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Biology Recapitulates Geology: the Distribution of *Megalagrion* Damselflies on the Ko'olau Volcano of O'ahu, Hawai'i[1]

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Abstract

Populations of endemic *Megalagrion* damselflies breeding in upland streams have exhibited a progressive decline in both range and numbers on O'ahu since the late 1970s, based on analysis of historical collection data and results of recent surveys. In particular, conservation status surveys conducted from 1991 onward determined that the 4 upland stream-breeding taxa on the island, 3 of which are endemic to O'ahu, have disappeared from many catchments they formerly inhabited, particularly in the Wai'anae Mountains and on the leeward side of the Ko'olau Mountains. The remaining populations on the island are now disproportionately concentrated on windward slopes of the latter range, where they are clustered around exposures of the core dike complex of the Ko'olau volcano. This geological formation traps groundwater in dike-segregated compartments, thereby producing permanent surface flow in the upper reaches of many windward Ko'olau gulches, coupled with naturally interrupted midreaches immediately below that block the upstream migration of invasive species. The discovery of this correlation between geology and damselfly distributions has allowed predictive location of additional colonies by using geological maps, permitting future surveys to be more accurately targeted, and providing an objective basis for the delimitation of habitat critical to the survival of these species.

Introduction

Endemic damselflies in the genus *Megalagrion* were formerly a common component of Hawaiian stream and wetland biotas at elevations ranging from sea level to at least 2000 m. In response to ecological opportunities offered by the topographically complex and geographically isolated Hawaiian archipelago, specialized species of *Megalagrion* evolved to exploit a wide variety of aquatic ecosystems as breeding habitats, ranging from anchialine pools and stream terminal reaches in the lowlands to rheocrenes and rushing streams in the highlands. Many of these habitat specialists also evolved as single island endemics, particularly on the geologically older main islands of Kaua'i and O'ahu. As of result of their bright colors, insular endemism, fascinating ecological specializations, and relatively large size in relation to most other Hawaiian insects, these damselflies have attracted continuing attention from researchers in taxonomic entomology, systematics, and ecology (Williams, 1936; Zimmerman, 1948; Polhemus, 1997; Jordan *et al.*, 2003).

With the advent of European contact and subsequent colonization, many *Megalagrion* species experienced significant range contractions or even extirpation on particular islands as a result of physical habitat modifications and introduction of invasive species (Polhemus & Asquith, 1996; Polhemus, 1996; Liebherr & Polhemus, 1997). Such impacts were particularly severe on O'ahu, the most heavily developed and populated island in the archipelago. Beginning in 1991, a comprehensive survey program for native damselflies, funded in large part by the U.S. Fish and Wildlife Service, was undertaken on O'ahu by staff from the Bishop Museum and other partner organizations, eventually covering 150 sites on the island (Fig. 1). These surveys demonstrated that at least one

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Table 1. **Distribution of stream-breeding *Megalagrion* damselfly populations on O‘ahu**. Populations are defined as demes separated by significant topographic barriers sufficient to preclude regular gene flow, and may include separate branches of the same overall stream catchment.

	NUMBER OF REMAINING POPULATIONS				
TAXON	**Leeward Wai‘anae**	**Windward Wai‘anae**	**Leeward Ko‘olau**	**Windward Ko‘olau**	**Total**
M. oceanicum	0	0	0	8	8
M. leptodemas	0	0	2	2	4
M. n. nigrolineatum	0	0	6	15	21
M. hawaiiense	2	2	2	10	16

lowland species, *M. pacificum*, had been completely extirpated from O‘ahu, and that another lowland species, *M. xanthomelas*, was reduced to a single remnant population (Liebherr & Polhemus, 1997). Both of these species bred in lentic habitats or stream terminal reaches, which experienced significant modification for agriculture beginning as early as the 19th century, and sustained similarly early impact from alien fishes imported for food sources by Asian immigrant laborers (Polhemus & Englund, 2003).

Similar declines, however, were also apparent by the late 20th century for three upland species breeding in lotic habitats: *M. oceanicum*, *M. leptodemas*, and *M. nigrohamatum nigrolineatum*. All three of these taxa are endemic to O‘ahu, and formerly occurred in both major mountain ranges on the island, the Ko‘olau and Wai‘anae (Polhemus & Asquith, 1996). By the late 1990s (and probably decades earlier) they had been completely extirpated from the Wai‘anae Mountains, and persisted to varying degrees only in streams draining from the Ko‘olau volcano. In addition, one other upland stream-associated species, *M. hawaiiense*, managed to retain a few small populations in the Wai‘anae Mountains and remained locally abundant in certain Ko‘olau catchments. The comprehensive surveys of the 1990s revealed a further interesting pattern in regard to these remnant distributions: they were to a large degree clustered on the windward slope of the Ko‘olau Mountains (Table 1), particularly in the northern windward quadrant, where deeply incised catchments reveal exposures of the core dike complex of the Ko‘olau volcano. It thus became apparent that in addition to biological determinants, the distribution of the remaining populations of O‘ahu-endemic stream-breeding damselflies was also being dictated to some extent by geomorphological and petrological factors. In the present paper, this possible relationship is examined, beginning with a review of the geology of O‘ahu and the Ko‘olau volcano, followed by an analysis of distribution patterns for the taxa in question.

Geology and Geomorphology of the Ko‘olau Volcano

The island of O‘ahu is the third largest in the Hawaiian chain, with an area of 1574 km^2, and lies in the eastern Pacific Ocean at approximately 21°30'N and 158°00'W. The bulk of the island consists of the heavily eroded remnants of a pair of shield volcanoes formed over the Hawaiian hot spot: the Wai‘anae volcano in the west, and the Ko‘olau volcano in the east (Fig. 2). The Wai‘anae volcano is the older of the two, with its earliest rocks dating from 3.7 My, while the Ko‘olau volcano is over a million years younger, with oldest rocks dating to 2.6 My (Carson & Clague, 1995). At their peak, the elevations of the Wai‘anae and Ko‘olau volcanoes are estimated to have reached 2200 m and 1900 m, respectively (Carson & Clague, 1995), but both have now been greatly lowered by erosion, with the current summit of the Wai‘anae Range (Mt. Ka‘ala) attaining 1231 m, and the summit of the Ko‘olau Range (Kōnāhuanui) standing at only 960 m. Despite its lower height, the Ko‘olau volcano is the wetter of the two, due to the prevailing trade wind patterns, with its windward flank receiving up to 7000 mm of rainfall a year, while the wettest secton of the Wai‘anae Mountains, the

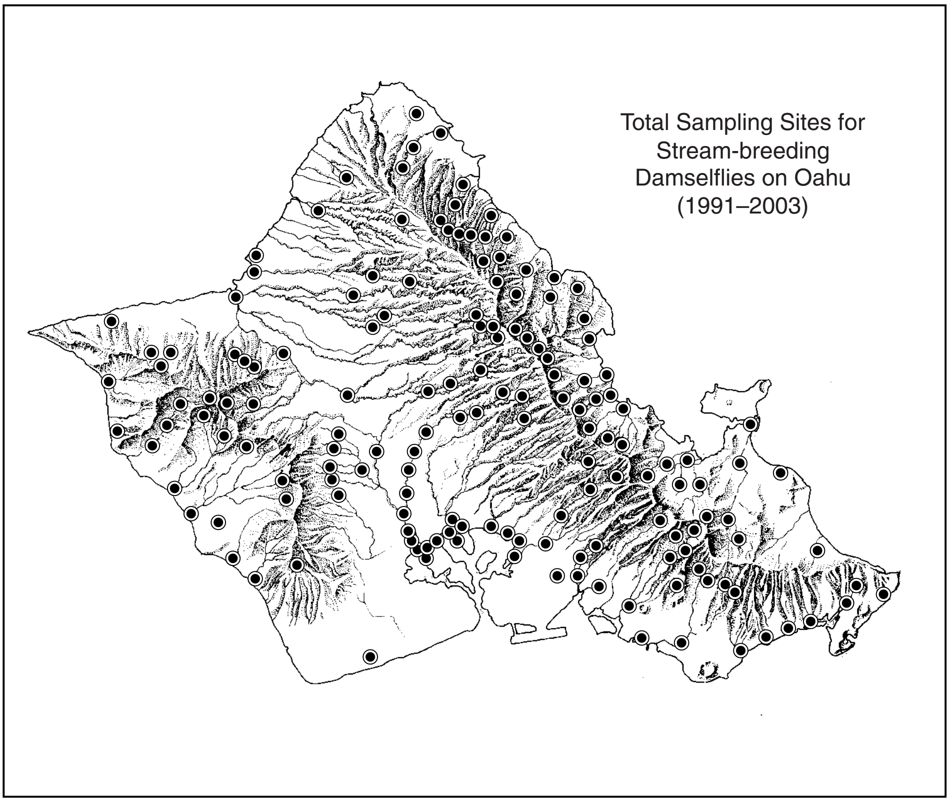

Figure 1. Sites on O‘ahu sampled for *Megalagrion* damselflies from 1991 to 2003 inclusive.

Mt. Ka‘ala massif, receives less than 2000 mm (Giambelluca *et al.*, 1986). This difference in precipitation regime has a marked effect on the number of perennial streams draining from the two mountain ranges; of the 57 perennial streams recognized on O‘ahu, the Ko‘olau volcano has 48, while Wai‘anae has only 9 (Hawaii Stream Assessment, 1990).

Erosion has also heavily reduced the flanks of both volcanoes, particularly on their seaward faces. Such erosion is strikingly asymmetrical, with the interior slopes of the volcanoes being gradual and sloping inward to a broad central valley formed in the dihedral between their two abutting lava shields, and the outer seaward slopes in large part precipitous, with tall cliffs and steep slopes. It was initially thought that these steep seaward slopes were simply the result of headward erosion by the combined action of wind, rain and sea, but bathymetric mapping initiated in the 1960s revealed enormous submarine debris fields offshore of the seaward faces of both the Wai‘anae and Ko‘olau volcanoes, leading to a hypothesis by Moore (1964) that these steep seaward flanks were the result of catastrophic slope failures associated with giant landslides. This hypothesis has been subsequently supported by more sophisticated bathymetric mapping techniques, including the GLORIA multibeam side-scan sonar system of the 1980s, and the JAMSTEC multibeam surveys combined with GPS navigation that were employed in the late 1990s (Moore & Clague, 2002).

The realization that giant landslides have been a significant factor in the erosional history of the Ko‘olau volcano allows a reassessment of the geomorphology of the Ko‘olau Mountains, and of the influence of such landslides on the development and bed profiles of stream catchments within the range. Based on most recent evidence, it appears that one major event, the Nu‘uanu landslide, was responsible for most of the mass wasting experienced by the windward Ko‘olau Mountains. This

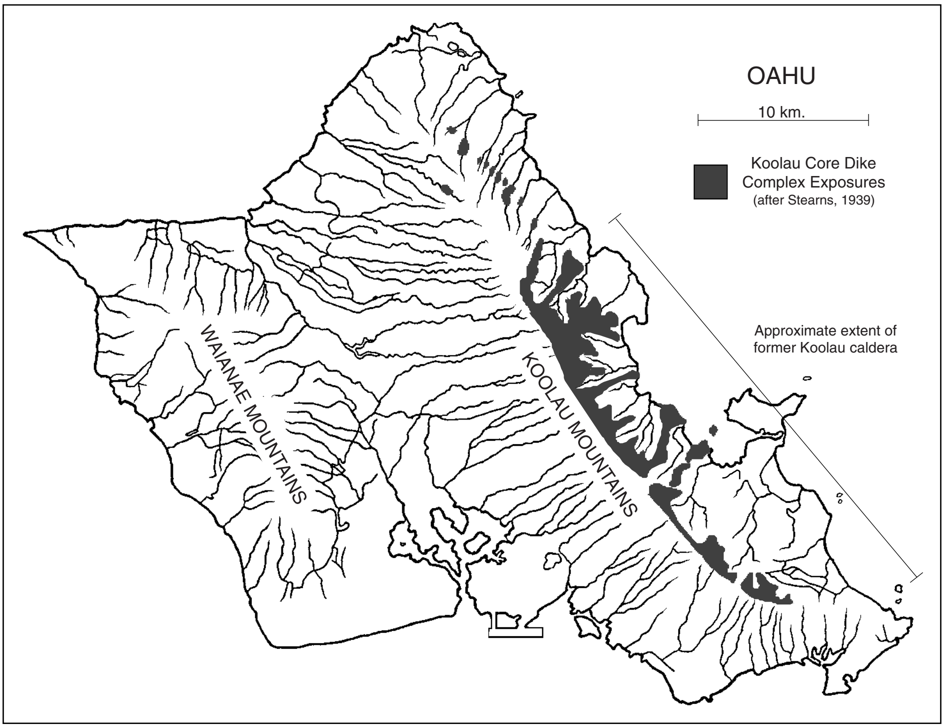

Figure 2. Map of O‘ahu showing location and extent of exposures of the core dike complex of the Ko‘olau Volcano and approximate former extent of the Ko‘olau caldera.

landslide occurred prior to 1.5 my (Clague *et al.*, 2002), and involved the entire northeastern flank of the Ko‘olau caldera, which formerly extended from Waimanalo to near Punalu‘u (Fig. 2), a distance of approximately 28 km (Macdonald *et al.*, 1983). This is the sector of the windward Ko‘olau Mountains that now exhibits bowl-shaped valleys with extremely steep headwater reaches, open midreaches, and long terminal reach estuaries. By contrast, the section of the windward Ko‘olau Mountains lying northwest of the old caldera, referred to subsequently as the northern windward Ko‘olau Mountains, laying beyond the rim of the caldera, did not experience giant landslides and has streams with very different catchment structure.

Unlike the bowl-shaped valleys formed in the old caldera, the streams of the northern windward Ko‘olau Mountains from Kaluanui Stream northward have perched headwater reaches with well integrated drainage patterns occupying open, hanging valleys modestly incised into the tholeiitic basalts of the Ko‘olau Volcanic Series that represent the remaining outer windward slope of the original volcano. These hanging catchments make abrupt transitions into narrow canyons up to 500-m deep entrenched into this old windward surface, and eventually debouch onto relatively short terminal reaches lacking extensive estuaries. The boundary between the perched headwaters and the midreach canyons in most of these northwest Ko‘olau systems (particularly Kaluanui, Ma‘akua, Kaipapa‘u and Koloa) is usually marked by one or more high waterfalls that form a significant break in the stream bed profile. In addition, the canyon bottoms are heavily infilled with coarse alluvium, creating a deep hyporheic zone into which the base flow sinks except during spates, making these stream ecosystems "naturally interrupted" according to the classification of Polhemus *et al.* (1992).

Examination of geological maps reveals that the transition from perched headwaters to midreach canyons in these northern windward Ko‘olau systems also correlates with the points at which these streams have eroded downward into the upper margin of the volcano's core dike com-

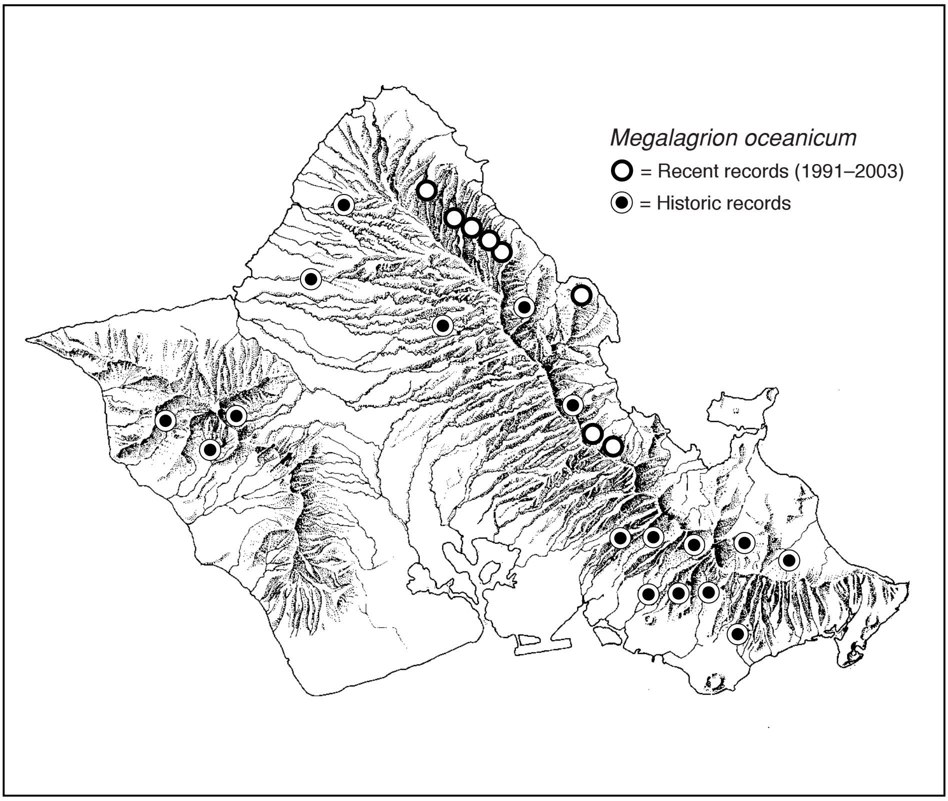

Figure 3. Former and current distribution of *Megalagrion oceanicum* on O'ahu.

plex (Stearns, 1939). This dike complex consists of numerous parallel, vertically-oriented dikes of hard, dense, microcrystalline basalt, in some cases up to 400/km (Macdonald *et al.*, 1983), that represent the remains of the lava conduits that fed the volcano's main rift zone, and are tightly clustered along the remains of this rift zone that forms the southeast to northwest longitudinal axis of the Ko'olau Range (Takasaki *et al.*, 1969). The exact definition of the "core dike complex" has varied among authors; Wentworth (1951) considered it to be the zone containing over 100 dikes per mile, while Takasaki *et al.* (1969) defined it as areas where dikes constitute more than 5 percent of the total rock volume (see Fig. 8 in this latter work for a graphic representation of dike densities in the upper Waiāhole and Kahana systems). Because of their structure, the dike rocks are relatively impermeable, and therefore trap groundwater in the more porous exposures of the Ko'olau Volcanic Series that intervene between them. As noted by Takasaki *et al.* (1969), the dikes generally retard the movement of groundwater in a seaward direction, instead forcing it to move laterally to points of discharge where the dike complex is cut by stream valleys. The dikes are also harder and less susceptible to erosion than the surrounding Ko'olau volcanics, and create vertical waterfalls where streams encounter them in the course of downcutting.

In the bowl-like valleys from Waimānalo to Punalu'u the core dike complex crops out broadly amid vertical cliffs along the valley heads at elevations between 180 and 240 meters (Takasaki *et al.*, 1969), having been exposed by the combined forces of the Nu'uanu landslide and subsequent headward erosion. In the entrenched catchments from Kaluanui to Mālaekahana, the core dike complex is by contrast exposed only to limited extents at or near the heads of the midreach canyons (Fig. 2) at elevations ranging from 200–400 m. These points of core dike complex exposure in turn correlate with the presence of high waterfalls, and the point at which base flow in these systems makes a tran-

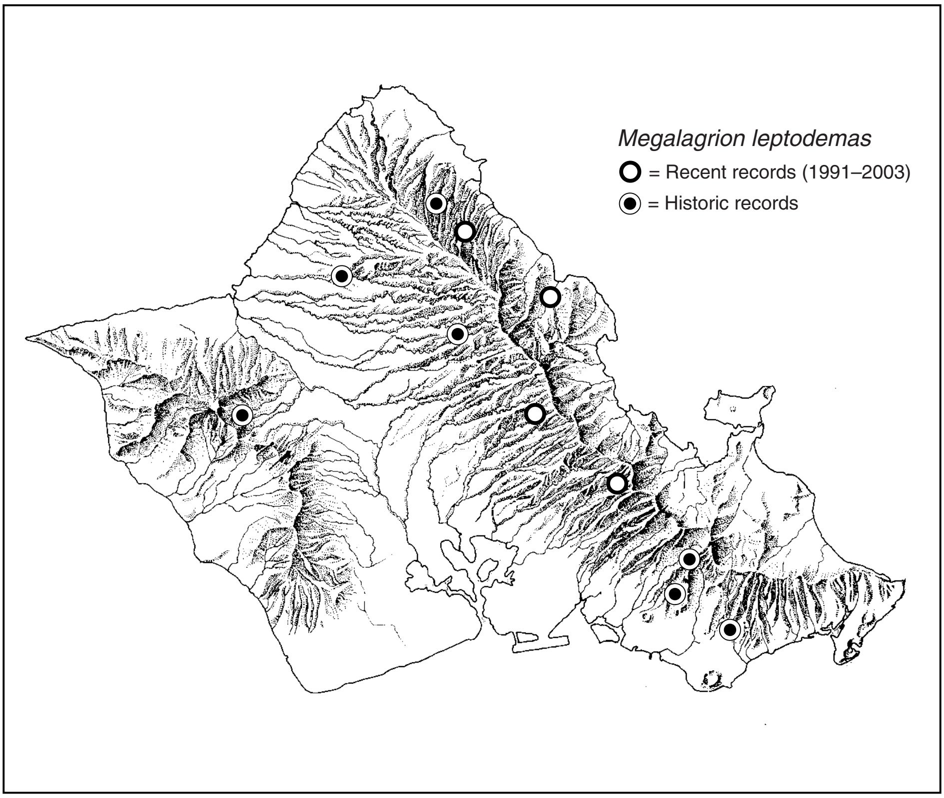

Figure 4. Former and current distribution of *Megalagrion leptodemas* on O‘ahu.

sition from perennial surface flow to hyporheic, suballuvial flow. These correlations have in turn had a significant influence on the distribution of the remaining populations of endemic stream-breeding damselflies on O‘ahu.

Distribution of Damselfly Populations on the Ko‘olau Volcano

The island of O‘ahu is known to have historically supported 8 damselfly species in the endemic Hawaiian genus *Megalagrion*. Of these, one, *M. oahuense*, breeds terrestrially beneath banks of *uluhe* ferns on upland ridges; another, *M. koelense*, breeds in the phytotelmata of the climbing pandanus (*Freycinetia arborea*) in similar habitats; and two more, *M. xanthomelas* and *M. pacificum*, breed in lentic habitats or slow stream terminal reaches (Polhemus, 1996). Of these four species, only *M. oahuense* is endemic to O‘ahu. These four are not considered further in the current paper.

The native damselfly biota of upland stream habitats, by contrast, consists of three species endemic to O‘ahu, plus one species more widespread across the Hawaiian chain. These species, which formerly co-occurred in many catchments throughout the island, are as follows:

Megalagrion oceanicum

This large orange-and-black species is endemic to O‘ahu and breeds in stream riffles and rapids, or on waterfall faces. Historic collection records show that *M. oceanicum* was originally present in the windward and leeward drainages of both the Ko‘olau and Wai‘anae mountain ranges, although it is now extirpated from the latter, with the last specimens from the Wai‘anae Range having been taken

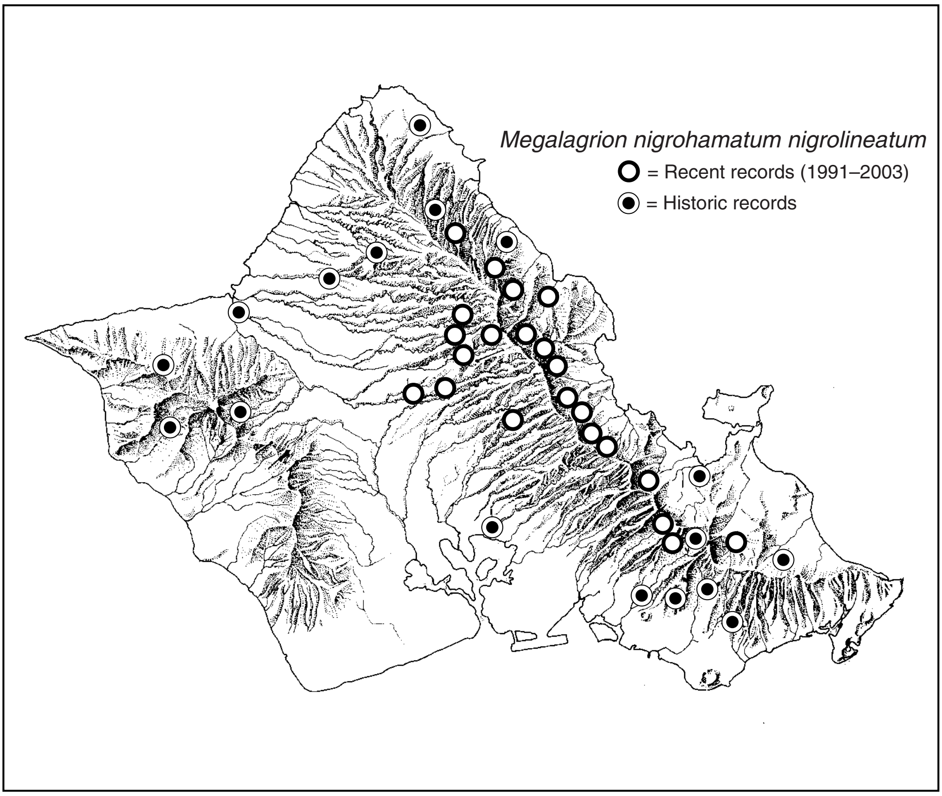

Figure 5. Former and current distribution of *Megalagrion nigrohamatum nigrolineatum* on O‘ahu.

above Wai‘anae in 1948. Current surveys indicate that the species has also been completely extirpated from the leeward Ko‘olau Mountains, and now occurs only as a series of scattered populations on the windward side of the Ko‘olaus, occupying 8 stream catchments from Kahalu‘u Stream in the southeast to Kahamainui Stream in the northwest (Fig. 3). The persistence of the two southernmost populations on branches of the ‘Āhuimanu system (Waihe‘e and Kahalu‘u) is in fact in doubt; neither has been reconfirmed in nearly a decade, despite several recent visits by the author to Kahalu‘u, and intensive scientific study of the Waihe‘e catchment from 1999–2001 by researchers from the Biological Resources Division of the U.S. Geological Survey (Brasher *et al.*, 2004).

Megalagrion leptodemas

This slender, predominantly bright red species is endemic to O‘ahu and breeds in headwater and upper midreach stream pools. Historic collection records indicate that this species occurred in certain windward drainages of the Wai‘anae Mountains (Hale‘au‘au), and on both the windward and leeward sides of the Ko‘olau Mountains. Current surveys have found that this species is now extirpated in the Wai‘anae Mountains, and survives in the Ko‘olau Mountains only as widely scattered colonies on both the windward and leeward sides of that range. Only four populations are known to exist at present, occupying the North Hālawa, Waiawa, Ma‘akua and Kahana drainages (Fig. 4).

Megalagrion nigrohamatum nigrolineatum

This endemic O‘ahu subspecies of *M. nigrohamatum* is characterized by broad panels of yellow, orange or reddish coloration on the pterothorax, uninterrupted by lateral stripes, and breeds in headwater and midreach stream pools. Historic collection records show that this species was originally

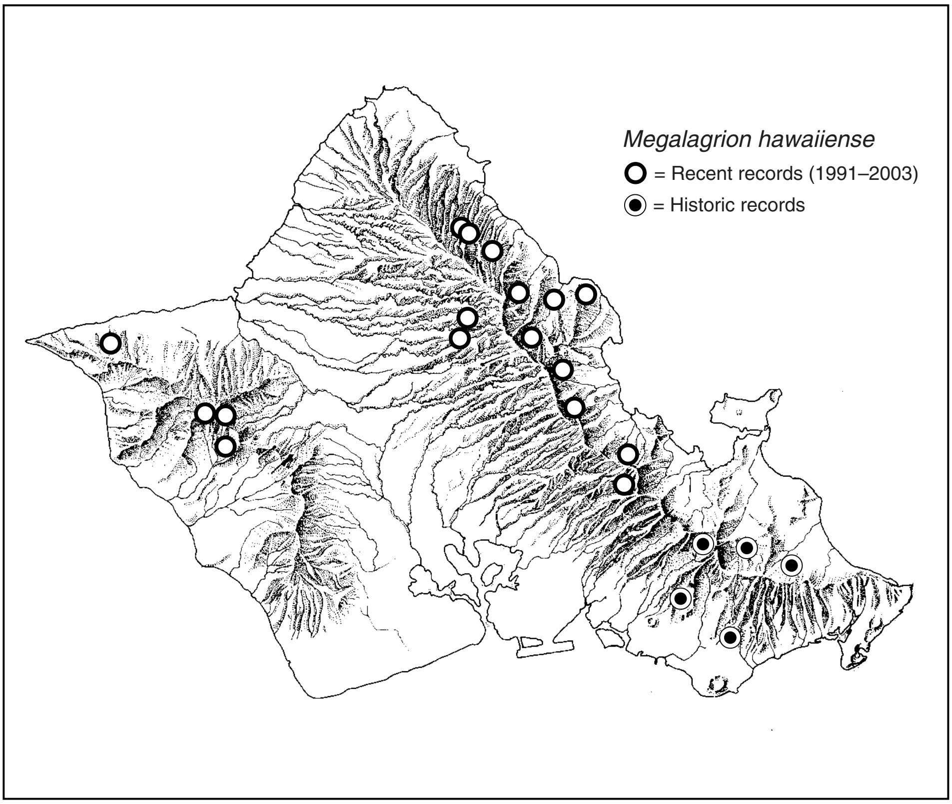

Figure 6. Former and current distribution of *Megalagrion hawaiiense* on O‘ahu.

present in the windward and leeward drainages of both the Ko‘olau and Wai‘anae ranges, but current surveys indicate that the species was completely extirpated in the Wai‘anae Mountains sometime after 1980 (the last record being from Pāhole Gulch in that year). The species persists in a modest number of drainages on both the windward and leeward sides of the Ko‘olau Mountains (Fig. 5). Some of the remaining populations are robust, and the species shows a degree of tolerance for physically disturbed habitats, provided these are free of introduced poeciliid fishes (Englund, 1999).

Megalagrion hawaiiense

This is a widespread species, occurring on all major high islands in the Hawaiian archipelago except Kaua‘i, and breeding on rheocrenes. Across its range it exhibits considerable color polymorphism; although the typical color pattern of males is orange-and-black, variants include aqua-and-black males from the Hāna coast of Maui, and a dark blue-and-black form from the windward Ko‘olau Mountains. On O‘ahu, historic collection records show that this species occurred in both the Wai‘anae and Ko‘olau mountain ranges at intermediate to high elevations. Of two color forms present on O‘ahu, the typical orange-and-black form occurs in the Wai‘anaes and northern leeward Ko‘olaus, while the unusual dark blue-and-black form is found in the southern and windward Ko‘olaus (Fig. 36 in Polhemus & Asquith, 1996). Recent surveys indicate that this species has been extirpated in the Wai‘anae Mountains south of Kolekole Pass (the last record from that section of the range being from Palikea Peak in 1957), but persists north of the pass in the Mt. Ka‘ala summit bogs and in the upper drainages of the Wai‘anae Kai area below Pu‘u Kalena. In the Ko‘olau Mountains the dark form of this species persists as numerous small populations associated with headwall seeps

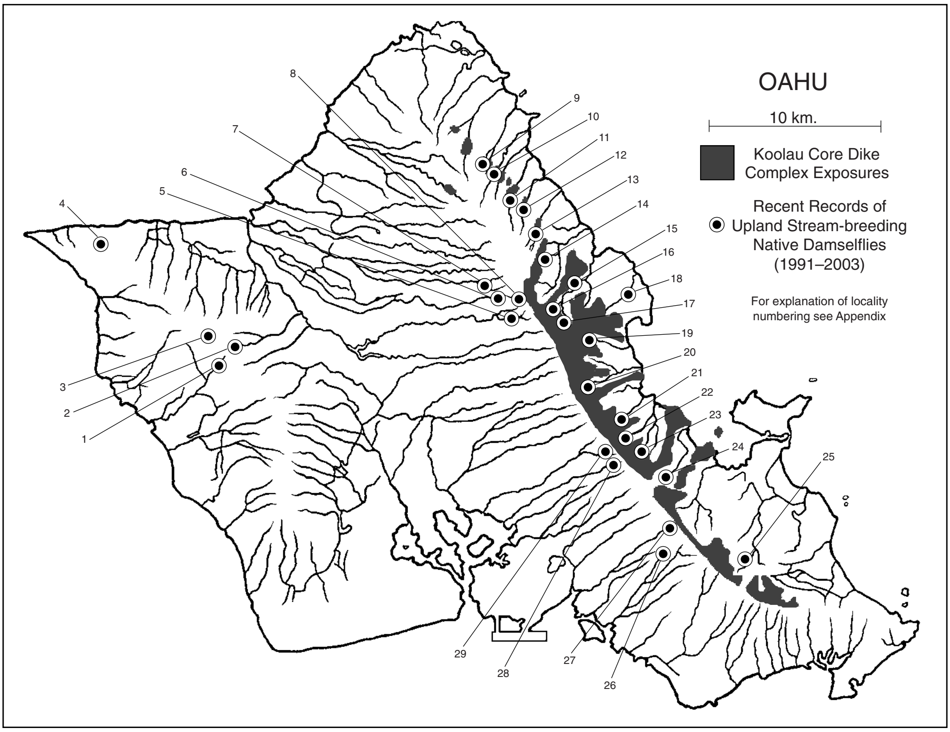

Figure 7. Distribution of currently known populations of upland stream-dwelling *Megalagrion* damselfly species on O'ahu in relation to exposures of the Ko'olau core dike complex. Site numbers correspond to those used in the Appendix, which provides details for each locality.

and riparian rheocrenes, particularly in the windward drainages (Fig. 6).

In examining the distributions of these stream dwelling damselflies on O'ahu (Figs. 3–7), it becomes clear that by far the majority of the remaining populations are confined to the windward drainages of the Ko'olau Mountains (Table 1, and see data presented in Englund, 1999). In addition, overall species richness is clearly greatest in the incised catchments of the northern windward Ko'olau Mountains, and correlates with exposures of the core dike complex. In particular, stream midreaches traversing the core dike complex in this section of the island are almost the only localities in which *M. oceanicum* may still be found. The open, bowl-like valleys of the old caldera from Waikāne southeastward are particularly deficient in native damselflies in comparison to the windward drainages from Kualoa Point northwestward, supporting only scattered populations of *M. nigrohamatum nigrolineatum* and *M. hawaiiense* (except for very small remnant populations of *M. oceanicum* in the 'Āhuimanu system which may already be extirpated—see previous discussion), and southeast of the 'Āhuimanu supporting only two populations of *M. nigrohamatum nigrolineatum*. All of these remaining populations in the southeast sector of the range are concentrated near the broad exposures of the core dike complex at the valley headwalls. Although it may be possible that additional populations of both *M. nigrohamatum nigrolineatum* and *M. hawaiiense* persist near some of the headwall springs behind Waimānalo, the fact remains that even on the windward flank of the Ko'olau Mountains, which represents the last refuge for O'ahu's endemic stream-breeding damselflies, the bowl-like valleys of the old caldera have lost nearly all of their original native damselfly populations, except those associated with the core dike complex exposures.

Discussion

The definition of critical habitat for insect species at risk is one of the more difficult and contentious issues in conservation biology. In some cases, such as insects restricted to particular host plant species, the matter is superficially straightforward, but the exercise then becomes definition of critical habitat for the host plant rather than the insect, and leads to questions of minimum viable patch size. In cases where the insect taxon is a generalist predator or ranges widely across a spectrum of local ecosystems, the matter can become even more complex. Aquatic insect taxa are conceptually more tractable in regard to delineation of critical habitat, since they occupy ecosystems with discrete boundaries, but even here there are differences between lentic habitats such as lakes, ponds and springs, which are discrete landscape features with uniform attributes, and lotic habitats such as streams, which are linear and vary in their characteristics along the length of a catchment.

The current study demonstrates that critical habitat for a particular group of aquatic insects at risk, native Hawaiian *Megalagrion* damselflies breeding in upland streams on the island of Oʻahu, can be accurately and predictably defined by evaluation of the geological structure of the catchments they inhabit. In particular, it is clear that colonies of four *Megalagrion* species breeding in upland streams are concentrated around exposures of the core dike complex of the Koʻolau volcano (Fig. 7), and that by using geological maps to locate such exposures it is possible to effectively focus survey efforts, and unambiguously define habitats essential to the continued survival of these species.

The correlation between the remaining populations of native, stream-breeding damselflies on Oʻahu and exposures of the core dike complex of the Koʻolau volcano is striking, and probably results from several factors:

1. *Precipitation* - Due to prevailing wind patterns in the northeastern Pacific, the windward sides of the Hawaiian Islands receive significantly more precipitation than the leeward sides. This in turn has an effect on the distribution of perennial streams within islands, and their associated aquatic biota, including *Megalagrion* damselflies. On Oʻahu, all remaining populations of upland, stream-breeding *Megalagrion* species are now found in areas that lie within the 2000 mm median annual isohyet (Giambelluca *et al.*, 1986). Even so, the 2000 mm median annual isohyet also covers large areas of the leeward Koʻolau and lower windward Koʻolau slopes that once supported native damselfly populations but now do not, and the remaining damselflies are distinctly clustered and discontinuous along stream reaches that lie within this precipitation zone. Additional factors must thus be involved in determining their current distribution.

2. *Catchment flow regime* - The core dike complex has been known for over a century to be an important aquifer, supplying significant groundwater inflow to collection systems such as the Waiāhole Ditch (Stearns & Vaskvik, 1935; Takasaki *et al.*, 1969; Hirashima, 1971). Exposures of this formation thus represent areas of predictable spring outflow for dike-confined groundwater at the headwalls of the bowl-like valleys in the southeastern Koʻolau Mountains, creating rheocrene habitats that are exploited by *M. hawaiiense*. Due to the dense and impermeable nature of the core dike complex rocks, they also create a zone of both augmented base flow and minimal hyporheos along the incised streams which cross them in the northern windward Koʻolau Mountains, and bring nearly the entire base flow to the surface over a certain distance. It is this feature which is apparently of greatest importance in correlating with the distributions of *M. oceanicum*, *M. leptodemas*, and *M. nigrohamatum nigrolineatum*. In the incised canyons of the north, the stream reaches lying immediately below exposures of the core dike complex make a sudden transition from bedrock to alluvial beds, and base flow makes a similar sudden transition from surface to hyporheic. This hyporheic base flow frequently remains subsurface for 1–2 km below the core dike complex contact, and surfaces again only near the seaward terminus where it floats on top of the inland-percolating marine water table. These naturally interrupted catchments therefore also produce a zone of relatively unsuitable habitat downstream of the core dike complex exposures, and confine damselfly populations to the vicinity of the core dike complex itself or to the headwater reaches upstream of it (see Fig. 4 in Englund, 1999).

3. *Invasive species* - The natural dichotomy of surface flow encountered below exposures of the core dike complex in the canyons from Kaluanui northwestward creates a barrier to the upstream migration of invasive aquatic species, particularly poeciliid fishes, which have been circumstantially implicated in predation on native damselfly populations. Englund (1999), in a study including the majority of windward Koʻolau catchments, demonstrated a strong negative correlation between the presence of poeciliids and that of native damselflies, and in the same paper provided figures that

detailed the elevational distribution of *Megalagrion* species in individual catchments at elevations now known to correspond with those of core dike complex exposures. The dry channels of the naturally interrupted midreaches below the core dike complex also appear to be effective barriers to the upstream migration of invasive amphibians and non-native damselflies. In the bowl-shaped valleys of the southeastern windward Koʻolaus, by contrast, no such zones of natural flow interruption originally existed due to higher base flows fed from more extensive exposures of the core dike complex at the valley heads, thus allowing more effective upstream penetration of invasive species.

4. *Urbanization* - The bowl-like valleys of the southeastern Koʻolau Mountains have open floors that are highly suitable for urban and suburban development, or for agriculture. As a result, they have been heavily altered in the past 200 years by the growth of towns such as Kāneʻohe, Kailua, and Waimānalo, coupled with extensive nursery and pasturing in the latter area extending up to 5 km inland. These land uses have both altered the physical habitat, through the channelization of stream terminal and midreaches, and promoted introduction of invasive species for mosquito control or via releases from home aquaria (Polhemus & Englund, 2003). In addition, the headwalls of the bowl-like valleys have been more readily bored for water development tunnels and trans-basin diversions, resulting in significant losses of base flow (up to 50%) in catchments such as Kahana, Waikāne, Waiāhole, Waiheʻe, and Kahaluʻu (Hirashima, 1963, 1965. 1971; Takasaki *et al.*, 1969). The incised catchments northwest of Kahana Bay, by contrast, have much smaller areas of open, relatively level land along their terminal reaches, and have consequently been less affected by urbanization and agriculture. The few towns that do exist in this area, Hauʻula and Lāʻie, are both set close to the coast, and residential or agricultural developments extend at most 1 km inland. The incised valleys also lack extensive ditch and tunnel systems, because their dike exposures were limited and difficult to utilize. The topography of these catchments cut into the intact windward slopes that were never subjected to giant landslides has thus served to buffer their damselfly populations from a wide spectrum of human impacts.

The hypothesis that the core dike complex exposures correlate with current damselfly distributions is testable to some extent, because not all catchments on Oʻahu containing exposures of the this formation have yet been sampled for native damselflies. Several moderately incised but incompletely surveyed gulches remain in the northern windward quadrant of the range, particularly ʻIhiʻihi and Wailele [the record of *M. oceanicum* from this latter catchment in Englund (1999) was in error]. Of equal interest, a single exposure of the core dike complex is also exposed leeward of the Koʻolau crest in the upper Waimea system, and would certainly repay examination. At the same time, not all streams with core dike complex exposures harbor native damselflies: although the complex crops out along the upper midreach of Mālaekahana Stream, surveys here have indicated an absence of *Megalagrion* species, possibly because this stream valley is relatively dry for a windward location, not deeply entrenched, and has therefore been easily colonized by invasive species and formerly subjected to sugarcane cultivation in its lower section. Finally, the geological factors correlating with native damselfly distributions on Oʻahu may also have analogs on other islands in the Hawaiian chain. On eastern Maui, for instance, the old, hard flows of the Honomanū basalts have been exposed in certain deeply incised catchments on the windward flank of Haleakalā, such as Hanawī, and these areas are also known to support populations of increasingly rare *Megalagrion* species.

Clearly, some form of protection and management for the remaining core dike complex exposures and their proximal stream reaches is an essential step in efforts to retain the endemic stream-dwelling damselfly fauna of Oʻahu. Even so, these localities now appear to represent the "last of the last" in regard to populations of retreating species such as *M. leptodemas* and *M. oceanicum*, and it is an open question as to whether these few particularly optimal catchments constitute sufficient minimum core range to ensure the long-term survival of these species. The same considerations also apply to other endemic, stream-dwelling species on Oʻahu, particularly native Diptera in the genera *Telamatogeton* and *Procanace*, the remaining populations of which are also largely confined to stream reaches in proximity to exposures of the core dike complex.

In summary, geomorphology and petrology appear to be acting as significant factors in determining the distribution of the remaining populations of endemic, stream-breeding damselflies and other lotic insects on the island of Oʻahu, and probably elsewhere in the Hawaiian Islands. As such, they should be taken into account in any future effort to delineate critical habitat for these increasingly endangered species.

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APPENDIX

Localities on O‘ahu at which native upland stream-breeding damselflies have been recorded from 1991–2003.

Locality numbers correspond to those in Figure 7 and represent sites at which one or more of the following species have been collected or unequivocably observed: *Megalagrion leptodemas*, *M. oceanicum*, *M. nigrohamatum nigrolineatum*, or *M. hawaiiense* (for detailed data on species occurring along particular streams and reaches see Englund, 1999). Dates in parentheses indicate the most recent year in which any of the preceding 4 species has been recorded at a given locality. Elevations are given in meters with foot equivalents in order to allow interface to USGS topographic maps.

1. Wai‘anae Mtns., Kānewai Stream (trib. to Honua Stream), upper Wai‘anae Valley, 425 m [1400 ft] (1994)
2. Wai‘anae Mtns., Mt. Ka‘ala, headwater tributary of Haleanau Gulch at edge of summit bog, 1160 m [3800 ft] (1991)
3. Wai‘anae Mtns., headwaters of Mākaha Stream below Mt. Ka‘ala summit bog, 1160 m [3800 ft] (1991)
4. Wai‘anae Mtns., small stream S. of Dillingham airfield, 150 m [500 ft] (1998)
5. Ko‘olau Mtns., upper Kaukonahua Stream, 460–520 m [1500–1700 ft] (1996)
6. Ko‘olau Mtns., Poamoho Stream, headwater reach, 520 m [1700 ft] (1996)
7. Ko‘olau Mtns., upper Helemano Stream, 490 m [1600 ft] (1996)
8. Ko‘olau Mtns., lake along upper Poamoho Stream, S. of Poamoho trail summit, 700 m [2300 ft] (1995)
9. Ko‘olau Mtns., upper Kahamainui Gulch, above Lā‘ie, 390 m [1280 ft] (1993)
10. Ko‘olau Mtns., Koloa Gulch, above Lā‘ie, from forks to first major waterfalls on each branch, 275–365 m [900-1200 ft] (1994)
11. Ko‘olau Mtns., Kaipapa‘u Stream, below first major waterfall, 305 m [1000 ft] (1994)
12. Ko‘olau Mtns., Ma‘akua Gulch, above Hau‘ula, at first waterfall, 150–215 m [500–700 ft] (1994)
13. Ko‘olau Mtns., upper Kaluanui Stream, above Sacred Falls, 670–760 m [2200-2500 ft] (1993)
14. Ko‘olau Mtns., Punalu‘u Stream, Waiho‘i Springs, north fork, 180 m [600 ft] (2001)
15. Ko‘olau Mtns., Kahana Stream, midreach, 30–270 m [100–880 ft] (1995)
16. Ko‘olau Mtns., Kahana Valley, headwaters of north branch of Kahana Stream at Intake 1 on Waiāhole Ditch tunnel, 245 m [800 ft] (1995)
17. Ko‘olau Mtns., Kahana Valley, headwaters of Kahana Stream at Intake 19 on Waiāhole ditch tunnel, 245 m [800 ft] (1995)
18. Ko‘olau Mtns., Makaua Gulch, above Ka‘a‘awa, 245 m [800 ft] (1994)
19. Ko‘olau Mtns., headwaters of Waikāne Stream at Waikāne Camp (site), 245 m [800 ft] (1995)
20. Ko‘olau Mtns., Uwau Stream (trib. to Waiāhole), headwaters, 245 m [800 ft] (1995)
21. Ko‘olau Mtns., Ka‘alaea Stream, near bridge on road, 25–30 m [80–100 ft] (1995)
22. Ko‘olau Mtns., Kahalu‘u Stream, headwaters of north branch, 150 m [500 ft] (2000)
23. Ko‘olau Mtns., Waihe‘e Stream, NW of Kāne‘ohe, waterfall and rocky stream at headwall, 215 m [700 ft] (2003)
24. Ko‘olau Mtns., He‘eia Stream in Ha‘ikū Valley, at Board of Water Supply pumphouse, 135 m [440 ft] (1995)
25. Ko‘olau Mtns., ‘Ōma‘o Stream, Maunawili Valley, 95 m [320 ft] (1995)
26. Ko‘olau Mtns., headwaters of Mo‘ole Stream (trib. to Nu‘uanu Stream) below Mt. Lanihuli, 520–610 m [1700–2000 ft] (1996)
27. Ko‘olau Mtns., headwaters of Kālihi Stream, above Wilson Tunnel, 305–365 m [1000–1200 ft] (1994)
28. Ko‘olau Mtns., North Hālawa Valley, tributary above highway tunnel, 305 m [1000 ft] (2000)
29. Ko‘olau Mtns., Waiwa Stream, upstream of rain gauge, 215–245 m [700–800 ft] (1995)