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THE MOSQUITOES OF YELLOWSTONE NATIONAL PARK (DIPTERA: CULICIDAE)

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ABSTRACT. Twenty-nine species belonging to 4 genera of mosquitoes are reported for Yellowstone National Park, WY (USA). Phenology, local distribution, and ecology of each species are addressed along with taxonomic notes on certain species. Mermithid (nematode) parasitism of some of the park's *Aedes* species is also discussed.

INTRODUCTION

Yellowstone National Park, encompassing nearly 1.0 million hectares (2.5 million acres) in northwestern Wyoming, is the largest national park in the lower continental United States. Straddling the Continental Divide, the park occupies a high mountainous plateau that includes narrow strips of Montana to the north and west and a small portion of Idaho to the southwest (Fig. 1). The area is covered mainly with montane forests of lodgepole pine (*Pinus contorta*) interspersed with open meadows, valleys, and lakes. Spruce (*Picea engelmannii*) and fir (*Abies lasiocarpa*) dominate the upper elevations. Yellowstone Lake in the central region of the park is the largest alpine lake in North America. Elevations range from 1,620 m (5,314 ft.) at the North Entrance to several peaks exceeding 3,000 m (10,000 ft.). Average elevation in the park is approximately 2,250 m (7,500 ft.). Heavy winter snowfall and numerous streams and springs provide water for innumerable mosquito breeding sites with considerable habitat diversity.

Several physiographic features isolate the Yellowstone Plateau ecologically from surrounding areas. Severe drops in elevation to the north, west, and east result in ecotones unfavorable for most of the Yellowstone mosquito species. To the south, Grand Teton National Park and Jackson Hole are drier, more sparsely forested, and lower in elevation (Jackson Lake is 2,064 m [6,772 ft.]). Much of the surrounding area is covered with grasses and sagebrush (*Artemisia tridentata*), and less than one-third of the species found on the Yellowstone Plateau occur here. Many of the snow pool *Aedes* species in Yellowstone are effectively isolated due to climatic and elevational differences on all sides.

The first published report on the mosquitoes of Yellowstone (Dyar 1923) listed 20 species and included brief notes on each. Additional papers contributing to the fauna include Dyar (1929), Rees and Harmston (1948), Nielsen (1969, 1982), and Savage et al. (1994). The known culicid fauna of the park now includes 29 species belonging to four genera (Table 1). The present study was undertaken to confirm and update the work of Dyar (1923, 1929) and others who have reported on the mosquito fauna of Yellowstone National Park. Our collections extend over a 30-year period. We collected all of the species in the current list, except *Aedes campestris, Aedes dorsalis,* and *Anopheles punctipennis.* Most specimens were collected as larvae using dippers and reared to adults in the laboratory. Adult females also were collected with killing tubes while biting and both sexes were netted by sweeping near larval habitats or in swarms.

Due to the great variation in annual snowfall and temperatures in the spring and early summer, the appearance of individual species in known larval sites may vary as much as 2 weeks from year to year. Therefore, we have not included dates for individual collections, choosing instead to discuss seasonal distribution in general terms later in this paper. Unfortunately, Dyar (1923) did not include dates for his collections. We believe his collections were made in late June and early July as these are the dates on specimens we have examined in the Smithsonian collection from his Yellowstone material. Specimens from our Yellowstone collections are now stored at the University of Utah.

NOTES ON THE SPECIES

Aedes campestris: This species was reported from the Gibbon Meadows by Rees and Harmston (1948). We have not collected *Ae. campestris* in the park and the reported specimens, which were not indicated as larval or adult, could not be located for confirmation.

Aedes canadensis: Widely distributed. Larvae are sometimes found associated with thermal areas. Immatures are able to tolerate highly mineralized and acidic conditions; we have collected them in pools with a pH as low as 3.2.

Aedes cataphylla: Widely distributed. Larvae occupy shallow grassy pools in open meadows, usually appearing as soon as snow melts at these sites.

Aedes cinereus: Widely distributed. Larvae of this very small species are most often collected from shallow pools associated with willows and where the bottoms are colored by the presence of yellow or orange growths of bacteria and algae. Especially common in the Bechler area in the southwestern corner of the park.

Aedes diantaeus: Sparsely distributed, having

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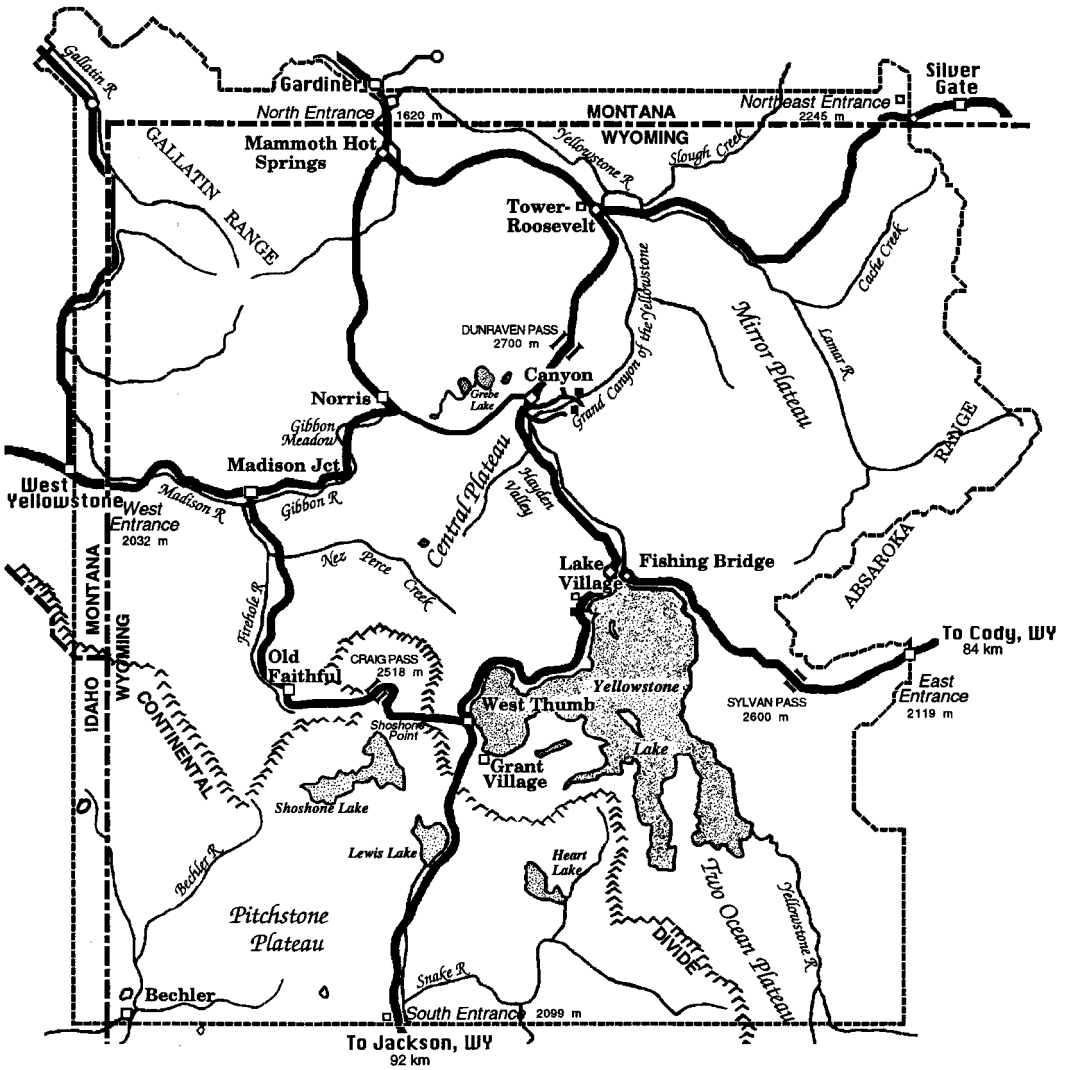

Fig. 1. Yellowstone National Park.

been collected only near Canyon, Lake Village, and Grebe Lake. Larvae occur in shallow grassy forest pools. This species is unique in that males do not swarm but mate with females as they are attempting to bloodfeed (Dyar 1922). Larvae have extremely long antennae that they extend ventrally and use as legs to move slowly across the bottom while their mouth brushes bring up food.

Aedes dorsalis: Dyar (1923) reported this species from 3 localities in the park: Camp Roosevelt, Old Faithful, and Canyon. Despite intense collection in these areas and other locations we have not been able to find this species. We have, however, obtained some of Dyar's specimens of Yellowstone material from the Smithsonian mosquito collections and have confirmed his collections of *Ae. dorsalis* at the 3 sites noted above.

Aedes euedes, Aedes excrucians, Aedes fitchii: These 3 banded-legged species are frequently found associated together as they share a common habitat. Larvae usually occupy deeper permanent and semi-permanent pools with emergent vegetation. *Aedes euedes* is rare in the park (Nielsen 1982), whereas *Ae. excrucians* and *Ae. fitchii* are among the more abundant species.

Aedes hexodontus: Dyar described this species from the Sierra Nevada in California in 1916, but did not report it from Yellowstone. Larvae are found throughout the park in shallow grassy pools and marshes in open areas in the higher meadows and valleys, generally above 2,250 m (7,500 ft.). This is one of the more abundant species in Yellowstone and the mosquito most often collected in biting counts during July.

Aedes impiger: This Arctic species moved south during Pleistocene glaciation into the northern

Table 1. Mosquito fauna of Yellowstone National Park. Footnotes refer to published records.

Aedes campestris Dyar and Knab[1]
Aedes canadensis (Theobald)[1,2]
Aedes cataphylla Dyar[1,2]
Aedes cinereus Meigen[1,2]
Aedes diantaeus Howard, Dyar, and Knab[2]
Aedes dorsalis (Meigen)[2]
Aedes euedes Howard, Dyar and Knab[3]
Aedes excrucians (Walker)[1,2]
Aedes fitchii (Felt and Young)[1,2]
Aedes hexodontus Dyar
Aedes impiger (Walker)[1]
Aedes implicatus Vockeroth[2]
Aedes increpitus Dyar[1,2]
Aedes intrudens Dyar[1,2]
Aedes nevadensis Chapman and Barr
Aedes pionips Dyar[2]
Aedes pullatus (Coquillett)[1,2]
Aedes punctor (Kirby)[1,2]
Aedes schizopinax Dyar[4]
Aedes spencerii idahoensis (Theobald)[1,2]
Aedes ventrovittis Dyar[5]
Anopheles earlei Vargas
Anopheles punctipennis (Say)[1]
Culex tarsalis Coquillett[1,2]
Culiseta alaskaensis (Ludlow)[2]
Culiseta impatiens (Walker)[1]
Culiseta incidens (Thomson)[1]
Culiseta inornata (Williston)[1,2]
Culiseta morsitans (Theobald)[6]

[1] Rees and Harmston (1948).
[2] Dyar (1923).
[3] Nielsen (1982).
[4] Dyar (1929).
[5] Nielsen (1969).
[6] Savage, Nielsen, and Miller (1994).

Rocky Mountains of the western United States. Larvae develop in shallow grassy pools in open meadows above 2,500 m (8,000 ft.). This species is a very abundant and annoying pest at the higher elevations.

Aedes implicatus: Although widely distributed, this is one of the less common species. Immatures are usually found in overflow pools along streams or in grassy willow-lined snowmelt pools. Larvae are often associated with *Aedes increpitus.*

Aedes increpitus: Occurs throughout the park and, with *Ae. cataphylla,* is the most abundant early species. Larvae usually appear in late April or early May. It occurs in a wide variety of shallow grassy snowmelt pools primarily in open or partially shaded areas. It is the most important pest species in the park during June.

Aedes intrudens: Dyar (1923) was uncertain as to the occurrence of this species in the park. Rees and Harmston (1948) listed records of this species as questionable. We have found this species to be widespread in the park and, due to its propensity to enter dwellings, one of the more annoying species for park employees and visitors in early summer. Larvae occur in small forest pools, usually associated with other species.

Aedes nevadensis: Both Dyar (1923) and Rees and Harmston (1948) reported *Aedes communis* (De Geer) from the park. Our collections throughout the area indicate that the larvae falling into the *Ae. communis* complex all conform to the comb scale characters for *Ae. nevadensis* as reported by Brust and Munstermann (1992). We assume that Dyar's, Rees's, and Harmston's collections were actually *Ae. nevadensis.* Larvae occur primarily in small snowmelt pools in forested areas. This mosquito is an important pest species in the park. Dyar reported it as the dominant species at all of his higher elevation camps.

Aedes pionips: Widespread in forested areas but not an abundant species. The large larvae are found in larger, deeper semipermanent and temporary forest pools. Adults are among the last species to emerge in July. Although *Ae. pionips* females have been collected on human hosts, they have not been observed attempting to bite.

Aedes pullatus: Occurs throughout the park in a greater variety of snowmelt pools than any other *Aedes* species. It is also found over a wider elevational range. This species readily invades new habitats and larvae are often found in man-made excavations such as roadside depressions and postholes. Depressions left by the roots of fallen trees are a frequent larval source. Larvae mature slowly and, with *Ae. pionips,* are the last of the *Aedes* to emerge in July. Females are very aggressive biters and are an important pest species in the park.

Aedes punctor: Occurs throughout the park. Larvae usually occur in small forest pools that are at least partially shaded, often occurring in pure cultures in pools with heavy growth of bacteria and algae. Females are aggressive biters, but rarely move far from the shade of the forest.

Aedes schizopinax: This species is rare in the park and was previously known only from the Mammoth area (Dyar 1929). We have found larvae in several localities near Mammoth and also in the Old Faithful area. Larvae usually occupy pools with a high organic content. Dyar reported larvae in scummy seepage water and in game and cattle tracks. Our collections have usually been in polluted marshy areas. We have never taken this species in biting collections in the vicinity of larval sources. Host preferences for this species and *Ae. pionips* need to be determined as neither species appears to be strongly attracted to humans.

Aedes spencerii idahoensis: Dyar (1923) reported both *Ae. spencerii* (Theobald) and *Ae. idahoensis* (Theobald) from the park. All of our collections at various sites in both the larval and adult stages conform to characters in the subspecies *Ae. spencerii idahoensis* as discussed by Nielsen and Rees (1959). A few females show slight integrating characters (some scattering of light scales on the dorsum of the abdomen) toward *Ae. spencerii spen-*

cerii, but we do not believe this subspecies occurs in the park. The greatest concentration of *Ae. spencerii idahoensis* occurs in the Slough Creek area in the northeastern region of the park, where it is an extremely annoying pest. Here, larvae occur in great concentrations in oxbow lakes formed during the spring runoff of Slough Creek. Populations of this subspecies also occur in Hayden Valley, Canyon, Mammoth, and Camp Roosevelt (Lodge) areas where the open habitat of this subspecies exists.

Aedes ventrovittis: Dyar (1923) described *Aedes cacothius* from a series of biting females collected in the vicinity of Shoshone Point at 2,483 m (8,200 ft.) east of Old faithful. Dyar recognized that *Ae. cacothius* may be the Rocky Mountain representative of *Aedes ventrovittis* of the high Sierras. Subsequent examination of the syntypes by Nielsen (1969) confirmed *Ae. cacothius* to be a synonym of *Ae. ventrovittis.* Immatures of this species have now been collected in the vicinity of Dyar's type locality and at several other locations in the park at higher elevations. Large populations exist near the Grebe Lake trail head and at several sites around Grebe Lake. *Aedes ventrovittis* is the earliest emerging *Aedes* species in the park. Eggs hatch quickly in water running off banks of melting snow and larvae occur in running rivulets and small pockets through which water is continually moving. Larvae are often associated with *Ae. impiger,* whose eggs often hatch in the same sites as soon as the water stops moving. Adults of *Ae. ventrovittis* are usually on the wing by late May or early June and are an extreme nuisance for 2–3 weeks.

Anopheles earlei: Rees and Harmston (1948) reported adults of *Anopheles occidentalis* Dyar and Knab from the West Entrance of Yellowstone Park. This record undoubtedly refers to *An. earlei,* which also has the light fringed area at the tip of the wing; *An. occidentalis* is now known to be restricted to Pacific coastal areas. *Anopheles earlei* females have been collected at various sites in the park and we have taken larvae in a permanent marsh in the Slough Creek area. Our larval collections were all made in July and August. We have not looked for overwintering sites of the adults.

Anopheles punctipennis: This species appears to be rare in the park. The only record is adults collected from the Mammoth Lodge in early September by Rees and Harmston (1948).

Culex tarsalis, Culiseta incidens, Culiseta inornata: Marshy areas that contain these 3 species occur in many areas of the park. Dyar (1923) mistakenly believed that *Cs. inornata* completely replaced *Cs. incidens* in the park. Actually, *Cs. incidens* is widespread and larvae often occur in smaller, colder pools that contain snow pool *Aedes* species earlier in the season. *Culex tarsalis* often occurs in pure culture in smaller, less polluted pools and larvae can tolerate unusually warm temperatures. In the West Thumb Geyser Basin, a large concentration of larvae was collected in a small pool where the water temperature was 38°C (101°F). All of our larval collections of these 3 species were made in June, July, or August. We have no data on overwintering habits in the park.

Culiseta alaskaensis: Dyar (1923) reported a single specimen at Lake Village and noted the date, June, 26 1922, as this was the first record from the United States and Wyoming. Adults of this large species with white-banded legs have been observed and collected at various locations in the park. The only larval collections were made in a permanent marsh in the Slough Creek area where larvae were associated with *Cs. inornata* and *An. earlei.*

Culiseta impatiens: This species is widespread in the park where larvae are usually collected in late summer in small permanent pools earlier occupied by snow pool *Aedes* larvae. It is the earliest mosquito to appear on the wing. Overwintering females become active in May while snow still covers the ground. They are aggressive biters and will readily enter buildings in search of a blood meal.

Culiseta morsitans: Larvae of this species were collected in a permanent pond on the west side of Yellowstone Lake north of West Thumb in late June (Savage et al. 1994). Larvae were concentrated at the bases of clumps of semiaquatic grasses. Adult males and females were reared from these collections. This appears to be a rare species and we have no other data on its distribution or habits in the park.

POSSIBLE ADDITIONAL RECORDS

Two additional species, *Anopheles freeborni* Aitken and *Culex territans* (Walker), likely occur in the park. Both species have been collected within 56 km (35 mi.) of the park where similar habitat exists. *Aedes melanimon* Dyar and *Aedes sticticus* (Meigen) have been collected near the park but these species typically occur at much lower elevations. We have also searched without success for tree hole species, particularly *Aedes hendersoni* Cockerell, in the few stands of deciduous trees that occur in the park.

QUESTIONABLE RECORDS

Dyar (1923) reported a single specimen of *Aedes vexans* (Meigen) taken at Yellowstone Lake. He noted that it seemed out of place at his highest collecting station (2,347 m [7,700 ft.]) and that a mistake was possible. *Aedes campestris,* as noted above, is also a questionable record.

SEASONAL DISTRIBUTION OF SPECIES

Due to normally heavy winter snowfall and the high elevation of most of the park, ideal conditions for larval development usually do not occur until

late April to early June in the open meadows and valleys, and 1–2 weeks later in forested areas where the snow melts more slowly. Therefore, species that prefer exposed habitats are the first to appear. These include *Ae. ventrovittis, Ae. impiger, Ae. cataphylla, Ae. increpitus, Ae. implicatus, Ae. hexodontus,* and *Ae. spencerii idahoensis.* These species usually are on the wing during June. The remaining *Aedes* species, which occupy shaded or partially shaded forest habitats, normally complete immature development in late June or early July. Species that occupy the deeper permanent or semipermanent pools rarely complete development before July. These include *Ae. excrucians, Ae. fitchii, Ae. euedes, Ae. pionips,* and *Ae. pullatus.* The first 3 banded-legged species are also the longest lived and the only *Aedes* females that occasionally persist into late August. Most *Aedes* females in the park typically reach a peak of abundance between the 3rd week of June and the 3rd week of July. Females rapidly decline in numbers in late July and most disappear by early August.

Culiseta species that overwinter as adult females emerge in May and June, with the first larvae appearing in late June. We have collected larvae of *Cs. incidens* and *Cs. impatiens* in some habitats just after *Aedes* species have pupated or eclosed. Both larvae and adults can be found throughout the summer until early September. The life histories of *Cs. alaskaensis* and *Cs. impatiens* appear to conform closely to the observations of Frohne (1953, 1954). Larvae of *Cx. tarsalis,* another species overwintering as adult females, generally appear in late June and persist until August. No adults or larvae have been collected after the first week in August. Females and larvae of *An. earlei* have been collected in June with larvae persisting into August. Adult females probably move into overwintering sites in September.

PARASITISM BY MERMITHID NEMATODES

Mermithid parasites (Nematoda: Mermithidae) have been found in mosquito larvae developing in vernal pools near Grebe Lake (elevation 2,447 m) and along DeLacy Creek (elevation 2,438 m) northwest of Shoshone Point (Blackmore and Nielsen 1990). Preparasites infect first- and 2nd-instar larvae in the early spring (April to early May) and postparasites emerge from 4th-instar larvae at the time pupation would otherwise occur (mid-May to mid-June). The predominant host species are *Ae. nevadensis, Ae. impiger,* and *Ae. hexodontus* at the Grebe Lake sites, and *Ae. punctor, Ae. nevadensis, Ae. pullatus,* and *Ae. hexodontus* at DeLacy Creek. Other infected species include *Ae. cataphylla, Ae. cinereus, Ae. diantaeus,* and *Ae. ventrovittis.* Parasite prevalence can be as high as 93% and is consistent across species within sites (Blackmore and Nielsen 1990). Infections are invariably fatal unless the parasites are encapsulated by the host (Blackmore 1989). Species-specific differences in the expression of host immune responses to these parasites were observed in both localities. Melanotic encapsulation of parasites by larvae of *Ae. nevadensis* and *Ae. hexodontus* permits survival of some infected individuals of these species (Blackmore 1989).

Field-collected mermithids from DeLacy Creek sites are significantly larger than those from the pools near Grebe Lake but laboratory studies indicate that these differences are due to environmental rather than genetic factors (Blackmore 1991). Although the taxonomic status of these nematodes has yet to be determined, they appear to be closely related to *Romanomermis nielseni* (Tsai and Grundmann), which infects *Ae. increpitus, Ae. nevadensis,* and other *Aedes* species in southwestern Wyoming.

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