Dragonflies and damselflies (Insecta: Odonata) of the Republic of the Marshall Islands

By Donald W. Buden*

Abstract
Seven species of Odonata are recorded from among the numerous atolls and mid-ocean reef islands that make up the Republic of the Marshall Islands (RMI). They include two Zygoptera (damselflies: Tanymecosticta sp. and Ischnura aurora) and five Anisoptera (true dragonflies: Anax guttatus, Diplacodes bipunctata, Pantala flavescens, Tholymis tillarga, and Tramea transmarina). The damselfly Tanymecosticta sp. is known only from a single WW II-era extralimital record reported here for the first time. Breeding is confirmed for the six other species, which are widely distributed in the Pacific and often further afield. The frequently cited record of Pantala flavescens as being the first odonate and one of the first insects to colonize Bikini Atoll after cessation of nuclear testing requires verification. Additional surveys on many of the Marshall Islands not yet sampled for odonates will doubtless result in many new locality records. However, small island size, limited habitat diversity and water resources for breeding, and large distances from potential source populations contribute to an impoverished odonate fauna, and few, if any, species are likely to be added to the list. The six species known to inhabit the Marshall Islands make up the entire known odonate faunas of many other low, coralline islands in the west-central Pacific.

*Author E-mail: don_buden@comfsm.fm
Introduction

The insect order Odonata, including the suborders Zygoptera (damselflies) and Anisoptera (true dragonflies), is poorly known in the Pacific island nation of the Republic of the Marshall Islands (RMI). Many of the 34 atolls and mid-ocean reef islands that make up the RMI have not been surveyed specifically for odonates, and others have been incompletely sampled, with specimens collected only opportunistically and often ancillary to other studies--records of odonates are confirmed for 15 atolls and one of five stand-alone islands.

Among the earliest records are the larvae and an imago collected by Reverend Benjamin G. Snow on Ebon Atoll and identified as *Anax guttatus* by Cabot (1881). Another larva that Snow collected on Ebon was identified by Cabot (1890) as “Tramea spec.” and referred to *T. transmarina propinqua* by Lieftinck (1962). Snow’s specimens are in the Museum of Comparative Zoology, Harvard University (MCZ). The collection dates are unknown but Snow was a missionary on Ebon from 1862 to 1877 and had visited the atoll earlier during the 1850’s (Buck 2005).

Schnee (1904) commented briefly on specimens of *A. guttatus*, *Diplacodes bipunctata*, and *Pantala flavescens* that he obtained on Jaluit Atoll, probably between 1899 and 1903. Baker (1951) stated that Schnee spent approximately one year (1899-1900) on Jaluit during which time he obtained records of birds, and Spennemann (2000) indicated that Schnee was the government physician on Jaluit from 1900 to 1903. Schnee’s odonate specimens were identified by Peter Kempny, who listed them in a separate publication (Kempny 1904).

Asahina (1940) provided the first comprehensive review of the Anisoptera (dragonflies) of Micronesia wherein he recorded *A. guttatus*, *D. bipunctata*, *Tholymis tillarga*, *P. flavescens*, and *T. transmarina* (under *T. limbata*) from the Marshall Islands. His sources included Schmidt’s (1938) check-list of the Odonata of Oceania, along with specimens from his own collection and
those in Kyushu Imperial University collected by Teiso Esaki on Wotje and Jaluit Atolls in November 1937.

Following WWII, numerous scientific studies were conducted in the Marshall Islands by visiting American scientists. Some specimens were also collected by military personnel, especially in the northern islands, including Bikini and Enewetak Atolls, which were being used for nuclear weapons testing, and Kwajalein Atoll, the site of a military base. New locality records of insects appeared in a few widely scattered publications during the 1940’s and 50’s, and sporadically thereafter, but few odonates were recorded.

Henry K. Townes, an entomologist with the U.S. Department of Agriculture, conducted an entomological survey of Micronesia during May-August 1946 that included visits to Enewetak, Kwajalein, Jaluit, Ailinglaplap, Majuro, and Likiep Atolls in the Marshall Islands. He (Townes 1946) briefly commented on odonates that were previously recorded in the Marshalls, and one specimen each of *D. bipunctata* and *T. transmarina* that he collected on Likiep Atoll and a *D. bipunctata* collected on Majuro Atoll are in entomology collections of the Smithsonian Institution.

Arthur C. Cole (entomologist, University of Tennessee) was a member of the Bikini Scientific Resurvey team in July and August 1947. The purpose of the resurvey was to assess insect populations on Bikini Atoll following Operation Crossroads atomic bomb tests. Cole (1949) recorded 13 species of ants from Bikini in one paper and 55 other species of insects (no odonates among them) in another (Cole 1951).

During the summer of 1950, Robert L. Usinger (University of California, Berkeley), and Ira La Rivers (University of Nevada) conducted insect surveys on Arno Atoll. Usinger and La Rivers (1953) reported that adult damselflies [presumably *Ischnura aurora*] were seen in the vicinity of taro pits and that dragonfly larvae were observed in wells, cisterns and taro pits. Anax
*guttatus* was the only odonate species mentioned in their report, but one each of *A. guttatus*, *D. bipunctata*, and *P. flavescens* collected by La Rivers on 21 May, 18 July, and 2 August, respectively, are listed in the Smithsonian Institution online entomology database.

In January, 1958, Typhoon Ophelia passed directly over Jaluit Atoll in the southern Marshalls. In April of that year, a team of seven scientists that included J. Linsley Gressitt, Chair of the Entomology Department, Bishop Museum, arrived at Jaluit to study the effects of the storm (Blumenstock 1961). Gressitt’s (1961) report on the terrestrial fauna states that larvae of a damselfly and two species of dragonflies were observed in many of the old Japanese water cisterns or oil tanks. Lieftinck (1962) recorded *I. aurora, D. bipunctata, and P. flavescens* collected by Gressitt on Jabwar (Jaluit) Island during April-May 1958.

Lieftinck’s (1962) review of the Odonata of Micronesia remains the most comprehensive study on odonates among the Mariana Islands, Caroline Islands, Gilbert Islands (now a part of Kiribati), and the Marshall Islands. This work includes locality records accompanied by detailed discussions of taxonomy and biogeography, and phylogenetic relationships.

William B. Jackson, Professor of Zoology, Bowling Green State University, observed dragonflies on Enewetak Atoll over several summers during the mid-1960s. He recorded exuviae and several larval instars present in a rain-filled concrete instrument bunker on Engebi Island that was constructed during the era of nuclear weapons testing in the 1940s and 50s (Jackson 1968). He collected one adult identified as *P. flavescens* by J. L. Gressitt and remarked that based on appearance alone, at least one other species was present (Jackson 1968).

Bernard B. Sugerman of the Entomology Program, U.S. Army, reported on insects and other arthropods that he and others collected on Kwajalein Atoll during the mid-to-late 1960s (Sugerman 1972). The list included four species of odonates—*A. guttatus, D. bipunctata, P.*
flavescens, and T. transmarina. In a later report on insects that he himself collected on Kwajalein during 1971-1974, Sugerman (1979) included Tholymis tillarga.

The 1987 publication of a two-volume treatise on the natural history of Enewetak Atoll (Devaney et al. 1987a,b) summarized the results of research conducted at the mid-Pacific Research Laboratory during its 30 years of operation (1954-1984). G. Allan Samuelson and Gordon Nishida, entomologists at the Bishop Museum, contributed the chapter on insects and other terrestrial arthropods (Samuelson and Nishida 1987). The only odonates they recorded for Enewetak Atoll are P. flavescens, based on Jackson’s (1968) report, and T. transmarina based on a sight record by E. H. Bryan, Jr. in 1975. No new locality records of Odonata in the Marshall Islands were published over the next three decades.

The present study reports odonates from Maloelap, Namdrik and Mili Atolls, and Mejit Island for the first time and new locality records for Ailinglaplap, Majuro, and Arno Atolls based on observations and collections I made during June-August 2016 and June-July 2017. I observed odonates on all islands visited during this study.

Study Area

The Pacific island nation of the Republic of the Marshall Islands (RMI) includes over 1,000 small, low-lying coralline islands scattered across nearly 2,000,000 km$^2$ in the west-central Pacific Ocean (between 4 and 15° N and 160 and 173° E), but with a total land area of only about 181 km$^2$ (Unicover Corporation 2016). The islands are distributed among 29 atolls and five stand-alone, mid-ocean reef islands in a double chain approximately 1,300 km long (northwest to southeast) and 1,150 km wide—the Ralik Chain in the west and Ratak Chain to the east (Table 1, Figure 1). None of the islands is more than 5.0 km$^2$ in area (most being less than 1.0 km$^2$), and most are no more than 2-4 m above sea level, with the highest point being 10 m on Likiep Island,
Likiep Atoll, The islands are geologically recent having emerged from the sea no more than a few thousand years ago (Dickinson 2003, 2004, 2009).

Annual rainfall ranges from as little as 635 mm in the northern Marshalls to more than 4,000 mm in the south (National Biodiversity Team of the Republic of the Marshall Islands 2000), and the vegetation correspondingly grades from xerophytic forest and scrub in the north to more mesic woodlands in the south (Mueller-Dombois and Fosberg 1998). Buden and Tennent (2017) give a brief overview of terrestrial environments in the RMI and Mueller-Dombois and Fosberg (1998) provide detailed descriptions of habitats.

There are no freshwater streams or lakes in the Marshall Islands (Johnson 2012, U.S. Fish and Wildlife Service, n.d.), although some islands support brackish ponds (U.S. Fish and Wildlife Service, n.d.). A water sample I collected about 10 cm below the surface along the southeastern shore of Mejit Island Pond, which occupies 5.0 ha on the northern end of the island, measured 6,442 micro-Siemens/cm, well within the range of brackish water (1,500 to 15,000 μS/cm) cited in Watling (2007); the pH was 9.23. Freshwater habitats are largely confined to transient pools of rainwater in natural or anthropogenically produced depressions such as taro pits (for cultivation of Cyrtosperma merkusii and other aroids), bomb craters from WW II, and roadside puddles and drainage ditches. Open wells that tap into the subsurface freshwater lens, plastic tanks and cement cisterns that collect and store rainwater, and rainwater that accumulates in tree holes and leaf axils (phytotelmata) also contribute to this limited resource.

MATERIALS AND METHODS
I observed and collected odonates in the Marshall Islands during two summers as part of a study assessing biodiversity in the RMI: in 2016--Namdrik Atoll (Namdrik Island, 28 June-5 July), Ailinglaplap Atoll (Buoj Island 8-10 July, Jeh Island 11-12 July), Mili Atoll (Mili Island 21-28 July), Arno Atoll (Arno Island 1-3 August), and Majuro Atoll (Majuro Island at various times
totaling about three weeks during 22 June-9 August, Eneko Island 14-15 July, and Anil Island 5 August); in 2017—Mejit Island (26 June-3 July), Maloelap Atoll (Tarawa Island 10-17 July), Majuro Atoll (Majuro Island, at various times totaling about four weeks during 15 June-26 July). An observation I made of *P. flavecens* ovipositing on Kwajalein Atoll, 20 June 2002, during an unscheduled, weather-related, in transit stop-over, is included.

Abundance categories are appraisals based on incidental observations during the 2016/2017 surveys: common (at least 25 encounters on most days, often many more), fairly common (approximately 10-25 encounters on most days), uncommon (usually no more than 10 sightings per day and unobserved on some days), scarce (known only from one or a few sightings). Codes for breeding criteria are: C (male and female in copula), T (male and female flying in tandem), O (female ovipositing), OT (female ovipositing in tandem with male), L (larvae), E (exuviae).

Records gleaned from the scanty and widely scattered literature and from museum specimens (some previously unreported in the literature) are summarized and consolidated, previous studies are briefly described, and at least one source (in most cases the primary source) is given for each locality record if not included in Lieftinck (1962). Place names and statistical data for islands, including number of islands and total land area are from Buden and Tennent (2017) and based largely on Bryan (1971). Specimens were netted during walks along roads, forest trails, broad, open areas, and wherever standing water was available; numbers of males and females collected during each of the 2016 and 2017 surveys are indicated in the species accounts. Measurements of salinity and pH of the Mejit Pond water sample were obtained with a Solinist conductivity meter and KRK KP-10 pH meter, respectively.
RESULTS
SPECIES ACCOUNTS
Suborder Zygoptera
Family Isostictidae

*Tanymecosticta* sp.
An extralimital record of an unidentified species of *Tanymecosticta* from Kwajalein Atoll is attributed to human-assisted transport and reported here for the first time—see discussion.

Family Coenagrionidae

*Ischnura aurora* (Brauer)
The Gossamer Damselfly ranges from Pakistan and India eastward to southern China and southeastward to the Indo-Australian Archipelago and Oceania (Dow et al. 2013). In the Marshall Islands, Lieftinck (1962) recorded it from Utrik, Wotje, Ailinglaplap, Arno, and Jaluit Atolls and Kili Island, and the Smithsonian online entomology database lists one specimen (USNMENT 331930) collected on Majuro Atoll, “in field” [probably on Majuro Island] by R. P. Owen on 20 April 1949. None was encountered during the summer 2016 survey but I observed it on all islands visited in 2017. Specimens: 2017--8♂/7♀. Breeding confirmed (Table 2) based on observations during this study and Gressitt’s (1961) remarks on damselfly larvae being present in many old Japanese water cisterns or oil tanks on Jaluit Atoll in April 1958. These almost certainly pertain to *I. aurora* as Lieftinck (1962) recorded adults collected by Gressitt on Jabwar (Jaluit) Island in April 1958. Excluding the single anomalous record of *Tanymecosticta* sp., no other species of damselfly is known from the Marshall Islands.

Suborder Anisoptera
Family Aeshnidae

*Anax guttatus* (Burmeister)
The Lesser Green Emperor ranges from the Seychelles to India, eastward to Japan and southeastward to the Indo-Australian Archipelago and Oceania (Sharma 2010); it has recently been recorded as far east as French Polynesia (Marinov et al. 2016). In the Marshall Islands, Lieftinck (1962) recorded it from Kwajalein, Wotje, Ailinglaplap, Arno, Jaluit, and Ebon Atolls, and Kili Island. Additionally, the Smithsonian online entomology database lists one specimen
during a recent visit to the MCZ, I examined two pinned *A. guttatus* from Ebon Atoll, presumably collected by Snow, but found no data to supplement what Cabot (1881) had written. This species was observed occasionally on all the atolls visited during the present study, and was usually seen in flight over water, roads, and broad, open, sparsely vegetated areas, including vacant lots, school yards, and airstrips. The one female collected during the 2016 survey had flown into a room at the Arno Beachcomber Lodge, and the only one collected in 2017 was at the edge of Mejit Island Pond. Specimens: 2016--6 ♂/1 ♀; 2017--9 ♂/1 ♀. Breeding confirmed (Table 2).

**Family Libellulidae**

*Diplacodes bipunctata* (Brauer)

The Red Percher Dragonfly ranges widely from Indonesia eastward to French Polynesia (Rowe and Marinov 2013). In the Marshall Islands, Lieftinck (1962) recorded it on Wotje, Ailinglaplap, Jaluit and Ebon Atolls. Additionally, the Smithsonian online entomology database lists specimens collected by H. K. Townes on Likiep Island, Likiep Atoll on 30 August 1946 (USNMENT 273781), and Majuro Atoll, [probably on Majuro Island] on 20 August 1946 (USNMENT 273780), and another (USNMENT 3737820) collected on Ulen Island, Arno Atoll by I. La Rivers on 18 July 1950. This species was scarce on Namdrik Atoll (only one seen over a period of one week), but was common on all other atolls visited during the 2016 and 2017 surveys. It was observed wherever water was present as well as in grassy, weedy areas along roadsides, fields, and vacant lots. Specimens: 2016--11 ♂/5 ♀; 2017--11 ♂/10 ♀. Breeding confirmed (Table 2).

*Pantala flavescens* (Fabricius)

The Wandering Glider is a circumtropical species recorded on all continents except Antarctica (Boudot et al. 2016). Lieftinck (1962) recorded it on Kwajalein, Wotje, Ailinglaplap,
Arno, Jaluit, and Ebon Atolls. It has been reported also from Bikini Atoll (Silsby 2001), but the record is unverified—see discussion. I observed *P. flavescens* regularly on all the islands I visited during this study, usually in flight over roads, water-filled cisterns, and open sparsely vegetated areas. Specimens: 2016--10♂/10♀; 2017--5♂/5♀. Breeding confirmed (Table 2).

*Tholymis tillarga* (Fabricius)

The Evening Skimmer is widespread throughout the Old World tropics, including Oceania (Clausnitzer 2016), but records from the Marshall Islands have hitherto been scanty. Lieftinck (1962) recorded it on Wotje Atoll citing Asahina’s (1940) paper that reported a male collected on Wotje Island by T. Esaki on 27 November 1937, and Sugerman (1979) recorded it on Kwajalein Atoll on Roi-Namur Island during at least one of his visits in the early 1970s. It is probably fairly common to common on most of the atolls, the paucity of records being in large part due to its crepuscular habits making it less likely to be encountered during daytime surveys. The 26 exuviae I collected from the walls of a single cistern on Namdrik Atoll are the most I obtained of a single species at one site during the present study--17 were collected on 28 June and nine on 5 July 2016, but how many, if any, of the latter were newly emerged and not simply overlooked earlier is unknown. I observed *T. tillarga* regularly over water on all islands surveyed during the present study, mainly at dusk and dawn, and occasionally flushed individuals from grassy, weedy, shrubby areas while walking along forest trails during midday. Specimens: 2016--6♂; 2017--9♂/1♀. Breeding confirmed (Table 2).

*Tramea transmarina* Brauer

The Red Glider Dragonfly ranges widely from Southeast Asia southward and eastward to the Indo-Australian Archipelago and Oceania (Wilson et al. 2013). Lieftinck (1962) recorded it in the Marshall Islands from Kwajalein, Likiep, and Arno Atolls. Asahina (1940) recorded a male and female collected by T. Esaki on Wotje Island, Wotje Atoll, on 24 November 1937, and a female collected by N. Tosawa on Ebon Atoll (Ebon Island?) on 14 February 1934. I observed *T.
transmarina regularly on all the atolls (and on Mejit Island) surveyed during the present study. It was often seen at open water-filled cisterns and on patrol over roadsides and open, sparsely vegetated areas. Specimens: 2016--11♂/5♀; 2017--11♂/5♀. Breeding confirmed (Table 2).

**DISCUSSION**

Excluding the single anomalous, extralimital record of *Tanymecosticta* sp. from Kwajalein, six species of odonates are known from the Marshall Islands. They include one zygopteran, *Ischnura aurora*, and five Anisoptera—*Anax guttatus, Diplacodes bipunctata, Pantala flavescens, Tholymis tillarga*, and *Tramea transmarina*. All are widely distributed in the Pacific and often well beyond and are included in the “Least Concern” category in the IUCN Red List of threatened species (IUCN 2017). All six have a high dispersal potential and an ability to utilize the limited and often transient natural and anthropogenic water resources available on these tiny remote islands. A relatively rapid larval development and ability to withstand drought conditions may also contribute to their success. *Pantala flavescens*, for example, is able to complete development from egg to imago in about five to six weeks (Suhling et al. 2004), and its larvae are able to remain dormant in dry mud for at least several months (Van Damme and Dumont 1999).

*Seasonality and breeding*

Little is known of seasonality and breeding of odonates in the Marshall Islands. Most of the collections and observations are from the summer months, June-August, with only a scattering of records from other times of the year. To what extent populations may at times include migrants is unknown. All six of the indigenous species have been recorded in summer (this study), and Esaki (in Asahina 1940 and Lieftinck 1962) collected all six on Wotje Atoll in November 1937. Warm, tropical conditions persist throughout the year and breeding probably takes place year-round. At
the Mejit Island Pond, during 26 June-3 July, I regularly observed *I. aurora*, and *D. bipunctata* in copula, and in tandem, with many *D. bipunctata* also ovipositing and with tenerals of both species being frequently flushed from the dense grasses and sedges along the edge of the pond. On Tarawa Island, Maloelap Atoll, 10-17 July, I observed females of *T. tillarga* ovipositing in the same cistern from which imagos were also emerging—nine exuviae were collected on the cistern walls on 14 July, two others from subsequent emergences were collected on 15 July, and five others on 16 July. On Majuro Island, Majuro Atoll, I observed many *P. flavescens* in tandem, in copula, and ovipositing during 15 June -26 July 2017, and all 34 larvae that I collected from a water-filled pit on 26 and 27 July were *P. flavescens* of different sizes ranging from 9.0 to 23.0 mm and presumably representing several different age groups.

To what extent breeding may be impacted by seasonal differences in rainfall is uncertain. Rainfall occurs throughout the year but is more frequent during May-November (wet season) than December-April (dry season). On Majuro, the only island for which I have data for the summers of both 2016 and 2017, incidental observations indicate a much higher incidence of breeding activity in 2017. Breeding activity in 2016 may have been negatively impacted by the severe 2015/2016 El Niño event that caused extreme drought conditions throughout the Marshalls and adjacent areas of the Pacific. The total accumulated rainfall on Majuro for November 2015-July 2016 was 1,229.4 mm compared with 2,797.1 mm over the same period during 2016/2017 (data from National Weather Service, Guam).

*Species assemblages*

Additional surveys to include the many islands of the RMI from which odonates have not yet been recorded, all or most of which presumably have not yet been searched for odonates, doubtless will produce many new locality records, but new additions to the species list are less likely. Small island size, limited and often temporary water resources (breeding sites), and
distance from potential source populations contribute to an impoverished odonate fauna in the Marshalls. The same six species appear to make up the entire odonate faunas of many island groups throughout the Marshalls (Table 1) as well as those of many other small, ecologically impoverished islands in the west-central Pacific. They are the only odonates known from the Gilbert Islands, eastern Kiribati (Lieftinck 1962), and the Republic of Nauru (Buden 2008), immediately to the south, and, with the exception of the single endemic species Hemicordulia erico, they compose the entire odonate fauna of Kosrae, a high, volcanic, and ecologically more diverse island in the eastern Carolines, immediately to the west of the Marshalls (Buden and Paulson 2003). In assessing ecological distribution of odonates on Pohnpei, eastern Carolines, Paulson and Buden (2003) indicated that these six species appear to be characteristic of open, disturbed lowland habitats including temporary ponds and artificial water bodies, which describes the predominant ecological conditions found throughout the Marshalls.

_Agrionoptera sanguinolenta_ Lieftinck co-occurs with these six species on many islands in the Carolines (Buden 2004, Buden and Paulson 2004) but is unrecorded in similar habitats in the Marshall Islands. However, the nominate subspecies, which is endemic to Pohnpei and its satellite islands, has been recorded as a probable storm transported vagrant in the Bonin Islands, Japan, about 2,600 km north of its native range (Karube and Sugimura 1997, Karube in Buden 2004), thus indicating a potential for long-distance dispersal. The absence of _A. sanguinolenta_ in the Marshalls (and on Kosrae) may qualify as another example for Marinov’s (2015) list of “oddities” in Pacific Odonata biogeography.

_Pantala flavescens_ on Bikini Atoll: A record in need of verification
An Internet search for information on _Pantala flavescens_ reveals numerous articles stating this species was the first odonate and one of the first insects to settle on Bikini Atoll following cessation of nuclear weapons testing. If a source is mentioned, it refers either directly or indirectly to Silsby’s (2001) book on dragonflies of the world, and presumably the statement on
Michael Parr reminded me that this species was one of the very first insects (of any Order) to recolonize Bikini Atoll in the Pacific after the cessation of atomic testing.” No date or other details are given, and Parr (pers. comm.—email to Milen Marinov 14 December 2016) indicated that he cannot now recall or locate the source for the statement.

Bikini Atoll was the site of 23 nuclear weapons tests beginning with Operation Crossroads in July 1946 and concluding with the Operation Hardtack series that was completed in July 1958; a hiatus of five years of no testing occurred during 1949-1953. Biological surveys were hastily made just before Operation Crossroads (but not before DDT was spread across the island to control flies bothersome to Navy personnel), and a resurvey was conducted a year later in July and August 1947 (Henson 2000). There are no records of odonates from Bikini from any time prior to the test and none in Cole’s (1951) report that included insect collections made during the resurvey. Hines (1966) remarked that teams of scientists examined Bikini annually from 1946 to 1950 and 1954 to 1958, and that an ecological resurvey was done in 1964 after six years of no testing and no visits by humans. However, there are no records of odonates from Bikini in Lieftinck’s (1962) comprehensive review of the Odonata of Micronesia, nor in more recent literature reviewed for the present study. Also, no unreported odonate specimens from Bikini were found during recent searches of the Smithsonian collections (Flint pers. comm.) or in the Bishop Museum collections (Polhemus pers. comm.), both institutions being principle recipients of insects collected in the northern Marshalls during and just after WW II.

The likelihood of *P. flavescens* being on Bikini Atoll is high given its widespread occurrence throughout the Marshalls (this study). Polhemus (pers comm.) remarked that the Bishop Museum has a male *P. flavescens* collected on Engebi Island, Enewetak Atoll, by Y. Oshiro on 6 January 1951 (slightly less than three years after conclusion of the Sandstone series of tests in May 1948). This specimen, together with several others in the Bishop Museum
collected on Kwajalein from January 1945 to November 1972, indicates the presence of *P. flavescens* in the northern Marshalls before and during the time of testing. But claims of its presence on Bikini and rapid recolonization after nuclear testing are unverified. Furthermore, stating that *P. flavescens* was the first odonate to settle on the atoll following cessation of testing presupposes its complete elimination from the atoll during the test and discounts the possibility of individuals surviving on islands elsewhere on the atoll at some distance from the blast site. Rats (*Rattus rattus*?), for example, appear to have survived nuclear tests that were being conducted at nearby Enewetak Atoll (Hines 1966, Jackson 1969, Jackson et al. 1987).

The Castle Bravo test conducted on Bikini Atoll in March 1954 released the greatest amount of energy of any test conducted in the Marshall Islands, the 15 megaton yield being more than twice the yield predicted (Ford 2015). Nine members of the detonation preparations team (firing party) remained on the atoll on Eneyu Island, about 33 km from the blast site, in a well protected bunker, and suffered no casualty (Clark and Cahn 1957). During nuclear testing in the Marshalls, the larvae of odonates, if not the adults, probably would receive some protection in wells or in water-filled cement-lined cisterns and bunkers, which are breeding sites that are frequently utilized by present day populations of odonates in the RMI (Jackson 1968 and this study). In any event, there does not appear to be any definitive evidence to support the claim that *P. flavescens* was the first odonate to recolonize Bikini, and apparently no published record of any odonate from Bikini Atoll. Possibly, in the initial report of this record, Bikini Atoll was confused with nearby Enewetak Atoll, where nuclear tests were also being conducted. A number of specimens of *P. flavescens* collected at Enewetak during and shortly after the period of testing are in the Bishop Museum, and Jackson’s (1968) account of *P. flavesens* breeding there was based on observations made during the mid 1960s, about six or seven years after cessation of testing in 1958.
Tanymecosticta sp. on Kwajalein Atoll: A probable instance of human-mediated transport

The damselfly family Isostictidae includes more than 40 species among 12 genera (Schorr and Paulson 2017) and ranges from the Moluccas eastward to Australia, New Guinea, New Britain, the Solomon Islands, and New Caledonia (Donnelly 1993, Kalkman and Orr 2013, Houston et al. 2014). The genus Tanymecosticta “is widespread on New Guinea, has a single species in New Britain, and another on Woodlark on the east, and occurs on Misool and Tanimbar on the west” (Donnelly 1993:125). Species of Tanymecosticta, as well as those of other isostictid genera, tend to occupy well shaded stream or riverine habitats (Michalski 2012, Polhemus pers. comm.).

The online entomology database of the National Museum of Natural History (Smithsonian Institution) includes a record of Tanymecosticta sp. (USNMENT 347632) collected on Kwajalein Atoll by David G. Hall on 5 August 1944. Additional information on a typewritten note accompanying the specimen and provided by Oliver Flint (pers. comm.: email 13 January 2017) states “abdomen incomplete/ Isostictidae/ Possibly a Tanymecosticta spec. (only a single ♀)/ Family quite new for the archipelago!/ It was determined by Lieftinck in 76.” In his email, Flint (pers. com.) indicated that the specimen lacks abdominal segments beyond the basal portion of segment six, that it may be a male though catalogued as female, and that authorship of the typed note is uncertain.

The natural occurrence of a species of Tanymecosticta (or of any isostictid) on Kwajalein is unlikely given the lack of suitable habitat [no freshwater streams; surface freshwater largely limited to pools of rainwater] as well as the distance from potential source populations across a broad expanse of open ocean. The isostictid population nearest to Kwajalein is that of T. filiformis on New Britain, about 2,300 km to the southwest. In all probability, the specimen from Kwajalein arrived on military transport, possibly with the shuttling of supplies and equipment, or, more likely in this instance, during the travels of military personnel engaged in entomological
surveys. David G. Hall, who collected the specimen, was a medical entomologist in the United States Army during WW II, being in service from 1942 to 1946. During the latter part of the war, he travelled extensively throughout the Pacific assigned to Air Transport Command with the general mission of reducing the impact of arthropod-borne pathogens on the war effort (R. D. Hall pers. com.). How much time he spent on Kwajalein is unknown but his son, R. D. Hall, remarked (pers. comm.) that he often spoke of his time there. The places he visited during and shortly before his stay on Kwajalein are also undetermined. The specimen of *Tanymecosticta* sp. collected on 5 August 1944 is the only specimen listed as collected by Hall on Kwajalein, and a gap of about eight months exists in the database before the entry of any of Hall’s specimens collected prior to that date—*Agrionoptera insignis*, Guadalcanal, October 1943. However, the military orders he received in September 1944 (photocopy provided by R. D. Hall--email 31 January 2017) directing him to spend the next 140 days conducting “sanitary, malarial and entomological surveys” in Saipan, Guam, Australia (Townsville, Amberley), New Guinea (Port Moresby, Nadzab, Hollandia), Guadalcanal, New Caledonia, Fiji, Tarawa (Gilbert Islands), Nanomea (Ellice Islands), and Canton, although well after the date of the Kwajalein record, nevertheless attest to his widespread travels among Pacific islands, including many localities within the geographic range of the genus *Tanymecosticta*.

Although the possibility of mislabeling exists in such cases of unusual extralimital records, there is no reason in this instance not to accept the locality data as being correct. Hall was a professional entomologist and a taxonomist of excellent repute—the only Army entomologist to receive the Legion of Merit in WW II (Hall et al. 1986). Also, relating to this anomalous distribution record, Polhemus (pers. comm.) pointed out that a number of unusual records have come out of Kwajalein in the past, probably attributable to the atoll being a logical and frequently used intermediate refueling point between Australia/New Guinea and Hawaii, but
that none of the species have become established owing to the absence of their ecological requirements in the Marshalls. Hall’s record of an isostictid damselfly on Kwajalein may serve as yet another example of the potential of human-assisted transport—a mode of dispersal in the Odonata that is sometimes overlooked (Marinov 2015).

ACKNOWLEDGMENTS

I thank Mabel Peter and Molly Helkena of the Historic Preservation Office, Majuro, for their assistance in the initial planning of this project and Clarence Luther, mayor of Namdrik Atoll for providing accommodations and local transport during my week-long stay at Namdrik. Mark Stege and Franky Erra of the Marshall Islands Conservation Society assisted with arranging travel to and accommodations at Mejit Island and Maloelap Atoll (Tarawa Island), Tuvuki Ketedromo, Paul Paul, and Dolores de Brum (Marshall Islands Environmental Protection Agency) provided measurements of salinity and pH for the Mejit Pond water sample, and Charles “Chip” Guard and Clint Simpson (National Weather Service, Guam) provided monthly rainfall summaries for Majuro Island. The inset for the Marshall Islands location map was provided courtesy of Marshall Weisler. I am also grateful to Dan Polhemus (Bishop Museum) and Oliver Flint (National Museum of Natural History) for information on specimens from the Marshall Islands in their respective institutions. I thank Milen Miranov, Michael Parr, and Pam Taylor for their efforts in attempting to locate the source of the Bikini Atoll record of *Pantala flavescens*, and appreciate information provided by R. D. Hall on his father, David G. Hall, relating to the Kwajalein record of *Tanymecosticta* sp. For addressing queries relating to Pacific odonates and odonate source materials, I thank Kari Anderson (librarian, University of Washington), John Abbott, Ron Clause, Rod Crawford, Rachel Hawkins, Michael Michalski, Dennis Paulson, and Richard Rowe. I also thank Phil Perkins for permission to examine
specimens in the Entomology Department at the MCZ and Whit Farnum for his invaluable assistance during my visit to the museum.

**Literature Cited**


Clark, J. C., and R. Cahn. 1957. We were trapped by radioactive fallout. Saturday Evening Post, July 1957. 230:17-19, 69-71.


Downloaded on 2 March 2017.


## TABLE 1

<table>
<thead>
<tr>
<th>Land Area (km²)</th>
<th>No. of Islands</th>
<th>Zygoptera</th>
<th>Anisoptera</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tany</td>
<td>Isch</td>
<td>Anax</td>
</tr>
<tr>
<td><strong>RALIK CHAIN</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ujelang Atoll</td>
<td>1.74</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>Enewetak Atoll</td>
<td>5.85</td>
<td>44</td>
<td>+</td>
</tr>
<tr>
<td>Bikini Atoll</td>
<td>6.01</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Rongelap Atoll</td>
<td>7.95</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>Rongerik Atoll</td>
<td>1.68</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Ailinginae Atoll</td>
<td>2.80</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Wotho Atoll</td>
<td>4.35</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>Ujae Atoll</td>
<td>1.86</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Lae Atoll</td>
<td>1.45</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Kwajalein Atoll</td>
<td>16.39</td>
<td>93</td>
<td>[+]b</td>
</tr>
<tr>
<td>Lib Island</td>
<td>0.93</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Namu Atoll</td>
<td>8.86</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td>Jabot Island</td>
<td>0.57</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Ailinglaplap Atoll</td>
<td>14.69</td>
<td>56</td>
<td>+</td>
</tr>
<tr>
<td>Jaluit Atoll</td>
<td>11.34</td>
<td>91</td>
<td>+</td>
</tr>
<tr>
<td>Kili Island</td>
<td>0.93</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Namdrick Atoll</td>
<td>2.77</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ebon Atoll</td>
<td>5.75</td>
<td>22</td>
<td>+</td>
</tr>
<tr>
<td><strong>RATAK CHAIN</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bokak Atoll</td>
<td>3.24</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Bikar Atoll</td>
<td>0.49</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Utrik Atoll</td>
<td>2.43</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Taka Atoll</td>
<td>0.57</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Mejit Island</td>
<td>1.87</td>
<td>1</td>
<td>+</td>
</tr>
<tr>
<td>Ailuk Atoll</td>
<td>5.36</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td>Jemo Island</td>
<td>0.16</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Likiep Atoll</td>
<td>10.26</td>
<td>65</td>
<td></td>
</tr>
<tr>
<td>Wotje Atoll</td>
<td>8.18</td>
<td>75</td>
<td>+</td>
</tr>
<tr>
<td>Erikub Atoll</td>
<td>1.53</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Maloelap Atoll</td>
<td>9.82</td>
<td>75</td>
<td>+</td>
</tr>
<tr>
<td>Aur Atoll</td>
<td>5.62</td>
<td>43</td>
<td></td>
</tr>
<tr>
<td>Atoll</td>
<td>Latitude</td>
<td>Longitude</td>
<td>9.17</td>
</tr>
<tr>
<td>---------------</td>
<td>----------</td>
<td>-----------</td>
<td>------</td>
</tr>
<tr>
<td>Arno Atoll</td>
<td>12.95</td>
<td>103</td>
<td>+</td>
</tr>
<tr>
<td>Mili Atoll</td>
<td>14.91</td>
<td>92</td>
<td>+*</td>
</tr>
<tr>
<td>Nadikdik Atoll</td>
<td>0.90f</td>
<td>28</td>
<td></td>
</tr>
</tbody>
</table>

*a Tany, Tanymecosticta sp.; Isch, Ischnura aurora; Anax, Anax guttatus; Dipl, Diplacodes bipunctata; Pant, Pantala flavescens; Thol, Tholymis tillarga; Tram, Tramea transmarina.

b Known only from a single anomalous extralimital record attributed to human-mediated transport.

*First report, this study.
TABLE 2

Evidence of Odonates Breeding\textsuperscript{a} in the Marshall Islands during this Study\textsuperscript{b}, with Additional Records from the Literature\textsuperscript{c}

<table>
<thead>
<tr>
<th>Locality</th>
<th>Isch</th>
<th>Anax</th>
<th>Dipl</th>
<th>Pant</th>
<th>Thol</th>
<th>Tram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enewetak</td>
<td>C, T</td>
<td>O\textsuperscript{SR}</td>
<td>C, OT</td>
<td>O\textsuperscript{SR}</td>
<td>O\textsuperscript{SR}</td>
<td>L\textsubscript{(L)}</td>
</tr>
<tr>
<td>Kwajalein</td>
<td>O\textsuperscript{SR}</td>
<td>C, T, OT</td>
<td>O\textsuperscript{SR}</td>
<td>O\textsuperscript{SR}</td>
<td>T\textsuperscript{SR}</td>
<td></td>
</tr>
<tr>
<td>Likiep</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mejit</td>
<td>C, T</td>
<td>O\textsuperscript{SR}</td>
<td>C, OT</td>
<td>O\textsuperscript{SR}</td>
<td>O\textsuperscript{SR}</td>
<td>L\textsubscript{(L)}</td>
</tr>
<tr>
<td>Maloelap</td>
<td>O\textsuperscript{SR}</td>
<td>OT</td>
<td>O\textsuperscript{SR}</td>
<td>T, E\textsuperscript{16}</td>
<td>C, T, E\textsuperscript{6}</td>
<td></td>
</tr>
<tr>
<td>Ailinglaplap</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Majuro</td>
<td>T</td>
<td>O\textsuperscript{SR}</td>
<td>C, T, O, OT,</td>
<td>C, T, OT, L\textsuperscript{34}</td>
<td>C, T, O, OT\textsuperscript{SR}</td>
<td></td>
</tr>
<tr>
<td>Arno</td>
<td>O\textsuperscript{SR}</td>
<td>OT\textsuperscript{SR}</td>
<td>C, T, O, OT,</td>
<td>C, T, OT, L\textsuperscript{34}</td>
<td>C, T, O, OT\textsuperscript{SR}</td>
<td></td>
</tr>
<tr>
<td>Jaluit</td>
<td>L\textsubscript{(G)}</td>
<td>L\textsubscript{(G)}</td>
<td>L\textsubscript{(G)}</td>
<td>C</td>
<td>E\textsuperscript{26}</td>
<td></td>
</tr>
<tr>
<td>Namdrik</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ebon</td>
<td>L\textsuperscript{(C1)}</td>
<td>L\textsuperscript{(C1)}</td>
<td>L\textsuperscript{(C1)}</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mili</td>
<td>O\textsuperscript{SR}</td>
<td>C, T\textsuperscript{SR}, O, OT</td>
<td>OT, E\textsuperscript{3}</td>
<td>E\textsuperscript{3}</td>
<td>T, E\textsuperscript{1}</td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{a}C, pair in copula; T, pair in tandem; O, female ovipositing; OT, female ovipositing in tandem with male; L, larvae (with number collected); E, Exuviae (with number collected); SR indicates sight record(s) only, all other records include one or more vouchers. Abbreviation of species names as in Table 1.

\textsuperscript{b}24 June-2 August 2016, 15 June-26 July 2017, and one \textit{P. flavescens} I observed ovipositing in a thin film of rain water at one end of an otherwise empty swimming pool on Kwajalein Island, Kwajalein Atoll, 20 June 2002. Records from Mejit Island and Maloelap Atoll are from 2017, Majuro records are given as 2016/2017, all others, excluding \textit{P. flavescens} on Kwajalein, are 2016.

\textsuperscript{c}Indicated as subscripts: (C1), Cabot (1881); (C2), Cabot (1890); (G), Gressitt (1961 and Gressitt in Lieftinck 1962); (J), Jackson (1968); (L), Lieftinck (1962).
Figure 1. Location map for the Marshall Islands.