Plants critical for Hawaiian land snail conservation: arboreal snail plant preferences in Puʻu Kukui Watershed, Maui

WALLACE M. MEYER III, LILY M. EVANS, CONNOR J.K. KALAHIKI
JOHN SLAPCINSKY, TRICIA C. GOULDING, DAVID G. ROBINSON
D. POMAIKAʻI KANIAUPO-CROZIER, JAYNEE R. KIM
KENNETH A. HAYES and NORINE W. YEUNG

Abstract The Hawaiian archipelago was formerly home to one of the most species-rich land snail faunas (> 752 species), with levels of endemism > 99%. Many native Hawaiian land snail species are now extinct, and the remaining fauna is vulnerable. Unfortunately, lack of information on critical habitat requirements for Hawaiian land snails limits the development of effective conservation strategies. The purpose of this study was to examine the plant host preferences of native arboreal land snails in Puʻu Kukui Watershed, West Maui, Hawaiʻi, and compare these patterns to those from similar studies on the islands of Oʻahu and Hawaiʻi. Concordant with studies on other islands, we found that four species from three diverse families of snails in Puʻu Kukui Watershed had preferences for a few species of understorey plants. These were not the most abundant canopy or mid canopy species, indicating that forests without key understorey plants may not support the few remaining lineages of native snails. Preference for *Broussaisia arguta* among various island endemic snails across all studies indicates that this species is important for restoration to improve snail habitat. As studies examining host plant preferences are often incongruent with studies examining snail feeding, we suggest that we are in the infancy of defining what constitutes critical habitat for most Hawaiian arboreal snails. However, our results indicate that preserving diverse native plant assemblages, particularly understorey plant species, which facilitate key interactions, is critical to the goal of conserving the remaining threatened snail fauna.

Keywords *Broussaisia arguta*, critical habitat, extinction, gastropod, Hawaiʻi, mollusc, niche, Pacific islands

Supplementary material for this article is available at doi.org/10.1017/S0030605320000873

WALLACE M. MEYER III (Corresponding author, orcid.org/0000-0001-9588-9794) Biology Department, Pomona College, 175 W. Sixth Street, Claremont, California, 91711, USA. E-mail wallace_meyer@pomona.edu

LILY M. EVANS, CONNOR J.K. KALAHIKI, TRICIA C. GOULDING, JAYNEE R. KIM and NORINE W. YEUNG Malacology, Bernice Pauahi Bishop Museum, Honolulu, USA

JOHN SLAPCINSKY Invertebrate Zoology, Florida Museum of Natural History, Gainesville, USA

DAVID G. ROBINSON USDA APHIS National Malacology Laboratory, Academy of Natural Sciences, Philadelphia, USA

D. POMAIKAʻI KANIAUPIO-CROZIER Maui Land & Pineapple Co. Inc., Puʻu Kukui Watershed Preserve, Lahaina, USA

KENNETH A. HAYES (orcid.org/0000-0002-0814-483X) Pacific Center for Molecular Biodiversity, Bernice Pauahi Bishop Museum, Honolulu, USA

Received 26 February 2020. Revision requested 1 June 2020.
Accepted 3 September 2020. First published online 25 May 2021.

Introduction

The Hawaiian archipelago was formerly home to one of the most species-rich land snail faunas (> 752 species; Cowie et al., 1995; Yeung & Hayes, 2018). This rich fauna resulted primarily from in situ speciation, leading to levels of endemism > 99% (Cowie, 1995). Unfortunately, many Hawaiian land snail species are extinct (Yeung & Hayes, 2018), and the remaining fauna, particularly ground-dwelling species, have been severely impacted. For example, only three of the estimated 300 endodontid species and 21 of 325 amastrid species remain (Yeung & Hayes, 2018; Yeung et al., 2018; Hayes et al., 2020). Although only nine of the 42 species in the genus *Achatinella*, the well-publicized Oʻahu tree snails listed as endangered under the Endangered Species Act (USFWS, 1981), remain, other native Hawaiian arboreal snails have fared better, particularly smaller (< 5 mm) achatinellids, succineids, and euconulids (Yeung & Hayes, 2018). However, reductions in range sizes and population densities of all extant species highlight the urgent need for effective conservation strategies (Solem, 1990; Yeung & Hayes, 2018).

Information on how resources influence the abundance and distribution of invertebrate species is often limited (Cardoso et al., 2011). For most Hawaiian snails, ecological information on critical habitat requirements is unknown (Solem, 1990). Understanding which plant species are preferred hosts for arboreal snails is key to determining which combination of native plant species can facilitate preservation of native snail diversity, and alternatively, how changes in abundance of native plant species can influence native snail populations (Meyer et al., 2014). Preferred host plants are determined by identifying which plants had more snails on them than expected by chance. Understanding the snails'

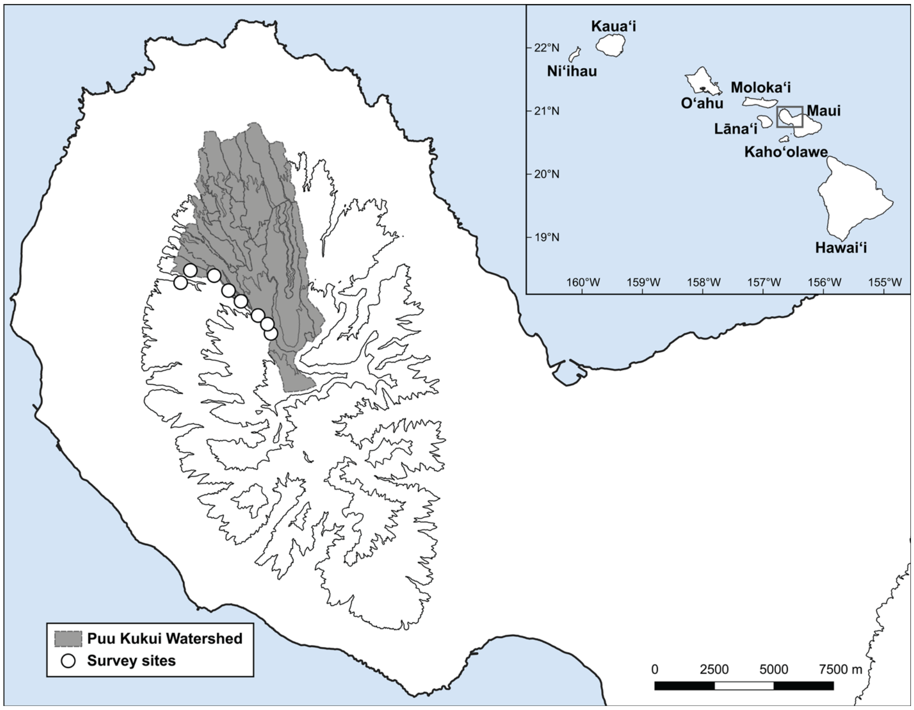

FIG. 1 Pu'u Kukui Watershed Preserve (shaded region) located on Maui Island, showing the nine survey sites (white circles) along an elevation gradient of 730–1,380 m. The inset map shows the main Hawaiian Islands.

preferences is the foundation required for further studies to test the mechanisms that underlie these preferences.

The purposes of this study were to: (1) examine the plant preferences of the native arboreal land snails in the Pu'u Kukui Watershed Preserve (hereafter, Pu'u Kukui; owned by Maui Land & Pineapple Company Inc.) on Mauna Kahalawai (West Maui), Hawai'i (Fig. 1), and (2) compare these results to similar studies on O'ahu (Meyer et al., 2014) and the Island of Hawai'i (Meyer, 2012) to examine if concordant patterns exist across islands. Pu'u Kukui is home to at least 40 extant native land snail species, most being arboreal (K.A. Hayes et al., unpubl. data), and the flora at higher elevations comprises primarily native species (Table 1). Studies in native forests are valuable for informing land snail conservation because these forests are where the remaining native snail species are found (Meyer & Cowie, 2010), and provide an ecological context for understanding interactions among native snails and plants (Meyer et al., 2014).

Studies examining plant preferences of arboreal snails on O'ahu and Hawai'i found that a diversity of native snails demonstrated strong preferences for a small proportion of plant species present (Meyer, 2012; Meyer et al., 2014). Explanations for such selectivity have largely focused on differing food (epiphytic fungi and bacteria: the phyllosphere) quality among plant species, and/or differing plant traits, such as robust (thick and/or static in varying conditions to provide protection from the rain) and smooth leaves that allow access to the phyllosphere and attachment of the aperture and epiphragm during estivation (Brown et al., 2003, 2006; Meyer, 2012; Meyer et al., 2014; O'Rorke et al., 2015; Holland et al., 2017; Sato et al., 2018). Using previous studies that examined plant preferences (Brown et al., 2003, 2006; Meyer, 2012; Meyer et al., 2014), we hypothesized that arboreal snails in Pu'u Kukui prefer a small subset of native plant species with robust and smooth leaves, and we predicted that *Broussaisia arguta*, a large-leafed native shrub, would be preferred by native snails in Pu'u Kukui.

Methods

To test these hypotheses, nine 5 × 5 m quadrats were surveyed in Pu'u Kukui over 2 days (14–15 June 2018; Fig. 1) by nine experienced malacologists (all authors except JRK). Quadrats were distributed along an elevation gradient of 730–1,380 m, at least 100 m apart. To determine the per cent cover of each plant species, we used the point intercept method, which is more precise and repeatable than visual cover estimates (Godinez-Alvarez et al., 2009). Each quadrat contained four parallel 5 m transects separated by 1 m, with the first 1 m from the edge. To estimate per cent cover for each plant species, a ¾ inch (c. 1.9 cm) diameter pole was positioned perpendicular to the ground at every 0.5 m along each transect. We recorded every plant species that the pole touched at each point for a total of 36 points per quadrat (we did not sample points at the edge of the transect; i.e. at 0 or 5 m).

All additional plant species not recorded in the point intercept surveys, but present in the quadrat, were then recorded. We assigned all plants to morphospecies and

Oryx, 2022, 56(1), 38–43 © The Author(s), 2021. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605320000873

TABLE 1 Plant selection by snails in Pu'u Kukui Watershed, Maui, in descending order by mean per cent cover. Values > 0 indicate preference, and values < 0 indicate avoidance. Preference values > 0.25 are in bold.

Plant species	Mean % cover	*Catinella* spp. (32 individuals)	*Philonesia* spp. (78)	*Elasmias luakahaense* (71)	*Auriculella uniplicata* (38)
Cibotium spp.	22.8	0.03	−1	−1	−1
Metrosideros polymorpha	19.4	−1	0.02	−0.15	−1
Nephrolepis cordifolia	11.4	−1	**0.52**	−1	**0.61**
Paspalum conjugatum	10.8	−1	−0.24	−1	−1
Dicranopteris linearis	10.8	−1	−1	−1	−1
Vaccinium reticulatum	10.5	−1	−1	−1	−1
Wikstroemia uva-ursi	10.5	−0.13	−1	0.02	−1
Myrsine spp.	10.4	−1	−1	**0.63**	−1
Adenophorus tamariscinus	9.3	−1	−1	−0.44	−1
Tibouchina herbacea[1]	8.6	−1	−1	−1	−1
Clermontia spp.	8.3	**0.92**	**0.76**	**0.96**	**0.64**
Freycinetia arborea	7.1	0.07	**0.80**	−1	**0.95**
Clidemia hirta[1]	6.8	−1	−0.35	−1	−1
Melicope spp.	6.8	−1	−0.33	**0.40**	−1
Cryptomeria japonica[1]	5.9	−1	**0.57**	−1	**0.67**
Elaphoglossum wawrae	4.3	−1	**0.66**	−1	0.23
Peperomia spp.	4.3	−1	−1	−1	−1
Cheirodendron trigynum	4.0	**0.87**	−1	−0.05	−1
Rubus argutus[1]	3.4	−1	−1	−1	−1
Nephrolepis multiformis	3.1	−1	−1	−1	−1
Unknown fern 2	2.7	**0.50**	−1	−1	−1
Broussaisia arguta	2.5	**0.75**	**0.79**	**0.64**	**0.80**
Psilotum complanatum	2.2	−1	−1	−1	−1
Dodonaea viscosa	1.9	−1	−1	−1	−1
Unknown fern 4	1.8	−1	−1	−1	−1
Astelia sp.	1.5	**0.84**	−1	−1	−1
Dianella sandwicensis	1.5	−1	−1	−1	−1
Schinus terebinthifolia	1.2	−1	−1	−1	−1
Unknown fern 1	1.2	−1	−1	−1	−1
Capparis sandwichiana	0.9	−1	−1	−1	−1
Kadua affinis	0.9	−1	−1	−1	−1
Leptecophylla tameiameiae	0.9	−1	−1	−1	−1
Juncus sp.	0.6	−1	−1	−1	−1
Sadleria cyatheoides	0.6	−1	−1	−1	−1
Smilax melastomifolia	0.6	**0.86**	**0.83**	−1	−1
Unknown fern 3	0.6	−1	−1	−1	−1
Alyxia oliviformis	0.3	−1	−1	−1	−1
Cyanea elliptica	0.3	−1	−1	−1	−1
Phaius tankervilleae	0.3	−1	−1	−1	−1
Pritchardia schattaueri	0.3	−1	**0.98**	−1	−1
Psidium cattleyanum[1]	0.3	−1	−1	−1	−1
Sacciolepis indica[1]	0.3	−1	−1	−1	−1
Unknown fern 5	0.3	−1	−1	−1	−1

[1]Non-native species.

identified all plants to the lowest taxonomic level possible, in most cases to species. Following plant surveys, we surveyed all plants for snails (top and bottom of leaves, stems and trunks). Most plants were < 2 m in height, allowing researchers to survey the whole plant. Plants > 2 m height were surveyed only up to 2 m. At the start of each survey, all surveyors were assigned a plant species, and collected all the snails from this species in the quadrat, recording the number of individuals of each snail taxon on that plant before being assigned another plant species. This was repeated until all plant species had been surveyed. Following surveys of all plants in a quadrat, individual snails were identified to the lowest taxonomic level possible, in most cases to species. Representatives of native snail morphospecies were collected, preserved, and deposited in the Bishop Museum, Honolulu (Supplementary Table 1). Native snails not collected for further taxonomic study were released back into the plots. Non-natives were either collected or euthanized.

To estimate the plant preferences of each snail species, we used the Jacobs' selectivity index (Jacobs, 1974), calculated as:

$$D_{ia} = (r_i - p_a)/ \ r_i + p_a - 2\, r_i p_a)$$

where D_{ia} is the selectivity index of snail species i for plant type a, r_i is the ratio of plant type a use to all other plant types used, and p_a is the ratio of plant a to all other plants. The index ranges from −1 to 1. Values > 0 indicate preference (proportion of snails on that species was higher than the relative per cent cover of the plant species). Values below zero indicate avoidance. Because both plant and snail species were patchily distributed, we calculated a global Jacobs' selectivity index for each snail species using mean per cent cover of all plant species and the proportional number of individuals of each snail species on each plant species across all plots (Table 1). To be conservative, we examined preference for snail species only if > 30 individuals were recorded, and we identified preference when Jacobs' index was > 0.25.

Results

We recorded 283 individual snails, but identifying most specimens to species in the field was not possible, and therefore individuals were assigned to 10 taxonomic groupings that were readily identifiable during surveys. The seven native taxonomic groups were *Catinella* spp., *Philonesia* spp., *Auriculella uniplicata*, *Elasmias luakahaense*, *Punctum* sp., *Lamellidea* cf. *polygnampta,* and *Tornatellidinae* spp. (Supplementary Table 2). Non-native groupings were *Oxychilus alliarius*, *Deroceras laeve* and *Deroceras reticulatum*. Four taxonomic groupings (hereafter, species: *Catinella* spp., *Philonesia* spp., *A. uniplicata* and *E. luakahaense*) were sufficiently abundant for preference analyses.

Consistent with previous studies on O'ahu and the island of Hawai'i, evolutionarily distant snails had relatively similar plant preferences (Table 1). For example, two plant species, *B. arguta* and *Clermontia* spp. were preferred by all four snail species. Consistent with our hypothesis, all preferred plant species are understorey plants. The dominant native tree species, *Metrosideros polymorpha*, which formed the canopy in many of the sites surveyed, and the common native mid canopy shrub, *Cibotium* spp., were not preferred.

Discussion

Concordant patterns in arboreal snail preferences across islands provide valuable insights into management strategies that may benefit snail conservation in the Hawaiian Islands. Firstly, arboreal snail preferences for a few species of understorey plants, and not the most widespread and abundant canopy and mid canopy species (*M. polymorpha* and *Cibotium* spp.) indicate that native forests without key understorey plant species may not support native snails. Secondly, consistent preference for *B. arguta* among various island endemic snails on three islands (Brown et al., 2003, 2006; Meyer, 2012; Meyer et al., 2014) indicates that this plant species is critically important in restoration to improve snail habitat. Other important native understorey species can also be identified by comparing studies. For instance, *Smilax melastomifolia* was a preferred plant species for two of the four snail species in our study, and four of the six snail species studied on O'ahu (Meyer et al., 2014). However, patterns within just one site may also be important, particularly if the plant species was preferred by many snail species. *Ilex anomala* was a preferred species of all snails examined on O'ahu, but no *Ilex* species were recorded in our study. Similarly, preference for *Clermontia* spp. had not been previously reported, but *Clermontia* spp. are sensitive to browsing mammals, and as such are rare, patchily distributed, and thus not likely to be recorded in previous experimental plots (Medeiros et al., 1986). Anecdotally, many native succineids were consistently found on two *Clermontia* individuals near Meyer's (2012) transects on the island of Hawai'i. As such, restoration efforts to enhance populations of these threatened plant species, and other understorey plants, may also benefit snails, and potentially other native invertebrates.

Understanding the plant preferences of snails not only provides insight into which combination of native plant species may facilitate preservation of native snail diversity, but also highlights that losses or changes in abundance of native plant species can influence extant native snail populations. There has been no evaluation of how rapid reductions in the ranges of many Hawaiian plant species over the last century (Burney & Burney, 2007) have affected native snail species. Even in areas not threatened by human disturbance, rooting and trampling by non-native pigs, and other non-native ungulates, significantly reduces native understorey plant richness and cover (Cole & Litton, 2014). In addition to reducing understorey plants, non-native plant species are often the first to colonize areas disturbed by pigs (Aplet et al., 1991), further changing the understorey plant community. Non-native plants are not often used by native snails, although invasive ginger species (*Hedychium* spp.) on the island of Hawai'i are a preferred plant of native succineid snails (Brown et al., 2003, 2006; Meyer, 2012). Identifying plants key to snail survival is a critical step in stemming the loss of this highly threatened fauna and provides important insights to help identify areas to protect and to restore areas to provide habitat for the remaining arboreal snails. This is fundamental information for areas where arboreal snails are present, reintroductions are being considered, and in enclosures built to protect native snails from introduced predators. Although additional research is required to quantify how snail fitness is influenced by various native plant species, consideration of the composition of plant assemblages could be a key management strategy for providing habitat to maintain stable arboreal snail populations.

Concordant patterns across islands help to indicate which plant species are critical for snail restoration but it is difficult to ascertain if leaf traits are good predictors of snail preferences. Although smooth ferns, *Elaphoglossum wawrae* and *Dryopteris* sp., were preferred, and the hairy *Cibotium* spp. were avoided on Maui, as on O'ahu and Hawai'i (Meyer, 2012; Meyer et al., 2014), consistent patterns across all plants are difficult to identify. For example, some common plants with both robust and smooth leaves, most notably, *M. polymorpha*, are not preferred at Pu'u Kukui or on other islands (Meyer, 2012; Meyer et al., 2014), but may be a preferred species for *Achatinella* spp. (O'Rorke et al., 2015; Holland et al., 2017; Sato et al., 2018). Similarly, although many plant species preferred by snails could be considered smooth (e.g., *Clermontia* spp., *Freycinetia arborea, Astelia* sp., *S. melastomifolia*), high numbers of *Philonesia* spp. on *Cryptomeria japonica*, a non-native cedar, were unexpected, as most were found on the rough bark. In addition, determining if *Pritchardia schattaueri*, a native Hawaiian palm, should be considered robust, probably depends on ecological context. Fronds of *P. schattaueri* can be heard crashing into one another in times of elevated winds, but snails are typically found on palms in protected valleys where winds are low. An objective examination of leaf trait preferences requires that all plant traits be defined before a survey is conducted, and analyses test if snails were found on plants with certain traits more than expected by chance. As this has not been done, our current understanding of which leaf traits are important are only anecdotal. We recommend field assessments be used to determine which plants snails prefer prior to any conservation action.

Synthesizing results from studies that examined snail feeding and host plant preferences highlights that our knowledge of what constitutes critical habitat for most snail species is still limited. For example, although O'Rorke et al. (2015) found that the phyllosphere did not differ among plant species within a site, they did not assess the phyllosphere of plants that did not serve as snail hosts. As such, it remains unclear whether snails choose host plants based on phyllosphere assemblages. Holland et al. (2017) found that one native snail species had reduced fitness when provided non-native plants compared to native plants. Plant species used by Holland et al. (2017) were not examined by O'Rorke et al. (2015), limiting comparisons between the two studies. Also, the findings of Holland et al. (2017) contrast with studies examining plant preferences in the Hawaiian Islands. For example, a non-native ginger species, *Hedychium coronarium*, used in the feeding trials, was preferred by native succineids on Hawai'i and reproduction on ginger in the wild seems robust (Brown et al., 2003, 2006; Meyer, 2012). However, *Hedychium* spp. were not utilized by snails on O'ahu (Meyer et al., 2014). *Hedychium* spp. were rare on O'ahu, making preference assessment for these species difficult. Also, *M. polymorpha*, a widespread native tree species used as one of the native species by Holland et al. (2017), was not preferred by all snail species in wet forests on Maui (Pu'u Kukui), Hawai'i or O'ahu (Meyer, 2012; Meyer et al., 2014). An approach that uses the same plant species and snail taxonomic groupings and incorporates snail plant preference observations, examination of phyllosphere differences among plant species, and laboratory rearing studies is required to elucidate whether differences in food resources underlie plant preferences and influence snail fitness.

Only through studies of the ecology of Hawaiian land snails can informed decisions be made regarding which management methods could be used to conserve the remaining Hawaiian land snail fauna. Calls for development of approaches to protect and expand suitable habitat for native Hawaiian snails have reverberated for 3 decades (Solem, 1990), but these efforts have primarily focused on limiting the impacts of non-native predators such as *Euglandina* species (Hadfield & Mountain, 1980; Hadfield et al., 1993; Meyer et al., 2017), rats (primarily *Rattus rattus*; Hadfield et al., 1993), and increasingly other overlooked predatory species such as *Oxychilus alliarius* (Meyer & Cowie, 2010; Curry et al., 2016). Unfortunately, examination of how changing plant assemblages could have influenced snail populations have been sparse. Until recently, ecological information on plant preferences were undocumented for nearly all extant Hawaiian snails. Identification of critical habitat for threatened arboreal snails in dry forests and snails that live in the leaf litter or surface soil has not been attempted.

Although elucidating mechanisms that underlie snail preferences in wet Hawaiian forests still requires further study, concordant patterns among numerous evolutionarily distinct, endemic insular land snail species in wet Hawaiian forests on three islands suggest conservation strategies that could improve preservation of extant native arboreal snails: (1) protect areas with diverse understorey plant assemblages, (2) restore understorey assemblages in degraded areas, and (3) ensure that important plant species (e.g. *B. arguta*) are a focus of restoration. Many questions remain, however: (1) How have plant distributions and abundances changed and do these changes correspond with changes in arboreal snail distributions and abundances? (2) How do different plant species influence the fitness of arboreal snails? (3) How have changes in plant assemblages interacted with introduced predators to influence arboreal snail distributions and population sizes? (4) What plant restoration efforts could best enhance land snail conservation efforts? We hope this study helps spur further holistic research to explore how plant restoration efforts could benefit not only native snails but also other native Hawaiian invertebrates.

Acknowledgements We thank Maui Land & Pineapple Co. Inc., Pu'u Kukui Watershed Preserve staff for field and logistical support, and Garrett Ancheta and Kainoa Pestana for their invaluable assistance with field work. Funding was provided by the National Science Foundation to NWY, KAH, and WMM (DEB-1819878), and to NWY and KAH (DEB-1120906, 1656254, 1656231, 1837849, DBI-1902328, DBI-1561774). This is contribution 2020-006 to the Hawaii Biological Survey.

Author contributions Study design: WMM, NWY, KAH; fieldwork: all authors except JRK; data analysis: LME, CJKK, WMM; writing: WMM, KAH, NWY; figure, supplementary tables: JRK; revision: all authors.

Conflicts of interest None.

Ethical standards This study abided by the *Oryx* guidelines on ethical standards. All collections of snails were under the provisions of state and local permits (FHM11-264, FHM12-294, FHM13-324, FHM15-357, I1053, I1271), in collaboration with Pu'u Kukui Watershed Preserve staff, and with minimization of impacts on remaining populations and their ecosystems.

References

Aplet, G.H., Anderson, S.J. & Stone, C.P. (1991) Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. *Vegetation*, 95, 55–62.

Brown, S.G., Spain, B.K. & Arizumi, A. (2006) A field study of the life history of the endemic Hawaiian snail *Succinea newcombiana*. *Malacologia*, 48, 295–298.

Brown, S.G., Spain, B.K. & Crowell, K. (2003) A field study of the life history of an endemic Hawaiian succineid land snail. *Malacologia*, 45, 175–178.

Burney, D.A. & Burney, L.P. (2007) Paleoecology and 'inter-situ' ecology on Kauai, Hawaii. *Frontiers in Ecology and the Environment*, 5, 483–490.

Cardoso, P., Erwin, T.L., Borges, P.A. & New, T.R. (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, 144, 2647–2655.

Cole, R.J. & Litton, C.M. (2014) Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. *Biological Invasions*, 16, 125–140.

Cowie, R.H. (1995) Variation in species diversity and snail shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution*, 49, 1191–1202.

Cowie, R.H., Evenhuis, N.L. & Christensen, C.C. (1995) *Catalog of the Native Land and Freshwater Molluscs of the Hawaiian Islands*. Backhuys Publishers, Leiden, The Netherlands.

Curry, P.A., Yeung, N.W., Hayes, K.A., Meyer, III. W.M., Taylor, A.D. & Cowie, R.H. (2016) Rapid range expansion of an invasive predatory snail, *Oxychilus alliarius* (Miller 1822), and its impact on endemic Hawaiian land snails. *Biological Invasions*, 18, 1769–1780.

Godinez-Alvarez, H., Herrick, J.E., Mattocks, M., Toledo, D. & van Zee, J. (2009) Comparison of three vegetation monitoring methods: their relative utility for ecological assessment and monitoring. *Ecological Indicators*, 9, 1001–1008.

Hadfield, M.G., Miller, S.E. & Carwile, A.H. (1993) The decimation of endemic Hawaiian tree snails by alien predators. *American Zoologist*, 34, 610–622.

Hadfield, M.G. & Mountain, B.S. (1980) A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae mountains of Oahu. *Pacific Science*, 34, 345–358.

Hayes, K.A., Slapcinsky, J., Sischo, D.R., Kim, J.R. & Yeung, N.W. (2020) The last known *Endodonta* species? *Endodonta christenseni* sp. nov. (Gastropoda: Endodontidae). *Bishop Museum Occasional Papers*, 138, 1–15.

Holland, B.S., Chiaverano, L.M. & Howard, C.K. (2017) Diminished fitness in an endemic Hawaiian snail in nonnative host plants. *Ethology Ecology & Evolution*, 29, 229–240.

Jacobs, J. (1974) Quantitative measurement for food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia*, 14, 413–417.

Medeiros, A.C., Loope, L.L. & Holt, R.A. (1986) Status of native flowering plant species on the south slope of Haleakala, East Maui, Hawaii. *University of Hawaii Cooperative National Park Resource Studies Unit Technical Report*, 59, Honolulu, USA.

Meyer, III. W.M. (2012) Native Hawaiian succineids prefer non-native ginger (*Hedychium* spp.) plant species in the Kohala Mountains, Hawaii: conservation ramifications. *American Malacological Bulletin*, 30, 147–151.

Meyer, III. W.M. & Cowie, R.H. (2010) Invasive temperate species are a threat to tropical island biodiversity. *Biotropica*, 42, 732–738.

Meyer, III. W.M., Gary, D.T., Yeung, N.W., Dirks, C., Leung, K., Léon, J.A. et al. (2014) Native arboreal land snails in the Mt Kaala Natural Area Reserve, Oahu, Hawaii, have similar plant preferences: implications for conservation. *Journal of Molluscan Studies*, 80, 469–472.

Meyer, III. W.M., Yeung, N.W., Slapcinsky, J. & Hayes, K.A. (2017) Two for one: inadvertent introduction of *Euglandina* species during a failed bio-control attempt. *Biological Invasions*, 19, 1399–1405.

O'Rorke, R., Cobian, G.M., Holland, B.S., Price, M.R., Costello, V. & Amend, A.S. (2015) Dining local: the microbial diet of a snail that grazes microbial communities is geographically structured. *Environmental Microbiology*, 17, 1753–1764.

Sato, A.Y., Price, M.R. & Vaughan, M.B. (2018) Kāhuli: uncovering indigenous ecological knowledge to conserve endangered Hawaiian land snails. *Society & Natural Resources*, 31, 320–334.

Solem, A. (1990) How many Hawaiian land snail species are left? And what we can do for them. *Bishop Museum Occasional Papers*, 30, 27–40.

USFWS (United States Fish & Wildlife Service) (1981) Endangered and threatened wildlife and plants: listing the Hawaiian (Oahu) tree snails of the genus *Achatinella* as endangered species. *Federal Register*, 46, 3178–3182.

Yeung, N.W., Bustamente, K.M., Sischo, D.R., & Hayes, K.A. (2018) Rediscovery of *Newcombia canaliculata* (Baldwin 1895) (Gastropoda: Achatinellidae) and *Laminella venusta* (Mighels, 1845) (Gastropoda: Amastridae). *Bishop Museum Occasional Papers* 123, 31–36.

Yeung, N. & Hayes, K. (2018) Biodiversity and extinction of Hawaiian land snails: How many are left now and what must we do to conserve them–a reply to Solem (1990). *Integrative and Comparative Biology*, 58, 1157–1169.