington, at a pond 5.5 mi. (9km) west of Stevens Pass, King County, on 17 June 1969. In California, Rosser W. Garrison collected large series of adults near Fort Bragg, Mendocino County, on 12 June 1976 and near Alpine Lake, Marin County, on 13 May 1978. George P. Doerksen (pers. comm.) has recorded mature adults in considerable numbers as late as 13 July (1978, Tahsis), the most northerly locality from which the species is known.

We suspect the relative rarity of *I. erratica* in collections owes mainly to its early flight season. It is one of the earliest species to appear everywhere it occurs (23 March in California, 23 April in Oregon, 21 April in Washington and 30 April in British Columbia). The last flight dates (15 June in California, 22 July in Oregon, 7 August in Washington and 8 August in British Columbia) fall in mid-summer when many species of Odonata are at their peak abundance. During the period when this species is flying in some numbers, weather conditions in its range are generally adverse for Odonata activity (cloudy, windy, often raining), and because of this it is seldom encountered even when the collector ventures into the field. Not until July do sunny, warm days become a regular feature of the climate in the range of *I.*

erratica, and in that month dragonflies become common and dependably present; by that time the flight season of this species is almost over.

ADULT BEHAVIOR

I. erratica is unique among Pacific coast *Ischnura* and different from other *Ischnura* species we have observed in the field (including all the North American species except the very rare *I. gemina*). Typically in this genus adults occur in marsh vegetation, often with the sexes in about equal numbers, the tenerals remaining in the vicinity of their emergence until maturity. Thus, the whole life cycle is passed in a relatively restricted area. In *Enallagma* and many other coenagrionid genera, on the contrary, tenerals leave the water and wander widely, returning to the water when mature. *I. erratica* is much more similar to an *Enallagma* or *Coenagrion* in its behavior than it is to other *Ischnura*. Young individuals can be found well away from the water. Males rest flat on rocks and logs as much as on vegetation, a trait shared by *Argia* but uncommon in other coenagrionids. They may be encountered entirely in the open, well away from edge vegetation, and they fly rapidly across the water when disturbed. Most *Ischnura* (including *capreola, cervula, damula, demorsa, denticollis, perparva, posita, prognatha* and *verticalis* of North America and *elegans* and *pumilio* of Europe) that we have encountered disappear into marsh vegetation when disturbed. *I. barberi* and *I. ramburi*, although somewhat larger and more conspicuous than most other *Ischnura*, also are strongly tied to herbaceous vegetation in or beside the water. Only *I. kellicotti* of eastern North America is as atypical as *I. erratica*; it is a species of open water that typically forages from, and breeds on, water lilies (*Nuphar* and *Nymphea*). Adults perch flat on water lily leaves, unlike other *Ischnura*, which usually perch on stems or leaf tips. *I. erratica* also commonly perches flat on floating leaves, for example *Potamogeton* and *Brasenia*, like *I. kellicotti*, as well as on substrates used by other species of *Ischnura*. These two species are similar in being more robust than is usual among other members of the genus, and *I. erratica* is the largest species (measured by hind wing length) of *Ischnura* in the New World.

Copulation has been recorded from 6 May (1976, Pitt Meadows) to 26 July (1978, Tahsis). Observed copulation has been timed to last from 62 to 84 minutes. CANNINGS & DOERKSEN (1979) reported that during copulation "The male occasionally vibrates the forewings, bringing them slowly forward to an angle of 45° in front, then vibrates them back again over the hindwings. At this time the female is lifted, by the grip of the male's anal appendages on the female's prothorax, 30° off her perch. At the climax of this action, the male's forewings are flicked back with an audible snap, apparently striking the female, who is then lowered to the grass blade." Doerksen (pers.

comm.) noted a variation on this action while observing a pair copulating on a *Carex* leaf on 26 July 1978 at Tahsis. The female, gripped by the male, was bounced off the platform three times in rapid succession, but without the wing slapping seen at Pitt Meadows. Doerksen also observed an instance of interspecific tandem linkage at Tahsis on 26 July 1978 involving a male *I. erratica* with a mature male *Lestes disjunctus* in tow.

Oviposition has been noted from 7 May (1976, Pitt Meadows) to 15 July (1978, Tahsis). Females oviposit unaccompanied by males, and the eggs are placed under water in plant tissue, either in standing stems or floating vegetation. Females have been observed laying eggs in the emergent culms of *Cinna latifolia* and *Dactylis glomerata*, in floating *Carex* stems and in submerged mats of *Sphagnum* moss. The larvae inhabit submerged vegetation.

BREEDING HABITAT

WHITEHOUSE (1941) felt the rarity of *I. erratica* might be attributed to "strict requirements in its breeding place" and described its preference as a "shallow, sun-lit, hard bottomed, reedy marsh". Now that we know more about the species we can agree its requirements are probably more stringent than those of its congeners in the region; nevertheless, it is evident it inhabits a greater range of habitats than Whitehouse assumed.

Most ponds at which *I. erratica* has been seen in Washington are beaver ponds, small and relatively shallow, with clear water and entirely or partially wooded banks. Aquatic vegetation varies greatly but is always present. This apparent habitat preference may in part be an artifact of the abundance of this type of pond, the only aquatic habitat appropriate for lentic dragonflies in much of forested western Washington. The ornamental pond at Shores Acres State Park, Oregon, is clearly not produced by beavers, but it is shallow, clear, and surrounded by trees. Another *I. erratica* pond, at Morton, Lewis County, Washington, is open, shallow and fringed with grasses. On the contrary, extensive cattail (*Typha latifolia*) marshes around large lakes such as Lake Washington and Lake Sammamish in Seattle do not appear to support populations of *I. erratica*. In British Columbia, too, almost all localities where the species is known to occur are ponds or small, shallow lakes in or near forests. Two localities differ from this: the "sunlit runway" at Cultus Lake (WHITEHOUSE, 1941) and the pond at Pitt Meadows, which is within the dykes of the Alouette River. The latter pond is periodically flooded by the river and is completely in the open, surrounded only by grasses. In addition, most of the British Columbia water bodies have soft, muddy bottoms rather than the hard one described by Whitehouse; the consistency of the substrate seems not to be a limiting factor in the distribution of the species.

Predominant plants at various British Columbia localities vary. At the Tahsis pond, major species are *Nuphar polysepalum*, *Sparganium minimum* and floating *Sphagnum*, while at Pitt Meadows the emergent vegetation is mainly the grasses *Dactylis glomerata* and *Cinna latifolia*. On Pender Island, *I. erratica* occurs at a pond surrounded by *Typha latifolia*, *Carex rostrata* and *C. aquatilis*, with *Eleocharis palustris* and *Hippuris vulgaris* the main emergent species. At Weston Lake on Saltspring Island *Utricularia vulgaris* and *Sparganium* sp. are the dominant plants where *I. erratica* occurs. At many of the Washington localities *Carex* spp. and *Lysichitum americanum* are common. At two ponds *Typha latifolia* is the dominant edge species, mixed with *Iris pseudacorus* at one of them. At two ponds bog vegetation is prevalent, including *Ledum groenlandicum* and *Kalmia occidentalis*. *Potamogeton* sp. is the dominant floating plant at two localities, mixed with *Brasenia schreberi* at one of them. Again it is clear that *I. erratica* occurs in a fairly wide variety of habitat types.

Most of the water bodies involved are either more or less neutral in pH or are slightly acid. The pond at Pitt Meadows had a pH of 7.2 on 2 May 1976 (CANNINGS & DOERKSEN, 1979). The ponds and lakes supporting *Sphagnum* normally would have a pH less than 6.5. Mike Lake, Golden Ears Provincial Park, which is surrounded by such acidophile plants as *Myrica gale*, *Ledum groenlandicum* and *Sphagnum*, has a pH of 4.5 in mid-summer.

RELATIONSHIPS

In many ways *Ischnura erratica* diverges from the other North American members of its genus. The position of the origin of vein M_2 has been repeatedly listed as diagnostic for *Ischnura*, at least to distinguish it from many other coenagrionid genera. In most specimens of *I. erratica* this vein arises near the fifth antenodal in the forewing and near the fourth antenodal in the hindwing, as in species of *Enallagma*. In all other North American *Ischnura* the same point of origin is nearer the fourth antenodal in the forewing and the third antenodal in the hindwing, irrespective of the size of the species. In addition, the females of *I. erratica* are rather *Enallagma*-like (WALKER, 1953, and our own observations), the behavior is definitely *Enallagma*-like, and the larva, although conforming for the most part to the generic diagnosis of *Ischnura* (CANNINGS & DOERKSEN, 1979), could pass for an *Enallagma* because of its robustness and the relatively less acuminate tips of its caudal lamellae.

We believe this species is indeed in the genus *Ischnura*, based on overall appearance, larval morphology and penis structure, but it is clearly an aberrant member of the genus. *Ischnura* is a worldwide genus, encompassing a wide variety of species, and it would be profitable to assemble enough

specimens and information to reassess its limits. The monotypic *Anomalagrion*, for example, is much more like typical *Ischnura* than are some of the species now included in the latter genus. North American genera that may be closely related to *Ischnura* include *Zoniagrion* and *Hesperagrion*, and it may be that *I. erratica* shares characters with some of these monotypic and poorly known genera.

The restriction of this species to the humid Pacific coastal region may indicate its antiquity within the genus *Ischnura*. The only other dragonflies endemic to this region are *Tanypteryx hageni*, which is one of the most primitive Odonata of North America, and *Gomphus kurilis*, *Octogomphus specularis* and *Ophiogomphus bison*, all three in a family generally considered of long existence. In addition, relict species of other ancient groups inhabit this area, for example the aplodontia (*Aplodontia rufa*) and the tailed frog (*Ascaphus truei*), among the most primitive living rodents and frogs respectively. Thus it is tempting to speculate that *I. erratica* is more like members of related genera than most *Ischnura* because of its possession of primitive character states than because of its divergence from a typical *Ischnura* mode.

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