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THE CONSERVATION STATUS OF TWO ENDANGERED MARIANA BUTTERFLIES, *HYPOLIMNAS OCTOCULA MARIANENSIS* AND *VAGRANS EGISTINA* (NYMPHALIDAE)

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ABSTRACT. The Mariana eight-spot butterfly (*Hypolimnas octocula marianensis*) and the Mariana wandering butterfly (*Vagrans egistina*) are endemic to the Mariana Islands and both have recently been listed as federally protected under the U.S. Endangered Species Act. We conducted both targeted surveys and grid transect searches on Guam and targeted surveys across the islands of Saipan, Tinian and Rota to locate native hostplants, eggs, caterpillars and adults of these rare insects. Despite having a relatively common hostplant, *V. egistina* was not found during this study, even in places it had last been found. Although various life stages of *H. o. marianensis* were documented, the hostplants of this species were heavily impacted by grazing of introduced ungulates; only in native limestone forest with jagged tower karst topography, did hostplants persist, and the butterfly with them. The reasons for the disappearance of *V. egistina* are not clear, but do not appear to be related to hostplant availability. Our surveys suggest that control of invasive ungulates on Guam will be the single most effective conservation action for Mariana eight-spot recovery, and is essential to any chance of long-term persistence for the species there. *H. o. marianensis* has significant, unoccupied, hostplant patches on the three northern islands (Rota, Tinian, and Saipan) which might be considered as sites for future translocation and reintroduction efforts, in order to reduce the risk of extinction.

Additional keywords: Commonwealth of the Northern Mariana Islands; Invertebrate conservation; Guam; Saipan; Rota; Tinian; Mariana Wandering butterfly; Mariana eight-spot butterfly

Insect conservation is often complicated by a dearth of information regarding the life histories of rare species, including crucial information such as life span, hostplants, sources of predation, and critical habitat (Medeiros et al. 2013). These challenges make the determination of meaningful measures of the status of threatened populations all the more essential to effective conservation. Because most insects are short-lived in the adult stage and cryptic in other stages, detection and assessment of minimum viable habitat size may require repeated visits over multiple years to properly assess occupied patches (e.g. Eiben & Rubinoff 2015). Further, species with distributions that are characterized by meta-populations, which are by definition both patchy and ephemeral, may be absent in many parts of their critical range every year, as adults move between patches of suitable habitat depending on fluctuating local environmental conditions (e.g. Harrison et al. 1988, Hanski & Singer 2001). Understanding predation and parasitoid pressure is both critical and challenging due to the presence of multiple life stages, i.e. egg, caterpillar, chrysalis, and adult, each with different ecologies, detection probabilities, threats and vulnerabilities. Thus, short-term studies risk drastically underestimating the minimum habitat requirements needed for the long-term survival of many endangered insects. For tropical butterflies, seasonal variations can be very difficult to discern, and populations of adults occur in lower numbers, temporally distributed across the year, rather than concentrated in a few weeks, as might occur for temperate species (Bonebrake et al. 2010). Given these challenges, it is important to establish parameters for conducting surveys of rare tropical insects, and to optimize ways of assessing their population status and stability. This project contributes directly to these goals by examining the occurrence, over time, of two rare butterflies across their current and historic ranges, including an assessment of re-introduction potential. The challenges of surveying for rare, tropical, butterflies with patchy distributions will be increasingly important as destruction of tropical rainforests across the planet continues. Our work exemplifies some of the challenges and potential for rare tropical butterfly conservation.

The Mariana eight-spot butterfly (Fig. 1), *Hypolimnas octocula marianensis*, and the Mariana wandering butterfly, *Vagrans egistina*, are both endemic to the Mariana Islands (the U.S. Territory of Guam and the U.S. Commonwealth of the Northern Mariana Islands [CNMI]) (Figs. 2, 3), and were both recently listed as endangered (USFWS 2015) under the U.S. Endangered Species Act, due to dramatic population declines. Over the past five years the U.S. Fish and Wildlife Service (USFWS) and U.S. Department of Defense funded dedicated surveys to seek and monitor populations of both species and to determine the full extent of their ranges across the

islands. Data collected during this study contributed to the USFWS's assessment of the need to list both species. Additionally, the information presented here will be useful in developing effective recovery plans for these two endangered butterfly species. The first step in effective management and initiating the recovery of these species is collection of basic distribution, conservation status, life history and critical habitat information, of which very little has been available until recently.

Historically, the Mariana wandering butterfly, *V. egistina*, was never considered common, but was once widespread in forest habitat on the islands of Guam and Rota (Schreiner & Nafus 1996). However, it has not been documented on Guam since 1979 where it is currently considered extirpated. On Rota in the mid-1990s, Schriener and Nafus (1996) were the last researchers to document *V. egistina* and recorded several males from a raised bench above a seabird reserve. *V. egistina* was reared from the endemic Mariana Islands tree *Maytenus thompsonii*, which occurs on the islands of Guam, Rota, Tinian and Saipan, though rearing records are sparse and may refer to a single incident (Swezey 1937 listed as 1942 in USFWS 2015). Very little information about the ecology and life history of the butterfly is available.

The Mariana eight-spot butterfly (*Hypolimnas octocula marianensis*) historically occupied a discontinuous range, occurring on Guam and Saipan, but apparently excluding the islands of Rota, Aguiguan and Tinian, which lie between Guam and Saipan (Fig. 3) (Schreiner & Nafus 1996). Further, there have been no records of the species from Saipan in decades, and it is likely extinct there (Schreiner & Nafus 1996). The goals of our surveys were to assess the occurrence of both butterfly species across the four main islands, Guam, Rota, Tinian, Saipan (Fig. 3), and to assess presence, condition and distribution of their hostplants, including plants on islands not currently occupied by the butterflies. By conducting multi-year surveys on a subset of sites we hoped to better understand multi-year patch occupancy and to consider the possibility that metapopulation dynamics might be important in developing a conservation strategy for the insects. Finally, we suggest a number of potential conservation and management activities aimed at increasing the numbers, stability and chances of persistence for these vulnerable insects.

Materials and Methods

The Mariana Archipelago is distributed in a north-south orientation, north of the equator in the western Pacific basin. The region is characterized by a tropical climate that is typically warm and humid, with a year-round average temperature near 27° C, and little seasonal variation in temperature. Relative humidity ranges from 65% to 75% during the day, and 85% to 100% percent at night. There are two climatic seasons, a relatively wet season from July to December, including occasional typhoon strikes, and a drier season from January to June, though rain can fall at any time of year and annual rainfall ranges between 203–279 cm.

Fig. 1. *Hypolimnas octocula marianensis* ovipositing on *Procris pedunculata*, one of the butterfly's two host plants; both plants are restricted to tower karst habitat.

We made seven multi-day survey trips to Guam between 2011–2015, and Saipan, Tinian and Rota each were surveyed once over the course of the study. Field surveys were generally conducted to locate extant populations of the butterflies on all islands, primarily by targeting areas likely to support hostplants. We also revisited known butterfly population locations to assess patch occupancy over time and address the possibility that the target species operate as meta-populations, recolonizing patches and then disappearing. Finally, to address the possibility of bias against finding butterflies away from hostplants during our targeted surveys, we

also conducted randomized grid surveys on Guam for 15 days, to determine if either butterfly species might congregate away from larval hosts (e.g. lekking), making visits to the hostplants a misleading measure of adult presence (Scott 1992). Additionally, we rigorously searched for and recorded the presence of suitable hostplants on both occupied and unoccupied islands, as this would be essential data for reintroduction programs. Due to the endangered status of the two butterfly species and the sensitive nature of Department of Defense land use, we are not able to release specific coordinates for surveys and sightings of the butterflies and hostplants. During the course of our surveys we also made note of other butterfly species present.

Surveys typically were conducted by teams of 2–4 experienced biologists including the authors, and were only undertaken during conditions when butterflies of other species were seen flying. While temperature was never a factor in the tropical climate, if rain was too heavy for butterflies of any species to fly, we delayed or canceled surveys to reduce the chances of underestimating patch occupancy. When hostplants were found, they were searched thoroughly for eggs, larvae and pupae, as well as potential feeding damage. We used a combination of targeted surveys and random transects to ensure that we did not bias our searches based on assumptions about where either butterflies' hostplants occurred, or where the adults might be found. As previously discussed, frequently adult butterflies have very different habitat preferences from their larvae, and searches focused on larval hostplants may not be effective in discovering adults (e.g. Scott 1992). Finally, we relied on the observations of colleagues, verified by photographic evidence, to augment the data we collected and provide a more complete assessment of the conservation status of the species over time. Specifically, our survey dates and locations were as follows: **2011** (8 days) Guam: 7/15–19 and 7/21, 22 Saipan: 7/19–21; **2012** (9 days) Guam 10/11–14, 19 Rota 10/15–18; 2013 (15 days) Guam 3/21–4/4; **2014** (11 days) Guam 3/25,26 and 6/15–21, Tinian 3/27, 28; **2015** (7 days) Guam 4/5–11 (See Table 1.).

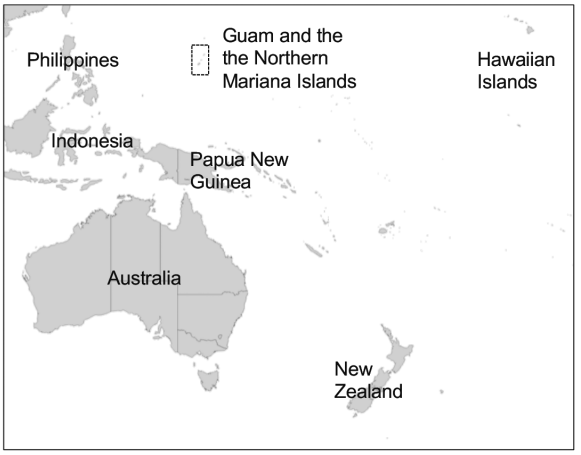

FIG. 2. Map of the Central and Western Pacific, showing the location of the Mariana Islands

Given the conservation status and low numbers of *H. o. marianensis*, we could not conduct mark recapture studies to assess movement between patches or estimate population sizes. However, by revisiting areas during the five years of the study, we were able to assess patch occupancy over time.

Guam. Guam is the largest island of the group with a total land area of about 545 km^2, and a maximum elevation of 406m. Guam is a combination of volcanic clay, largely in the southern 2/3 of the island, and limestone karst due to secondary uplift predominantly

TABLE 1. Hostplant Survey dates and locations

Island	Dates of surveys	Presence of *H. o. marianensis* host plants	Presence of *V. egistina* host plants	Hours searching (team size varied from 2–10 people)
	2011:7/15–19 , 7/21–22			2011: 53
	2012: 10/11–14, 19			2012: 46
	2013: 3/21–4/4			2013: 150
	2014:3/25,26 and 6/15–21			2014: 79
Guam	2015: 4/5–11	yes	yes	2015: 85
Rota	2012: 10/15–18	yes	yes	41
Tinian	2014: 3/27–28	yes	no	18
Saipan	2011: 7/19–21	yes	no	23

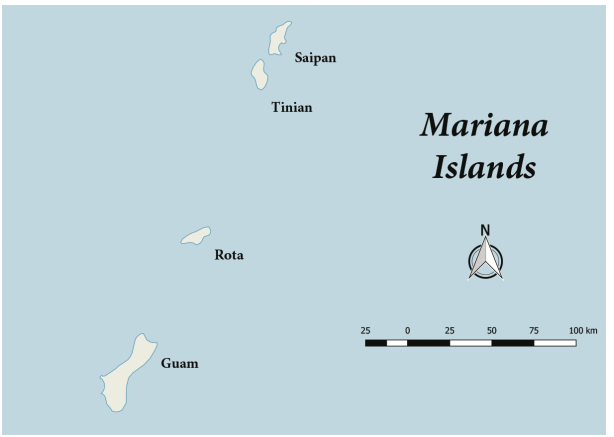

Fig. 3. Map of the four islands included in this study, showing proximity, relative areal extent, and position in the western Pacific. These four islands comprise the southern portion of the Mariana Archipelago.

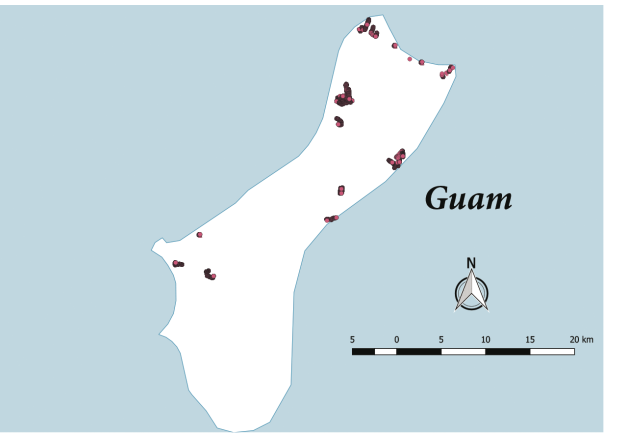

Fig. 4. Map of the island of Guam, the largest and most populated island in the Marianas. Waypoints (red) and survey tracks (black) are overlain. Note that the survey work on Guam focused on the northern portion of the island, which harbors the majority of native limestone forest habitat.

across the northern third. The other islands have more evenly distributed, though spotty, karst deposits, making Guam's soil types largely exclusive. These two soil types have dramatically different characteristics including pH, drainage and particle size, all of which impact plant community composition and distribution. We surveyed Guam seven times over a five-year period (2011–2015), recording GPS tracks, observations of adult butterflies, caterpillars, chrysalides, eggs, egg fragments, hostplants and evidence of caterpillar feeding damage (Table 1., Fig. 4). Our most extensive surveys on Guam occurred during a two-week period in March/April 2013. These surveys followed randomized grid transects through habitat that sometimes included unsuitable butterfly and butterfly hostplant habitat, non-native forest, open grasslands, and residential areas. We conducted these transect surveys over a two-week period in March/April 2013, in collaboration with colleagues at the University of Guam. Between 6 and 15 trained participants followed each transect, ensuring that any hostplants were thoroughly searched. These transect surveys were designed to cover a swath of the limestone soil types common on the north half of the island. Most previous surveys focused on cliff edges, where the Urticaceous hosplants, *P. pedunculata* and *E. calcareum*, are most common. We wished to confirm this assumption through direct surveys across the island interior as well as testing for the possibility of lekking in either butterfly species. Additionally, *Maytenus thompsoni* occurs outside of the rough karst typical of the cliff edges, and these transects provided an opportunity to assess its abundance on the island. All additional surveys at different times of year consisted of non-random transects, and focused on native limestone forest, with the goal of finding hostplants based on optimal microhabitat conditions (especially tower karst and along upper as well as lower cliff boundaries, including beach backstrand forest, where *Procris pedunculata* and *Elatostema calcareum* tend to persist). Accordingly, our targeted surveys were conducted in March, April, June, July and October, to account for seasonal variations in insect abundance. All potential *H. o. marianensis* hostplants were recorded as waypoints.

Rota. Rota is the second southernmost island of the Marianas Archipelago, located 74 km northeast of Guam. With its highest point at around 496 m, this island shows the impacts of agriculture across the low-lying areas of the island's perimeter, the rugged interior still maintains some native forest.

Tinian. Tinian Island is located in the southern CNMI just south of Saipan. With a total land area of 102 km^2, Tinian's terrain is characterized essentially by a low, flat, transversely tilted limestone platform, broken by a few relatively gentle ridges, slopes and cliffs. The maximum elevation is 178 m. Due to its flat topography and rich soils, 95% of Tinian's surface of the island was converted to sugar cultivation for several decades. There are patches of remnant native forest isolated in a few spots of karst along the central spine of the island. Due to its use for agriculture and the military, it was the most heavily impacted of all the islands.

Saipan. Saipan is both the largest and most populated island of the CNMI, second only to the main island of Guam in the Mariana Archipelago and 190 km north of Guam and just 9.3 km northeast of Tinian. The

land area of the island is 115 km² with a maximum elevation of 480 m. Intensive agriculture, ungulates and on-going development have caused significant habitat damage. Karst outcrops in the northern part of the island host the best remaining native forest.

RESULTS

Guam. Our transect surveys were well-distributed across large portions of Guam from 2011 to 2015 (Fig. 4). Most transects and surveys encountered patches of *Maytenus thomsonii* trees, suggesting that it is still fairly abundant across northern Guam. We stopped and conducted thorough visual searches for caterpillars, eggs and feeding damage of any kind at each *Maytenus* tree we encountered. No signs of *V. egistina* were observed anywhere.

In contrast to *Maytenus*, *Procris pedunculata* and *Elatostema calcareum*, were quite rare on many of the transects on Guam. During the targeted hostplant surveys in tower karst between 2011 and 2015, we found the Mariana eight-spot butterfly hostplants in small patches irregularly distributed almost exclusively along the cliff edges or embedded in tall towers of karst along the shore, where ungulates, specifically feral pigs and Philippine Deer, were unable to reach them (Table 1). Specifically, we observed a total of 13 patches of *P. pedunculata/E. calcareum* at five locations (not shown) and these generally appeared to be well-hydrated, and other than damage due to ungulate browsing, in good condition. In most cases, if the hostplants occurred in patches of more than five or six plants, there were signs of the butterfly presence, including eggs and pupal exuvia. Overall we observed butterflies, hostplants, or both in five locations in 2014–2015 surveys.

Approximately 86% (30 of 35) of Mariana eight-spot butterfly eggs we observed during all surveys appeared black in color, indicating a possible infestation by native or introduced parasitoid wasps. An exit hole was also evident in numerous black eggs indicating that the parasitoid had already emerged. The most abundant butterflies observed were the recently introduced swallowtail, the Common Mormon (*Papilio polytes*), and the widespread indigenous Nymphalid, the Blue-Banded King Crow (*Euploea eunice*). Two additional *Hypolimnas* congeners of *H. octocula marianensis* were also observed in smaller numbers, the guardian (*H. anomala*), and the blue moon (*H. bolina*). Eight adult *H. o. marianensis* were observed during reconnaissance and meander searches during 2014 surveys, but none during 2015.

Rota. We visited the same Sagua'gaga Seabird Sanctuary as Schreiner and Nafus (1996) as part of our surveys on Rota, and *Maytenus thompsonii* continue to be very abundant (broad thickets of small trees with multiple stems forming an impenetrable barrier) on the site, extending for hundreds of square meters with no apparent breaks. However, we did not see any *V. egistina* butterflies, eggs or larvae despite targeted searches on consecutive days. Elsewhere on the island, we were able to locate several extensive (50–100 stems) patches of *Procris pedunculata* and one site with *Elatostema calcareum*.

Tinian. The central karst escarpment in the region of Mt. Lasso supported at least four colonies of *Procris pedunculata*, all of over 200 stems, and one of which exceeded 600 stems. The four populations were easily accessible and larger than colonies of the hostplant on Guam (which supported *H. o. marianensis* populations). Ungulate hunting pressure is much higher on Tinian, and there is no restricted military land, resulting in relatively low feral ungulate grazing pressure and, apparently, allowing *P. pedunculata* to thrive in higher density and more accessible places on the island, than on Guam. The steep perimeter cliffline did not appear to support any hostplants, despite several search attempts. No *M. thompsonii* was found during our surveys.

Saipan. Focused surveys on Saipan revealed just two colonies, of 50–100 stems of *Procris pedunculata* in the northern region of the island, on the Laderan escarpment. Despite extensive searching, no signs of *H. o. marianensis* at any life stage were found. These patches were of sizes that were more than adequate to support larvae of the butterfly. No *Maytenus* was observed during our searches.

DISCUSSION

Invasive species and conversion of native forest have imperiled a variety of wildlife and plants across the Marianas, many species of plant and animal are extinct or nearly so. Loss or fragmentation of native plant communities can be particularly damaging for species such as butterflies, which have obligate hostplants, and cannot reproduce when plant populations become too small or scarce (Scott 1992; Rubinoff 2001, 2002). As hostplants become isolated, butterflies which are habitat specialists cannot readily disperse, or recolonize across heavily altered terrain to find random fragments of hostplant following local extirpation (e.g. Harrison et al.1988). Most of the land on all four islands that had been cleared for cultivation purposes in the 20th century and by activities during World War II now consists of secondary forest dominated by invasive species. This forest tends to have an open understory and invasive trees in the genera *Albizzia*, *Delonix*, *Acacia* and *Casuarina* which are often associated with

Leucaena leucocephala the most widespread invasive tree (Engbring et al. 1986; USFS:https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046690). The second most common habitat type across the Marianas is now grassland due to cattle ranching and intentional burns by hunters to increase Philippine deer habitat (Wiles et al. 1999). While this plant community might be favorable for a few native bird taxa, grasslands do not support most native butterflies or their hostplants.

There are some encouraging opportunities; on several occasions, we located extensive patches of *H. o. marianensis* hostplant, particularly in the central areas of the Tinian. While the butterfly has never been recorded from this island, the habitat appears adequate to support a population of the species. Because ungulate densities on Tinian are much lower than Guam, this island might provide an important refugium for the species.

The decline and scarcity of *V. egistina*, is a mystery. Future targeted surveys on Rota might reveal it to persist even still, an understanding of the principle factors leading to declines is crucial to its recovery. Unlike *H. o. marianensis*, which seems limited primarily by hostplant availability, *M. thompsonii*, is abundant on Rota and Guam, some of the trees being over four meters tall, and occasionally forming dense stands, especially on Rota. Possibly, introduced predators or parasitoids are to blame (e.g. Howarth 1991), though the reasons *V. egistina* would have been particularly vulnerable to such invasive species are unclear. Either *V. egistina* populations are impacted by some other cause, or the main hostplant is not *Maytenus*, but rather some other, much rarer, plant. The sole record of it being reared by Swezey (1942) is likely to be accurate, though the rarity of the butterfly suggests the possibility that other hostplants may be important.

In contrast, *H. o. marianensis* was found on Guam in many of the locations where its hostplants occurred, and it seems likely that hostplant availability and connectivity may be important challenges to its recovery. Philippine deer and feral pigs were recorded as extremely common over 100 years ago (e.g. Safford 1905) and have likely been putting pressure on native vegetation for much longer than that. Conry (1989) noted the severe impacts of invasive ungulates on native vegetation and, nearly 20 years ago, Wiles et al. (1999) were specifically concerned about the impacts of the deer on *H. o. marianensis* hostplants and subsequent declines of the butterfly. During our surveys we also noticed that *Procris pedunculata* and *Elatostema calcareum*, were both highly susceptible to the impacts of introduced ungulates, and are restricted to the roughest terrain in native limestone forest, characterized by sharp edged tower karst, often with 1m jagged pits, that impedes access for invasive deer and feral pigs. If the intense ungulate pressure on the hostplants on Guam can be reduced, the plants should recover and might lead to much larger butterfly populations. Further, potentially suitable sites for translocation / re-introduction on the CNMI islands of Rota, Tinian and Saipan appear to exist, with large stands of the hostplants and lower ungulate densities than on Guam. It is unclear why *H. o. marianensis* does not occur on the other islands, hostplant abundance and distribution appeared to be greater than on Guam. With successful establishment of populations on the other islands, and elimination of ungulates from most of the range on Guam, it is possible that *H. o. marianensis* could make a full recovery. Aside from our work, conducted between 2011 and 2015, relatively few surveys have been carried out to determine the population size and distribution of *H. o. marianensis*, or its hostplants, and no formal studies have been conducted to increase our understanding of appropriate conservation measures for this species. Although we located a number of *H. octocula marianensis* during surveys, we did not see adult butterflies of this species during our most recent surveys, in 2015. Because the butterfly only occurs on a few patches on the northern and central parts of Guam, it is very vulnerable to extinction. The hostplant is extremely patchy in its distribution across what is otherwise suitable habitat (karst with a closed canopy); the butterfly is, in turn, patchy on the hostplant, not occurring at all plant locations.

Metapopulation dynamics. Butterflies, particularly, can exhibit a metapopulation structure in which populations colonize new patches as others are extirpated, leading to an on-off temporal patchwork of localized occupation and extinction (Harrison et al. 1988; Hanski & Singer 2001). For such species, many areas of suitable habitat may not be occupied during a given time frame. Based on our surveys, we cannot exclude the possibility that *H. o. marianensis* operates under such a metapopulation structure. For example, the Pagat Cave area supported *H. o. marianensis* prior to our surveys (K. Campora, pers. com.), but we never found the insect there and only very limited hostplant. However, in 2015, after several years of repeated visits, a colleague reported the presence of caterpillars (C. Fiedler, pers. com.), and we located a patch of hostplant that had not been evident in previous years. Thus, we surmise that the Pagat Cave area is only occasionally occupied, but may be important in

supporting connectivity between populations along the coast. As expected, some areas were always occupied by *H. o. marianensis*, including Haputo Ecological Reserve and Tanguisson /Lost Pond. It is likely that protection from ungulates and the presence of large stands of hostplant support these important, larger, populations and that they may be more persistent as a result.

Hostplants for *H. o. marianensis* appear to be confined to a very particular circumstance on Guam, occurring in a narrow band of jagged tower karst along and below the cliff line. Thus, populations of the butterfly could easily become isolated by loss of native habitat as invasive plants expand or habitat continues to be developed, since many tropical forest butterflies are unlikely to fly through open terrain (Laurance et al. 2002). While Asiga Cave is the southernmost and most isolated population recorded (C. Fiedler, pers. com.), the southeastern part of Guam has some karst along the ocean which may hold other, patches of the hostplant and butterfly. These areas should be surveyed more thoroughly as part of a comprehensive management plan.

The continued presence of ungulate damage throughout the karst ecosystem on Guam (herds of deer and pigs were observed regularly) is a primary concern, and indicates that hostplant health and distribution continue to be limited by grazing pressure (Wiles et al. 1999). We encourage future studies to determine longevity of plants inside versus outside of ungulate exclusion fences, especially where hunting-based control measures are in place, as this is entirely unknown.

Three primary impacts on hostplants were observed during surveys: native larval butterfly herbivory, damage due to invasive ungulate herbivory, and pest insect infestation. By far the most common and severe damage observed was due to ungulate grazing and trampling, most frequently browsing by Philippine deer or feral pigs. In general larval feeding does not kill the hostplant as it was usually spread over several adjacent plants. Ungulate herbivory on the other hand, typically included structural damage of hostplants, broken main stems, evidence of crushing, in some cases with regrowth in the vicinity of breakage. The most severe ungulate herbivory was observed at the edges of hostplant patches and on more accessible branches rather than the plants concealed amongst the sheer karst towers.

Other threats to hostplants. Invasive *Pseudococcus* sp. (Family: Pseudococcidae) mealy bugs occurred on both *P. pedunculata* and *E. calcareum* and this pest was observed on several patches. Mealy bug infestations did not appear extensive and negative impacts from the infestation were not clear. One of the more important broad scale threats includes the periodic incidence of strong typhoons in the region. It is relatively common for the Mariana Islands to be impacted by tropical storms and typhoons, particularly during the wet season, from July to December. Typhoons have been a regular natural occurrence in the region for many thousands of years, and therefore the local marine and terrestrial ecosystems and their native flora and fauna, have adapted to the periodic disruptive impacts of such natural catastrophic events. But given recent anthropogenic stresses on Mariana ecosystems, recovery of rare species from such events becomes more challenging, especially with smaller and more fragmented populations.

The current situation is bleak, with *H. o. marianensis* being restricted to declining stands of hostplant, increasingly isolated in the most severe formations of tower karst and limited to narrow bands of the cliffs and coastal escarpment. If no relief is given from the intense grazing pressure of very high ungulate densities, as appears to be the case, the remaining hostplants are likely to decline further, and populations of *H. o. marianensis* may reach a critical lower threshold and disappear, as the recolonization pattern typical of meta-populations collapses. Insect populations under metapopulation dynamics do not always demonstrate gradual decline, and may go from relatively numerous to extinct in as little as a few years (Harrison et al. 1988).

Future research. Females of other butterfly species that utilize multiple hostplants and exhibit metapopulation structure exhibit a marked preference for certain species, possibly with a genetically mediated component (Hanski & Singer 2001). Thus, it is possible that particular female *H. o. marianensis* prefer *E. calcareum* and others, *P. pedunculata*. This may further restrict the species' ability to recolonize patches of hostplants, since, in addition to reduced hostplant availability, the effective population size feeding on either hostplant is a subset of the total, already fragmented, population size. Research to establish the basis for hostplant use and possible oviposition preferences in *H. o. marianensis* might prove critical to successful reintroductions and reserve planning on Guam.

Finally, the impact of introduced ants and parasitoids has not been evaluated. It is possible that either, or both, may be working in concert to reduce populations of the butterflies through larval and egg predation. Controlled exposure trials (e.g. King et al. 2010) for larvae and eggs may be an effective way to determine

the impact of these predators on the early life stages. These impacts may be all the more important as the distribution of the hostplants becomes increasingly restricted and isolated by ungulate grazing.

Management recommendations. It is possible that *V. egistina* persists in very low numbers, and concerted, long-term survey efforts should be engaged on Rota, where it was last seen and where its hostplant remains abundant.

H. o. marianensis may persist as meta-populations across karst topography on Guam, with a few larger, possibly permanent populations. However, the sparse, spotty distribution of the hostplants, and the constant pressure from intense ungulate grazing puts the species at grave risk of extinction. Elimination of invasive ungulates from karst topography, specifically—but not exclusively—on military land would likely conserve the majority of remaining *H. o. marianensis* hostplant populations. While hunting pressure off military bases is higher, public support for maintaining game species will likely keep ungulates at levels which suppress hostplant regeneration.

Additionally, the abundance of the two hostplants on Tinian, Rota, and Saipan suggests an opportunity for reintroduction (or new populations in the case of Rota and Tinian) of the butterfly to establish additional populations. The reasons that *H. o. marianensis* was never recorded from Rota and Tinian, despite being geographically situated between Saipan and Guam, may never be clear. Establishing populations of the butterfly on these other islands would be further insurance against extinction. Such out of range introductions have been important in other insular species (Reynolds & Klavitter 2006; Freifeld et al. 2016). Due to hunting pressure, ungulate densities on Rota, Tinian and Saipan are lower than on Guam, leading to more secure hostplant populations, at least in the near future. In addition to ungulate control, spreading the butterfly across the islands would decrease the chance of a catastrophic event, like a typhoon, eliminating the species. As part of efforts to enhance the number of the hostplants, greenhouse propagation trials could be conducted, to optimize growth and survivorship of these fragile plants in captivity. Both *Procris pedunculata* and *Elatostema calcareum* could be raised in greenhouses, and once established, eggs could be brought in, and caterpillars reared, with butterflies released in the wild. Propagation of hostplants ex situ, and then outplanting the captive raised plants in suitable, fenced off micro 'reserves'—for example in areas that have benefited from ungulate control—could substantially increase the availability of high quality endangered butterfly habitat. Without these actions, the status quo of simply monitoring populations and patch occupancy is likely to track the decline and eventual extinction of *H. o. marianensis*.

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