

## Characterization of a Small Population of the Orangeblack Hawaiian Damselfly (*Megalagrion xanthomelas*) in Anchialine Pools at Kaloko-Honokōhau National Historical Park, Hawai'i Island

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**Abstract.** The endangered orangeblack Hawaiian damselfly (*Megalagrion xanthomelas*) is a lowland inhabitant of freshwater and brackish wetland environments. Formerly one of the most widely distributed native insects in Hawai'i, it now appears restricted to small populations on the islands of O'ahu, Moloka'i, Maui, and Hawai'i. On Hawai'i island, anchialine pools provide important habitat for *M. xanthomelas*, and Kaloko-Honokōhau National Historical Park (Park) supports one of only a few documented populations on the western side of the island. This study aimed to estimate the population size of *M. xanthomelas* at this Park, characterize its habitat, and identify substrates on which females oviposit eggs. We conducted visual surveys for adult *M. xanthomelas* at anchialine pools during June 2016–August 2017. On average, the observed population was 10.7 individuals per month (range = 5–20; standard error = 1.3). Males were observed 6.1 times more frequently than females, likely reflecting the less cryptic nature of males compared to females. Females exhibited oviposition behavior on a variety of substrates, but small branches were used most frequently. Factors restricting this population are poorly known, but invasive fish may limit its distribution across the Park. Removal of invasive fishes from anchialine pools and 'Aimakapā Fishpond may restore much habitat for this rare species in the Park.

**Key words:** anchialine pool, Hawai'i, *Megalagrion xanthomelas*, damselfly, endangered species

Damselflies (Odonata) are common inhabitants of many shallow-water aquatic ecosystems, with nearly 3000 species recognized worldwide (Suhling et al. 2015). Most species are restricted to the margins of lakes, ponds, and streams, although some species reside in brackish environments. In Hawai'i, a single radiation within the endemic genus *Megalagrion* (Coenagrionidae) has resulted in 23 species and 5 subspecies across the

high islands of the archipelago (Polhemus 1993). *Megalagrion* occupy a variety of habitats, including streams, seeps, springs, bogs, swamps, marshes, coastal wetlands, and anchialine pools (Polhemus 1996). Additionally, *Megalagrion* have evolved to occupy moist habitats novel to Odonata, including the base of leaf axils and in litter beneath ferns and other plants (Perkins 1913, Polhemus 1996). The Hawaiian damselfly fauna also includes three intro-

duced species with which *Megalagrion* share some habitats. In contrast to most *Megalagrion*, the introduced damselflies are widespread across the Hawaiian Islands and are common in many aquatic habitats.

Ranges and population sizes of many *Megalagrion* are declining, and several species may be extinct. In recognition of these declines, six species have received federal protection under the Endangered Species Act. Included among these species is the orangeblack Hawaiian damselfly, *M. xanthomelas* (USFWS 2016). *Megalagrion xanthomelas* is unique among native damselflies in that it lives in brackish (mixohaline) coastal wetlands and anchialine pools as well as some freshwater environments. *Megalagrion xanthomelas* was once a common inhabitant of lowland habitats, including Honolulu gardens, and was found as high as 915 m elevation on the Kona Coast of Hawai'i island (Perkins 1913). Although its former range is uncertain, it may have occurred on all the high islands across the archipelago (Polhemus 1996). *M. xanthomelas* populations have declined dramatically over the past 100 years, and the species now appears to be restricted to relatively few populations on O'ahu, Moloka'i, Maui, and Hawai'i island (Polhemus 1996, Polhemus et al. 1999, USFWS 2021). This damselfly was thought to have been extirpated from O'ahu until the discovery of a solitary population in 1994 (Polhemus 1996). Considerable effort has been made to protect and expand this tenuous population (Englund 2001, Preston et al. 2007). *Megalagrion xanthomelas* is most common on Hawai'i island with several populations reported across the island (Polhemus 1996, Jordan et al. 2007).

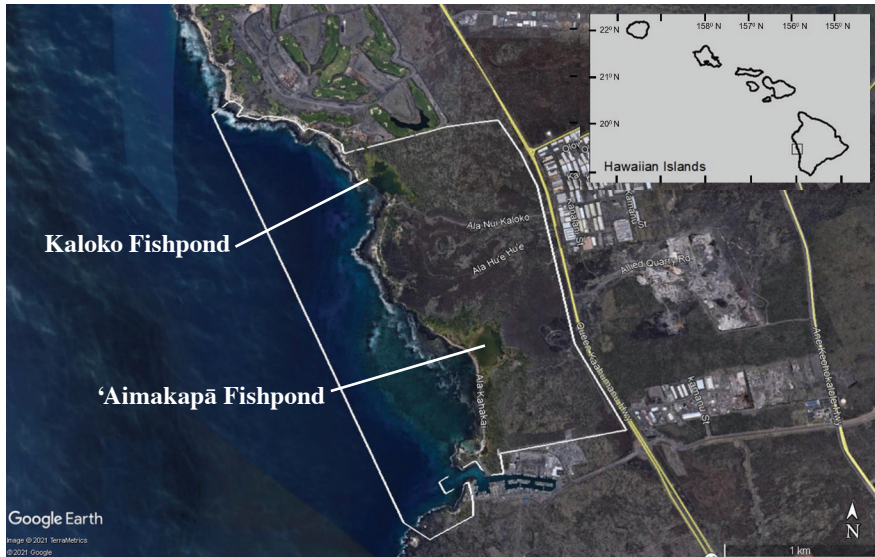
The distribution and abundance of *M. xanthomelas* is poorly known across its range, including within anchialine pool ecosystems. Anchialine pools are coastal bodies of brackish water that lack a sur-

face connection to the ocean but receive varying amounts of freshwater and seawater through subterranean cracks and other interstices (Holthuis 1973). Anchialine pools also provide important habitat for several rare and endangered shrimp species (Sakihara 2012; Seidel et al. 2015; USFWS 2020, 2021). Many anchialine pools are under pressure from a variety of anthropomorphic forces, including habitat loss from development (Hoover and Gold 2006), groundwater pollution (Brock and Kam 1997, Hoover and Gold 2006, Marrack et al. 2015) and development (Oki 1999, USFWS 2016), and the introduction of invasive fishes (Dalton et al. 2013, Havird et al. 2013, Marrack et al. 2015, Seidel et al. 2015). A longer-term threat includes rising sea level, which is projected to result in higher salinity levels and the inundation of many pools (Marrack et al. 2015, Marrack 2016, Marrack et al. 2020).

The aims of our study were to document the distribution and abundance of *M. xanthomelas*, describe its habitat, and identify preferred substrates for ovipositing in anchialine pools at Kaloko-Honokōhau National Historical Park (Park). The Park contains the highest density of anchialine pools along the Kona Coast of Hawai'i island and protects important habitat for *M. xanthomelas* and other anchialine pool invertebrates.

## Methods

**Study site.** Kaloko-Honokōhau National Historical Park protects nearly 5 km<sup>2</sup> (Marrack and Beavers 2011) of coastal land, 6 km north of Kailua-Kona on the dry western side of Hawai'i island (Figure 1). Honokōhau Small Boat Harbor, Queen Ka'ahumanu Highway, and the Kohanaiki Private Club Community border the Park on the south, east, and north, respectively. The Park was formed in 1978 to protect a rich assemblage of archaeological, cul-



**Figure 1.** Location of Kaloko-Honokōhau National Historical Park along the Kona Coast of Hawai‘i. Anchialine pools supporting *Megalagrion xanthomelas* are located centrally in the Park between Kaloko and ‘Aimakapā Fishponds.

tural, and historical features, including two large brackish fishponds. Brackish wetland habitat within the Park includes over 200 anchialine pools (Marrack and Beavers 2011; K. Annandale, National Park Service, written communication, 2022) as well as Kaloko and ‘Aimakapā Fishponds. Anchialine pools range in size from  $<1 \text{ m}^2$  to about  $570 \text{ m}^2$ , and many of the smaller pools dewater during low tide. Kaloko and ‘Aimakapā Fishponds are considerably larger, occupying about 4.5 and 12 ha, respectively. The Park is dissected by several ‘a‘ā and pāhoehoe lava flows ranging in age from 1000 to 10,000 yrs (Marrack and Beavers 2011). Anchialine pools are located throughout both flow types. Vegetation is largely dominated by alien plants, although numerous native species persist, particularly in coastal strand and wetland habitats (Pratt 1998).

Anchialine pools occur throughout the Hawaiian Islands, but the majority lie along the rocky coasts of the leeward

side of Hawai‘i island. Most of the pools at Kaloko-Honokōhau are found within the younger (1000–3000 yrs) ‘a‘ā lava flows located in the central and southern parts of the Park. Containing a mix of freshwater provided through the subsurface aquifer and saline ocean water input from the ocean, anchialine pools in the Park ranged in salinity from about 8.9 to 29.5 ppt between 2007 and 2009 (Marrack and Beavers 2011). Tidal fluctuations result in pool salinity, temperature, and volume varying over the course of the day. Bottom surface habitat within the pools naturally varies and includes silt, sand, pebbles, cobbles, and rock slabs, in addition to leaves and twigs that fall into pools from nearby vegetation. A thick layer of fine organic sediment largely derived from fish feces lined the bottoms of some pools that contained invasive fish. Types and amounts of vegetation immediately peripheral to pools vary, with the native milo (*Thespesia populnea*) and beach

naupaka (*Scaevola taccada*), and invasive Christmas berry (*Schinus terebinthifolius*), most common. Emergent vegetation, where present, primarily includes the native makaloa (or umbrella sedge, *Cyperus laevigatus*) and ‘ākulikuli (or sea purslane, *Sesuvium portulacastrum*), and the invasive pickleweed (*Batis maritima*). Many pools within the ‘a‘ā flow are devoid of peripheral and emergent vegetation.

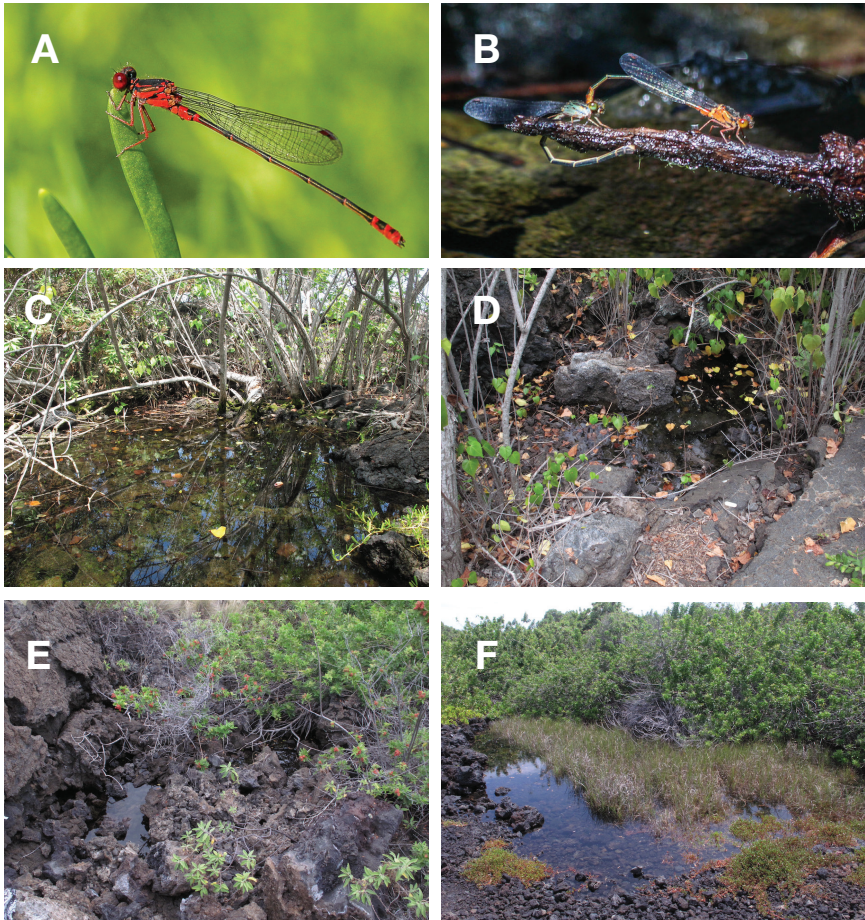
**Population census.** We conducted observations of *M. xanthomelas* at seven pools that composed “core” habitat and four pools that composed “peripheral” habitat. Core pools (7, 45, 50, 58, 62, 64, 65; Figure 2) were pools where *M. xanthomelas* were commonly found just prior to the study. Peripheral pools (11, 12, 32, 46) were pools in proximity to core pools (<50 m) and contained habitat considered favorable to supporting the damselfly (e.g., did not dewater at low tide, contained emergent or peripheral vegetation), but where *M. xanthomelas* had been observed less frequently in the recent past. Six of the seven core habitat pools are part of a complex of closely associated pools (each within about 20 m of the nearest pool). The seventh pool is located about 150 m northwest of the other six core pools. Two peripheral pools contained invasive guppies (*Poecilia reticulata*) and emergent or poolside vegetation. We surveyed core pools 1–2 times per month from June 2016–August 2017 (21–24 observation days). Peripheral pools were surveyed opportunistically over the same period (6–13 observation days). Most surveys (94.3%) were conducted during 0830–1230 although a few took place from 1230–1330 (6.7%). We did not consider the tidal cycle to influence damselfly abundance or activity, so survey dates and times were conducted independent of tides. Note that the National Park Service uses site-specific codes that designate island and ahupua‘a (a traditional Hawaiian land

subdivision) preceding unique anchialine pool numbers; all pools included in this study use the prefix HA\_Kaloko (e.g., HA\_Kaloko\_007), which has been omitted throughout the paper for brevity.

*Megalagrion xanthomelas* occupancy and abundance were estimated by quietly observing core pools for damselfly activity during one or more 15-min sessions during each observation day. Pools were generally surveyed simultaneously by 2–3 individuals, with the observers rotating among the pools each day. This rotation often resulted in pools being surveyed more than one time each day. Observers surveyed near the edge of each pool. All core pools except one were small enough so that the entire pool could be observed from one strategic location; the larger pool required changing positions 2–3 times within the observation period. *Megalagrion xanthomelas* can be difficult to detect if stationary, but individuals generally change locations, defend territories via aerial interactions with other individuals, or search for food within 15-min periods. If no damselflies were detected during the survey, then the observer gently swept the pool margins with a stick to dislodge individuals that may have gone undetected. Individual *M. xanthomelas* were identified as male or female based on color (Figure 2A and 2B). Peripheral pools were surveyed in the same manner as core pools, but on fewer occasions.

Daily abundance estimates were based on the average number of individuals observed at each pool. Similarly, surveys conducted on one or more occasions during a calendar month were averaged for analysis. In addition to surveys at core and peripheral pools, most other pools within the Park were surveyed for damselflies on one or more occasions during the study period. These additional surveys contributed to our understanding of the distributions of other Odonata in the Park but are not reported here.





**Figure 2.** Male *Megalagrion xanthomelas* perched on pickleweed (A), a tandem pair of *M. xanthomelas* perched on a small branch (B), and four of the core pools where *M. xanthomelas* were surveyed (C–F). Note that the female *M. xanthomelas* (B) is probing the tip of her abdomen on the side of a branch that is above the surface of the water. The wetness of the branch suggests that it will be submerged during high tide.

**Oviposition behavior.** *Megalagrion xanthomelas* oviposition behavior was recorded at core pools by quietly observing female activity during October 2016–August 2017. Pools selected to observe oviposition behavior were based on activity identified during the occupancy surveys conducted earlier in the day.

We considered females to exhibit oviposition behavior if they touched the

distal tip of their abdomen onto a substrate above, at, or below the surface of the water (Figure 2B). Abdominal contact with the substrate often resulted in a series of probing events at a single location. It was not possible to see if eggs were released during contact with the substrate. Oviposition behaviors were recorded as discrete events if the female flew to a new location, even if on the same substrate. At each

location where an oviposition event was observed, we recorded the substrate, the contact point relative to the surface of the water (above, at, or below), and if the female was alone or part of a tandem with a male. Male *M. xanthomelas* attach the tip of their abdomen (claspers) to the female's pronotum during and after mating (Figure 2B). This connection is generally maintained while the female oviposits on substrates within the pools and is considered a form of sperm-guarding by the male (Battin 1993).

The length of time a pool was observed depended upon damselfly activity and was generally 30–90 min in duration. Occasionally, a female departed the pool, and the same or another female returned during the observation period. It was not possible to differentiate among females, so in these instances, females observed separately were considered to be different individuals. On occasion, more than one female was observed ovipositing at a pool at the same time. Ovipositing behaviors were observed opportunistically at several other pools over the course of the study.

**Pool properties.** A suite of pool properties was measured at the core and peripheral pools. Water temperature, salinity, and pH were measured on one occasion near high tide during the survey period using a YSI Sonde (YSI Incorporated, Yellow Springs, Ohio) placed on two locations on the pool bottom. A submersible HOBO conductivity data logger (model UL24-002-C; Onset Computer Corporation, Bourne, Massachusetts) placed on the bottom of four core pools (45, 50, 58, 64) recorded changes in water temperature, salinity, and pressure (an index of the changing water levels driven by the tide) at 5-min intervals during 9 September–3 November 2016.

The physical structure of each pool was determined in several ways. First, we estimated the proportion of the pool

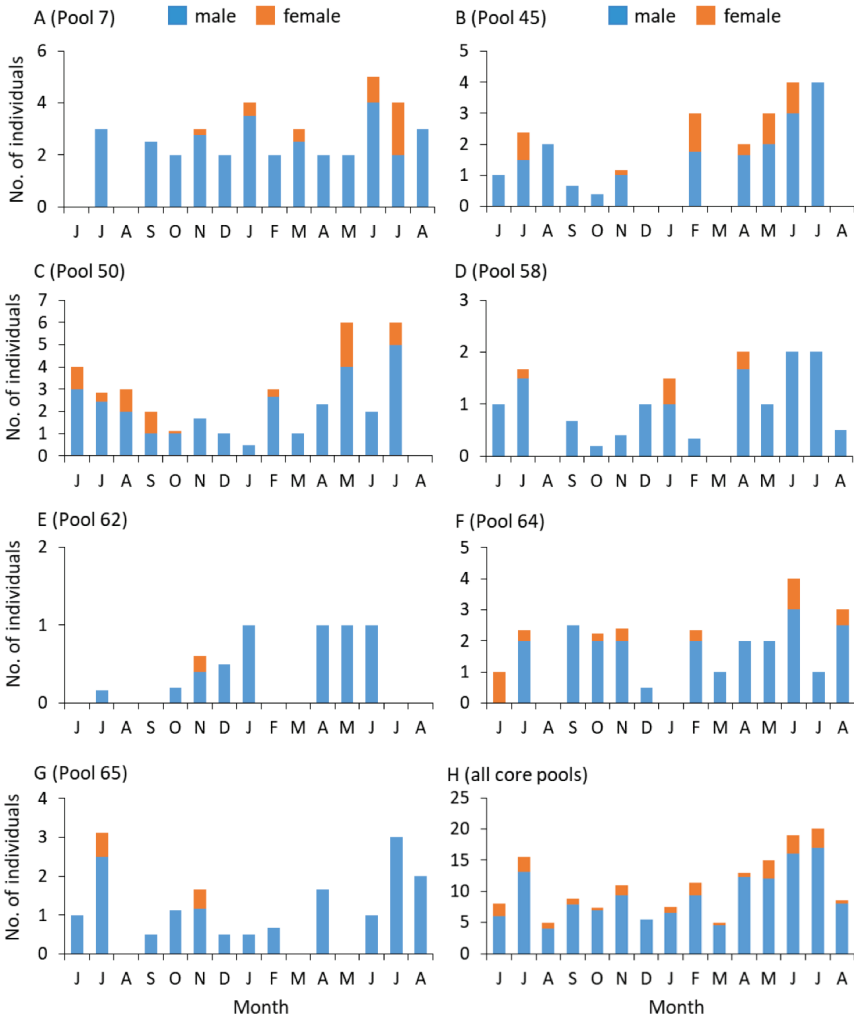
bottom occupied by substrate differing in size. The following categories were used to characterize the pools: silt and sand (<1 mm); pebbles (2–64 mm); cobbles (64–128 mm); boulders (128–512 mm); and rock slab (>512 mm). Similarly, the amount of cover (%) above the bottom substrate occupied by leaves and twigs was estimated. Finally, the amount of cover (%) provided by poolside vegetation was measured using a spherical densiometer held 0.5 m above the edge the pools at four approximately equidistant locations. The four points were averaged to provide a single value for each pool.

*Data availability.* Data and metadata associated with this paper are available at <https://doi.org/10.5066/P9W9T3ZK> (Peck and Nash 2022).

## Results

*Megalagrion xanthomelas* were recorded during all months of the study (Figure 3). The mean number of individuals observed across all of the core pools each month was 10.7 (range = 5–20; standard error of the mean (SEM) = 1.3). No clear temporal pattern in abundance emerged, although numbers were highest during July 2016 (15.5 individuals) and June and July 2017 (19.0 and 20.0 individuals, respectively) and lowest during August 2016 and March 2017 (5.0 individuals). Overall, males were 6.1 times more abundant than females (mean = 9.2 and 1.5 individuals/mo., respectively). Females were observed during all months except December 2016.

Abundance varied considerably among core pools with the highest number of individuals found in pools 7 and 50 (2.7 and 2.3/mo., respectively) and the lowest number in pool 62 (0.4/mo.). Overall, females were most abundant at pools 45 and 50 where they composed about one-fifth of all individuals (19.6 and 21.0%, respectively). Individual males and females rarely left pools during our observation



**Figure 3.** Mean number of male and female *Megalagrion xanthomelas* observed at the seven core pools (A–G) and at all core pools combined (H) during June 2016–August 2017.

periods, although tandem pairs were occasionally observed leaving one core pool in the direction of another core pool. At the peripheral pools, *M. xanthomelas* were observed at pool 11 during four of nine observations (0.7 males and 0.1 females/observation), at pool 12 during eight of 13 observations (0.8 males and 0.1 females/observation), at pool 32 during four of 14

observations (0.3 males and 0.1 females/observation), and at pool 46 during three of six observations (0.5 males/observation).

Physical and chemical properties varied considerably among pools (Table 1). The mean size of the core pools was 7.7 m<sup>2</sup> (range = 1.8–22.0 m<sup>2</sup>); in contrast, two of the four peripheral pools were much larger in size (295.3 and 566.9 m<sup>2</sup>).

One-time mean measurements ( $n = 2$ ) of water temperature, salinity, and pH at each pool were 22.6 °C, 11.8 ppt, and 7.9, respectively. Canopy cover ranged from 21.1 to 65.8% (mean = 42.8%) in core pools and 11.0 to 100% (mean = 44.0%) in the peripheral pools. Leaves and twigs were present on the bottoms of all pools, covering 5–30% (mean = 18.6%) of the core pools and 1–80% (mean = 24%) of the peripheral pools. The bottoms of the core pools were primarily composed of pebbles, cobbles, and boulders, although a layer of silt and sand dominated core pool 7. In contrast, silt and sand dominated the bottom of two of the peripheral pools.

**Ovipositing behavior.** Female *M. xanthomelas* were recorded exhibiting oviposition behaviors 299 times at six of the core pools during the study. Females were locked in tandem with males during 94.7% of the observations. Overall, oviposition behavior was observed on branches most frequently (46.8%), followed by rocks (25.9%) and leaves (floating or attached to branches; 18.3%) (Figure 4). Other substrates on which ovipositing behaviors sometimes occurred included floating algal mats, floating flowers, and emergent vegetation (9% combined). Preference for oviposition substrates varied among pools, but branches were used most frequently at three pools, while rocks and leaves were each used most frequently at one pool. The majority (58.5%) of oviposition probes took place just above the surface of the water (generally <2 cm) while slightly less than one-third (29.9%) of the probes took place below the water surface (generally <2 cm); 11.6% of the probes were at the surface (not distinguishable as above or below) (Figure 4).

## Discussion

**Distribution and population size.** Kaloko-Honokōhau National Historical Park supports a small but apparently stable population of the endangered *M.*

*xanthomelas* that is largely restricted to a complex of closely associated anchialine pools. The natural range of this population is not known, but other anchialine pools, as well as the vegetated margins of Kaloko Fishpond, may have been occupied by this damselfly in the past (Polhemus 1996). Other locations where *M. xanthomelas* have been documented along the Kona Coast include Kīholo Bay and ‘Anaeho‘omalū Bay (approximately 30 and 68 coastal km north of Kaloko-Honokōhau, respectively; Polhemus 1996) and at Pu‘uhonua o Hōnaunau National Historical Park (about 35 coastal km south of Kaloko-Honokōhau; Tango et al. 2012); the population at Pu‘uhonua o Hōnaunau was last observed in 2010 and is considered extirpated (M. Hayes, National Park Service, written communication, 2021). Elsewhere on Hawai‘i island, the nearest extant population may exist in a brackish pond at Whittington Beach Park, approximately 125 coastal km south of Kaloko-Honokōhau (Polhemus 1996). Other Hawai‘i island populations have been reported at wetlands along the Ka‘ū Coast, in anchialine pools at Keaukaha near Hilo, and along lower stretches of several streams along the Hāmākua Coast (Polhemus 1996, Jordan et al. 2007, Tango 2010). Overall, the status of *M. xanthomelas* on Hawai‘i island is poorly known and no recent surveys have been conducted.

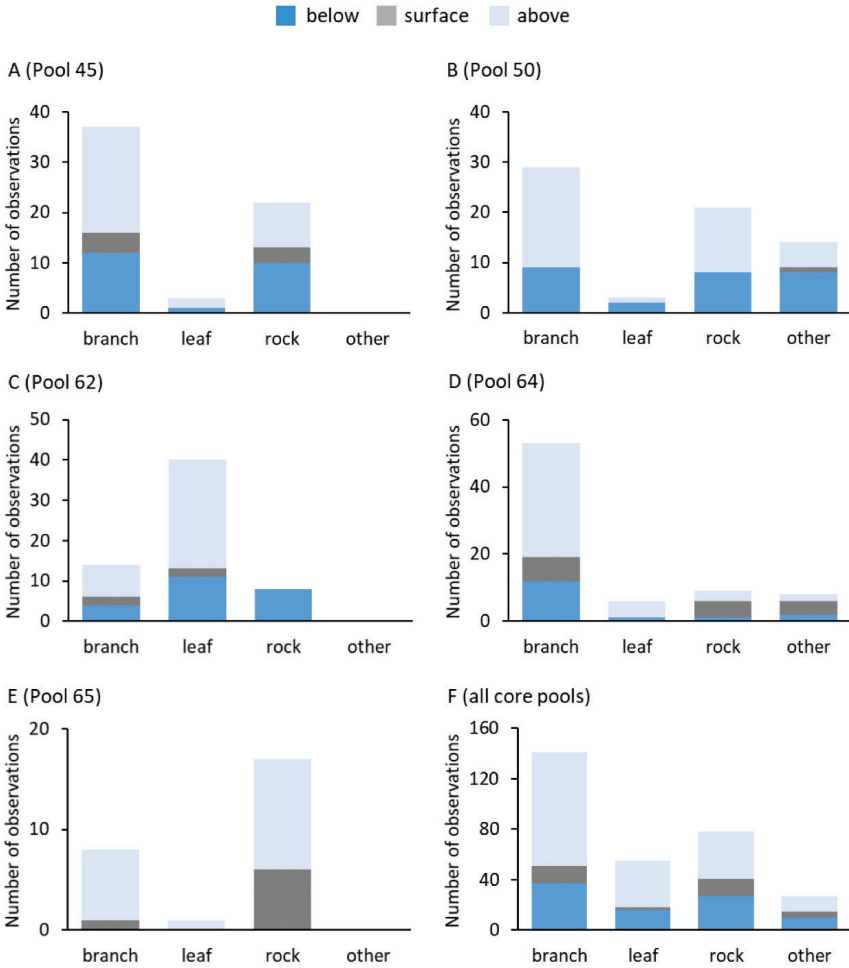
We estimated the breeding population of *M. xanthomelas* at Kaloko-Honokōhau to range from 5 to 20 individuals each month over the course of our study. Overall, males were observed 6.1 times more often than females. Because our surveys focused on the margins of pools, where damselflies were most abundant, active, and readily observed, we would have missed individuals that were in vegetation away from the pools. We expect this number to be relatively small, at least for reproductively active males, as they typi-



**Table 1.** Water conditions and physical attributes of core and peripheral anachialine pools surveyed for *Megalagrion xanthomelas*. Water property values (temperature, salinity, and pH) are the average of two measurements taken near high tide on 15–17 August 2017.

Pool number	Area (m <sup>2</sup> )	Temp (°C)	Salinity (ppt)	pH	Canopy cover (%)	Leaf/twig cover (%)	Bottom substrate <sup>1</sup> (% cover)				
							Silt & sand	Pebbles	Cobbles	Boulders	Slab
Core pools											
HI_Kaloko_007	22.0	25.0	14.1	8.1	30.0	20	80	0	10	10	0
HI_Kaloko_045	5.5	20.7	12.5	7.6	50.2	20	0	30	40	30	0
HI_Kaloko_050	13.8	21.4	11.8	7.6	34.6	20	0	30	30	40	0
HI_Kaloko_058	1.8	22.5	11.3	7.9	21.1	5	0	30	40	30	0
HI_Kaloko_062	3.1	20.8	12.3	7.4	30.9	15	0	10	40	50	0
HI_Kaloko_064	4.0	23.5	10.6	8.1	63.4	30	0	5	35	60	0
HI_Kaloko_065	3.9	24.6	10.3	8.3	65.8	20	0	5	45	50	0
Peripheral pools											
HI_Kaloko_011	295.3	26.6	9.7	8.0	11.0	1	5	0	15	60	20
HI_Kaloko_012	566.9	22.9	13.8	8.0	15.0	5	60	0	5	35	0
HI_Kaloko_032	27.8	23.9	10.6	7.9	100.0	80	85	0	5	10	0
HI_Kaloko_046	1.7	20.8	13.3	7.9	50.0	10	0	5	55	40	0

<sup>1</sup>Substrate size classes: silt and sand = <1 mm; pebbles = 1–64 mm; cobbles = 64–128 mm; boulders = 128–512 mm; slab >512 mm



**Figure 4.** Frequency of ovipositing behavior on substrates relative to the water surface in the five core pools where most observations were made and in all seven core pools combined. Ovipositing behavior was rarely observed at two core pools (7 and 58) and those data are not displayed individually.

cally compete for territories along pool margins. In contrast, we probably missed females that were in reproductive pause, and both males and females that had emerged but not yet reached reproductive maturity; individuals within these states may have resided away from the pools. Females appear to lack antagonistic interactions with other females, and unless

engaged in reproductive activities, are less active than males and more easily undetected during our surveys. Nearly 60% of all females observed were coupled with males. Females that were not prepared to mate at the time of our observations may have been perched away from the edge of the pool, as was observed along stream habitats on O’ahu (Preston et al. 2007).

The carrying capacity of *M. xanthomelas* in the core anchialine pools at Kaloko-Honokōhau is not known but may be lower than found in freshwater habitats in Hawai'i. Within the core anchialine pools, we found adult damselfly density to range from 0.1 to 0.4 individuals/m<sup>2</sup> over the course of the study (5–20 individuals total from 54.1 m<sup>2</sup> in core pools). The highest density we observed was considerably lower than the highest density observed at Tripler Army Medical Center (TAMC) on O'ahu, the only other population where abundances have been reported. For example, along a 95-m stretch of stream habitat at TAMC, peak *M. xanthomelas* abundances were estimated to be 2.3 and 5.6 individuals/linear m of stream during surveys conducted in 1997 and 2003, respectively (Preston et al. 2007). The highest estimated abundance at TAMC during those surveys was 535 individuals, 27 times greater than at Kaloko-Honokōhau. Similarly, as many as 2.7 individuals/m<sup>2</sup> were observed within three 21.9-m<sup>2</sup> artificial ponds built to provide supplemental habitat for the stream population at TAMC during May 1997–February 2000 (Englund 2001).

Relatively low numbers in the artificial ponds at TAMC were attributed to a lack of preferred oviposition substrate, competition, or predation from introduced odonates and other insects, and unfavorably high water temperatures (Englund 2001). It is unclear if oviposition substrates are limiting at Kaloko-Honokōhau, but unlike at TAMC, other odonates were rare in pools occupied by *M. xanthomelas*, except for pool 7, where the introduced damselfly *Ichnura ramburii* (Coenagrionidae) and several dragonfly species were common. Water temperature and other water properties at the Park are relatively stable within the range affected by the tidal cycle. As expected, we observed the greatest number of individuals at peripheral

pools during the months when counts were highest in the core pools, indicating that individuals dispersed away from the core area at that time. The greatest distance that *M. xanthomelas* was observed from the core area was about 250 m, where a single male was observed on one occasion.

**Pool properties.** *Megalagrion xanthomelas* is the only native damselfly to populate brackish habitats, although the introduced *I. ramburii* also tolerates brackish water and co-exists with *M. xanthomelas* at some locations, including one core pool at Kaloko-Honokōhau. Salinity in core pools at the Park ranged from 10.3 to 14.1 ppt during measurements made on a single day around high tide. Within-pool salinity also varies, reflecting tidal influences. For example, measurements made by data loggers placed at the bottom of four core pools (45, 50, 58 and 64) during 16 September–31 October 2016 recorded salinity to fluctuate 4.2 ppt within one calendar day (12 Oct 16; 9.6–13.8 ppt; pool 50) and 5.8 ppt over nine days (11 Oct 16 and 20 Oct 16; 9.0–14.8 ppt; pool 50). These salinities are within the range found to successfully support the development of *M. xanthomelas* eggs and naiads (Tango 2010). The maximum salinity in which *M. xanthomelas* can successfully reproduce is not known.

All core pools contained peripheral terrestrial vegetation, primarily Christmas berry and milo, that provided perching sites, varying degrees of overhead cover, and organic material that littered the pool bottoms. We did not quantify the use of perching substrates by males, but *M. xanthomelas* were most often observed perching on low-lying (<0.5 m above the water or ground surface) branches along the pool margins. Rarely were *M. xanthomelas* observed perching on perimeter rocks. The importance of overhead canopy cover (>1 m above the surface of the pool) is unclear, but may provide protection

from larger, actively flying dragonflies or avian predators.

Overhead cover may also moderate water temperature (Englund 2001) although the regular exchange of freshwater and saltwater in anchialine pools is likely a more important moderator of water temperature than is cover. The largest one-day fluctuation in water temperature recorded during 52 days of continuous monitoring in the four core pools was 2.9 °C (18 Sep 16; pool 64), a relatively small range considering the generally sunny and hot conditions at Kaloko-Honokōhau. Peripheral vegetation may provide an important source of organic material such as leaves, stems, and feces from perched animals into the pools (Naiman and Decamps 1997, Dudley et al. 2017). This input likely contributes to resources that support a prey base for naiads feeding on aquatic invertebrates and adults consuming Diptera and other flying insects that are attracted to water. Overall, *M. xanthomelas* were rarely observed at pools that lacked peripheral vegetation, indicating the importance of this substrate.

**Ovipositing behavior and substrate choice.** Female *M. xanthomelas* displayed ovipositing behavior on a wide range of substrates, both below and above the surface of the water. We could not observe eggs being laid so our observations may not represent egg-laying *per se*. A thorough search of the substrates for eggs or incisions made on the substrates during oviposition would be needed to determine if the behaviors we observed directly correlated with egg-laying. Regardless, we expect that the probing of substrates made by a female is generally representative of egg-laying behavior. Therefore, it appears that small branches were the preferred oviposition substrate within the pools. Females often perched on the branch just above the surface of the water and probed the branch with the tip of her abdomen just

above or below the water surface (Figure 2). Although most (58.5%) oviposition probes took place above the surface of the water, the substrate on which the probing took place was wet in all cases indicating that the substrate would likely be submerged during high tide or was in suitably wet conditions. To our knowledge, the influence of periodic exposure to air on the development of *M. xanthomelas* eggs is unknown.

We did not measure the amount of potential oviposition substrate in each pool so we cannot say if *M. xanthomelas* oviposits on substrates at a frequency that differs from the availability of the substrate. However, our observations indicate that *M. xanthomelas* uses a variety of substrates to lay eggs. The heavy use of branches and leaves for oviposition underscores the importance of peripheral vegetation for sustaining *M. xanthomelas* populations in these pools. Their ability to use a variety of substrates for oviposition, at Kaloko-Honokōhau and elsewhere (Englund 2001), may contribute to the capacity of this species to occupy a wide range of habitats.

**Potential limiting factors.** *Megalagrion xanthomelas* occupied only a small subset of potential habitat at Kaloko-Honokōhau. Factors limiting their distribution are clear in some instances, but less so in other cases. For example, some anchialine pools dewater (or completely drain) during low tide and become inhospitable for naiad survival. Similarly, pools that occupy unvegetated lava fields appear to provide poor habitat due to a lack of peripheral or emergent vegetation.

None of the core pools contained invasive fish, and these fish likely limit *M. xanthomelas* distribution and abundance across the Park as they do other anchialine pool invertebrates (Capps et al. 2009, Carey et al. 2011, Havird et al. 2013, Marrack et al. 2015, Seidel et al. 2015). In-

vasive fish have been suspected to reduce the survival of *Megalagrion* naiads in stream habitats throughout Hawai'i, either through predation or competition for food resources (Williams 1936, Polhemus 1993, Englund 1999). Globally, damselflies often share habitats with fish, but Hawaiian *Megalagrion* have evolved to inhabit environments that are free, or largely free, of predatory fish; their naïve evolutionary track may make them more vulnerable to pressures exerted by invasive fish than are introduced damselflies (Polhemus 1996). The influence of provenance may be exemplified by the presence of *I. ramburii* in anchialine pool and fishpond habitats at the Park that contain tilapia and guppies. At Kaloko-Honokōhau, invasive fish occupied about 19% of the anchialine pools and both Kaloko and 'Aimakapā Fishponds (K. Annandale, National Park Service, written communication, 2022).

In contrast to the core pools, *M. xanthomelas* were observed on several occasions at two peripheral pools that contained guppies. At one of these pools (pool 32), a female coupled with a male was observed ovipositing on milo branches just above the surface of the water. However, this is the only instance in which a female *M. xanthomelas* was observed at this pool and the pool is unlikely to sustain these damselflies. Similarly, a female in tandem with male was observed ovipositing on a leaf at the water surface of a narrow milo-lined section of an adjacent peripheral pool (pool 11) that also contained guppies. An exception to these observations is the occasional occurrence of males at a pool (pool 12) that contained several species of native reef fish that likely colonized the pool during an extreme high tide or storm surge event. Male *M. xanthomelas* now sometimes occupy a dense mat of pickleweed in that pool that has become established in sediment deposited by the 2011 Tōhoku tsunami. Overall, it is likely

that these peripheral pools, all located within about 50 m of the nearest core pool, provide marginal habitat that is occasionally occupied by individuals that have dispersed from the core area. The farthest distance that *M. xanthomelas* was observed from the core pools during our study was about 250 m.

Other invasive arthropods may also affect *M. xanthomelas* at Kaloko-Honokōhau. For example, ants are common around the pools and may prey on damselfly nymphs that emerge from pool water onto emergent substrates to complete development into adults. Ants were observed attacking a debilitated male *M. xanthomelas* that was removed from a pool following a possible act of sexual cannibalism (see below), suggesting that terrestrial-stage nymphs or teneral adult damselflies may be prey for ants. Scavenging by ants may explain the rarity of cast, post-emergence *M. xanthomelas* skins (exuviae) at the pools. Additionally, the non-native garden spider *Argiope ap-pensa* has become common in vegetation at anchialine pools at Kaloko-Honokōhau and elsewhere along the Kona Coast. This spider uses its orb web to capture flying insects and bears attention as a threat to *M. xanthomelas*.

**Cannibalism in *Megalagrion xanthomelas*.** During our surveys we observed what we believe was a case of cannibalism. On 15 October 2016, a single female *M. xanthomelas* was observed attacking and killing two male *M. xanthomelas* at one core pool (pool 50) during separate events. In both instances, the female tussled with the male in flight, forced it to the surface of the water, stood on its floating body, and used its mandibles to extract and consume small parts of the male's thorax near the base of its wings. Also on both occasions, the female stopped her attack before killing the males and flew onto a nearby perch.



The second attack began about 20 minutes after the first attack had been completed. Each attack lasted about five minutes. Immediately after the attacks, the males were removed from the water by an observer (U.S. Geological Survey volunteer Alex Clark), placed on a dry rock by the side of the pool, and watched for signs of recovery. Both males had pieces of thorax removed by the female, although the damage was considerably worse on the first male. Both males died shortly after being removed from the pool. The female had been observed exhibiting ovipositing behavior prior to the attacks. Because we did not observe mating with these males before the attacks, it is unclear if the acts are considered sexual cannibalism (Birkhead et al. 1988, Elgar and Crespi 1992, Lawrence 1992), a behavior that is often thought to be a way for females to gain immediate nutritional benefit following mating to enhance fecundity (Barry et al. 2008, Welke and Schneider 2012) or a density-dependent response to stress on resources (Fincke 1994, Johansson 1996).

### Management Considerations

Anchialine pools at Kaloko-Honokōhau represent critical habitat for a small population of the endangered *M. xanthomelas* on Hawai'i island. Implementing management actions that expand the range of this damselfly in the Park may contribute to protecting the species against unexpected events such as severe storms, the introduction of additional invasive predators, and sea level rise. In particular, maintaining or enhancing emergent and peripheral vegetation at pools could provide important structural habitat. Additional study would be beneficial to identify factors that limit *M. xanthomelas* abundance within and among anchialine pools at Kaloko-Honokōhau; however, based on generalized knowledge of the effects of invasive fish on aquatic invertebrates, it is likely

that tilapia, guppies, and western mosquitofish contribute to *M. xanthomelas* being restricted to a small set of anchialine pools in the Park. Removing those fish from pools that otherwise appear suitable for *M. xanthomelas* (e.g., does not dewater during low tide, contains emergent or peripheral vegetation and some overhead cover, and are within salinity tolerance limits) may be an important first step toward increasing damselfly populations in the Park. Further study, particularly efforts that focus on the ecology and requirements of the aquatic naiad stage, may help elucidate factors that affect the distribution of *M. xanthomelas* in the Park. Observations made during this study indicate that *M. xanthomelas* may be able to disperse naturally into nearby habitats provided they are suitable for reproduction. Translocation of eggs, naiads, or adults from the core pools into other suitable pools could be used if natural dispersal to additional pools is not observed.

### Acknowledgments

We thank Theo Black, Sammy Buechner, Andrea Centola, Alex Clark, Audrey Curtis, Klaus DeBoer, Andrew Hanano, Noah Hunt, Kamal Islam, Kelly Jaenecke, Jason LaBrie, Savannah Miller, Nicole Richardson, Shannon Schlater, and Jonny Shepard for their help surveying damselflies. We acknowledge Alex Clark for his astute observations and photographs of sexual cannibalism during one of his surveys. We thank Kaloko-Honokōhau National Historical Park for logistical support, issuing permits, and continued interest in our research. Funding was provided through the Natural Resource Protection Program, jointly sponsored by the National Park Service and the U.S. Geological Survey. Logistical and administrative support was provided by Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo. The manuscript was

greatly improved by comments made by Sallie Beavers, Kaile'a Annandale, Will Haines, and an anonymous reviewer. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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