The Importance of Insect Monitoring to Conservation Actions in Hawaii

Matthew J. Medeiros[1, 2*], Jesse A. Eiben[3], William P. Haines[4], Raina L. Kaholoaa[5], Cynthia B.A. King[6], Paul D. Krushelnycky[4], Karl N. Magnacca[7], Daniel Rubinoff[4], Forest Starr[8], and **Kim Starr[8]**

[1]Urban School of San Francisco, San Francisco, CA 94117. [2]University of California, Department of Integrative Biology, Berkeley, CA 94720. [3]University of Hawaii at Hilo, College of Agriculture, Forestry and Natural Resource Management, Hilo, HI 96720. [4]University of Hawaii at Manoa, Dept. of Plant and Environmental Protection Sciences, Honolulu, HI 96822. [5]Haleakala National Park, Makawao, HI 96768. [6]Hawaii Division of Forestry and Wildlife Native Invertebrate Program, 1151 Punchbowl Street, Room 325, Honolulu, Hawaii 96813. [7]Oahu Army Natural Resources Program, PCSU, Schofield Barracks, HI 96857. [8]Starr Environmental, Makawao, HI 96768. *Author to whom correspondence should be addressed: matt.j.medeiros@gmail.com

Abstract. Endemic insect species make up the overwhelming majority of Hawaii's native fauna, and play many important ecological roles. Despite this, insects receive low levels of conservation funding, likely due to their small size, fluctuating population sizes, and lack of baseline data necessary to determine if they are threatened with extinction. To determine which insects are at risk, how insect populations fluctuate in natural areas, and which management actions are most beneficial to Hawaiian ecosystems, we propose that insects be monitored whenever possible. Insect monitoring should be broad, generating community-based metrics such as species richness, rather that focusing on individual species. Resultant data should be entered into a stable, central database. Rather than individual insect species being the explicit target of conservation, we emphasize that measures of insect diversity can provide an assessment of restoration efforts, and serve as a metric for prioritizing areas for conservation. We provide lists of additional recommendations for land managers and research entomologists who wish to assist with insect conservation efforts.

Key words: database, endemic species, indicator species, invasive species, monitoring, population trends

I. Hawaiian insect diversity and the importance of insect conservation

Most biologists would agree that a primary global goal of conservation is the protection of biodiversity, whether it is measured in terms of species (Myers et al. 2000), evolutionary lineages (Williams et al. 1991), or ecological diversity (Soule et al. 2003). By any of these measures, insects account for the majority of Hawaiian terrestrial biodiversity. In terms of sheer number of species, insects are the major components of biodiversity in virtually any terrestrial ecosystem, and this is especially true in Hawaii, where the current native terrestrial vertebrate fauna consists only of birds and a single species of bat. At last count, Hawaii had nearly 5500 described native insect species, nearly all of these endemic (Nishida 2002), and this number grows steadily as new species are described. In fact, insects comprise 53% of all described endemic life forms in Hawaii and 70% of all endemic animals, including both terrestrial and marine organisms (Figure 1; Eldredge 2000). Invertebrates as a whole, including other arthropods and mollusks, account for 82% of all endemic life forms and 97% of endemic animals (Eldredge 2000).

Because insects are such an important component of Hawaiian ecosystems in terms of species richness, it stands to reason that they fill many ecological niches and provide important ecological services. Although little is known about specific plant-pollinator relationships in Hawaii, insects are certainly the primary pollinators of native plants. Based on floral morphology, 67% of endemic flowering plants are thought to be insect pollinated, compared to only 19% bird pollinated, and 14% wind-pollinated (Sakai et al. 2002). Insects are also important parts of food webs, being the primary native consumers of plants (especially in the absence of herbivorous mammals), and important decomposers of organic matter. Insects are critical sources of protein for all native forest birds, especially when nesting and raising young (Mountainspring 1987, Ralph and Fancy 1994), and the relationships between birds and their insect prey can be highly specific (Banko et al. 2002). The Hawaiian hoary bat or ōpeapea (*Lasiurus cinereus semotus*), an endangered species, feeds exclusively on insects and other arthropods (Whitaker and Tomich 1983, Jacobs 1999, Fullard 2001). Of course, insects also serve as food for each other, with extremely complex relationships among native herbivorous insects and their predators and parasitoids (Henneman and Memmott 2001).

Yet, this high diversity among insects is not indicative of the security of their persistence, and insect species in Hawaii have almost certainly suffered extinction rates as high as, or higher than other groups (McKinney 1999). Moreover, it is possible that the continued decline and extinction of plants and birds that are already favored with conservation resources (e.g., the endemic birds poouli, *Melamprosops phaeosoma*; alala, *Corvus hawaiiensis*; palila, *Loxioides bailleui*) may be due to the disintegration of ecosystems more broadly, and the decline of native insects, specifically. Thus, ignoring the plight of native insects may contribute to the disappearance of those more 'charismatic' elements of biodiversity. Ultimately, focusing nearly all conservation resources on plants and birds may not serve the long term interests of those taxa, if the insects on which they directly or indirectly depend are left to disappear.

II. Challenges to insect conservation

Despite insects being such a crucial component of Hawaiian biodiversity, vertebrates and plants continue to receive the lion's share of conservation attention and funding. To make matters worse for insect conservation efforts, Hawaii's share of nation-wide conservation funding is vastly underrepresented (Leonard 2008). Lack of funds for insect conservation is likely due to a combination of factors that complicate such efforts, including practical problems faced by land managers, as well as negative or indifferent public attitudes towards insects. In general, the United States lags in its efforts to conserve invertebrates, with disproportionately poor representation of arthropods on the endangered species list (one arthropod per 16 vertebrates and plants). Hawaii, which lacks most of the vertebrates that garner the attention of continental conservationists but has a much higher percentage of endemic insects, might be expected to do better than the national average. Regrettably, Hawaii is doing worse: a lower percentage

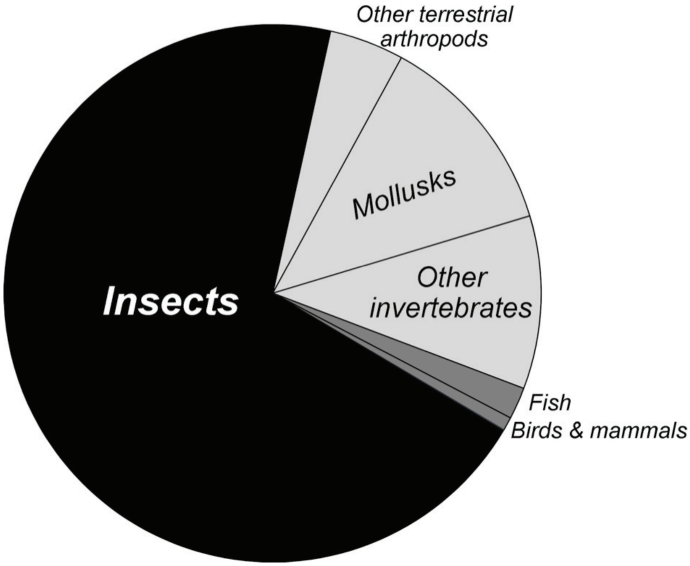

Figure 1. Insect species account for 70% of Hawaii's total number of endemic animal species.

of the Hawaiian arthropod fauna is listed as endangered than at the national level (one arthropod for every 19 vertebrates and plants), and current practice largely ignores the conservation of insects. For example, the Kauai green sphinx (*Tinostoma smaragditis*) has been collected less than 20 times since its discovery. Despite very little being known about its life history, no studies are currently being funded to learn more about it, even though this moth is the sole species of an endemic genus. Only a few Hawaiian insects are now federally listed, and these represent a small fraction of the species at risk and an insignificant proportion of Hawaii's overall insect diversity.

Why does this lack of emphasis on insect conservation exist in the first place? Perhaps the most obvious difficulty regarding insect conservation is that most insects are very small and cryptic, often noticed only after careful observation of an ecosystem. Many insects are nocturnal, or spend all or most of their lives under rocks, high in the tree canopy, or buried in moss or leaf litter. This means that assessments of population status or extinction of individual species require a highly focused search effort. Additionally, the adult life stages of many insects are able to fly and are therefore highly dispersive, making it extremely difficult to follow individuals over time. Tracking insects using GPS or radio technology is currently impossible for all but the largest insects, although marking with paints or tags is feasible for some species (see McGeoch et al. 2011 for an introduction to the broader literature regarding insect monitoring).

Compared to vertebrates and many plants, insects usually have relatively short lifespans, rapid generation times and often high reproductive output, meaning that populations can fluctuate greatly, both temporally and spatially. Some native insects exhibit "boom or bust" population dynamics, persisting at unnoticeable levels most of the time, but then experiencing occasional population explosions when they are common, or even considered pests. For most species, the underlying causes of population fluctuations are not understood, likely being dependent on interactions between climate, resources, and mortality factors such as predators and pathogens, and not always following predictable seasonal patterns. Because of these short-term fluctuations, it can be difficult to detect long-term trends in insect populations, even when they can be accurately sampled. To account for seasonal variation, it is usually necessary to sample multiple times per year, sometimes over several years. This can quickly become a daunting task when dealing with multiple species and multiple locations. Thus, these methods are essentially abandoned in practice, despite the fact that such data are necessary to understand conservation needs and large scale population patterns.

Assessing the long-term viability of insect species can be difficult because of this lack of historical baseline information on distributions and abundances. For most native Hawaiian birds and plants, scientists have at least some records of where species formerly occurred, and how common they once were. In contrast, historical information regarding insect distributions is far from complete, and for most species, is spotty or completely missing. Some insects that are currently rare or localized may have always been rare, while for others, rarity may be a symptom of decline due to novel threats. Many insects that were among the most common in the 1890s, and some even more recently, have become extinct or nearly so. Three examples include the carabid beetle *Blackburnia tantalus* (Liebherr and Polhemus 1997), the bee *Hylaeus facilis* (Daly and Magnacca 2003), and the wasp *Euodynerus nigripennis* (Williams 1927). For any species that has been rare for most of its documented history—which includes the vast majority of Hawaiian insects, particularly in highly-diverse radiations—it is especially difficult to ascertain when species are declining or under threat, since they may not be detected for years or even decades at a time.

Given the challenges and limitations outlined above, how should researchers, land managers, administrators and others interested parties proceed to make insects a more integral part of conservation in Hawaii? We offer our perspectives on how best to approach this question in the following sections.

III. How and why should we monitor insects?

As mentioned above, knowledge of how to conserve insects often suffers from a dearth of information. This applies to understanding both the status of species or populations and, to a somewhat lesser extent, how to mitigate threats to them. Some threats to insect species and communities are fairly well characterized (such as invasive social Hymenoptera, see below), and the solutions to these problems are theoretically straightforward, if often difficult to implement. Other forces degrade Hawaiian ecosystems more broadly and often interact with one another, and these likely exert impacts on insects that are complex, are challenging to measure, and as a result are currently poorly supported with empirical data. This also means that the best ways to alleviate these impacts for insects may not always be clear. We therefore suggest that a critical need at this juncture is an increased investment in insect monitoring, which will serve several inter-related goals.

First, increased monitoring will begin to allow more accurate assessments of population or species trends for at least a subset of the native fauna, which are currently almost entirely lacking. Second, monitoring insect communities will provide much additional information to land managers and state officials about overall patterns and trends in diversity within protected natural areas. We reiterate that insects and their relatives comprise the majority of the biodiversity that is the object of this protection. A third benefit is that the monitoring of insect communities, when conducted in conjunction with management actions, can begin to clarify whether commonly used management strategies actually do provide significant benefit to insects (as is often assumed or at least hoped), and ideally whether some are more effective than others. For a more thorough discussion of the advantages of using arthropod diversity to inform conservation practices, see the arguments of Kremen et al. (1993) and Oliver and Beattie (1996).

Of course, the effectiveness of monitoring efforts is dependent on the continuation of the sort of general collecting and taxonomic research that has been a mainstay of entomological work. This research provides critical information that gives conservation assessments meaning and validity, and at the same time can provide an alternate means to evaluate species status. Finally, an effective way to aggregate this information is needed: a centralized invertebrate database is critical to synthesizing abundance and distribution information generated from all types of collecting and monitoring efforts (McGeoch et al. 2011). We elaborate on these points below.

A. Using a broad approach to insect monitoring. The use of specific indicator groups presents an appealing way to deal with the complexity of monitoring insect communities (McGeoch 1998, Niemi and McDonald 2004, Gerlach et al. 2013). However, different insect groups often respond differently to different factors, so it is not likely that population trends in a single group will consistently indicate trends for all or possibly even most other groups. Similarly, one group may be especially sensitive to one type of stressor, and thus be a good "indicator" for that impact, but another group may be a better indicator for another impact. For example, Krushelnycky and Gillespie (2010) found that native spiders and beetles were among the most sensitive taxonomic groups to invasive ants in Hawaii, that other groups were much more variable in their responses, and that trophic group and population density were generally more effective for predicting sensitivity to ants than was taxonomic identity. In comparison, preliminary assessments suggest that Hawaiian Orthoptera and larval Lepidoptera may be particularly sensitive to predation by rodents, but also that the vulnerability of taxa may vary between sites and be context-dependent (P. Krushelnycky, unpublished data). Non-native plant invasions may produce yet a different pattern for insect communities. Therefore, it will often be difficult to know which indicators to select until more comprehensive sampling demonstrates which groups respond to a particular stressor and which do not. Practically speaking, this means that broad sampling is the best current approach, until such datasets can be used to determine whether a smaller subset of taxonomic or functional groups can be used as indicators for the health of the larger insect community (Basset et al. 2004).

When assessing the impacts of threats or management actions, community-wide metrics, such as endemic species richness, diversity or proportion of the community that is native (by species or individuals) should be evaluated, even if trends within specific taxonomic or functional groups are also investigated. Community-wide metrics are important to use because measures that span multiple insect groups will be much less sensitive to the idiosyncratic fluctuations of particular species or populations. Changes in these gross-level, synthetic metrics over time between different inventory or sampling efforts may be insightful even when different methods were used, although we strongly suggest being as consistent as possible in sampling methodology if a known goal is to make such comparisons. For example, an inventory of arthropods at Haleakala National Park (Krushelnycky et al. 2007) conducted roughly 25 years after an earlier one (Beardsley 1980) allowed for some limited comparisons regarding overall patterns of adventive species establishment, but differences in the goals and methods between the two surveys hampered detailed assessments of faunal changes over the intervening period. Assessments of native arthropod diversity require that insects be identified to low taxonomic levels, necessitating both expertise and time investment. However, because the insect fauna of Hawaii is disharmonic, with many groups absent, species-level identification is considered more feasible than continental tropical ecosystems. Additionally, many groups of insects can be classified as native or non-native after identification to genus, family, or even order, and it may be possible to use morphospecies to quantify diversity within some groups.

That said, while we generally advocate that researchers and land managers attempt to sample insects as broadly as possible, specialized monitoring focusing on single species or groups of interest may sometimes be needed or valuable (see McGeoch et al. 2011 for a list of examples of species of interest from South Africa). In some cases, when land managers request conservation recommendations from entomologists, enough may be known about a specific insect to confirm not only that the insect is threatened with extinction, but also to make a species-specific recommendation to conserve it. Some of the well-known Aeolian-dependent species such as the wekiu bug (*Nysius wekiuicola*) (Eiben and Rubinoff 2010) and Haleakala grasshopper moth (*Thyrocopa apatela*) (Medeiros 2009) are specific examples; other well-known species with a high level of cultural or ecological importance may benefit from species-specific monitoring as well, such as yellow-faced bees in the genus *Hylaeus*. In each of these cases a significant investment into the species' life history is or was necessary. In addition, research on specific taxonomic groups has provided clear evidence of the wider impacts of native habitat conversion: Leblanc et al. (2013) found that a suite of Hawaiian Drosophilidae was strongly tied to native forest stands.

In sum, we suggest that land managers partner with entomologists to conduct general arthropod monitoring in locations and situations of interest, especially before and after conducting particular management actions. Even when insects are not a specific target of management actions, they can serve as a valuable measure of the effectiveness of habitat protection. By tracking increases or decreases in the proportion of native insect diversity or abundance, we can use insects as a kind of "conservation currency." Initial monitoring will establish species lists and/or community composition at a given locality, with repeated observations providing important information about how specific management actions affect insect conservation and recovery. Whenever possible, it is important to simultaneously monitor at a comparable site where management actions are not implemented, to tease apart the effect of climate and other factors unrelated to management.

Our goal here is not to provide a list of specific sites and methods for this monitoring, because the decision to undertake insect monitoring will depend heavily on available funding, manpower, and other logistical and situation-specific considerations. Similarly, appropriate methods can also be highly site- and goal-specific. However, several examples that illustrate our aim include efforts by the Oahu Army Natural Resources Program to monitor insect community response to intensive rodent trapping in the Waianae Mountains, an effort by Pacific Rim Conservation and the Hawaii Department of Land and Natural Resources (DLNR) to monitor insect response to the construction of a predator-proof fence at Kaena Point Natural Area Reserve, and an effort by DLNR, the U.S. Geological Survey and the Maui Forest Bird Recovery Program to survey insect diversity and abundance to ascertain food resources for endangered forest birds on East Maui. Given sufficient progress and momentum in this direction, a working group could be established to provide more specific guidance and perhaps make recommendations for a network of monitoring sites.

B. Establishing a statewide invertebrate database. The continued description of native Hawaiian insect diversity is critical to its conservation, especially considering its high level of endemism. All conservation assessments and decisions are ultimately based on our understanding of the native biota. As a result of this constraint, previous attempts at compiling complete lists of species for a given time and place within Hawaii have been made with varying degrees of success. For example, Beardsley (1980) published a catalog of all insect species, native and non-native, found in the crater district of Haleakala National Park. There, he wrote (p. 1),

> The Catalog is still relatively incomplete. Specimens belonging to certain taxonomic groups have not yet been identified. In other groups, many identifications are still incomplete due to the unavailability of specialists in these groups, or to an inadequate present state of taxonomic knowledge concerning the groups.

This passage highlights the importance of current taxonomic work, as well as identification of specimens by experts.

In addition, the compilation of information generated in taxonomic studies and other types of "general collecting" can in some cases yield insight into species trends and conservation status. For example, Vorsino et al. (2013) found a substantial distributional shift and range reduction over time in *Omiodes continuatalis,* by comparing data from historical collections with those from modern surveys. The consistent entry of this type of collecting information, as well as information from broader inventories and monitoring efforts, into a central statewide database will provide a vast amount of information that would be difficult to compare and synthesize otherwise. For instance, Howarth and Preston (2007) recently documented insect species found on lands surrounding Kahului airport on Maui. While this information is extremely useful for monitoring long-term changes in insect communities, it is currently not easy to conduct a quick search of these data. To aid scientists, land managers, and environmental planners gathering information on the changing distributions of taxonomic groups, a new online State Invertebrate Database (SID) is being developed. The database is being generated by the State of Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife, and will be a specimen-level database that includes geographical (GIS) locality data whenever available. An ultimate goal of the database is to catalogue all museum specimens from collections made in Hawaii, and provide a central repository into which future specimen and collection data can be integrated. The SID will allow users to generate distribution maps for given species, species lists for given localities, and answer broad questions which to date have been difficult to address. For example, researchers will be able to analyze changes in habitat use by species over time, land managers will be able to better prioritize locations for management and conservation efforts, and groups planning for new protected areas will be able to determine whether rare species have been documented from a particular location of concern.

IV: Recommendations for land managers

Generally, species tend to have high extinction rates in fragmented habitats (Hanski 1999, Rybicki and Hanski 2013). Therefore, as with many other organisms, the best strategy is often to protect large tracts of land, rather than many small, widely spaced patches of high-value habitat (Samways 2007). That said, minimum habitat sizes for insects are often smaller than for vertebrates, so efforts to protect even small areas may have a significant payoff in terms of insect conservation. Some rare and elusive insects can be conserved effectively in small ranges that offer some natural protection, perhaps partly due to remoteness and/or inaccessibility, though some invasive species still pose problems in such areas (New 2009).

With the caveat that there may sometimes be exceptions, we agree with Samways (2007) that the most effective conservation strategy is a generalized approach, protecting habitats from universal threats, rather than attempting to protect insects on a case-by-case, species-by-species basis. This is largely for two reasons: First, the most important limiting factor for any given insect species is not often known with certainty, whether it be a parasitoid, predator, scarcity of host plant, or complex interactions between all of these. Second, even when the primary threat to an insect species is known, if that threat is highly specific and difficult to alleviate, doing so may not be the wisest use of resources, given the large number of species that would be ignored in the process. The general action of keeping ecosystems as intact as possible maximizes management efficiency by benefiting an entire suite of species (Asquith 1995; Gagné 1982; Howarth and Gagné 2012).

When a species-specific approach is warranted or required (e.g. under the Endangered Species Act), it is best to target species whose protection will benefit many other species or even entire ecosystems. *Drosophila* flies are a good example: They mainly breed in subdominant trees and require moderately dense shade, so protecting their hosts requires maintaining a native canopy and eliminating factors that hinder plant reproduction, such as pigs and rats. Management actions that benefit the flies therefore also benefit a number of other species, including plants.

How should ecosystems in Hawaii be broadly protected? As stated above, there is little robust evidence that common management practices are effective for conserving insects in Hawaii, though many of us assume that they are. Until more information becomes available, we suggest following recommendations that are based on our understanding of important threats. For example, Beardsley (1980) listed four management actions that he considered critical to preserving endemic insect biodiversity, particularly at high elevations. These four actions are no less relevant today than they were over thirty years ago when first suggested. We highly recommend that management agencies direct available resources toward these actions, when relevant to the ecosystem in question. To paraphrase and update

Beardsley's (1980) recommendations, these four actions are:

1. Ungulate control. Beardsley wrote that feral ungulates are a threat to insects and should be excluded, since they contribute to the decline of plant communities (though alien weed control within fenced areas is also important; see Cabin et al. 2000). Host plant specialists as well as the consumers that feed upon them are therefore harmed by ungulate rooting and browsing. Ungulate damage in Hawaii has been well documented by a number of papers; the literature has been synthesized in two position papers by the Hawaii Conservation Alliance (2005; 2007). We add that rodent control is important as well, since rodents are direct predators of arthropods as well as major seed predators of plants they depend on.

Ungulate exclusion and control techniques have been mastered in Hawaii and have become standard practice for most natural areas. There are many examples of successful ungulate control and eradication (Cole et al. 2012; Tunison et al. 1995). If the island is large, eradication will likely only be local and fences must be maintained forever. Smaller islands, such as Kahoolawe, can have all the ungulates removed, requiring no additional costs for ungulate control.

Rodent control is much harder than ungulate control and is usually done over a limited area. There are many examples of successful rodent eradication on small islands and atolls (Howald et al. 2007). However, control of rodents on large islands will likely be restricted to small high value locations, through the use of persistent trapping or installation of predator-proof fences.

2. Ant control. Entomologists since Perkins (1913) have noted the devastation that ants have caused to the Hawaiian insect biota. Hawaii is believed to have no native ant species, and although the impacts of ants are complicated and not always easy to document, it is nonetheless clear that ants pose a serious threat to many endemic insects (Cole et al. 1992, Krushelnycky and Gillespie 2008, 2010). Numerous ant species have invaded many habitats in Hawaii, and some continue to spread (e.g., Hartley et al. 2010). Eradication or control of ants using baits and toxicants would benefit a wide range of species (Krushelnycky et al. 2005), although the non-target effects of control methods must be considered, especially if treatments are conducted area-wide on a regular basis.

Unfortunately, ant eradication is usually very difficult, and success depends on various factors including the identity of the target species and most importantly the size of the infestation. There are now many examples of relatively small scale eradications globally (Hoffmann et al. 2011), including the eradication of *Pheidole megacephala* from an Oahu offshore islet (Plentovich et al. 2011) and the likely eradication of *Wasmannia auropunctata* on Maui (Vanderwoude et al. 2010). However, we know of only a single instance where more than one invasive ant species was simultaneously eradicated from a managed area (Hoffmann and O'Connor 2004), and in Hawaii multiple problematic ant species often co-occur, which can present greater management challenges. For example, the eradication of bigheaded ants (*P. megacephala*) from Mokuauia Islet was followed by a dramatic increase in the number of yellow crazy ants, *Anoplolepis gracilipes* (Plentovich et al. 2011).

3. Wasp control. Invasive yellowjackets (*Vespula pensylvanica*) have played a major role in diminishing native insect populations through direct predation (Gambino 1992, Wilson et al. 2009), though as Howarth and Gagné (2012) point out, quantifying the extent of wasp impacts is difficult. Regardless, yellowjackets are major pests of both humans and other animals and their nests should be destroyed when possible. Although wasp control is resource intensive and must be done on a continuous basis, techniques for successful wasp control are known, and local control can also benefit humans that frequent those areas. Yellowjackets have been documented to displace native pollinators (Wilson and Holway 2010), and management of yellowjackets has been shown to increase seed set of native plants (Hanna et al. 2013).

4. Ask visitors to stay on trails. This is the most habitat-specific recommendation in Beardsley's (1980) report, as the alpine cinder desert is such a small area, and a place where many arthropods take shelter under rocks. However, trampling any area in Hawaii still dominated by native plants will have detrimental impacts to the habitat, and this is worth reminding people.

Howarth and Gagné (2012) also provide an updated list of general management actions relevant to insect conservation in Hawaii, though some of these actions are geared more toward government agencies rather than individual land managers or researchers. Their suggestions include calls to control invasive species, improve quarantine measures for shipments to Hawaii, and improve the testing and review for potential biocontrol introductions. We recommend these actions as well. One of the biggest threats to native Hawaiian species is the introduction of invasive alien species, often insects themselves (see McGeoch et al. 2011). When invasive species are introduced into already shrinking native habitats, they may displace native plant species, directly prey upon native insects, or otherwise degrade existing habitats. Resource managers must be aware of any new invasive species, and regular monitoring of insect populations (see above) can help to detect these new introductions and to track population trends as native species respond to the invasives.

To prevent invasive species from entering native habitats, transportation of materials into these areas should be closely monitored. For example, insects such as ants can colonize construction materials while they are stored in baseyards, and entire colonies can then be transported into natural areas. Construction equipment and materials that have previously been in an area with invasive species should be power-washed and closely inspected for seeds, dirt, and insects before being allowed into conservation areas. Fence construction is an important management tool used to protect native habitats in Hawaii from ungulate damage, and predator-proof fences may become a more specific tool for insect conservation (Watts et al. 2008). However, fence lines also frequently serve as corridors for the spread of non-native species. Equipment sanitation and post-construction monitoring are integral to reducing the introduction and spread of invasive species into conservation areas, and these kinds of actions should be triggered when construction is proposed and written into contracts before construction begins. Plants and associated planting media used within natural areas should be closely inspected before they are brought into the field.

We recommend planting native plants wherever practical. Many native insects can only utilize native plants, and even if common native plant species are established far away from natural areas, the potential resource opportunities increase for native insects (see Roets and Pryke 2013). For example, the native tephritid fly (*Trupanea artemisiae*) is only known from the native hinahina (*Artemisia australis* and *A. mauiensis*). When *A. mauiensis* was planted at a number of sites many miles from the known range of this fly, the fly was able to find the plants and successfully breed (Starr and Starr 2012). This type of scenario is also believed to have occurred on the once mostly barren island of Kahoolawe: As more host plants were planted on the island, native insect species associated with these plants were discovered (Starr and Starr, personal observations).

On the other hand, non-native plant control is not always immediately desirable. Though many native Hawaiian insects are very host specific and can only utilize native plants, other endemic insects are able to utilize non-native plants. For example, the native tephritid fly *Trupanea crassipes* has only been reared from the non-native Spanish needles (*Bidens pilosa*). Many native *Hylaeus* bees heavily utilize the non-native tree heliotrope (*Tournefortia argentea*) (Magnacca and King 2013). Assuming this non-native tree does not display invasive tendencies, removing it from locations where there are native bees would not be in the bees' best interest unless an equally attractive plant resource was immediately available. The native Hawaiian grass leafroller moth (*Omiodes continuatalis*) utilizes many non-native grasses as a larval host, including the non-native kikuyugrass (*Cenchrus clandestinus*). Perhaps the most conspicuous example is the endangered Blackburn's sphinx moth (*Manduca blackburni*) that mostly uses the non-native tree tobacco (*Nicotiana glauca*), a common roadside weed, as its larval host plant. Some generalist native insects such as predators and detritivores may rely on the structural complexity provided by stands of mature trees, regardless of whether they are native or non-native, so removal of large non-native trees may not be advisable until outplanted native trees have become established. Managers should take into account potential deleterious effects on native insects when weighing costs and benefits of non-native plant control, as non-native plants in some circumstances can still harbor a number of endemic insects. We are not suggesting that invasive plants ever be included in restoration efforts, only pointing out that a knee-jerk reaction of rapidly removing all non-native plants is not always the best approach.

In sum, our recommendations for land managers are as follows:

1. Incorporate monitoring of insect communities (including funding these efforts) into management plans, especially when these plans include important new management actions
2. Ungulate and rat control
3. Ant control
4. Wasp control
5. Asking visitors to stay on trails
6. Control and monitoring of other invasive species (often plants and insects)
7. Frequent cleaning and sanitation of all construction and fence-building equipment
8. Close inspection of plants and soil that are to be brought into the field
9. Planting and restoring native vegetation wherever practical (with the caveat that stands of non-native plants should not be destroyed without some consideration of their possible role in insect conservation)
10. Encourage general collecting of insects by research entomologists (see below)

We recognize that many of these recommendations are practices that land managers are already doing, or attempting to do, and managers may feel frustrated with the current lack of novel methods of insect conservation. However, long-term monitoring of insect communities is glaringly absent from most management plans. Although such monitoring can be challenging, and requires significant financial investment, we feel strongly that one of the most important ways in which insects can inform conservation is *via* the data they provide. This requires a shift in perspective on the part of both land managers and entomologists. In addition to asking, "What can we do to conserve Hawaiian insects?" we might ask, "What can insects tell us about how well we are conserving Hawaiian biodiversity?" Rather than being the explicit target of conservation, insect diversity can provide a measure of success of restoration efforts, or serve as a metric for prioritizing areas for conservation. Of course, our hope is that more data on how conservation practices affect insect communities will eventually inform us as to which are most effective for conserving particular insect groups, enabling us to revisit the question, "What can we do to conserve Hawaiian insects?"

V. Recommendations for research entomologists

We suggest that communication between resource managers and research entomologists is a necessary prerequisite for effective and long-term insect conservation in Hawaii. Information that can help managers prioritize activities or formulate management plans include insect inventory and distribution data (such as that to be compiled in the SID, and that already available in various publications), specific threats to native insect species in these areas if known, and sometimes, what can be done to alleviate these threats. Dialogue between researchers and managers can lead to insect conservation actions that benefit multiple species and resources. Here, we outline several ways research entomologists can help land managers plan for conservation actions.

We recommend that research entomologists, when practical to do so, "check in" with land managers before starting research projects, particularly those involving new collections. This provides an opportunity for managers to discuss the research in the context of ongoing management interests. While time and resource constraints don't always make it practical for entomologists to gather data relevant for conservation, there are certainly instances when useful data can be generated relatively easily while conducting a larger research program. For example, many endemic Hawaiian birds rely heavily on caterpillars as a source of protein, and it is likely that the decline in endemic caterpillars is a contributing factor in the decline of these birds (see Asquith 1995 for an overview of this issue). Land managers might ask a field lepidopterist doing a taxonomic revision to collect data on the abundance of caterpillars observed during their fieldwork. Depending on the biology of the target species, and the frequency at which sites are visited, the lepidopterist may be able to generate a useful ecological dataset on caterpillar diversity and abundance. Such information may not be the primary objective of the entomologist, but this type of communication between managers and entomologists may lead to publications that would not otherwise have been possible. We do stress, however, that small datasets or those that sample for only a short period of time will be highly subject to error due to sometimes large natural fluctuations in population sizes of insects, and such data must therefore be interpreted with caution.

We recognize that land managers may sometimes be frustrated when looking for relevant information in the academic literature, in particular when ecological information such as distributions, host plants, and rarity are buried in species descriptions and the legends of phylogenetic trees. Research entomologists are therefore encouraged to highlight relevant information for insect conservation, such as maps, lists of species by localities, and host plant records, and ideally report it directly to land managers. In addition, data-free statements in papers declaring, for example, that a given insect group "can be used as an indicator for overall ecosystem health," are of limited utility. Publishing such statements without indicating *how* and *why* a particular group are biological indicators, and without making specific management recommendations, is nearly meaningless to land managers who are attempting to take real conservation actions on a daily basis. When applicable, researchers should report any information to managers if they believe that an aspect of current management practices may be harming native insects, or if changes in management practices could significantly benefit native insects.

One major trend in contemporary entomology is the decline of the "general entomologist." Starting in graduate school, entomologists—like practitioners of other fields—tend to become more and more specialized as they progress toward a degree. For non-applied entomologists, keeping up with the exponential increase of relevant scientific papers coupled with the joint pressures to publish and earn grants in fields as diverse as phylogenetics to biomechanics leads most students to focus narrowly on one group. This ultimately leads to researchers who are experts in one area but would be hard-pressed to evaluate conservation concerns, much less identify other types of arthropods, outside of their narrow study system.

A related problem is that entomologists typically only collect their target group of organisms during fieldwork. Reasons include lack of ability to identify non-target organisms, lack of time to curate them, and also reluctance on the part of land-management agencies to approve the collection of non-target specimens. The result is fewer and fewer specimens in research collections, many of which have an abundance of specimens collected decades ago and very few collected recently. Clearly, this makes it difficult for experts in any given group to track the changing distribution of endemic insects using natural history museums.

To remedy these problems, we make two recommendations: First, although it may not be realistic in the grant-driven modern world to expect graduate students and researchers to have time to become the kinds of general entomologists more commonly seen in decades past, it is possible for students and researchers alike to participate in regular "bioblitzes." These are carefully organized and intense collecting expeditions that focus on gathering as many specimens as possible in a short time, and identifying them as quickly as possible. With a variety of specialists attending a bioblitz together, there is excellent opportunity to learn things outside of one's own area of expertise. We encourage the organization of additional bioblitzes and other detailed biological inventories (see Howarth and Preston 2007) in the future. We recommend that land management agencies suggest areas they would like to learn more about as possible sites for future bioblitzes, since such activities can provide at least a qualitative assessment of native arthropod diversity.

Second, we recommend that when practical to do so, researchers request on research permit applications that they be allowed to collect generally while in the field, and that they collect, curate, and deposit as many specimens into museums as time permits (with the exception of threatened and endangered, or otherwise known rare species). This would help to alleviate the huge gaps in data currently suffered by existing natural history collections and allow experts for given groups to use recently collected museum material to quickly learn about the status of species even when they don't have the time or resources to conduct field work themselves.

Field researchers may not always have the time or resources to curate and identify specimens that are not directly related to an ongoing research project, but when they are willing to undertake the effort of properly preparing specimens, we believe it is in the best interests of land managers to allow it. Having specimens in natural history museums that can later be identified by experts would be preferable to the current dearth of recent specimens.

Of course, this practice depends on cooperation from land managers and others who review and approve collecting permits: We recommend that when considering collecting permit applications, resource management agencies should reassess the current standard of only allowing small numbers of "target" specimens to be collected by a particular researcher. Rather, whenever an entomologist goes on a collecting trip, permitting agencies could encourage them to collect, curate, and deposit specimens from a wide variety of groups. We have listed this recommendation in the above section ("Recommendations for land managers"). Opportunistic collecting by entomologists is very unlikely to negatively impact insect populations, given several aspects of insect biology (Morris 1987).

In sum, our recommendations for entomologist researchers are as follows:

1. Check in with land managers before projects, when possible, to determine whether it is feasible to generate datasets that are of conservation utility
2. Refrain from making statements in publications that suggest conservation utility of taxa without stating how this is possible; rather, present land managers with easy-to-interpret distribution maps, hostplant records, and checklists for species you study, as well as any practical recommendations or suggestions you may have
3. Participate in bioblitzes and other collaborative collecting efforts
4. When practical, ask for permission to collect generally, and quickly deposit specimens outside your area of expertise into natural history museums.

Lastly, we remind research entomologists who have the opportunity to do so that sharing fun, interesting, and important insights into insect natural history with interpretive staff and even visitors can help give staff and visitors alike a broader understanding and appreciation of the insect world, ultimately leading to increased support for protection of insect populations. Posters given to interpretive centers, classroom visits, and even impromptu conversations while in the field, are all examples of ways we can positively impact the future of insect conservation.

Notes

This paper was conceived in large part by discussions that took place during a symposium that took place at the 2012 Hawaii Conservation Conference entitled "They Are the 99%: Challenges and Successes of Conserving Invertebrates, Hawaii's Smallest Majority." Other than the corresponding author (MM), authors are listed alphabetically.

Acknowledgments

Collectively, we thank Frank Howarth, Betsy Gagné, Wayne Gagné, Rosemary Gillespie, Sam Gon, Ken Kaneshiro, Bill Mull, Steve Montgomery, Jim Liebherr, Dan Polhemus, George Roderick, Fred Stone, and Lorena "Tap" Wada, among others, for being inspirational advocates for Hawaiian insect conservation. Robert Dudley provided logistical support for MM. Michael Samways provided valuable comments that improved the manuscript. Funding was provided in part by the National Science Foundation (NSF) award #DEB-0918341, USDA Cooperative

State Research, Education and Extension (CSREES) projects HAW00942-H and HAW00956-H administered by the College of Tropical Agriculture and Human Resources, University of Hawaii, Manoa, and the Office of Mauna Kea Management at the University of Hawaii at Hilo. Partial funding support provided by the UH Hilo Office of Mauna Kea Management (S. Nagata), the Mauna Kea Observatories, and the UH Manoa Institute for Astronomy.

Literature Cited

Asquith, A. 1995. Alien species and the extinction crisis of Hawaii's invertebrates. Endangered Species Update 12: 1–8.

Banko, P.C., P.T. Oboyski, J.W. Slotterback, S.J. Dougill, D.M. Goltz, L. Johnson, M.E. Laut, and **T.C. Murray.** 2002. Availability of food resources, distribution of invasive species, and conservation of a Hawaiian bird along a gradient of elevation. Journal of Biogeography 29: 789–808.

Basset, Y., J.F. Mavoungou, J.B. Mikissa, O. Missa, S.E. Miller, R.L. Kitching, and **A. Alonso.** 2004. Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. Biodiversity and Conservation 13: 709–732.

Beardsley, J.W. 1980. Haleakala National Park Crater District resources basic inventory: insects. Technical Report 31. Cooperative National Park Resources Studies Unit, Department of Botany, University of Hawaii, Honolulu, Hawaii, USA.

Cabin, R.J., S.G. Weller, D.H. Lorence, T.W. Flynn, A.K. Sakai, D. Sandquist, and **L.J. Hadway.** 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conservation Biology 14: 439–453.

Cole, F.R., A.C. Medeiros, L.L. Loope, and **W.W. Zuehlke.** 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology 73: 1313-1322.

Cole, R.J., C.M. Litton, M.J. Koontz, and **R.K. Loh.** 2012. Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. Biotropica 44: 463–471.

Daly, H.V., and **K.N. Magnacca.** 2003. Insects of Hawaii. Vol. 17. Hawaiian Hylaeus (Nesoprosopis) bees (Hymenoptera: Apoidea). University of Hawai'i Press, Honolulu.

Eiben, J.A., and **D. Rubinoff.** 2010. Life history and captive rearing of the Wekiu bug (*Nysius wekiuicola*, Lygaeidae), an alpine carnivore endemic to the Mauna Kea volcano of Hawaii. Journal of Insect Conservation 14: 701–709.

Eldredge, L. 2000. Numbers of Hawaiian species. Supplement 5. Bishop Museum Occasional Papers 63, 3–8.

Fullard, J.H. 2001. Auditory sensitivity of Hawaiian moths (Lepidoptera : Noctuidae) and selective predation by the Hawaiian hoary bat (Chiroptera: *Lasiurus cinereus semotus*). Proceedings of the Royal Society of London Series B—Biological Sciences 268: 1375–1380.

Gagné, W.C. 1982. Working towards an assessment of the conservation status of Hawaii's endemic anthropods, with an emphasis on the moths or Lepidoptera. p. 63–72 *In* C.W. Smith (ed.), Proceedings of the Fourth Conference in Natural Sciences Hawaii Volcanoes National Park. University of Hawaii at Manoa, Department of Botany, Honolulu.

Gambino, P. 1992. Yellowjacket (*Vespula pensylvanica*) predation at Hawaii Volcanoes and Haleakala National Parks: Identity of prey items. Proceedings of the Hawaiian Entomological Society 31: 157–164.

Gerlach, J., M. Samways, and **J. Pryke**. 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. Journal of Insect Conservation 17**:** 831–850.

Hanna, C., D. Foote, and **C. Kremen.** 2013. Invasive species management restores a plant-pollinator mutualism in Hawaii. Journal of Applied Ecology 50: 147–155.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press.

Hartley, S., P.D. Krushelnycky, and **P.J. Lester.** 2010. Integrating physiology, population dynamics and climate to make multi-scale predictions for the spread of an invasive insect: the Argentine ant at Haleakala National Park, Hawaii. Ecography 33: 83–94.

Hawaii Conservation Alliance. 2005. Controlling Ungulate Populations in native ecosystems in Hawaii. Position paper. Available to the public on the HCA website: http://hawaiiconservation.org.

Hawaii Conservation Alliance. 2007. Controlling wild sheep and deer on conservation lands in Hawaii. Position paper. Available to the public on the HCA website: http://hawaiiconservation.org.

Henneman, M.L., and **J. Memmott.** 2001. Infiltration of a Hawaiian community by introduced biological control agents. Science 293: 1314–1316.

Hoffmann, B.D., and **S. O'Connor**. 2004. Eradication of two exotic ants from Kakadu National Park. Ecological Management and Restoration 5: 98–105.

Hoffmann, B., P. Davis, K. Gott, C. Jennings, S. Joe, P. Krushelnycky, R. Miller, G. Webb, and **M. Widmer.** 2011. Improving ant eradications: details of more successes, a global synthesis and recommendations. Aliens 31: 16–23.

Howald, G., C.J. Donlan, J.P. Galvan, J.C. Russell, J. Parkes, A. Samaniego, Y.W. Wang, D. Veitch, P. Genovesi, M. Pascal, A. Saunders, and **B. Tershy.** 2007. Invasive rodent eradication on islands. Conservation Biology 21: 1258–1268.

Howarth, F.G., and **B.H. Gagné.** 2012. Chapter 16, Development of insect conservation in Hawaii, p. 359–376. *In* T.R. New (ed.), Insect conservation: past, present and prospect. Springer, Dordrecht.

Howarth, F.G., and **D.J. Preston.** 2007. Monitoring for arthropods (insects and relatives) occurring within the Kahului Airport environs, Maui, Hawaii, Phase II. Final report submitted to Edward K. Noda and Associates, Inc. and the State of Hawaii, Department of Transportation, Airports Division. Available at http://hbs.bishopmuseum.org/publications/pdf/kahului-II.pdf.

Jacobs, D.S. 1999. The diet of the insectivorous Hawaiian hoary bat (*Lasiurus cinereus semotus*) in an open and a cluttered habitat. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77: 1603–1608.

Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, and **M.A. Sanjayan.** 1993. Terrestrial arthropod assemblages - their use in conservation planning. Conservation Biology 7: 796–808.

Krushelnycky, P.D., and **R.G. Gillespie.** 2008. Compositional and functional stability of arthropod communities in the face of ant invasions. Ecological Applications 18: 1547–1562.

Krushelnycky, P.D., and **R.G. Gillespie.** 2010. Correlates of vulnerability among arthropod species threatened by invasive ants. Biodiversity and Conservation 19: 1971–1988.

Krushelnycky, P.D., L.L. Loope, and **R.G. Gillespie.** 2007. Inventory of arthropods of the west slope shrubland and alpine ecosystems of Haleakala National Park. Pacific Cooperative Studies Unit Technical Report 148, University of Hawaii at Manoa, Honolulu.

Krushelnycky, P.D., L.L. Loope, and **N.J. Reimer.** 2005. The ecology, policy and management of ants in Hawaii. Proceedings of the Hawaiian Entomological Society 37: 1–25.

Leblanc, L., D. Rubinoff, and **M.G. Wright.** 2013. Conservation implications of changes in endemic Hawaiian Drosophilidae diversity across land use gradients. PloS One 8: e62464.

Leonard, D.L. 2008. Recovery expenditures for birds listed under the US Endangered Species Act: The disparity between mainland and Hawaiian taxa. Biological Conservation 141: 2054–2061.

Liebherr, J.K., and **D.A. Polhemus.** 1997. Comparisons to the century before: the legacy of R.C.L. Perkins and the Fauna Hawaiiensis as the basis for a long-term ecological monitoring program. Pacific Science 51: 490–504.

Magnacca, K.N., and **C.B.A. King.** 2013. Assessing the presence and distribution of 23 Hawaiian yellow-faced bee species on lands adjacent to military installations on Oahu and Hawaii island. Pacific Cooperative Studies Unit Technical Report 185, University of Hawaii at Manoa, Honolulu.

McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73: 181–201.

McGeoch, M.A., H. Sithole, M.J. Samways, J.P. Simaika, J.S. Pryke, M. Picker, C. Uys, A.J. Armstrong, A.S. Dippenaar-Schoeman, I.A. Engelbrecht, B. Braschler, and **M. Hamer.** 2011. Conservation and monitoring of invertebrates in terrestrial protected areas. Koedoe 53: Art. #1000 doi:10.4102/koedoe.v53i2.1000.

Mckinney, M.L. 1999. High rates of extinction and threat in poorly studied taxa. Conservation Biology 13: 1273–1281.

Medeiros, M.J. 2009. A revision of the endemic Hawaiian genus *Thyrocopa* (Lepidoptera: Xyloryctidae: Xyloryctinae). Zootaxa 2202: 1–47.

Morris, M.G. 1987. Changing attitudes to nature conservation - the entomological perspective. Biological Journal of the Linnean Society 32: 213–223.

Mountainspring, S. 1987. Ecology, behavior, and conservation of the Maui Parrotbill. Condor 89: 24–39.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. Da Fonseca, and **J. Kent.** 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

New, T.R. 2009. Are regional strategies for insect conservation feasible? Journal of Insect Conservation 13: 263–265.

Niemi, G.J., and **M.E. Mcdonald.** 2004. Application of ecological indicators. Annual Review of Ecology Evolution and Systematics 35: 89–111.

Nishida, G. 2002. Hawaiian terrestrial arthropod checklist. Fourth edition. Bishop Museum, Honolulu.

Oliver, I., and **Beattie, A.J.** 1996. Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. Ecological Applications 6: 594–607

Perkins, R.C.L. 1913. Introduction. *In* D. Sharp (ed.), Fauna Hawaiiensis. Cambridge: Cambridge University Press.

Plentovich, S., J. Eijzenga, H. Eijzenga, and **D. Smith.** 2011. Indirect effects of ant eradication efforts on offshore islets in the Hawaiian Archipelago. Biological Invasions 13: 545–557.

Ralph, C.J., and **S.G. Fancy.** 1994. Timing of breeding and molting in 6 species of Hawaiian honeycreepers. Condor 96: 151–161.

Roets, F., and **J.S. Pryke.** 2013. The rehabilitation value of a small culturally significant island based on the arthropod natural capital. Journal of Insect Conservation 17: 53–65.

Rybicki, J., and **I. Hanski**. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. Ecology Letters 16, Suppl. 1, Sp. Iss. SI: 27–38.

Sakai, A.K., W.L. Wagner, and **L.A. Mehrhoff.** 2002. Patterns of endangerment in the Hawaiian flora. Systematic Biology 51: 276–302.

Samways, M.J. 2007. Insect conservation: A synthetic management approach. Annual Review of Entomology 52: 465–487.

Soule, M.E., J.A. Estes, J. Berger, and **C.M. Del Rio.** 2003. Ecological effectiveness: Conservation goals for interactive species. Conservation Biology 17: 1238–1250.

Starr, F., and **K. Starr.** 2012. Presentation at 2012 Pacific Entomology Conference, available at http://www.starrenvironmental.com/publications/2012_native_tephritid_flies_of_subalpine_east_maui.pdf.

Tunison, J.T., R.L. Loh, and **J.A.K. Leialoha.** 1995. Fire effects in the submontane seasonal zone, Hawaii Volcanoes National Park. Pacific Cooperative Studies Unit Technical Report 97, University of Hawaii at Manoa, Honolulu.

Vanderwoude, C., K. Onuma, and **N. Reimer.** 2010. Eradicating *Wasmannia auropunctata* (Hymenoptera: Formicidae) from Maui, Hawaii: The use of combination treatments to control an arboreal invasive ant. Proceedings of the Hawaiian Entomological Society 42: 23–31.

Vorsino, A.E., C.B. King, W.P. Haines, and **D. Rubinoff.** 2013. Modeling the habitat retreat of the rediscovered endemic Hawaiian moth *Omiodes continuatalis* Wallengren (Lepidoptera: Crambidae). PloS One 8: e51885.

Watts, C., I. Stringer, G. Sherley, G. Gibbs, and **C. Green.** 2008. History of weta (Orthoptera: Anostostomatidae) translocation in New Zealand: lessons learned, islands as sanctuaries and the future. Journal of Insect Conservation 12: 359–370.

Whitaker, J.O., and **P.Q. Tomich.** 1983. Food habits of the Hoary Bat, *Lasiurus cinereus*, from Hawaii. Journal of Mammalogy 64: 151–152.

Williams, F.X. 1927. Notes on the habits of the bees and wasps of the Hawaiian Islands. Proceedings of the Hawaiian Entomological Society 6: 425–464.

Williams, P.H., C.J. Humphries, and **R.I. Vane-Wright.** 1991. Measuring biodiversity: taxonomic relatedness for conservation priorities. Australian Systematic Botany 4: 665–6679.

Wilson, E.E., and **D.A. Holway.** 2010. Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. Ecology 91: 3294–3302.

Wilson, E.E., L.M. Mullen, and **D.A. Holway.** 2009. Life history plasticity magnifies the ecological effects of a social wasp invasion. Proceedings of the National Academy of Sciences of the USA 106: 12809–12813.