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# Comparisons to the Century Before: The Legacy of R. C. L. Perkins and *Fauna Hawaiiensis* as the Basis for a Long-Term Ecological Monitoring Program[1]

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ABSTRACT: As one means of assessing the impact of the past 100 yr of development and biological alteration in Hawai'i, the damselfly (Odonata: Coenagrionidae) and carabid beetle (Coleoptera: Carabidae) collections of R. C. L. Perkins made in the 1890s are compared with similar collections made one century later during the 1990s. Two islands that have experienced very different histories of development are compared: O'ahu and Moloka'i. Of eight native damselfly species originally inhabiting O'ahu, one has been extirpated from the island, another is now reduced to a single population, and three more are at risk. Of the eight species originally found on Moloka'i, by contrast, there is only one species that has not been rediscovered, although there is reasonable probability that it has simply eluded capture because of inherent rarity, whereas the remaining species retain large and stable populations. Capture frequencies (based on specimens collected per decade) are lower now than in the preceding century for most species on O'ahu, even allowing for modern collectors retaining fewer specimens. The only species on O'ahu for which captures have increased between the 1890s and the 1990s are those that breed away from lotic and lentic habitats, indicating a severe negative impact from introduced aquatic biota for species that breed in such freshwater situations. On Moloka'i, all damselfly species except one have higher capture rates now than in the 1890s, explainable in large part to improved access to previously remote terrain. Among the Carabidae studied, 1990s surveys on Moloka'i have found 12 of 15 species Perkins sampled in the 1890s. Overall, recent surveys have failed to rediscover five species, all of which have been relatively rarely encountered over all decades of the past century. Recent surveys on O'ahu have recollected 17 of the 21 species Perkins found in the 1890s. The most dramatic change in the O'ahu carabid fauna over the past 100 yr is the extinction of the most common O'ahu species of the 1890s, *Colpocaccus tantalus* (Blackburn). This species was broadly distributed across the island, possessed a well-developed flight apparatus, and accounted for 39% of the specimens captured in the 1890s. It has not been collected since 1940 in spite of intensive collecting during the 1950s and 1990s. The elevational preference of *C. tantalus* was lower than that for the aggregate balance of the O'ahu carabid fauna, suggesting an altitudinally associated factor in the extinction: most likely ants such as *Pheidole megacephala* (F.). The loss of a previously dominant generalist species is viewed as an ecological catastrophe, substantially different in quality from extinction of geographically restricted island specialists.

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THE HAWAIIAN ISLANDS offer the supreme example of an extremely rich endemic biota existing on an isolated, geographically restricted archipelago (Zimmerman 1948). That this intense diversity is associated with a detailed historical baseline dating from the previous century is unique in the world and is due in large part to the thorough collections made by R. C. L. Perkins from 1892 to 1901 for *Fauna Hawaiiensis* (Manning 1986). Perkins' collections provide an accurate snapshot of the insect fauna as it existed at the end of the nineteenth century against which we can compare relative abundance and diversity a century later.

As one means of assessing the impact of the past 100 yr of development and biological alteration in Hawai'i, we have compared the damselfly and carabid beetle collections of Perkins to surveys made during the 1990s. We focus on two contrasting islands, O'ahu and Moloka'i, in this report: O'ahu, the most highly developed and populated of the Hawaiian Islands, and Moloka'i, its nearest neighbor in geological age, but occupied by only 5000 people. Both islands possess similar topographic diversity, with O'ahu's Mount Ka'ala rising 1231 m, comparable with Moloka'i's highest peak, the 1515-m Mount Kamakou. O'ahu's 608-ha surface area is about 2.5 times Moloka'i's 261 ha.

Perkins' collections made between 1892 and 1901 provide an unparalleled and unduplicated profile of the Hawaiian insect biota at a time of great transition. Sugarcane production increased 20-fold from 1875 to 1898 (Cuddihy and Stone 1990). By the 1890s, many lowland forests and shrublands had been either converted to plantation agriculture or heavily grazed by introduced goats and sheep (Hobdy 1993). Moreover, new insect predators, such as ants, were appearing in the Islands and undergoing population explosions. Even in 1892, soon after his arrival, Perkins noted of central O'ahu that "Thick forest, no doubt, once came down at least to 700 feet, for there were many traces of fires, some very old and some comparatively recent. . . . In all the lower forest there is an almost total absence of native insects, though the variety of trees should, one would expect, produce many beetles. Their absence seems to be due entirely to the vast numbers of ants (*Pheidole*) which infest the lower mountains" (Perkins 1892). Collecting in the remnants of these lower-elevation communities, Perkins was able to capture species that are now extremely rare or altogether extinct: "well below any continuous forest, on a bare dry ridge, I found three isolated trees standing together and in very bad condition. On these I took specimens of a *Clytarlus* new to me, the trees being much infested with the larvae and nearly dead" (Perkins 1892). In certain cases, collections made by Perkins soon after his arrival could not be duplicated even a few years later, as in 1896 when he visited the leeward Wai'anae Mountains and noted that: "Once or twice I made my way to the exact spot where I had collected the unique specimen of *Rhynchogonus funereus* and several rather good species of the '*Brachypeplus*' group, but the trees which were alive, but unhealthy, in 1892, were now quite dead and dry" (Perkins 1896).

## MATERIALS AND METHODS

Although Perkins' collections provide a remarkable historical baseline against which we can compare modern insect distributions and abundances within the Islands, the limitations of his methods must still be taken into account. Perkins concentrated disproportionately on certain groups, such as Coleoptera, Lepidoptera, Hymenoptera, and Odonata, while comparatively neglecting others such as Heteroptera, Homoptera, and Diptera. In addition, his O'ahu collections were primarily accomplished via short forays from established houses and plantations (Perkins 1892), and as such he did little of the tent camping at higher elevations that characterized his later work on Moloka'i and East Maui (Manning 1986). This meant that he did little comprehensive sampling at night on O'ahu, even though we now know many Hawaiian insect species are primarily nocturnal.

As a result, we have chosen to make our comparisons in groups for which Perkins provided a relatively comprehensive sample. The *Megalagrion* damselflies (Odonata: Coenagrionidae) were among his favorites because of their large size and bright coloration, and between 1892 and 1897 he captured examples of all native species known to inhabit the Islands. All but one of these were described by the completion of *Fauna Hawaiiensis* (Perkins 1899, 1910), the exception being *Megalagrion paludicola* from Kaua'i, which was taken by Perkins in 1894 but not recognized as a distinct taxon until Maciolek and Howarth did so (1979).

Perkins also made extensive collections of Carabidae (Coleoptera), focusing on this family because of carabid beetles' availability for collecting owing to their presence as adults throughout much of the year and their greater relative abundance among insects in native Hawaiian montane ecosystems. His focus was also determined by the interests of his mentor, Dr. David Sharp of Cambridge University, who wrote early on during Perkins' field studies, "I am very sorry you have not got Carabidae yet; I am inclined to think one reason may be your working to *[sic]* much in the forest; but of course this is only a guess. However you must correspond with Mr. Blackburn on the subject, for it certainly looks very blank that you should in five months have only got 2 species out of the 60 Blackburn discovered" (Sharp 1892). Perkins went on to discover the ways of the Hawaiian Carabidae, personally collecting more species than any other individual (e.g., of the 128 known species of the carabid tribe Platynini, Perkins collected 92 [unpubl. data]).

### *Survey Localities*

Manning (1986) summarized the collecting localities surveyed by Perkins in the 1890s. We have revisited all of these sites on O'ahu and Moloka'i, except where this has been precluded by the urbanization of O'ahu. Carabid beetles and upland damselflies were also collected at additional O'ahu localities not noted by Perkins in any extant field notes, including (1) Palikea and Pu'u Kaua summits in the Wai'anae Mountains, (2) the Poamoho-Ko'olau Crest Trail junction, (3) Pu'u Ka'aumakua, (4) 'Eleao peak, and (5) the Keahiakahoe-Tripler Ridge Trail junction, all of the latter in upper elevations of the Ko'olau Range. Stream-dwelling damselflies were also collected from a wide range of elevations in nearly every catchment on the island of O'ahu and from most catchments supporting perennial flow on the island of Moloka'i. Many of these catchments were not visited by Perkins; thus the modern damselfly surveys must be considered more geographically comprehensive than those from the 1890s.

### *Damselflies*

Surveys for *Megalagrion* damselflies are based primarily on visual searching for flying adults in their preferred habitats during sunny periods. As such, they are highly dependent on good weather, suitable habitat, and an intimate understanding of individual species' ecological preferences. Much of the recent data presented herein for damselflies is based on Bishop Museum's intensive conservation status surveys funded by the U.S. Fish and Wildlife Service between 1993 and 1996, which often used several collectors to investigate a particular stream reach. The data from these surveys, along with historical records from Perkins' specimens housed in the Bishop Museum, have been captured in a specimen-level database, which may be searched online via the Internet by accessing the Bishop Museum Hawai'i Biological Survey Arthropod Checklist Query system (http://www.bishop.hawaii.org/bishop/HBS/arthrosearch.html). Information in the database includes (1) locality; (2) day, month, and year; (3) elevation; (4) ecological notes; (5) collector; (6) species; (7) number of specimens; and (8) repository. Additional information—including color images of many species (Polhemus and Asquith 1996), distribution maps, and literature citations—is available via the Bishop Museum *Megalagrion* damselfly home page.

Additional historical specimen capture records were compiled from the collections of the University of Hawai'i at Mānoa, The Natural History Museum in London, the Smithsonian Institution in Washington, D.C., and several private collections. These collections in aggregate comprise the majority of the world's Hawaiian damselfly specimens, and the records obtained provide a relatively comprehensive data set with which to assess specimen captures over time. Based on species concepts adopted in a revision currently in progress, O'ahu originally supported eight native damselfly taxa, four of them endemic. Moloka'i also supported eight species, but only one of these was endemic. Of the remaining seven taxa on Moloka'i, four are widespread taxa shared with most other islands in the chain, including O'ahu, whereas three are shared with Lāna'i, Maui, or Hawai'i, but not O'ahu.

### *Carabid Beetles*

Carabid beetles have been surveyed in a semiquantitative manner using repeatable techniques across the localities visited. During daytime, emergent vegetation is beaten, with all beetles (and other insects) collected from a beating sheet. Collecting time varies with weather conditions and travel requirements, but 4 to 6 hr are preferred for daytime collecting at a site. Host plant data are retained by separating collections from the various plant species at a site. The greatest carabid densities are found on plants with abundant moss mats surrounding branches or resting in crotches. These are raked and shredded to expose arthropod inhabitants. Nighttime searching is standardized by searching on exposed ground, especially trails, for 2 hr per site. In addition, vegetation is beaten at night for 2 hr.

Our reported findings for carabid beetles are summarized from a series-specific database of the over 21,000 available specimens of the tribe Platynini, currently being taxonomically revised (Liebherr and Zimmerman, in press). This database summarizes all specimens in the Bishop Museum (BPBM); The Natural History Museum, London; the Cornell University Insect Collection (CUIC), as well as 13 other institutions holding smaller amounts of Hawaiian carabid material. Information in the database includes (1) locality; (2) day, month, and year; (3) minimum and maximum elevation; (4) ecological notes; (5) collector; (6) species; (7) number of specimens; and (8) repository. Results are restricted to the tribe Platynini, because the species-level taxonomy for that tribe is now well understood. Such restriction still allows generalization to all of Carabidae, because Platynini is the only tribe that has undergone extensive radiation on all of the high islands.

## RESULTS

### *Damselflies on O'ahu*

Perkins collected eight species of damselflies on O'ahu in the 1890s (Perkins 1899, 1910), of which seven are still extant based on our surveys in the 1990s (Table 1, Figure 1). No additional species have been discovered since Perkins' collections, but *Megalagrion pacificum* (McLachlan), formerly widespread in terminal reaches of perennial streams throughout the island chain, has apparently been extirpated on O'ahu, although it still persists on Moloka'i and Maui (Polhemus 1993, Polhemus and Asquith 1996). Of the seven species still remaining on O'ahu, *Megalagrion xanthomelas* (McLachlan), which Perkins found to be locally abundant in coastal wetlands, has been reduced to a single population in a stream reach bounded by culverts at Tripler Army Medical Center on the outskirts of Honolulu (Figure 2) (Polhemus 1996). This population was recently relocated to an artificial refugium to prevent its elimination in the face of new building construction at the site. *Megalagrion leptodemas* (Perkins), which Perkins captured at only one site in the 1890s, and at a total of only three sites between 1900 and 1910, has continued to remain uncommon and elusive. Although this species is now extirpated from the sites where Perkins found it, four additional populations have been located in the Ko'olau Mountains. *Megalagrion oceanicum* McLachlan, which was abundant in the 1890s, is now completely extirpated from the Wai'anae Mountains whence Perkins' type series came, and is apparently now confined to a set of 10 gulches in the windward Ko'olau Mountains. Similarly, most of Perkins' specimens of *Megalagrion nigrohamatum nigrolineatum* (Blackburn) came from the Wai'anae Mountains, where the species is now extirpated, although it is still locally abundant in the Ko'olaus. Only three species that do not breed in stream or pond habitats, the seep-breeding *M. hawaiiense* (McLachlan), the

TABLE 1

NATIVE HAWAIIAN *Megalagrion* DAMSELFLY SPECIES COLLECTED IN SURVEYS OF THE 1890S AND 1990S

| 1890s/1990s | O'AHU | MOLAKA'I |
|---|---|---|
| +/+ | 7 | 7 |
| +/− | 1 | 1 |
| −/+ | 0 | 0 |
| −/− | 0 | 0 |
| Total no. species | 8 | 8 |

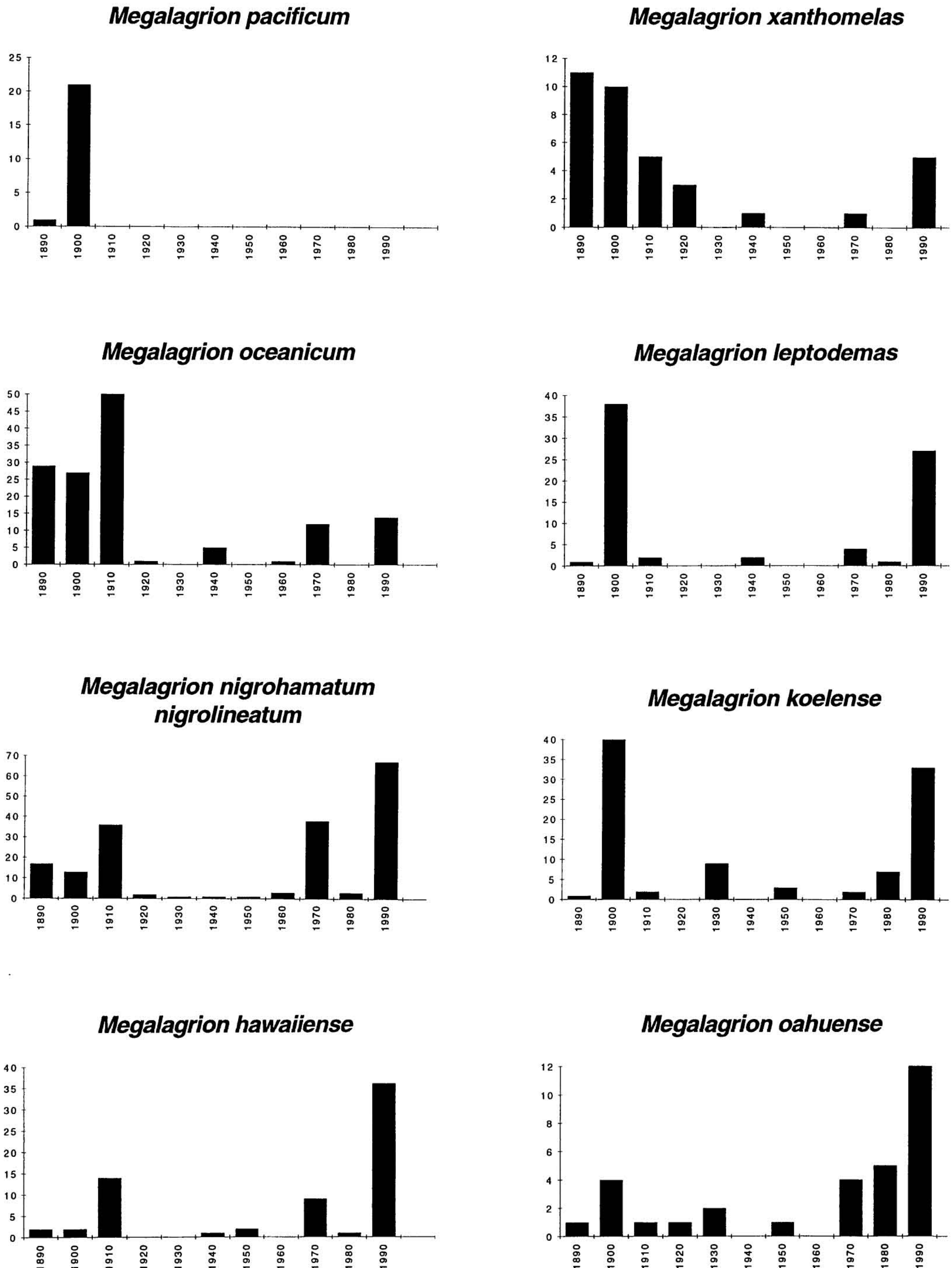


FIGURE 1. Total numbers of specimens collected by decade for eight *Megalagrion* damselfly species on O'ahu.

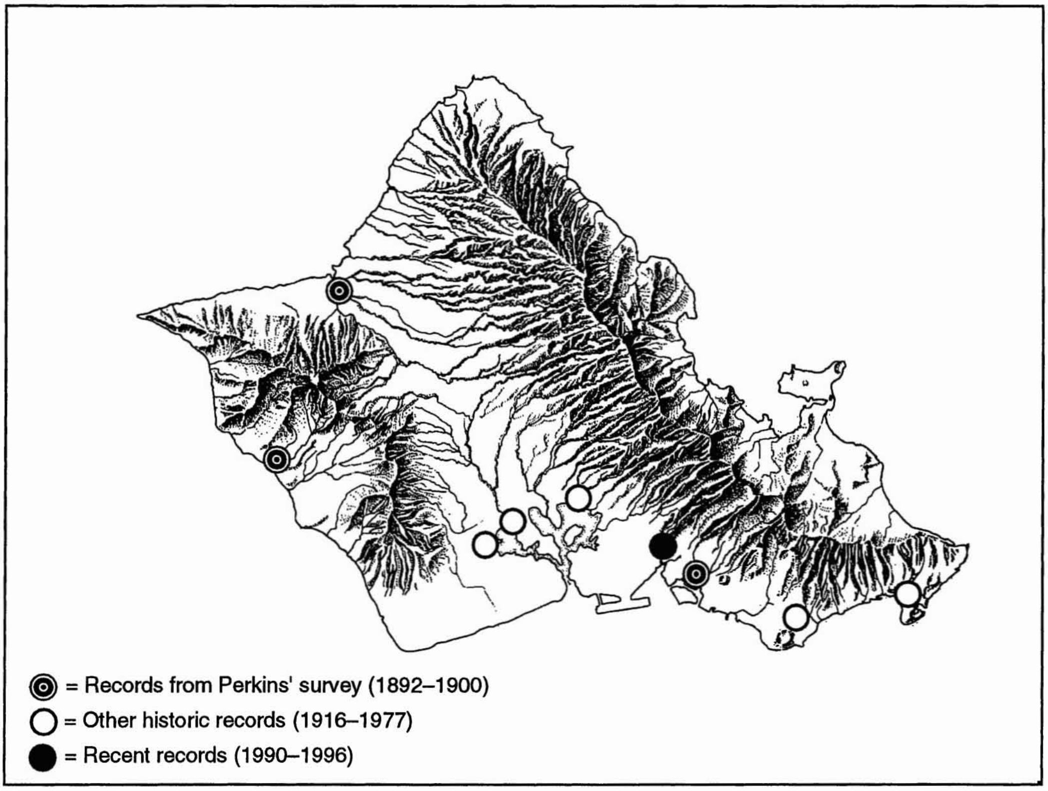


FIGURE 2. Current and historical records for *Megalagrion xanthomelas* (McLachlan), a lowland damselfly species that has been nearly extirpated on O'ahu.

phytotelmata-breeding *M. koelense* (McLachlan), and the terrestrially breeding *M. oahuense* (Blackburn), still appear to be as widespread and abundant in the 1990s as they were in the 1890s, indicating that introduced aquatic organisms, primarily frogs and fishes, have had a substantial negative impact on the other species (Polhemus 1993).

Summarizing Perkins' capture data for damselflies in the 1890s and 1900s (Figure 1) in comparison to captures resulting from recent surveys permits several facts to emerge. First, Perkins seems to have expended more effort collecting damselflies in the 1900s than in the 1890s. Second, the increased effort in the 1900s resulted in larger catches of rare species such as *M. koelense, M. pacificum,* and *M. leptodemas,* but not in the discovery of any additional species. Third, certain species, such as *M. hawaiiense* and *M. oahuense,* still eluded him because he did not understand their breeding habits; it was only in 1912 that Perkins finally secured a long series of *M. hawaiiense,* whereas modern collectors who understand this species' fondness for seeps have taken relatively large numbers of specimens. Captures of *M. xanthomelas, M. oceanicum,* and *M. leptodemas* were greater during Perkins' surveys in the 1890s and 1900s than during our recent 1990s surveys (Figure 1). To some extent this reflects more conservative collecting associated with status surveys for these endangered species that sought solely to establish presence or absence at a particular locality, but in addition the capture differential also seems to reflect lower overall population densities (Polhemus 1996). Only three species, *M. oahuense, M. hawaiiense,* and *M. nigrohamatum nigrolineatum,* show an increase in capture numbers in the 1990s over the 1900s (Figure 1). As noted above, the first two of these may be explained by modern knowledge of species' ecology. By contrast, the explanation of increased captures for *M. nigrohamatum nigrolineatum* appears to lie in the greater geographic coverage of contemporary surveys in comparison to those of Perkins. In fact, this species has seen a marked contraction of its range on O'ahu since 1900, although this is not reflected in total capture numbers because it is still locally abundant where it persists in the Ko'olaus. Finally, the capture numbers for *M. koelense* are somewhat equivocal, being low in the 1890s, high in the 1900s, and moderate in the 1990s. The explanation once again lies in species ecology; *M. koelense* is a phytotelmata breeder whose adults fly on ridge crests or above the canopy and are thus not easily caught. Recent immature surveys have shown that this species is, in fact, widespread and abundant in both the Wai'anae and Ko'olau ranges, even though stands of *Astelia,* one of the host plants utilized by this species for breeding, have been greatly reduced over the last several decades because of foraging by feral pigs (Stone 1985).

These examples reveal important limitations to the use of historical capture data. Such numbers are dependent not only on relative species abundance in any given decade, but also on collecting effort and the possession of specialized knowledge concerning habitats. At the same time, such data do reveal basic trends, especially when compared across the interval of a century. The lack of recent captures of *M. pacificum,* for instance, is not an artifact of sampling design in the 1990s; the species is actually extirpated on O'ahu.

### *Damselflies on Moloka'i*

Eight species of native damselflies were taken by Perkins on Moloka'i (Perkins 1899, 1910), of which all but one were recaptured during the surveys in the early 1990s. The exception is *M. molokaiense,* the only damselfly species endemic to Moloka'i, which is hypothesized on cladistic grounds to have a terrestrial larval ecology similar to that of *M. oahuense* (Polhemus 1993, 1997). Because the latter species still maintains healthy, albeit scattered populations on O'ahu, *M. molokaiense* may well be an inherently rare species with colonies remaining at remote, poorly sampled locations in the mountains of eastern Moloka'i. In sharp contrast to O'ahu, the remaining seven species of native damselflies on Moloka'i retain robust populations, including the lowland species *M. pacificum* and *M. xanthomelas,* both extirpated or nearly so on O'ahu.

Historical damselfly capture data by decade for Moloka'i show that the capture rates for all species except *M. molokaiense* have either held steady or increased between the 1890s and the 1990s. This is due both to the absence of substantial habitat disturbance and alien aquatic species introduction in the stream catchments of eastern Moloka'i, and to the increased mobility of entomologists, who have been able to use four-wheel-drive vehicles and helicopters to reach areas that were inaccessible to Perkins. Clearly the lesser degree of development and lower human population density on Moloka'i have resulted in the better retention of its damselfly biota in comparison with O'ahu.

### *Carabid Beetles on O'ahu*

Perkins' O'ahu collections from the 1890s included 21 of the currently known 32 species (Table 2), based on a total of 906 specimens (Table 3). Of these species, 17 have been recollected in the 1990s. Four species collected by Perkins in the 1890s have not yet been recollected in the 1990s, and conversely, six species have been collected in the 1990s survey that were not seen during Perkins' 1890 survey. Comparison of survey efficiency suggests similar success across 100 yr, because 66% of the known fauna was observed by Perkins versus 72% by us. That our survey efficiency is based on over two times the number of specimens

TABLE 2

NATIVE HAWAIIAN PLATYNINE CARABID SPECIES COLLECTED IN SURVEYS OF THE 1890S AND 1990S

| 1890s/1990s | O'AHU | MOLOKA'I |
|---|---|---|
| +/+ | 17 | 12 |
| +/− | 4 | 3 |
| −/+ | 6 | 4 |
| −/− | 5 | 2 |
| Total no. species | 32 | 21 |

suggests that current sampling techniques result in larger series of specimens at a site, but not necessarily in greater rate of discovery of rare species. We have spent a total of 45 days collecting sites on O'ahu in the 1990s. Perkins spent portions of 16 months collecting on O'ahu from 1892 to 1897 (Manning 1986), and though he spent relatively little time focusing on Carabidae (Perkins 1892), he encountered specimens over a wider variety of seasons and situations than we have.

Examination of relative species abundance in the two surveys led to a surprising conclusion. The most abundant species of the 1890s—*Colpocaccus tantalus* (Blackburn)—is absent from recent collections (Table 3). *Colpocaccus tantalus* exhibited a broad geographic distribution over the time span of its collections (Figure 3), occurring in both the Wai'anae Range and along the length of the Ko'olau Range. From a dominant position where it accounted for 39% of the specimens collected in the 1890s, it has decreased in relative abundance during the twentieth century (Figure 4), with the last observation at Hale'au'au, below Mount Ka'ala, in 1940 (BPBM, unpubl. data). The absence of *C. tantalus* since 1940 seems unequivocal, because of extensive surveys of Carabidae from native habitats made during the 1950s by E. J. Ford (1952), resulting in 974 total platynine specimens representing 25 of the 32 native species (BPBM, unpubl. data), followed by the 1990s surveys (Table 3).

*Colpocaccus tantalus* was collected on a variety of plants, including *Acacia koa, Cibotium chamissoi, Pipturus, Pritchardia, Broussaisia, Metrosideros,* and *Suttonia.* It occurred in moss mats on trees and under bark of dead *koa.* Most

TABLE 3

PLATYNINE CARABIDAE COLLECTED BY PERKINS' O'AHU SURVEY DURING THE 1890S, COMPARED WITH THOSE FROM SURVEYS OF THE 1990S

| RANK IN 1890s | SPECIES | NO. OF SPECIMENS 1890s | 1990s |
|---|---|---|---|
| 1 | *Colpocaccus tantalus* (Blackburn) | 357 | 0 |
| 2 | *Metromenus epicurus* (Blackburn) | 126 | 55 |
| 3 | *Metromenus fraternus* (Blackburn) | 99 | 106 |
| 4 | *Metromenus mutabilis* (Blackburn) | 76 | 146 |
| 5 | *Metromenus caliginosus* (Blackburn) | 51 | 240 |
| 6 | *Mesothriscus muscicola* (Blackburn) | 47 | 84 |
| 7 | *Metromenus palmae* (Blackburn) | 36 | 76 |
| 8 | *Chalcomenus corruscus* (Erichson) | 28 | 7 |
| 9 | *Blackburnia insignis* Sharp | 22 | 0 |
| 10 | *Metromenus cuneipennis* (Blackburn) | 13 | 1 |
| 11 | *Metromenus protervus* (Blackburn) | 9 | 16 |
| 12 | *Metromenus fugitivus* (Blackburn) | 8 | 173 |
| 13 | *Derobroscus micans* Sharp | 7 | 0 |
| 14 | *Mysticomenus tibialis* Sharp | 7 | 0 |
| 15 | *Metromenus fossipennis* (Blackburn) | 6 | 193 |
| 16 | *Anchotefflus gracilis* Sharp | 4 | 6 |
| 17 | *Metromenus bardus* (Blackburn) | 3 | 2 |
| 18 | *Brosconymus optatus* Sharp | 2 | 63 |
| 19 | Undescribed sp. "paludicola" | 2 | 23 |
| 20 | *Meteromenus perpolitus* Sharp | 2 | 14 |
| 21 | *Metromenus meticulosus* (Blackburn) | 1 | 99 |
| 22 | *Atelothrus fractistriatus* Perkins | 0 | 159 |
| 23 | *Metromenus audax* Perkins | 0 | 58 |
| 24 | *Metromenus hilaris* Perkins | 0 | 46 |
| 25 | Undescribed sp. "hihia" | 0 | 260 |
| 26 | Undescribed sp. "fordi" | 0 | 56 |
| 27 | Undescribed sp. "huhula" | 0 | 9 |
| Total no. of specimens | | 906 | 1,902 |

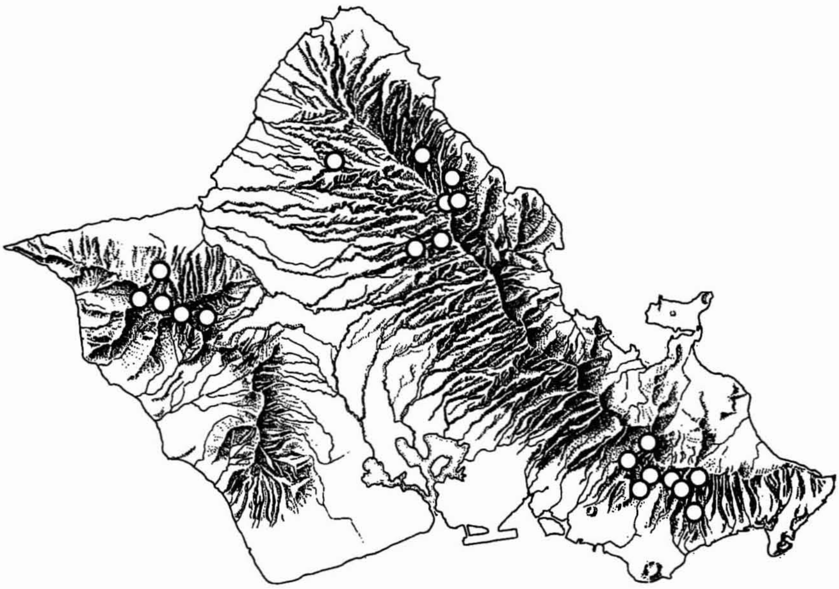

FIGURE 3. Distribution of recorded localities for *Colpocaccus tantalus* (Blackburn).

specimens were collected at elevations from 455 to 600 m, though limited numbers were collected from near the summit of Mount Ka'ala, at 1060 m elevation (Figure 5). The elevational preference of *C. tantalus* is significantly lower than those of the other species of O'ahu platynine carabids, suggesting that an altitudinally related factor was responsible for the serious decline in population levels of this species.

The other taxa missing in our recent survey were relatively much rarer in the 1890s, holding ranks 9, 13, and 14 among the 21 species collected by Perkins (Table 3). Conversely, many less-common species in Perkins' collections have been observed in large numbers by us. There may be a variety of reasons for this: (1) we have collected in regions inaccessible to Perkins, (2) we have used techniques Perkins did not use, (3) long-term fluctuations in population density may have occurred. As an example of the first reason, the undescribed species "fordi" is known from the crest of the northern Ko'olau range, distributed from Kaipapa'u on the north to Keahiakahoe on the south, a region denoted as "unsurveyed inaccessible" by Perkins (Liebherr and Polhemus 1997). Of his work at the Kawailoa Ranch, closest of his various bases to the northern Ko'olaus, Perkins wrote, "A long tramp was necessary before one could really get amongst the native insects, almost all of these for a long distance above the house having been cleaned out by the *Pheidole* ant. . . . Apart from the wet weather, the mountains of the Kawailoa district . . . were very unsatisfactory for collecting, the ridges . . . covered with masses of staghorn fern, impenetrable except at the expense of much toil and exertion" (Perkins 1892).

We also know that we have used collecting techniques that differ from Perkins', because he did little night collecting on O'ahu except for moths (Perkins 1892), whereas we have employed both active searching with headlamps

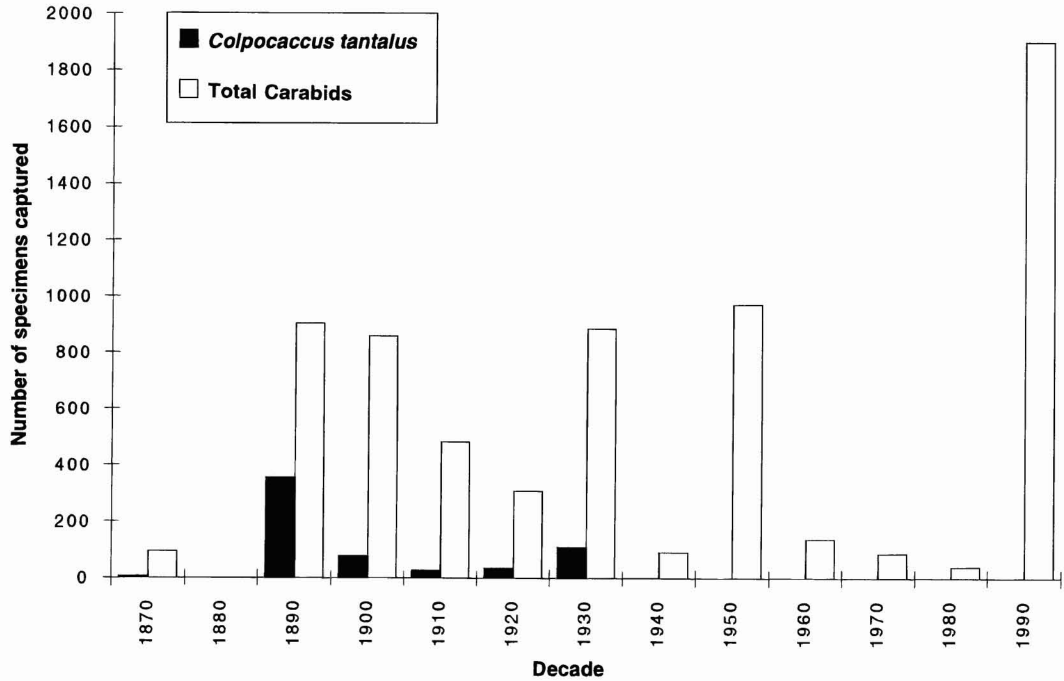


FIGURE 4. Total numbers of specimens collected by decade for *Colpocaccus tantalus* (Blackburn) (*filled bars*) and numbers for other O'ahu platynine carabids (*open bars*).

and beating of vegetation at night; of the 1902 specimens of the 1990s O'ahu survey, 746 or 39% were collected by these means. For example, the increase from 8 to 173 specimens of *Metromenus fugitivus* (Blackburn) (Table 3) is directly attributable to recent nighttime collecting; 146 of the 1990s specimens were collected at night (CUIC, unpubl. data). Also, the large numbers of *Brosconymus optatus* Sharp and its sister species, the undescribed species "hihia," observed in the 1990s (Table 3) are directly ascribable to an understanding of where these species live (i.e., under mosses and liverworts on thinner branches of *'ōhi'a* [Bridwell 1918]). This type of habitat is best sampled by beating, a technique Perkins apparently did not utilize extensively.

It is not possible to accurately determine relative population levels for all of the various species from historical collections because we do not know the amount of time Perkins spent employing his various collecting techniques. Therefore, comprehensive study of long-term fluctuations in populations must await future comparison with our recently completed and more repeatable sampling schemes. Nonetheless, several species distributed in areas that Perkins sampled are candidates for increased relative population densities over the past century, including *Metromenus fossipennis* (Blackburn), *M. meticulosus* (Blackburn), *Atelothrus fractistriatus* Perkins, *M. audax* Perkins, and *M. hilaris* Perkins (Table 3). Excluding nocturnal collections, specimen totals still show increases of 6 to 107, 1 to 93, 0 to 158, 0 to 58, and 0 to 46, when comparing the 1890s samples with 1990s samples (BPBM, CUIC, unpubl. data). That the latter three species were first collected by Perkins himself in the early 1900s suggests that they were relatively rarer in the 1890s than they are today.

Of the five species known from O'ahu but not seen in the 1890s or 1990s, two have not been recorded since Blackburn's collections in the 1870s: *Deropristus blaptoides* (Blackburn) from Kōnāhuanui and *Mysticomenus mysticus* (Blackburn) from the Wai'anaes. The former species was most probably collected by Perkins

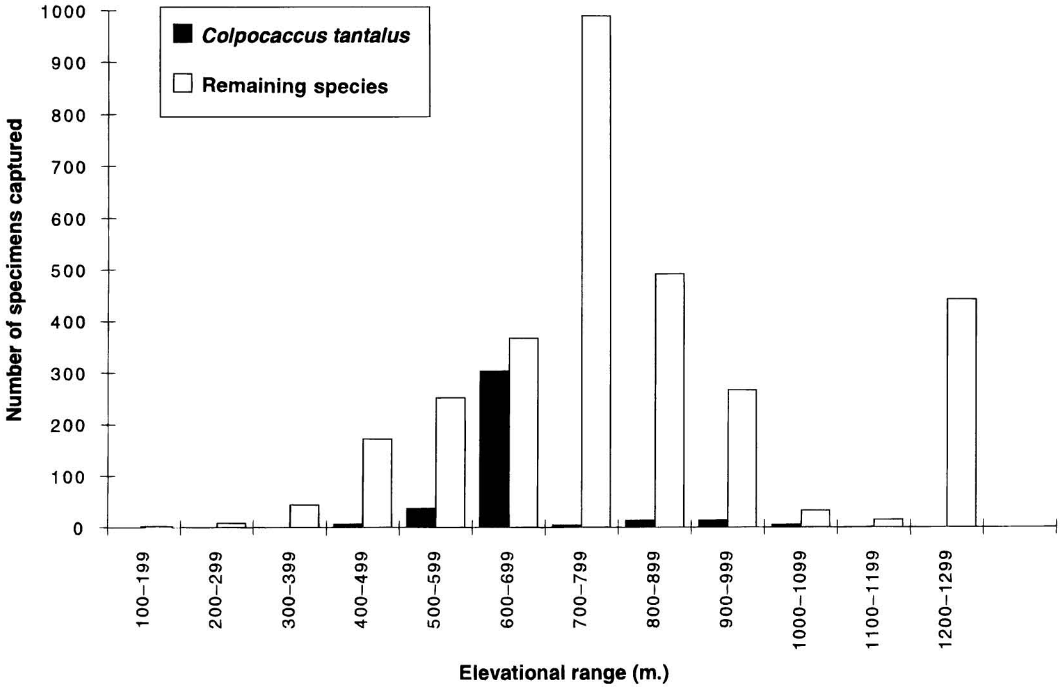


FIGURE 5. Numbers of specimens collected in elevational intervals for *Colpocaccus tantalus* (Blackburn) (*filled bars*) versus elevational profile for the aggregate balance of O'ahu platynine Carabidae (*open bars*). Elevational distribution of *C. tantalus* differs significantly from that of other species ($\chi^2$ = 1021.8, df = 11, $P << .001$).

in 1892; however his specimen was carried away from his room by marauding *Pheidole* ants when he answered a telephone call (Perkins 1892). Nonetheless, both of these species have been absent for over 100 yr and rediscovery seems unlikely.

The other three species absent from both the Perkins and recent surveys include the Wai'anae endemic *Atelothrus metromenoides* Perkins and the Ko'olau endemics *Metromenus oceanicus* (Blackburn) and the undescribed species "paloloensis," known from three series collected in the mountains above Honolulu from 1900 to 1906. It might be tempting to suggest the loss of these species; however, their inherent rarity makes discovery at any time unpredictable. The discovery of *Metromenus cuneipennis* (Blackburn) on Lanihuli by D.A.P., A. Asquith, and C. Ewing in 1996 follows its last previous collection on the Poamoho Trail in 1954 (BPBM, unpubl. data), suggesting that continuing survey efforts are the necessary means to ascertain the long-term prospects for the rarer endemic species.

*Carabid Beetles on Moloka'i*

Of the known Moloka'i platynine carabid fauna, 12 were sampled in the 1890s and again 100 yr later (Table 2). Three species observed by Perkins in the 1890s have not been seen by us. Conversely, we have collected four species not seen by Perkins. The species collected by Perkins but not observed in the 1990s include *Metromenus moerens* Sharp, *Atrachycnemis perkinsi* Sharp, and *Colpocaccus lanaiensis* Sharp; the former two are Moloka'i endemics, the latter is distributed on Moloka'i, Lāna'i, and Maui. *Metromenus moerens* has been collected 17 different times, with no series larger than six individuals. It was last seen in 1973, when a single individual was collected by W. C. Gagné (BPBM, unpubl. data). Thus *M. moerens* represents a relatively rarer species that has been recollected in relatively recent times. *Atrachycnemis perkinsi* is a member of a clade of exceedingly rare species (Liebherr and Zimmerman, in press); the four species in the clade are known from an aggregate 32 specimens, with two species represented by unique specimens. *Atrachycnemis perkinsi* is known from two series collected by Perkins in 1896 and 1902. The last specimen of any *Atrachycnemis* was collected in 1913 (BPBM, unpubl. data). The only bionomic information concerning *Atrachycnemis* is stated in Sharp (1903) as personal communication from Perkins: "Like *Deropristus,* never under stones." Rediscovery of any of the four *Atrachycnemis* and their habits remains a challenge. The Maui Nui species, *Colpocaccus lanaiensis,* is closely related to O'ahu's *C. tantalus,* with Moloka'i records spanning the 1890s to 1952. It has been collected on Maui in the 1990s: Kīpahulu Valley in 1991 (CUIC, unpubl. data). In summary, the species profiles of the 1890s and 1990s surveys of Moloka'i Platynini do not differ substantially. Species' absences in recent samples are best explained by lack of knowledge concerning where to find them, and their presumed relative rarity.

## DISCUSSION

Extinction probability is often assumed to be inversely proportional to species abundance; however, when extinction is based on environmental catastrophe (i.e., major ecological disturbance) large population size may not serve to buffer a species from extinction (Pimm 1991). Documenting the extinction of extremely rare species is a difficult undertaking, as illustrated above by the rediscovery of *Metromenus cuneipennis* on Lanihuli after a 42-yr hiatus of collections. Adopting a century-long (or longer) view, as done here, is perhaps the best means to explore long-term prospects for potentially endangered island endemics.

Among the Carabidae, the most defensible claim for extinction of a native Hawaiian species involves the species most commonly collected during the 1890s, *Colpocaccus tantalus.* The defensibility of a hypothesis of extinction for this species rests most strongly on the species' previous dominance in the fauna and secondarily on the lack of any collections since 1940. Its putative loss is therefore not correlated with extreme rarity during its known period of collection. In this, *C. tantalus* resembles the Rocky Mountain grasshopper, *Melanoplus spretus* (Walsh), which flew in swarms as large in extent as the state of Colorado, yet is extinct today, presumably because of modifications of its much more geographically limited breeding habitat (Lockwood and DeBrey 1990). The concentration of records for *C. tantalus* near 600 m elevation suggests that this elevation represented its primary breeding habitat. The relatively fewer individuals found at higher elevations could have represented less-dense breeding populations or nonresident volant individuals of this macropterous species. If *Pheidole* (Perkins 1892) or other ants (Reimer 1994) preyed on *C. tantalus* larvae or pupae in a manner similar to that shown for interactions of *Pheidole megacephala* (F.) and native *Tetragnatha* spiders (Gillespie and Reimer 1993), or Argentine ant, *Iridomyrmex humilis* (Mayr), and the Haleakalā carabid, *Mauna frigida* (Blackburn) (Loope et al. 1988, Cole et al. 1992), then elimination of the most-dense populations could have contributed to the final elimination of *C. tantalus.* Of course, the association of habitat disturbance due to nonnative plant introductions with the presence of alien pestiferous arthropods makes tenuous any final assignment of culpability (Howarth 1985).

Regardless of causation, this interpretation suggests that populations in lower-elevation, higher-population-density core areas contributed to those in higher-elevation marginal habitats through the rescue effect (Brown and Kodric-Brown 1977). Elimination of such core-area populations through predation and/or habitat destruction then led to collapse of the species over its entire range. Such an interpretation is appropriate only for species with highly developed dispersal abilities, which, based on its macropterous flight-wing configuration, *C. tantalus* apparently possessed. All other O'ahu species of platynine Carabidae except *Chalcomenus corruscus* (Erichson) are vestigially winged (Liebherr and Zimmerman, in press), so they probably do not exhibit differential core and marginally inhabited areas. More likely, their areas of habitation are already highly fragmented, with populations in isolated montane forest habitat on different peaks or in different mountain ranges operating largely independently of each other. These species might be expected to persist in bastions of suitable habitat until the last population is overrun. That they still persist is due to their occupation of higher-elevational, less-disturbed habitats than those utilized by *C. tantalus*.

The damselfly results are somewhat more easily explained. *Megalagrion pacificum* occupied an inherently vulnerable habitat in side pools along lowland stream reaches that had already been greatly modified in the cultivation of taro, and later rice, before Perkins arrived. This species was rare even in the early 1890s and appears to have vanished from O'ahu entirely by 1910. *Megalagrion xanthomelas,* although also an inhabitant of vulnerable lowland sites, had somewhat greater ecological plasticity and persisted as scattered populations in the Pearl Harbor area until at least the 1970s (Polhemus 1996). That was the same time at which other O'ahu stream-breeding species also experienced serious range contractions, indicating a sudden increase in the level of ecological disturbance in that decade. By contrast, the ranges of species that bred in montane areas removed from streams did not exhibit similar reductions, further indicating a causal agent, most likely biological, associated directly with freshwater habitats.

Both the beetle and damselfly cases demonstrate a loss of lowland and mid-elevational biota on O'ahu between the 1890s and the 1990s, which may in many ways seem an obvious conclusion. What has been less clear previously, however, is the likelihood of substantial shifts in relative abundance among species within these groups, particularly the carabid beetles, with certain formerly common species becoming rarer and other previously rarely encountered species now found in relatively greater numbers. This observation is consistent with an ongoing and dynamic community-level response to the protracted ecological perturbations experienced on O'ahu and reiterates the importance of continued standardized surveys to provide the historical baseline from which to assess long-term changes in the island's community structure.

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