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ARTICLE

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Reproductive response of the Samoan swallowtail butterfly to variability in host plant and habitat characteristics

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Abstract

The Samoan swallowtail butterfly (*Papilio godeffroyi*) has become restricted to Tutuila Island, American Samoa. Factors driving its extirpation on other islands may be partly due to the availability and suitability of habitat, given the singular association we observed of *P. godeffroyi* with its host plant, *Micromelum minutum*. We expected that as a host plant specialist, *P. godeffroyi* might respond to variation in the physical traits and habitat context of *M. minutum*, which could help identify conservation opportunities throughout its present and former range. Because the ecology of *P. godeffroyi* is largely unknown, we conducted systematic surveys during 15 months in 2013 and 2014 on Tutuila to investigate its reproductive response to the physical and phenological variability of individual host trees and to the structural and geographical variability of the stands in which they occurred. We searched foliage for eggs, larvae, and pupae and monitored seasonal trends in herbivory and production of leaves, flowers, and fruits on 117 host trees in 8 rainforest stands, mostly within the National Park of American Samoa (NPSA), starting in March 2013 and ending in August 2014. We observed high variability in butterfly reproductive output between individual trees and stands, due largely to a strong negative relationship between leaf biomass (at both tree and stand levels) and oviposition density (number of eggs per foliar biomass) and frequency (number of eggs per survey). Distribution patterns of larvae and pupae were less distinct but generally followed trends in oviposition. Our findings indicate that the butterfly is reproducing widely across Tutuila and is likely to respond positively to management to increase the availability of small host trees in low-density stands. Thus, the species is a good candidate for conservation management focusing on habitat.

KEYWORDS
American Samoa, butterfly demography, host plant and habitat relationships, *Micromelum minutum*, *Papilio godeffroyi*

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INTRODUCTION

Butterflies are widely appreciated and enthusiastically collected globally, but relatively few endemic species are known from the most remote oceanic islands (Howarth & Ramsay, 1991). For example, only two native butterflies, both endemic, are known from Hawai'i (Zimmerman, 1958), the most remote of all archipelagos. The Samoan Archipelago, also remote but closer to other island and continental populations, is home to about 31 butterfly taxa, 7 of which may be endemic (Patrick & Patrick, 2012; Tennent, 2006). Among the Papilionidae, a largely tropical family with ecological, cultural, and economic significance (Collins & Morris, 1985), about 14% of species were considered threatened or declining 30 years ago (New & Collins, 1991), but now nearly 23% of species are threatened and an additional 15% are classified as nearly threatened (IUCN, 2019). In the central Pacific, one of the most charismatic species is the strikingly marked Samoan swallowtail (*Papilio godeffroyi* Semper 1866, pepe ae), which is the only papilionid in the Samoan Archipelago.

Although *P. godeffroyi* is endemic to the Samoan Archipelago, Tennent (2006, p. 154) credits the report of at least one specimen, presumably a stray, from Fiji during the mid-to-late 1800s. Once widespread across the Samoan Archipelago, populations of *P. godeffroyi* on some islands have declined substantially over the past few decades (Patrick et al., 2018). A recent archipelago-wide survey failed to locate the species on the large westernmost islands of Upolu and Savai'i in Samoa, where it was last confirmed in 1979 (Edwards, 2012; Patrick et al., 2018). *P. godeffroyi* is now restricted to the much smaller island of Tutuila, American Samoa, where it is widespread but uncommon. Overall, the butterfly occupies relatively undisturbed rainforest habitat in only about 6% of its original range (Patrick et al., 2018). Based on reductions in range and population, it is classified as endangered in the IUCN Red List (Patrick et al., 2018).

Causes for the decline of *P. godeffroyi* are unclear, but habitat loss and cyclones may have played roles (Patrick et al., 2018). The butterfly's apparent preference for relatively intact forest on Tutuila indicates that both habitat availability and quality may be important factors (Patrick et al., 2018). Native forests on Upolu and Savai'i have been greatly reduced due to logging and conversion to agriculture and agroforest. Between 1954 and 1990, native forest cover on those islands decreased from 73% to 36% of the total land area, although agricultural forests, which supported some native tree species, increased from 12% to 46% (Olson, 2001). Conversion of forest habitat on Tutuila was less pronounced, presumably due to the island's exceptionally steep, rugged terrain and smaller human population. During 1960–1985, forest cover on Tutuila declined from 70% to 61% and 32% of land cover was converted to agricultural forest (Olson, 2001). Today, 4260 ha of relatively intact native forest on Tutuila is preserved in the National Park of American Samoa (NPSA, Craig, 2009). Despite the reduction in habitat on Upolu and Savai'i, considerable tracts of forest remain on those islands, indicating that habitat degradation or other factors also may have contributed to the decline of the butterfly.

Species of Rutaceae (rue family, including citrus) are host plants of many *Papilio* (Dethier, 1941), and the larvae of *P. godeffroyi* feed (apparently exclusively) on the leaves of *Micromelum minutum* (talafalu; Rutaceae). This host plant–herbivore relationship was initially confirmed by M. A. Schmaedick on Tutuila in 2006. This small tree is indigenous to the Samoan Archipelago and ranges in the Indo-Pacific from Thailand, the Philippines, and Northern Australia to western Polynesia (Whistler, 2004). In the Samoan Archipelago, its distribution is considered occasional within its habitat of coastal and foothill forest, which ranges from near sea level to 300-m elevation (Whistler, 2004). *M. minutum* has become rare in Samoa but is patchily distributed in relatively undisturbed forest stands on Tutuila (Patrick et al., 2018).

Our observations confirm the singular association of *P. godeffroyi* with *M. minutum* in the wild. We expected that as a host plant specialist, *P. godeffroyi* might respond to variation in the physical traits and habitat context of *M. minutum*. We therefore predicted that oviposition would be distributed in approximate proportion to the density of host tree stands, in accordance with the resource concentration hypothesis, which predicts that herbivores, and by extension herbivore reproduction, should occur at higher densities where resources are most abundant (Long et al., 2003; Root, 1973). Additionally, *Papilio* behavior is thought to depend largely on vision (Nagaya et al., 2021), raising the question of whether physical characteristics of individual host trees influence ovipostion behavior. Our goal in answering these questions was to provide a scientific basis for developing habitat management strategies for *P. godeffroyi* conservation.

Because the ecology of *P. godeffroyi* is largely unknown, we conducted systematic surveys during 15 months in 2013 and 2014 on Tutuila to investigate its reproductive response to the physical and phenological variability of individual host trees and to the structural and geographical variability of the stands in which they occurred. We surveyed *M. minutum* trees and stands located mostly within or near the NPSA, where forests were relatively undisturbed and likely to provide high-quality habitat for oviposition and juvenile development. Our approach was to compare the number of eggs, larvae, pupae, and exuviae (empty pupal case, indicating emergence of adult) per unit of foliage (reproductive density) and per survey

(reproductive frequency) among trees and stands and to model the response of reproductive output to a suite of habitat variables. We also examined the influence of tree phenology on reproductive output, although we anticipated that tree phenology would have little effect because many wet forest tropical trees are only weakly seasonal, especially in terms of producing new leaves (Craig, 2009; Lamoureux et al., 1981; Reich, 1995).

METHODS

Study area

The U.S. Territory of American Samoa is located approximately 3700 km southwest of Hawai'i, and along with the independent nation of Samoa, comprises the Samoan Archipelago (Figure 1). Overall, American Samoa occupies about 200 km^2 of land, with the island of Tutuila comprising 68% of the total land area, Ta'ū comprising 23%, the nearby islands of Ofu and Olosega together comprising 6%, and the remaining small islands and atolls comprising 3% (Craig, 2009). Collectively, the Islands of Ta'ū, Ofu, and Olosega make up the Manu'a Islands and are located about 95 km east of Tutuila. The climate of American Samoa is warm, humid, and wet year-round, with daily temperatures averaging about 28°C and annual rainfall totaling >300 cm (Craig, 2009). Nevertheless, American Samoa has an 8-month hotter, wetter season (October through May) and a 4-month cooler, drier season (June through September; Craig, 2009). The topography is generally

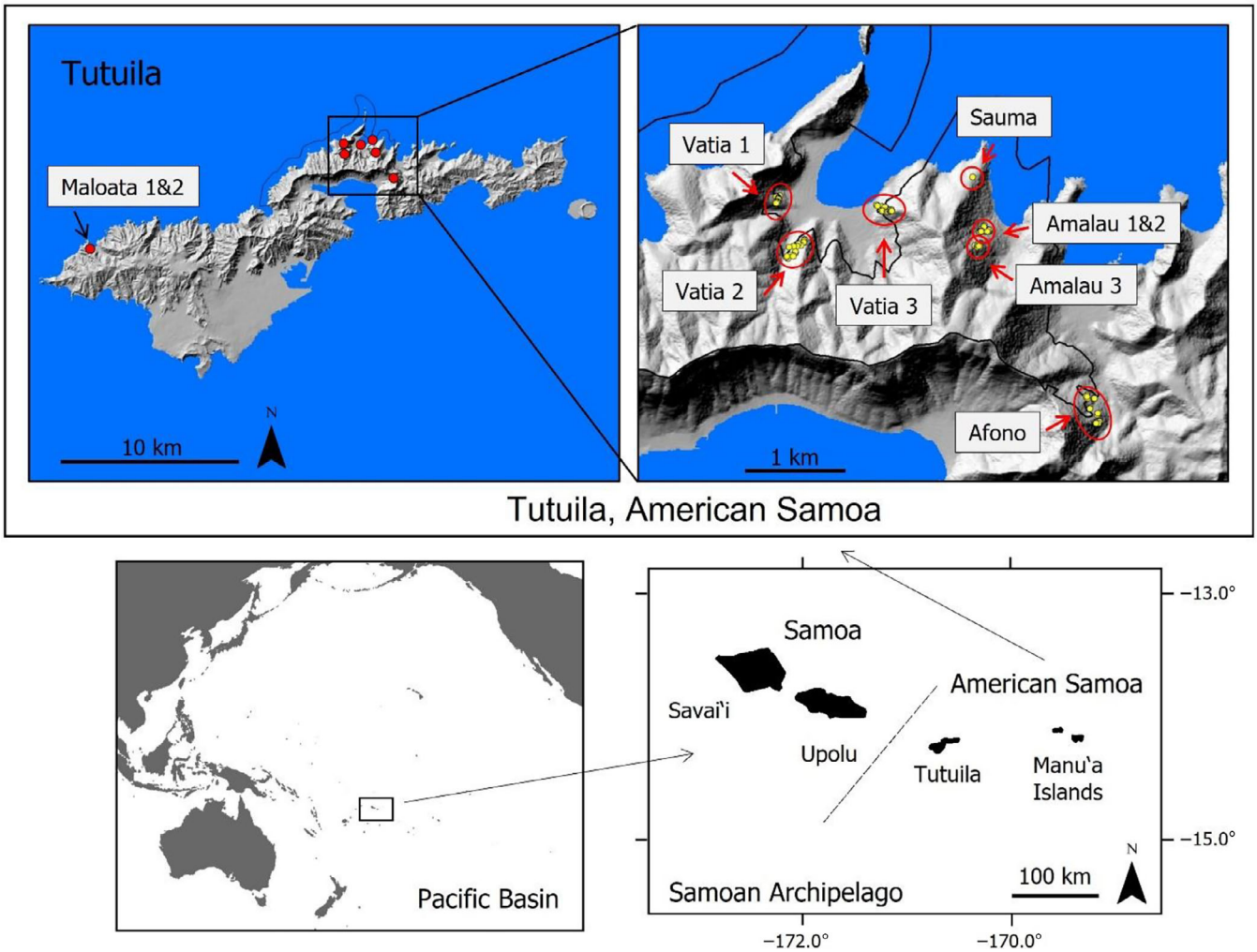


FIGURE 1 Location of the Samoan Archipelago and eight stands where *Papilio godeffroyi* was studied on the island of Tutuila, American Samoa. Two adjacent *Micromelum minutum* stands were combined for analysis at Amalau 1&2 and Maloata 1&2. The black polygon encompassing the north-central part of Tutuila indicates the boundary of the National Park of American Samoa. Red dots in the top left panel show the distribution of *M. minutum* stands. Yellow dots circled in red in the top right panel show the distribution of *M. minutum* trees within stands. Because some trees are close together, the yellow dots overlap at the geographic scale shown. The Manu'a Islands shown in the lower right panel refer to the Islands of Ta'u, Ofu, and Olosega. The dashed line shows the separation of Samoa and American Samoa.

steep with the few existing foot trails limited mainly to ridge tops and valleys. The highest point in the territory is the summit of Lata Mountain on Ta'ū (966 m above sea level [m asl]) and the highest point on Tutuila is Matafao Peak (653 m asl).

Eight stands, named with reference to nearby villages, were selected on Tutuila based upon the presence and accessibility of *M. minutum*, the host plant of *P. godeffroyi*. Seven of the eight stands were located on northeastern Tutuila within or adjacent to the Tutuila Section of NPSA, and one stand, Maloata, was located on the western end of Tutuila (Figure 1). Stands were located primarily within *Rhus* secondary forest that typically also contained elements of primary rainforest and secondary scrub vegetation (Liu et al., 2011). The stands ranged in elevation from 56 to 197 m asl at Vatia 1 and Maloata 1&2, respectively.

Each stand consisted of 1–40 *M. minutum* trees. Stands were functionally defined as clusters of ≥10 *M. minutum* trees with distances among neighboring trees <50 m; however, stands at Afono ($n = 21$ trees) and Maloata 1&2 ($n = 40$ trees) were more diffuse, with 4 trees at Afono 50–100 m apart and 7 trees or small clusters of trees at Maloata 1&2 100–250 m apart. The stands were similar in terms of elevation and vegetation structure regardless of stand size. At Sauma, the stand consisted of a single large tree. Two stands each at Amalau and Maloata were originally identified as being separate but were later combined for analysis due to being <100 m apart. These amalgamated stands were subsequently designated as Amalau 1&2 and Maloata 1&2.

Sampling design

In the 8 stands, we systematically surveyed 117 *M. minutum* trees for *P. godeffroyi* eggs, larvae, pupae, and exuviae at approximately 30-day intervals for 9–15 months, depending on logistical constraints, from 6 June 2013 to 7 August 2014 (Appendix S1: Table S1). We searched all the foliage of small trees (<2-m height) and the foliage of larger trees that could be reached from the ground or by safely climbing on adjacent trees and logs. The average height of survey trees was about 3 m; therefore, we were able to thoroughly survey the lower two thirds of most trees. We also assessed the phenological status (see *Host tree phenology*, below) on all 117 trees plus 74 additional trees from 13 March 2013 to 7 August 2014. Branches too high to sample for *Papilio* were nevertheless assessed for phenological status. All 191 trees were tagged with a unique identification number and geolocated using a Garmin global positioning system (GPS) device.

Characteristics of *Micromelum* stands, trees, and foliage

The area of each *M. minutum* stand was estimated by creating a polygon connecting perimeter trees using the Minimum Bounding Geometry feature in ArcMap (ArcGIS 10.3.1, ESRI, 2011). Stand density was then determined by dividing the number of trees by the estimated stand area. The single tree at Sauma was excluded from estimates of stand area, tree density, and tree basal area per unit of area.

Stands were characterized by recording and pooling several variables at each tree sampled. Measurements included the slope (as a percentage, using a clinometer), aspect (degrees determined using a compass oriented toward the four cardinal directions), elevation (using a GPS unit), and canopy cover (as percent cover using a spherical densiometer).

M. minutum typically grows as a small, spindly, understory tree, only occasionally reaching 8 m in height. Individual trees were characterized by recording their height, basal diameter (measured at 20 cm above the ground), and location within the forest (forest interior, forest edge, or forest gap). Because of the generally steep terrain, tree height was determined by measuring the vertical distance between the extrapolated plane of the ground and the highest point of the tree. The location of *Micromelum* trees within the forest was included as a gross metric to determine whether trees and associated *Papilio* were more likely to be found near light gaps or under shade.

We estimated the amount of foliage of each *M. minutum* within the stand. Leaves of *M. minutum* are typically composed of 7–15 leaflets arranged pinnately along the rachis. Leaves grow laterally from the main stem of small individuals, and they grow laterally from the main stem and primary and secondary branches of larger individuals (Figure 2A,B). From 28 October to 3 November 2014, we counted the number of leaves surveyed for *Papilio* according to leaf length class (in centimeters): <10, 10–25, 25–50, 50–75, and >75. Foliage surface area and mass were then estimated for each tree using regression equations associating leaf length to leaf area and mass, as described below. We differentiated between branches that were surveyed for *Papilio* and those that were too high to survey. Foliage quantity of out-of-reach leaves was estimated by multiplying the number of these unsurveyed leaves by the average area and mass of leaves that were surveyed on the same tree. For trees that were not surveyed for *Papilio*, we estimated foliage production using regressions of foliage area and mass with tree basal diameter. We used only leaves that were surveyed for *Papilio* when relating leaf area and mass to

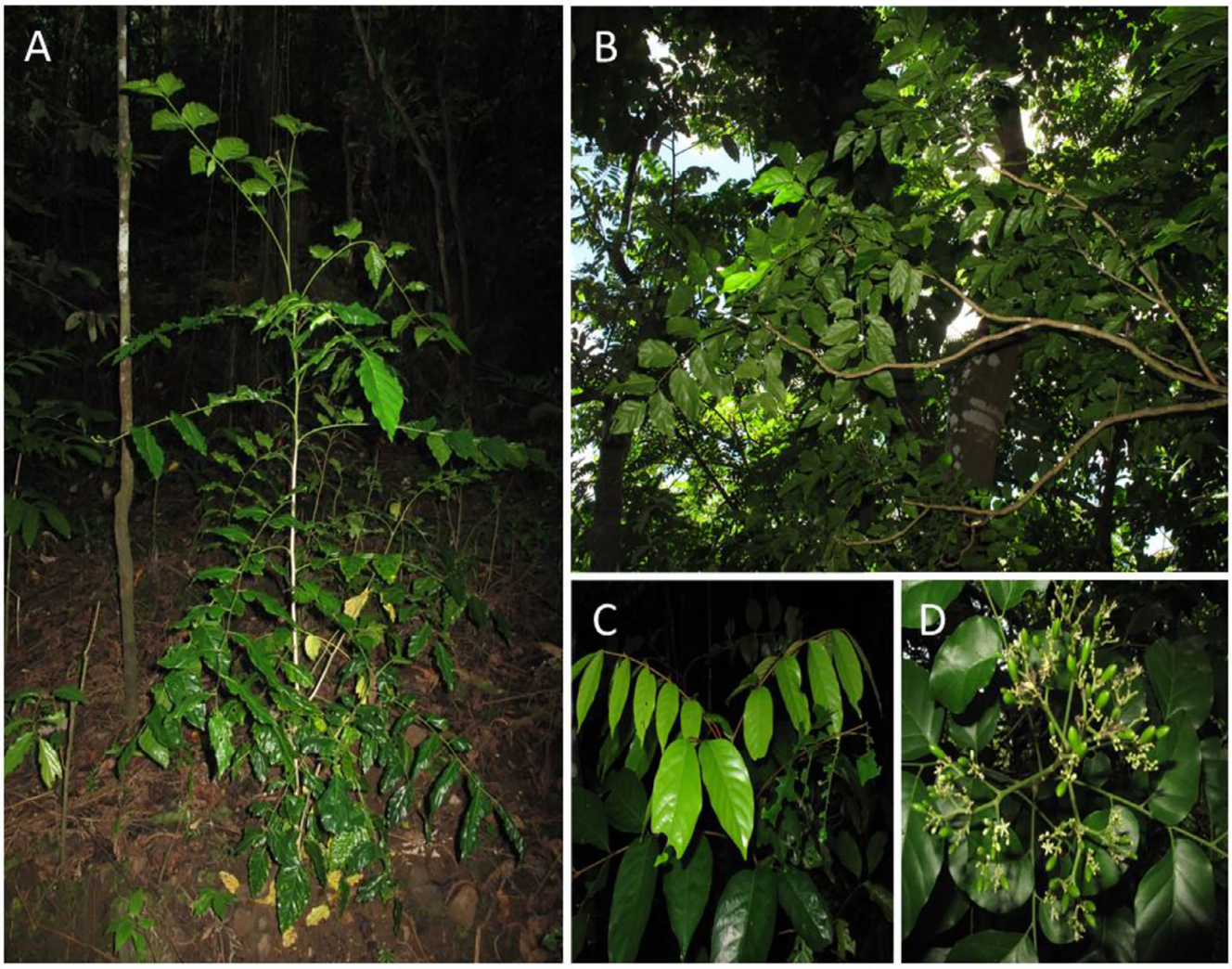


FIGURE 2 An immature *Micromelum minutum* growing in the forest understory (A). Leaves grow from the main stem of small, unbranched plants, but in larger individuals they primarily grow from the branches (B). New leaves are light green; leaves are pinnate with generally 7–15 leaflets (C). Note heavy herbivory, likely due to *Papilio godeffroyi* larvae, on older leaves in shaded background on the right side of image (C). Flowers and fruit (immature green fruit shown here) often occur simultaneously on a panicle (D). Photographs by R. W. Peck, Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo.

Papilio density (*Papilio* per kilogram of foliage per month) at the tree and stand levels.

The length, surface area, and dry mass of leaves, ranging from the smallest to the largest leaves available, were determined to allow an estimate of total leaf area and mass at the level of both individual trees and stands. On 30 October 2014, 11 leaves, which spanned the size range of leaves in this and other stands, were collected from Amalau 3 and transferred to the laboratory at American Samoa Community College for processing. The stand at Amalau 3 was selected because it contained a typical number of trees ($n = 23$) and was generally representative of other stands. In the laboratory, the length of each leaf was measured to the nearest millimeter and individual leaflets ($n = 116$) were removed, labeled, scanned on a flatbed scanner, oven-dried at 50°C for 48 h, and weighed to the nearest 0.01 g. The area (in square millimeters) of each leaflet was calculated from scanned images using ImageJ software (version 1.48, Rasband, 1997–2015). Leaflet area and mass were summed for each leaf. We also collected 43 leaves spanning the full range of leaf sizes from Amalau 2, Sauma, Vatia 2, and Vatia 3 during 3 November 2014 to supplement the sample of leaves from Amalau 3 and to include variation in leaf–leaflet characteristics potentially occurring in other stands. The 363 leaflets from these 43 leaves were pooled, dried, and weighed as described above, but they were not scanned for area measurement. Regression equations were used to identify the relationships between leaf length, area, and mass from the 54 leaves collected from these 5 stands.

Host tree phenology

Several variables were used to characterize monthly phenological patterns of *M. minutum*, including the presence or absence of the following features: new leaves, open flowers, green fruit, and red fruit (Figure 2). New leaves were differentiated from old leaves by their brighter color, smaller size, and terminal location. After their initial training, observers periodically calibrated their perceptions of color and brightness with one another to ensure standardization. Flowers were considered "open" when petals had separated enough to expose reproductive structures to pollinators. Fruit displayed a continuum of color, but red fruit was differentiated from green fruit when mature in size (~10 mm) and showing at least some reddish color. Leaf development was summarized for all trees, but data on flower and fruit production were presented only for trees >2 m in height because smaller trees rarely flowered.

In addition, the extent to which leaves were consumed by *Papilio* or other herbivorous insects was assessed by visual inspection of the whole tree on each survey and categorized as low (0%–10% consumed), moderate (11%–25% consumed), high (26%–50% consumed), and severe (51%–100% consumed).

Papilio location and abundance patterns

Foliage from each survey tree was systematically searched by hand for all *P. godeffroyi* developmental stages during each sampling event (Appendix S1: Table S1). We did not determine the probability of detecting *Papilio* specimens, but their eggs are large, conspicuous, and generally distinct compared with other insect eggs and their larvae and pupae are large and strikingly colored (Figure 3). We recorded the height above the ground, the leaf side (top or bottom), and leaf age (new or old) where each *Papilio* specimen was found. We described their developmental stage and recorded the stand, tree ID number, and height of their host tree. We did not record the elapsed time of the total survey, but leaves of similar size received about the same amount of search time.

Each *Papilio* specimen was collected and returned to the laboratory where, if viable, it was maintained on the foliage from which it was collected (intact eggs and pupae) or provided with fresh foliage (larvae) and allowed to develop (adults were released to the wild). This allowed us to visually confirm species identity as *P. godeffroyi* and to gather life history information (not reported here). In the field, we distinguished between eggs with intact shells (eggs) and broken, fragmentary shells (eggshells), collectively referred to as "ovi." We recorded the number of leaves (consisting of multiple leaflets) that were examined for *Papilio* on each tree every month. Because we collected all specimens during each visit, we considered each survey to be independent in terms of numbers of specimens per leaf, leaf area, and leaf mass.

Modeling stand and tree effects

We examined the effect of stand characteristics on reproductive output, as measured by the number of ovi detected, with hierarchical mixed-effects models. We used the log of the number of ovi as a response, with an offset of log(leaf sample mass) to account for sampling effort. We examined stand area, density, slope, aspect, cover, and mass as linear predictors of ovi detections within a random stand effect. Stand elevation was not used, as it varied only within a narrow range of values to properly fit a model; neither was aspect, as it is a circular variable with relatively few observations. The tree at Sauma was not included in the stand analysis. We compared models by the Akaike information criterion with a sample size correction (AIC_c) to assess the relative weight of evidence for those stand-level predictors affecting ovi detections.

We also used mixed-effects models to examine effects of the biophysical characteristics of individual trees on the number of ovi detections. These characteristics were tree height, basal diameter, total leaf area, total leaf biomass, number of leaves, and canopy cover. These models assessed the effect of tree-specific covariates on the log of the number of ovi, again with a log (sample mass) offset to account for sample size. Stand was added as a random effect to control for stand-specific effects on oviposition. We compared models by the AIC_c to assess the relative weight of evidence for those tree-level predictors affecting ovi detections.

Means are presented with standard errors (mean ± SE) unless otherwise noted. To compare means, we used two-sample *t* tests with either no correction when variances were equal or with a Hoech correction for unequal variances in Microsoft Office Specialist Excel 365 ProPlus.

All data used in the analyses that follow are available at https://doi.org/10.5066/P9A6CXQX; Banko et al. (2022).

RESULTS

Host tree and stand characteristics

The eight stands were characterized by high canopy cover (mean = 94.5%, range = 84.1%–98.4%) and were situated on steep slopes (mean = 34.4°; range = 20.4–52.0°) at relatively low elevation (mean = 135.8 m; range = 88–158.4 m; Appendix S1: Table S2). The stands were generally easterly

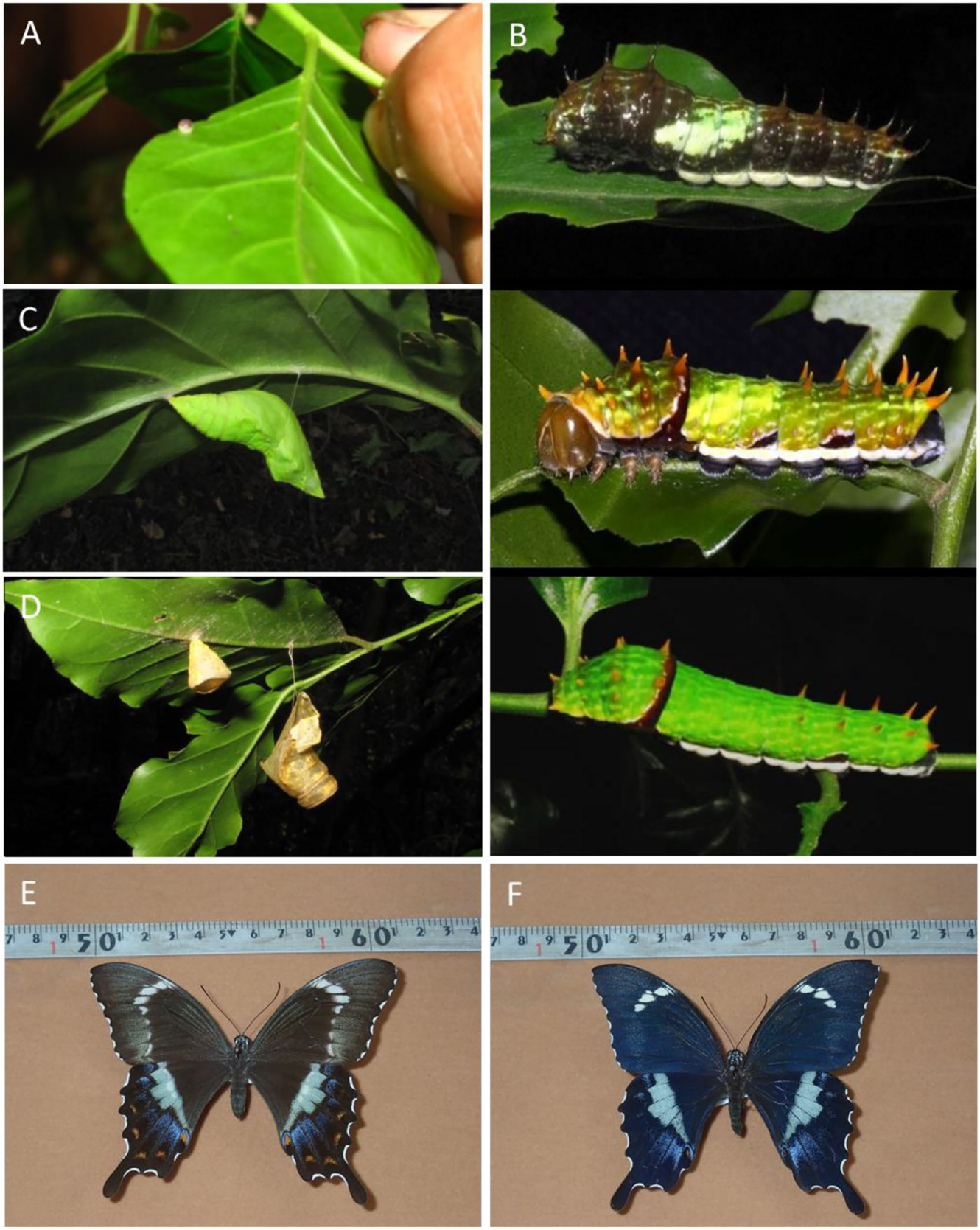


FIGURE 3 *Papilio godeffroyi* developmental stages include egg (A), larvae (B, increasing in age from top to bottom), and pupa (C). A butterfly emerged from its exuviae (empty pupal case; split into two pieces, D). The butterfly (adult male [E], adult female [F]) is the largest Lepidoptera in the Samoan Archipelago, with a wingspan approaching or exceeding 10 cm. Photographs (A–D) by R. W. Peck, Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo. Photographs (E) and (F) by M. A. Schmaedick, American Samoa Community College.

or northerly in aspect. Nearly all (232 of 238) *M. minutum* surveyed for *Papilio* or assessed for phenology were located within the forest interior. Four trees stood at the forest edge while two others were within forest gaps.

Measurements of leaves collected in the field revealed significant relationships between leaf length, area, and mass (Appendix S1: Table S3). Combining these results with measurements of tree size and foliage production, we found highly significant positive effects of basal diameter on estimates of the total leaf area and total leaf mass of individual trees (Appendix S1: Table S3), which explained much of the variation in leaf production between stands (Table 1). Consequently, mean leaf area and mass were twice as great per tree at the two stands with the largest diameter trees (Vatia 1 and Vatia 2) compared with the stand with the smallest diameter trees (Afono).

The biophysical characteristics of *M. minutum* stands varied greatly among stands, with tree numbers ranging from the single tree at Sauma to 40 trees at Maloata 1&2, which at 17.8 ha, covered 4.7 times more area than all other stands combined but had the lowest tree density (Table 2). Stand differences were also evident in tree density and basal area, with the largest values exceeding the smallest by 100-fold. Accordingly, total leaf area and mass per stand were highly variable.

TABLE 1 Biophysical characteristics (mean ± SE) of *Micromelum minutum* trees surveyed for *Papilio* or assessed for phenology at eight stands.

Stand	No. trees	Height (m)	Basal diameter (cm)	Basal area (cm^2)	Leaf area (m^2)	Leaf mass (g)
Afono	21	3.1 ± 0.29	3.4 ± 0.33	10.9 ± 2.38	1.9 ± 0.43	97 ± 21.9
Amalau 1&2	37	3.8 ± 0.33	4.6 ± 0.46	22.3 ± 4.93	2.8 ± 0.58	146 ± 30.0
Amalau 3	23	3.2 ± 0.37	3.5 ± 0.38	12.2 ± 2.86	2.5 ± 0.53	126 ± 26.3
Maloata 1&2	40	4.8 ± 0.25	4.6 ± 0.32	19.5 ± 2.88	2.9 ± 0.35	150 ± 18.2
Sauma	1	5.0	8.0	50.3	14.1	771.0
Vatia 1	23	3.1 ± 0.47	4.9 ± 0.66	26.4 ± 6.98	3.5 ± 0.71	182 ± 36.7
Vatia 2	20	3.9 ± 0.46	5.2 ± 0.58	26.6 ± 5.49	3.8 ± 0.64	195 ± 32.5
Vatia 3	26	3.5 ± 0.40	3.9 ± 0.45	15.8 ± 4.33	2.6 ± 0.54	134 ± 27.5
All trees	191	3.8 ± 0.14	4.3 ± 0.18	19.5 ± 1.71	2.9 ± 0.21	150 ± 11.0
Papilio trees	117	2.9 ± 0.14	3.6 ± 0.19	13.6 ± 1.81	2.1 ± 0.26	109 ± 13.5

Note: Tree height was measured above the base and basal diameter was measured at 20-cm height. Leaf area and mass were calculated from the number and length of leaves observed at the end of the study using regression equations derived from a sample of leaves that were measured, dried, and weighed in the laboratory (Appendix S1: Table S3). Trees surveyed for *Papilio* ($n = 117$) were smaller on average than the combined (survey and phenology) sample of trees ($n = 191$), reflecting the physical constraints of sampling tall trees in the field. A single large tree comprised the sample at Sauma.

TABLE 2 Biophysical characteristics of *Micromelum minutum* stands (see Table 1 for biophysical characteristics of trees).

Stand	Stand area (m^2)	No. trees	Density (no. trees/ha)	Total basal area (cm^2/ha)	Total leaf area (m^2/ha)	Total leaf mass (kg/ha)
Afono	1493.0	21	14.07	153.53	27.01	1.36
Amalau 1&2	340.9	37	108.54	2417.89	305.25	15.86
Amalau 3	112.3	23	204.81	140.41	520.58	25.90
Maloata 1&2	17,828.5	40	2.24	43.84	6.55	0.34
Sauma	na[a]	1	na[a]	na[a]	na[a]	na[a]
Vatia 1	133.0	23	172.93	4558.20	611.08	31.40
Vatia 2	1213.4	20	16.48	438.38	63.04	3.21
Vatia 3	494.8	26	52.55	831.46	138.03	7.02
All stands (total)	21,615.9	191	8.84	1.20	25.90	0.59
All stands[b]	3088.0 ± 2464.99	24 ± 4.2	81.7 ± 30.93	1226 ± 636.7	238.8 ± 92.87	12.2 ± 4.72

[a]Value not available because there was only one tree at Sauma.
[b]Values are mean ± SE.

Host tree phenology

We recorded the presence or absence but not the abundance of new leaves, flowers, and fruits on trees each month. We observed new foliage on most trees (range = 89%–100%) throughout the study with no indication of seasonality (Figure 4A). Relatively few trees flowered each month, but twice as many trees flowered from February through July (36%) compared with October through January (18%). Green fruit production was relatively aseasonal, but few trees were fruiting two months after the low flowering period. Green fruit was present on an average of 15% (range = 5%–23%) of trees each month, but red fruit was present on only 2.3% (0%–7.1%) of trees. We observed few or no trees with red fruit from March through July, when flower production was more frequent.

Herbivory, presumably by *P. godeffroyi* larvae, was noted on all trees throughout the year with 80% of trees (range = 60%–93%) at low levels and 20% of trees (range = 7%–40%) at moderate levels, but only three trees experienced heavy herbivory (Figure 4B). The intensity of herbivory was relatively consistent from March 2013 through March 2014, but it increased from May through August 2014.

Abundance patterns and location of eggs and juvenile stages

During June 2013 to August 2014, we conducted a total of 115,908 leaf-surveys and found 1545 *Papilio* specimens, or 13.33 specimens/1000 leaf-surveys

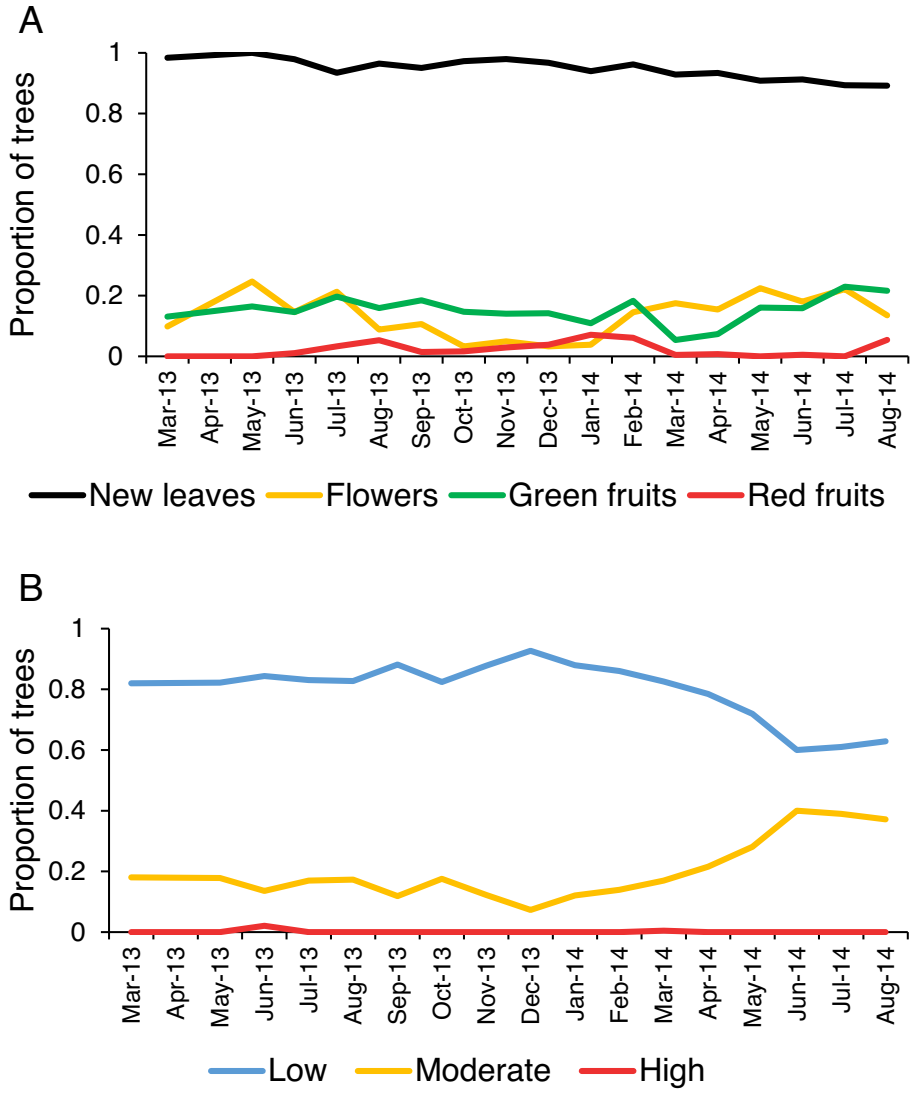


FIGURE 4 Proportion of *Micromelum minutum* trees ($n = 191$) producing new leaves, flowers, green fruit, and red fruit (A), and proportion of trees displaying low, moderate, or high levels of herbivory (B) each month from March 2013 to August 2014.

(discounting 13 leaf-surveys with multiple specimens; Appendix S1: Table S4). Our monthly searches for *P. godeffroyi* on the 117 designated trees in the 8 stands covered approximately 45% of the total standing crop of *M. minutum* in terms of leaf mass (12.7 of 28.7 kg) and leaf area (250.0 of 559.8 m^2). The cumulative area of foliage covered by leaf-surveys was 1878.74 m^2, which yielded 0.82 *Papilio* specimens/m^2. The cumulative dried mass examined during leaf-surveys was 96.1 kg, which produced 16.07 specimens/kg. In terms of live eggs, the most frequent active life stage, we found 3.88 eggs/1000 leaves, 0.24 eggs/m^2 leaf area, and 4.68 eggs/kg leaf mass. Despite thorough searching, we failed to find *Papilio* of any life stage during 114,363 leaf-surveys (98.7% of total).

Of the 1545 *Papilio* specimens found on survey trees, we collected 450 eggs, 942 eggshells, 90 larvae, 20 pupae, and 43 exuviae. Because each leaf was carefully inspected and all specimens were removed during each visit, the survey results approximate the rate of monthly reproduction, assuming low rates of specimen removal by predators and high rates of detection during surveys. Therefore, the 1392 eggs and eggshells indicate a total of 12.01 ovi/1000 leaves, 0.74/m^2 leaf area, and 14.48/kg dried leaf mass (Appendix S1: Table S4). Nevertheless, we recorded female butterflies landing and ovipositing, or apparently ovipositing, on only four occasions at survey trees and once at a phenology tree. Juvenile *Papilio* were encountered 92% less often than were ovi. Because the developmental time of *Papilio* exceeded our 30-day sampling interval (M. Schmaedick, pers. obs.), late-stage larvae, pupae, and exuviae that we found represented specimens that we either overlooked during the previous survey or that moved from leaves that were out of reach previously. The 90 larvae and 20 pupae yielded a combined incidence of 0.95 juveniles/1000 leaves, 0.06 juveniles/m^2 leaf area, and 1.14 juveniles/kg leaf mass. The 43 exuviae we collected presumably represented successful reproductive outcomes for an incidence of 0.37 exuviae/1000 leaves, 0.02 exuviae/m^2 leaf area, and 0.45 exuviae/kg leaf mass.

Reproduction was highly variable between stands (Figure 5; Appendix S1: Table S4). Stands with the highest incidence of oviposition per unit of foliage were Afono, Maloata 1&2, and Vatia 2. Oviposition frequency was intermediate at Vatia 3 and lowest at Sauma, Amalau 1&2, Amalau 3, and Vatia 1.

To address whether variation in the reproductive output of stands might be influenced by host plant density, we evaluated reproduction as a function of the total estimated density of leaves of all survey and phenology trees in each stand (in kilogram of leaves per hectare). We found that the oviposition density (in ovi per kilogram) on surveyed leaves was negatively related to the foliage density of all trees at stands (data log-transformed; $n = 1366$ ovi, $df = 6$, $R^2 = 0.78$, $F = 17.9$, $p = 0.008$; Sauma excluded; Figure 5A). In other words, stands with the lowest overall densities of trees and leaves (Maloata 1&2, Afono, and Vatia 2) yielded the most ovi per unit of surveyed foliage. The stand at Sauma, however, consisted of a single isolated tree that yielded the fewest ovi (3.77 ovi/kg leaves; Appendix S1: Table S4), indicating that there may be a threshold of stand density that is attractive or discernable to ovipositing females.

The output of juvenile stages mirrored the trend seen for oviposition. Larvae and pupae were negatively related to the density of *Micromelum* leaves in the stands (data log-transformed; $n = 110$ juveniles, $R^2 = 0.82$, $F = 22.5$, $p = 0.005$; Figure 5B). Because only 43 exuviae were found, trends in eclosion frequency relative to leaf density were not clear. Nevertheless, the highest numbers of exuviae were found at two of the three stands with high oviposition and juvenile production: Vatia 2 (1.73 exuviae/kg leaves) and Afono (0.54 exuviae/kg leaves; Appendix S1: Table S4).

Using a hierarchical mixed-effects model, we investigated the effects of stand characteristics (slope, forest cover, stand area, tree density, and leaf mass) as linear predictors of oviposition rates within a random stand effect. Models were compared with AIC_c to assess the relative weight of evidence for those stand-level predictors affecting oviposition. The model AIC_c indicated no evidence that stand covariates affected oviposition rates (Table 3). The two models showing the greatest effect (still with higher AIC_c values than the null model) were leaf mass and tree density. Those two predictors were highly correlated (coefficient of determination $[R^2] = 0.94$) and together may indicate that foliage density is a potential factor warranting further study.

Among all 117 trees monitored for reproduction, 103 (88%) yielded ≥1 ovi during the study, but the range in ovi number was wide (1–109 ovi/tree). The top 12 (10%) oviposition hosts accounted for 345 (25%) of all ovi collected and 50% of ovi/100 g leaves (Figure 6A). These super-host trees were concentrated in stands where overall *Papilio* reproduction per unit of foliage was high (Maloata 1&2, Vatia 2, and Afono) or intermediate (Vatia 3; Figure 5A). In fact, only 1 tree from the other 5 stands ranked among the top 30 ovi hosts. Forty-two (36%) trees produced <1 ovi/100 g leaves, and all but two were in low-yield stands. An additional 14 (12%) trees yielded no ovi, and 10 of these were in low-yield stands. Somewhat unexpectedly, four no-ovi trees were in Maloata 1&2, the highest yield stand.

On ovi-producing trees, ovi density (ovi/100 g leaves) and frequency (ovi/survey) were positively

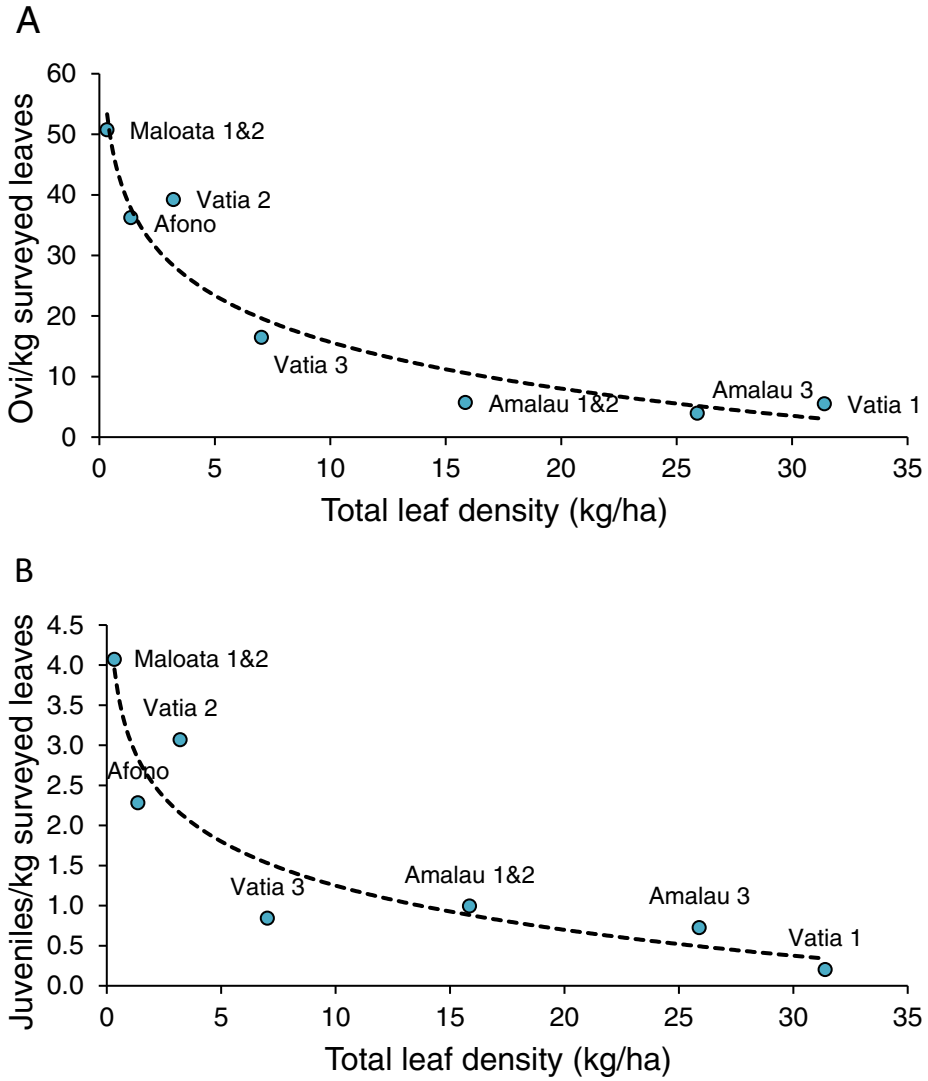


FIGURE 5 *Papilio godeffroyi* oviposition (A) and juvenile production (B) on surveyed leaves relative to overall *Micromelum minutum* leaf density in seven stands. The single tree at Sauma was not included in the analysis. Leaf density (in kilograms per hectare) was calculated from the estimated mass of all *Micromelum* leaves recorded from October through November 2014 from all *Papilio* survey and phenology trees in the stand. The prevalence of ovi (eggs and eggshells) trended negatively relative to leaf density ($R^2 = 0.92$, $y = -11.1\ln[x] + 41.289$). Juvenile (larvae and pupae) production also trended negatively relative to leaf mass ($R^2 = 0.79$, $y = -0.796\ln[x] + 3.085$).

TABLE 3 Akaike information criterion (AIC) comparison table for models to assess stand-level predictors.

Model	*K*	AIC_c	ΔAIC_c	Weight (%)	Cumulative weight (%)
Null (leaf mass)	3	311.5	0.00	34.1	34.1
Stand mass	5	311.6	0.18	31.2	65.3
Stand density	5	313.4	1.91	13.1	78.4
Stand area	5	314.1	2.61	9.2	87.7
Stand slope	5	314.3	2.79	8.4	96.1
Stand cover	5	315.8	4.34	3.9	100.0

Note: Stand predictors were nested within stand, and all models (including the null) had an offset of log(leaf sample mass) to control for sampling effort.

but weakly related ($df = 102$, $R^2 = 0.13$, $F = 14.51$, $p = 0.0002$), and ovi were found more often on the top 12 ovi trees (65.1% of surveys ±6.95) compared with all other trees that yielded ≥1 ovi/survey (43.16 ± 2.88; two-tailed $t = 2.92$, $df = 101$, $p = 0.01$). Only 5 (4.3%) of the 117 trees yielded ovi on every survey, whereas

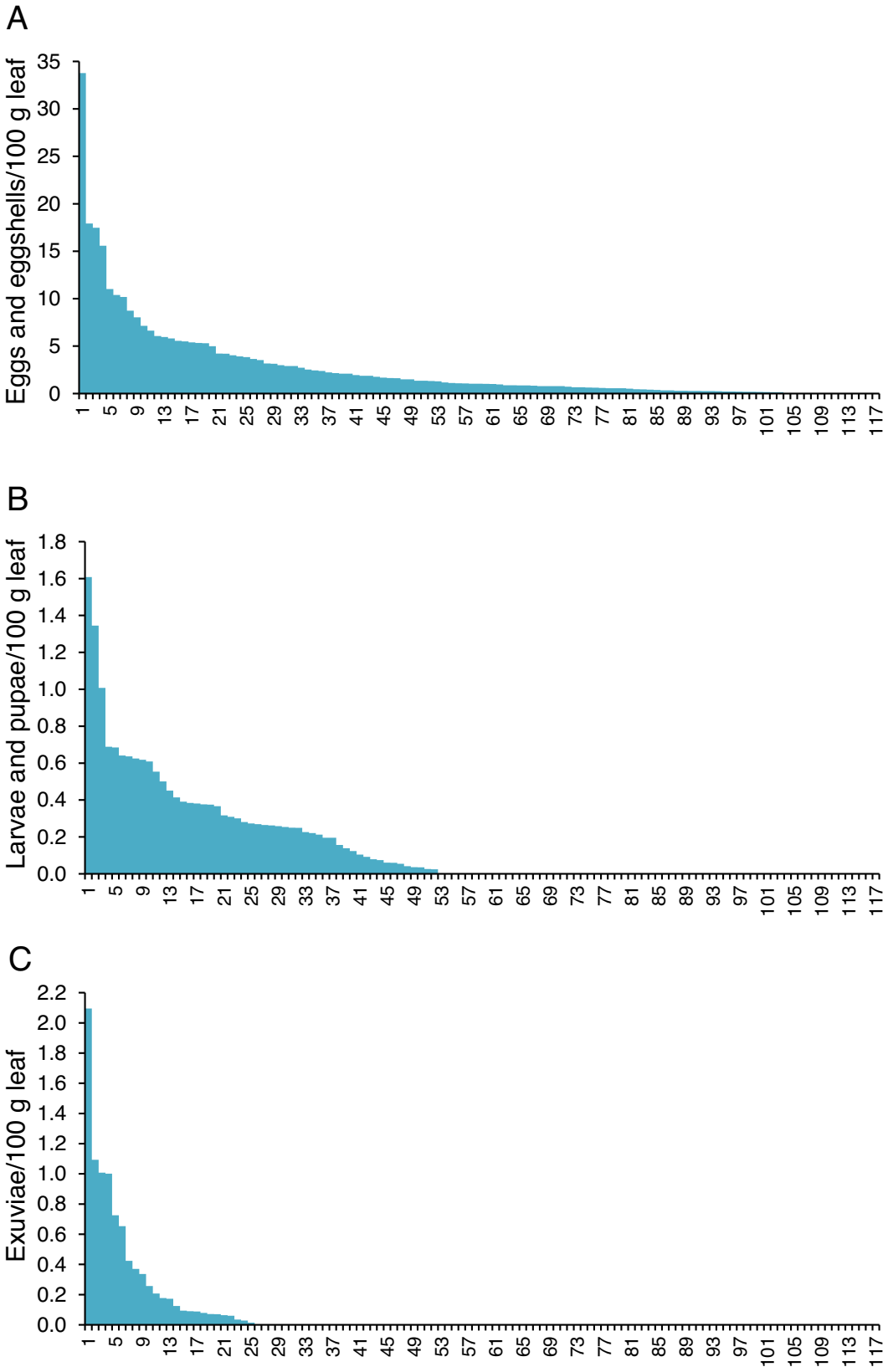


FIGURE 6 Distribution of *Papilio godeffroyi* ovi (eggs and eggshells, A), juveniles (larvae and pupae, B), and exuviae (C) on surveyed leaves relative to leaf mass among 117 *Micromelum minutum* trees. Except for the 13 trees on which no *Papilio* were ever found (tree numbers 105–117 on the *x*-axes), trees represented by 1–104 were usually different individuals on each graph.

72 (61.5%) yielded no ovi or ovi less than half of the time (Figure 7).

Of the 12 top ovi trees, 5 were ranked among the top 10% for juveniles/100 g leaves and 2 were ranked among the top 10% for exuviae/100 g leaves. The top 10% of juvenile-hosting trees accounted for 22 (20%) larvae and pupae and 53% of juveniles/100 g leaves (Figure 6B). They were distributed in stands with high (Maloata 1&2, Vatia 2, and Afono) and low (Amalau 3) *Papilio* reproduction. No juveniles were found on 65 trees (56% of total). Only one of the top juvenile-hosting trees was also ranked in the top 10% of exuviae-hosting trees. The top 10% of trees with exuviae accounted for 60% of the total and 89% of exuviae/100 g leaves, but no exuviae were found on 92 trees (79% of total; Figure 6C). The top 10% of exuviae-producing trees were distributed in stands with high (Vatia 2 and Afono), intermediate (Vatia 3), and low (Amalau 1&2, Amalau 3, and Vatia 1) *Papilio* reproduction. No *Papilio* specimens of any type were found on 13 of the 117 trees, which were distributed in stands with high (Maloata 1&2) and low (Amalau 1&2, Amalau 3, and Vatia 1) reproduction.

To evaluate how individual tree size and leaf mass might affect the density of oviposition, we compared the 12 top ovi-hosting trees (i.e., ovi/100 g surveyed leaves) with the remaining 105 trees in terms of basal diameter, height, and total leaf mass (including both surveyed and nonsurveyed leaves). We anticipated that these highly correlated tree attributes would produce trends similar to those observed for oviposition at the stand level, such that smaller trees with less foliage would generally yield more ovi per unit of foliage. In fact, we found that the 12 top ovi trees were 30% smaller in diameter (2.6 cm ± 0.24 vs. 3.7 cm ± 0.21; two-tailed $t = -3.58$, df = 115, $p = 0.001$), 30% shorter (2.1 m ± 0.33 vs. 3.0 m ± 0.14; two-tailed $t = -2.55$, df = 115, $p < 0.05$), and had 59% less foliage mass (33 g ± 9.4 vs. 81 g ± 9.2; two-tailed $t = -3.64$, df = 115, $p = 0.0008$).

The mixed-effects models to assess how tree-level covariates affected oviposition density produced three covariates that performed better than the null model (Table 4). Two of those, leaf area and mass, accounted for 50.5% and 43.1% of the model weight, respectively, with tree diameter weighing in at 4.8%. Linear coefficients for the leaf area (−0.1 ± 0.03) and mass (−1.9 ± 0.57) models indicated a negative association between general "foliage density" and oviposition, similar to the result obtained when comparing the 12 top ovi trees with all others (see above). The negative coefficient for diameter (−0.1 ± 0.04) corresponded to a tendency for smaller trees to host more oviposition.

Despite the continual production of new foliage, *Papilio* specimens were almost always found on old leaves: 92% of eggs (eggshells not included because leaves may have been young when eggs were laid), 98% of larvae, and all pupae and exuviae. Ovi were found on the underside of leaves (abaxial) 79% of the time. Larvae were found on the topside of leaves (adaxial) 98% of the time, but pupae and exuviae were always found on the underside. Most *Papilio* were found singly on leaves, but 2–4 ovi were collected from the same leaflet or leaf on 41 occasions. Nearly all ovi were found on the leaflet lamina, but one was on a leaf rachis, one was on a flower panicle, and one was on a branch. Our results showed that larvae moved to slightly higher branches to pupate and eclose (emerge as adults). Ovi and larvae were collected at a mean height of 2.2 m ± 0.02 ($n = 1472$) and pupae and exuviae were collected at

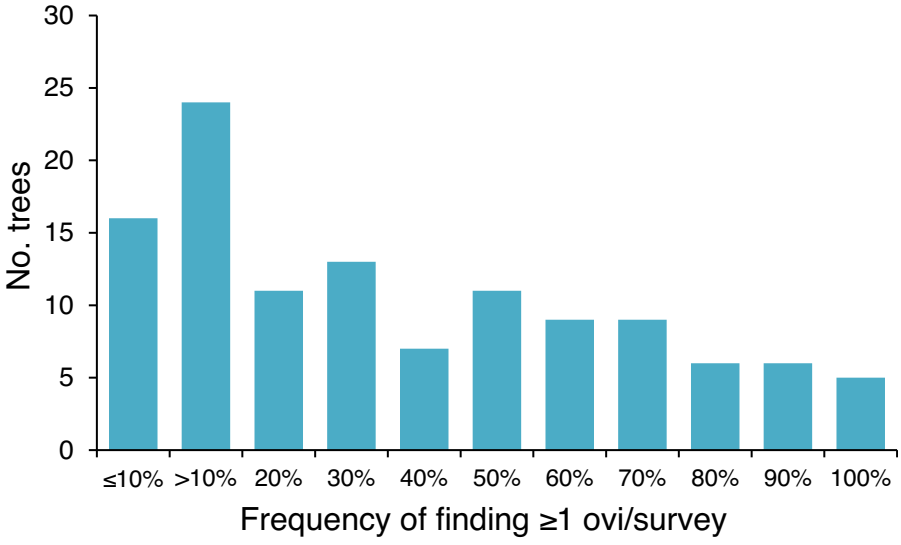


FIGURE 7 Frequency at which ovi (eggs and eggshells) were found on each of 117 *Micromelum minutum* trees during monthly surveys.

2.7 m ± 0.12 ($n = 58$) above the base of host trees (two-tailed $t = -3.43$, df = 1528, $p = 0.001$). This difference could be an artifact of our sampling, which did not include the upper parts of tall trees from which a portion of the larvae might move into the sampled zone and pupate there if vertical movement was not biased up or down.

We found a positive correlation between monthly egg production (in eggs per kilogram foliage) and temperature (Pearson's $r = 0.75$, $F = 12.86$, $p = 0.005$; Figure 8) but not with precipitation (Pearson's $r = 0.10$, $F = 0.11$, $p = 0.75$). Temperatures (Appendix S1: Table S5) were warmer from October through May (mean = 27.9 ± 0.12 SE), the nominally hot, wet season (Craig, 2009), and cooler from June through September (27.1 ± 0.20; one-tailed $t = 3.60$, df = 10, $p = 0.008$), but precipitation (Appendix S1: Table S5) was similar (26.9 ± 4.37 vs. 26.9 ± 2.81; one-tailed $t = 0.004$, df = 10, $p = 0.50$). Mean egg production was 5.5 eggs/kg ± 0.58 SE during the warmer months and 3.7 ± 1.12 during the cooler months, but the difference was not significant (one-tailed $t = 1.37$, df = 10, $p = 0.11$). Sampling did not always occur at the same time each month, which may have obscured seasonal trends. Eggs ($n = 450$) represented the most reliable index of seasonal reproduction because sample sizes of larvae ($n = 90$) and pupae ($n = 20$) were relatively small and because eggshells ($n = 942$), which were often cryptic, and exuviae ($n = 43$) might have remained longer on leaves, potentially biasing results by their accumulated numbers on the first sampling date at each stand.

TABLE 4 Akaike information criterion (AIC) comparison table for mixed-effects models to assess the properties of individual trees on the log of the number of ovi (egg and eggshell) detected.

Model	*K*	AIC_c	ΔAIC_c	Weight (%)	Log-likelihood	Cumulative weight (%)
Tree leaf area	4	302.7	0.00	50.5	−147.2	50.5
Tree leaf mass	4	303.0	0.32	43.1	−147.3	93.6
Tree diameter	4	307.4	4.70	4.8	−149.5	98.5
Null	3	311.5	8.78	0.6	−152.6	99.1
Tree height	4	312.7	9.97	0.3	−152.1	99.4
Tree canopy cover	4	312.7	10.02	0.3	−152.2	99.8
Tree leaves	4	313.5	10.85	0.2	−152.6	100.0

Note: All models (including the null) had an offset of log(leaf sample mass) to control for sample size. Stand was added as a random effect to control for stand-specific effects on oviposition.

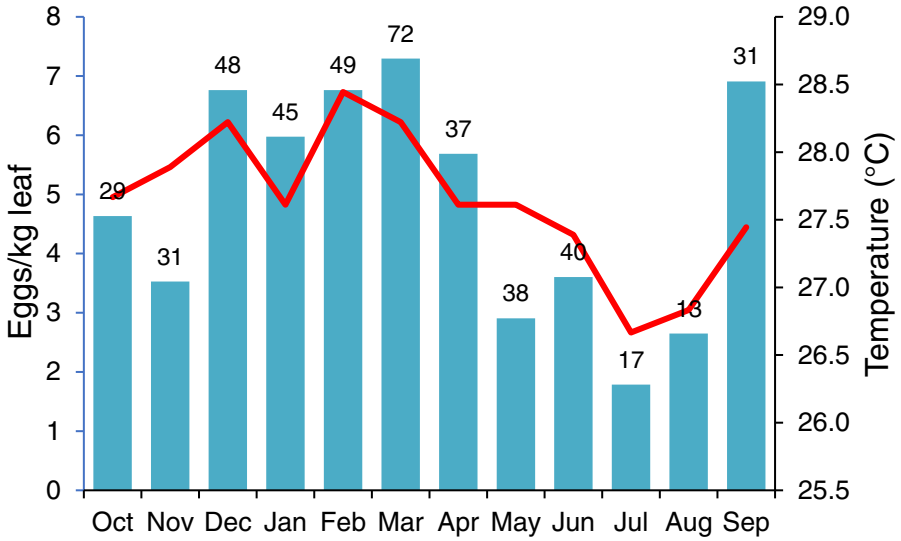


FIGURE 8 Monthly distribution of *Papilio godeffroyi* eggs ($n = 419$) weakly tracked temperature. Egg data for 2013 and 2014 were combined for June, July, and August to increase sample sizes for those months. Numbers of eggs are shown above each bar. Temperature data from NOAA (red line; see Appendix S1: Table S5). Seasonal differences in photoperiod are relatively minor, but the period during October–May tends to be hotter and wetter, whereas the period during June–September is generally cooler and drier (Craig, 2009). There is no clear seasonal pattern in *Micromelum minutum* phenology, indicating little relationship with oviposition patterns.

DISCUSSION

Scope and limitations of survey

Our study is the first to investigate patterns of *P. godeffroyi* reproduction relative to host plant and habitat characteristics anywhere in the Samoan Archipelago since the brief, early observations of Mathew (1885) and Hopkins (1927). We found eggs, larvae, pupae, and exuviae on most trees within all eight *M. minutum* stands, indicating that this butterfly is reproductively active across a range of environmental conditions. Although most stands were scattered along the north-central coast of Tutuila (within the NPSA), one was located on the far western tip of the island and another consisted of just one tree, demonstrating that the butterfly may be reproducing wherever *M. minutum* occurs and in whatever abundance it is found.

Monthly surveys of *Papilio* reproduction on the 117 designated *Micromelum* trees covered about 45% of the total standing crop of foliage in all stands, and the 1545 specimens (mostly eggs and eggshells) we collected provided sufficient statistical power to assess at least some responses of the butterfly to a range of habitat and host plant conditions, as discussed later. Nevertheless, we found specimens on about 1% of the leaves that were examined, indicating the intensity of effort likely needed to replicate our results. We observed females ovipositing on only five occasions and rarely saw males, and from this we conclude that studies of adult mating and feeding behavior would be logistically challenging.

Eggs of some local sphingid moths resemble those of *P. godeffroyi*, but we did not find them on *M. micromelum*. *P. godeffroyi* eggs are firmly attached to the leaf and seem resistant to being dislodged, but we could have underestimated their abundance if oviposition disproportionately occurred more frequently in the foliage above our reach. Although we found larvae and pupae slightly higher in trees, there was no indication that they became more abundant in the higher foliage.

M. minutum as host plant

As one of over 2000 species within the Rutaceae, or citrus family, *M. micromelum* has a wide distribution in the Indo-Pacific region, ranging from Thailand to Northern Australia to western Polynesia (Whistler, 2004). Within the Samoan Archipelago, it is found on Savai'i and Upolu Islands in Samoa and on Tutuila, Aunu'u, Ta'ū, Ofu, and Olosega Islands in American Samoa. Elsewhere *M. minutum* is host to several other species of *Papilio*, including *P. schmeltzi* in Fiji (Chandra et al., 2013), *P. aegeus* and *P. fuscus* in Australia (Braby, 2000), and *P. ambrax*, *P. fuscus*, and *P. aegeus* in Papua New Guinea (Parsons, 1991).

Globally, other species of Rutaceae host larvae of swallowtail butterflies (Braby, 2000), and additional surveys might reveal *P. godeffroyi* on one or more of the several, relatively rare species of *Melicope* or on agricultural species of *Citrus*. Chandra and Hodge (2021) found that the closely related *P. schmeltzi* oviposited on *Citrus reticulata*, and larvae successfully developed on this host in cage studies with potted plants, although they did not find it on *Citrus* in the field aside from a single oviposition reported from a 2008 survey (Chandra et al., 2013). Early work on Upolu and Tutuila Islands in the late 1800s reported larvae of *P. godeffroyi* to be "not uncommon" and feeding on "young stunted plants of '*Aralia*' growing in shady and sheltered places" (Mathew, 1885). No species of *Aralia* are known from American Samoa, although four native species of Araliaceae are in the Samoan Archipelago, along with some ornamental species of *Schefflera*. We cannot explain Mathew's observation, but *M. minutum* may have been the "*Aralia*" he mentioned, given the strong host plant association we observed.

M. minutum was the only plant species on which we observed *P. godeffroyi*, although additional surveys might discover alternative hosts. Although we did not search systematically for *Micromelum* stands, the species seems to be common but patchily distributed across Tutuila. The eight stands we studied occurred at low elevation on relatively steep slopes within the forest interior under dense canopy cover. Only six trees stood at the forest edge or within forest gaps. The stands varied greatly in area and tree density as well as total leaf area and mass.

We observed new foliage on most trees throughout the study with no indication of seasonality. We also assessed herbivory, most presumably by *P. godeffroyi* larvae. Only three trees showed signs of heavy herbivory; otherwise, herbivory occurred at low or occasionally moderate levels. The intensity of herbivory was relatively consistent from March 2013 through March 2014, but it increased from May through August 2014. Low levels of herbivory on individual leaves could indicate that larvae moved within and possibly between trees to feed. Our data may indicate that larvae moved slightly higher in trees, presumably sometimes beyond our reach, before pupating compared with where we found eggs or larvae. Movement to higher leaves may reduce predation from ground-based predators (e.g., reptiles, ants; Campbell & Torgersen, 1983; Weseloh, 2012) or provide more favorable microclimatic conditions for development (e.g., warmer due to Sun exposure; Bryant et al., 2002; Veldtman et al., 2007). Alternatively, pupae and exuviae we found may have originated from eggs and young

larvae that were missed in the previous survey, or they may represent larvae that moved into the sampled (lower) portions of the trees from the unsampled (higher) portions during the interval between surveys. Although not tested, the latter scenario would more likely lead to pupae and exuviae being found higher in the sampled portion of trees.

Relatively few trees flowered each month, but twice as many trees flowered from February through July than from October through January. We never observed *P. godeffroyi* visiting *M. minutum* or other flowers, so seasonal use of potential sources of energy for adults is unknown. Green (unripe) fruit production was not strongly seasonal, but few trees were fruiting two months after the low flowering period. We observed green fruit on about 15% of trees each month and red (ripe) fruit on about 2.3% of trees, with no trees having red fruit from March through July. The low incidence of red fruit relative to green fruit might indicate that frugivores are harvesting much of the ripe fruit crop or that ripe fruit persists for only short periods of time before falling from the tree. We did not observe instances of frugivory or record the prevalence of fallen fruits, but birds or other animals that may eat *M. minutum* fruit might also prey on *P. godeffroyi* caterpillars or pupae at the same time.

Oviposition patterns in response to host plant and environmental characteristics

Variability between *M. minutum* stands in oviposition density provides a starting point for developing habitat management strategies to enhance *P. godeffroyi* conservation. All stands yielded ovi, but oviposition was not distributed in proportion to the availability of trees. The resource concentration hypothesis predicts that herbivores, and by extension we assume herbivore reproduction, should occur at higher densities where resources are most abundant (Long et al., 2003; Root, 1973). To the contrary, we found that stands with the lowest densities of trees and total mass of leaves yielded relatively high numbers of ovi per unit of foliage. We recorded the highest densities of ovi at Afono, Maloata 1&2, and Vatia 2; intermediate density at Vatia 3; and lowest densities at Sauma, Amalau 1&2, Amalau 3, and Vatia 1. The exception to this tendency was the low ovi density at the single Sauma tree, raising the possibility of a minimum threshold of tree and foliage density that may be attractive or discernable to ovipositing females. Other studies have found that oviposition rates decrease with increasing host plant density, likely due to an increase in female selectivity as host density increases (Rausher, 1983).

We also found a negative relationship between tree and foliage density and the densities of larvae and pupae. Too few exuviae were found to support a conclusion, but we would expect a similar relationship with a larger sample size. Nevertheless, no exuviae were found at Maloata 1&2, raising the question of whether it might function as a population sink despite high rates of oviposition and juvenile recruitment.

Our hierarchical mixed-effects model to evaluate the influence of stand characteristics on oviposition density provided no evidence of an effect due to slope, forest cover, stand area, tree density, or leaf mass. Nevertheless, the mixed-effects models for tree-level covariates indicated a negative relationship with leaf area and tree leaf mass. This was consistent with the differences in oviposition density between the three high-oviposition and five low-oviposition stands, as discussed above.

Just as ovi density was higher in stands with low tree and foliage density, small trees with relatively little leaf mass also yielded higher densities of ovi, although this could have been partly due to our inability to sample much above 2 m in tall trees. This result contrasts with the results of Veldtman et al. (2007), who found that the largest trees within stands were overutilized by wild silk moths, *Gonometa postica* and *G. rufobrunnea* (Lasiocampidae), independent of the actual size of the host plant. Larger individuals of herbaceous host plants also have been shown to be selected for oviposition more often by Lepidoptera (Thompson & Pellmyr, 1991) and Coleoptera (Heisswolf et al., 2005). Instead, we found that the top 10% of trees in terms of oviposition density were on average 30% shorter and smaller in diameter and had 72% less leaf mass than all other trees. This top 10% of trees disproportionately hosted 25% of all ovi and nearly 50% of ovi/100 g leaves. These super-oviposition trees were concentrated in the three most productive stands, which likely contributed to stand productivity, especially because only one tree ranked in the top 30 of ovi hosts was in a low-yield stand. Moreover, two of the three high-yield stands included only one tree ranked in the lower 50% of oviposition, although four trees at the highest yield stand, Maloata 1&2, yielded no ovi. Oviposition density and frequency were positively related, and relatively few trees yielded ovi on >80% of surveys. Overall, this indicates that the physical characteristics of individual trees affect stand productivity, but tree size and foliage mass do not explain all the variation we observed in oviposition patterns at the stand level.

Neither do tree and foliage density entirely account for oviposition patterns seen among individual trees, although the negative relationship between oviposition rate and tree or leaf density may indicate that females become more selective on smaller trees having fewer

leaves on which to oviposit, similar to the negative relationship we observed between oviposition rates and leaf density at the stand level (as discussed above; also see Rausher, 1983). *Papilio* behavior relies heavily on vision, and oviposition may be affected by multiple visual features, perhaps supplemented by olfactory, gustatory, and tactile cues (Nagaya et al., 2021). Higher levels of green reflectance of leaves increased oviposition rates in caged *Papilio xuthus* (Nagaya et al., 2021), and if leaves of small *M. minutum* trees tend to be younger and appear brighter (Figure 2A,C), *P. godeffroyi* females would likely oviposit more frequently on small trees. Nevertheless, we found nearly all eggs, larvae, and pupae on leaves that appeared dark green, indicating that they were older compared with leaves that were a lighter shade of green. Without evidence of differences in leaf quality between small and large host trees, we cannot evaluate variation in oviposition behavior relative to host size or age. Factors such as local microclimate, leaf chemistry and physical characteristics, and predator abundance may be useful variables to examine in future studies if specialization on *M. minutum* has heightened the butterfly's sensitivity to variation in host plant and environmental conditions. The *P. godeffroyi* we observed appeared to be strong fliers that would have little difficulty moving within or between trees or stands to select suitable oviposition sites.

Oviposition occurred during all months but with higher densities during the warmer, wetter months of December–April. Mechanisms underlying this pattern are unclear. Egg-laying in herbivorous insects often coincides with leaf flush, as new leaves are often higher in nitrogen and are more tender (Rausher, 1981). We observed new *M. minutum* leaves throughout the year, but eggs, larvae, pupae, and exuviae were nearly always found on older leaves. We have no knowledge of *M. minutum* leaf nutrition or palatability to *P. godeffroyi*, but we fed both young and old leaves to larvae in the laboratory while generally avoiding very young or very old leaves. Our anecdotal observations lead us to suspect that differences in larval feeding preferences, growth, and survival might be found in experimental feeding trials using leaves of various ages. For example, Chandra and Hodge (2019) found *P. schmeltzi* first instars grew faster on younger *M. minutum* leaves, but fifth instars grew faster on mature leaves.

P. godeffroyi reproduction was marginally greater during the hotter, wetter months, but eggs and larvae of the Fijian swallowtail, *P. schmeltzi*, were most abundant from June through September, roughly corresponding to the cooler, drier season (Chandra et al., 2013). It is also possible that the seasonal pattern we observed was due to higher survival, or greater fecundity, of adult females. For example, adult survivorship of the Jamaican swallowtail (*P. homerus*) has been positively associated with higher numbers of flowers suitable for foraging (Garraway et al., 2008). *M. minutum* flowering declined during the hotter months, but flowering patterns of other plants in our study area have not been reported. Additional studies might find that variation in predation rates also influence seasonal trends in adult survival and reproduction. Regardless of the proposed mechanism, our observations of seasonal patterns included data for only 9–16 months at each stand. Longer term studies might identify more definitive seasonal trends.

Conservation implications

P. godeffroyi breeds broadly across Tutuila in both primary and secondary rainforest habitats, and reproduction likely occurs wherever *M. minutum* is found, even in relatively isolated trees and stands such as some of the ones we surveyed. Although the species may seem at relatively low risk of extinction on the face of this evidence, it raises questions about why it disappeared from other islands, what measures would help to reestablish it in former range, and how can it be protected from present or emerging threats in its present range. We take note of the invasive species already documented in American Samoa (Craig, 2009) as well as potentially disruptive invaders that may not currently be recognized or that may yet become established and create conditions unfavorable to the butterfly and its habitat. Similarly, environmental conditions could change rapidly due to a cyclone or more gradually from climate change (Craig, 2009), potentially increasing the risk of extinction. Starting therefore with the situation of the butterfly on Tutuila, a more comprehensive survey of host tree distribution may facilitate the development of a spatially explicit conservation plan for the butterfly and its habitat that could consider threats to butterfly populations and habitats from environmental events and biological agents. Following this, host plant surveys on other islands within the former range of the butterfly could guide decisions about habitat management and eventual reintroductions of the butterfly to reduce the risks inherent to single-island populations. Additional surveys could also reveal alternative host plants that could broaden the scope of habitat conservation actions, although studies of the Fijian endemic, *P. schmeltzi*, showed that the primary host, *M. minutum*, promoted greater larval growth and survival compared with three alternative hosts (Chandra & Hodge, 2021).

We found that butterfly reproduction varied significantly between stands of the host plant due in part to a negative relationship between oviposition rates and host tree density and total stand foliage mass. Variation in

oviposition rates between individual trees was also largely explained by their negative relationship with foliage mass. Further investigation of these relationships could help guide habitat management by identifying potential differences in microclimate or predator behavior due to variation in tree and foliage density and other stand characteristics. Nevertheless, our results provide a starting point for planning habitat management strategies that increase butterfly reproduction. For example, host plant stands with a relatively high proportion of young, small trees may support higher rates of oviposition. Anecdotally, in November 2014, we observed numerous larvae in the small trees that had been planted, beginning in March 2013, along the edge of the forest behind American Samoa Community College. As young stands mature, monitoring changes in rates of butterfly reproduction and mortality of different developmental stages would provide valuable insights for developing habitat management plans. At the same time, it would be helpful to evaluate changes in stand structure and dynamics; leaf chemistry and physical characteristics; and predator–prey and parasitoid–host interactions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Banko et al., 2022) are available from the USGS ScienceBase-Catalog: https://doi.org/10.5066/P9A6CXQX.

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REFERENCES

Banko, P. C., R. W. Peck, and M. A. Schmaedick. 2022. "Samoan Swallowtail Butterfly Reproductive Response to Host Plant Characteristics, 2013–2014." U.S. Geological Survey Data Release. https://doi.org/10.5066/P9A6CXQX.

Braby, M. F. 2000. *Butterflies of Australia: Their Identification, Biology and Distribution*, Vol 1. Collingwood: Australian Biological Resources Study/CSIRO Entomology, CSIRO Publishing.

Bryant, S. R., C. D. Thomas, and J. S. Bale. 2002. "The Influence of Thermal Ecology on the Distribution of Three Nymphalid Butterflies." *Journal of Applied Ecology* 39: 43–55.

Campbell, R. W., and T. R. Torgersen. 1983. "Effect of Branch Height on Predation of Western Spruce Budworm (Lepidoptera: Tortricidae) Pupae by Birds and Ants." *Environmental Entomology* 12: 697–9.

Chandra, V., and S. Hodge. 2019. "The Effects of Leaf Age and Host Plant on Larval Development of an Endemic Fijian Butterfly *Papilio schmeltzi* (Lepidoptera: Papilionidae)." *Weta* 53: 15–23.

Chandra, V., and S. Hodge. 2021. "Fijian Swallowtail Butterfly *Papilio schmeltzi* (Papilionidae: Lepidoptera) Shows Clear Preference-Performance Relationships on Both Native and Exotic Host Plants." *Austral Entomology* 60: 225–33.

Chandra, V., T. A. Inoue, and U. R. Khurma. 2013. "Field Studies on Fiji's Endemic Swallowtail Butterfly, *Papilio schmeltzi*: Habitat, Activity Pattern, Phenology and Distribution." *South Pacific Journal of Natural and Applied Sciences* 31: 51–60.

Collins, N. M., and M. G. Morris. 1985. *Threatened Swallowtail Butterflies of the World*. Gland and Cambridge: IUCN Red Data Book, IUCN.

Craig, P., ed. 2009. *Natural History Guide to American Samoa*, 3rd ed. Pago Pago: National Park of American Samoa, Department of Marine and Wildlife Resources, American Samoa Community College. https://www.nps.gov/npsa/learn/nature/upload/NatHistGuideAS09.pdf.

Dethier, V. G. 1941. "Chemical Factors Determining the Choice of Food Plants by *Papilio* Larvae." *American Naturalist* 75: 61–73.

Edwards, E. 2012. "Report on the Moths and Butterflies (Lepidoptera) of Upland Savai'i." In *Rapid Biodiversity Assessment of Upland Savai'i, Samoa*, edited by J. Atherton and B. Jefferies, 113–39. Apia: Secretariat of the Pacific Regional Environment Programme. https://www.sprep.org/attachments/Publications/BIORAP_Upland_Savaii.pdf.

ESRI. 2011. *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.

Garraway, E., A. J. A. Bailey, B. E. Freeman, J. R. Parnell, and T. C. Emmel. 2008. "Population Studies and Conservation of Jamaica's Endangered Swallowtail Butterfly *Papilio* (*Pterourus*) *homerus*." *Journal of Insect Conservation* 12: 383–97.

Heisswolf, A., E. Obermaier, and H. J. Poethke. 2005. "Selection of Large Host Plants for Oviposition by a Monophagous Leaf Beetle: Nutritional Quality or Enemy-Free Space?" *Ecological Entomology* 30: 299–306.

Hopkins, G. H. E. 1927. *Insects of Samoa and Other Samoan Terrestrial Arthropoda, Part III. Lepidoptera, Fasc. 1 Butterflies of Samoa and Some Neighbouring Island-Groups*, Vol 1, 1–64. London: British Museum.

Howarth, F. G., and G. W. Ramsay. 1991. "The Conservation of Island Insects and Their Habitats." In *The Conservation of Insects and Their Habitats: 15th Symposium of the Royal Entomological Society of London, 14–15 September 1989*, edited by N. M. Collins and J. A. Thomas, 71–107. London and San Diego, CA: Academic Press.

IUCN. 2019. "The IUCN Red List of Threatened Species. Version 2019-3." http://www.iucnredlist.org.

Lamoureux, C. H., D. Mueller-Dombois, and K. W. Bridges. 1981. "Temporal Variation of Organism Groups Studies: Trees." In *Island Ecosystems: Biological Organization in Selected Hawaiian Communities. U.S. International Biological Program Synthesis Series 15*, edited by D. Mueller-Dombois, K. W. Bridges, and H. L. Carson, 391–407. Stroudsburg, PA and Woods Hole, MA: Hutchinson and Ross.

Liu, Z., N. E. Gurr, M. A. Schmaedick, W. A. Whistler, and L. Fischer. 2011. *Vegetation Mapping of American Samoa*. Vallejo, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region. General Technical Report. (R5-TP-033). 19 pp. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd937236.pdf.

Long, Z. T., C. L. Mohler, and W. P. Carson. 2003. "Extending the Resource Concentration Hypothesis to Plant Communities: Effects of Litter and Herbivores." *Ecology* 84: 652–65.

Mathew, G. F. 1885. "Life History of Three Species of Western Pacific Rhopalocera." *Transactions of the Entomological Society of London, Part V* 33: 357–68.

Nagaya, H., F. J. Stewart, and M. Kinoshita. 2021. "Swallowtail Butterflies Use Multiple Visual Cues to Select Oviposition Sites." *Insect* 12: 1047.

New, T. R., and N. M. Collins. 1991. *Swallowtail Butterflies: An Action Plan for their Conservation*. Gland: IUCN. https://portals.iucn.org/library/sites/library/files/documents/1991-011.pdf.

Olson, M. D. 2001. "Development Discourse and the Politics of Environmental Ideologies in Samoa." *Society and Natural Resources* 14: 399–410.

Parsons, M. 1991. *Butterflies of the Bulolo-Wau Valley*. Honolulu, HI: Bishop Museum Press.

Patrick, B., E. Edwards, and M. Böhm. 2018. "*Papilio godeffroyi*. The IUCN Red List of Threatened Species." e.T122530997A122603026. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T122530997A122603026.en.

Patrick, B., and H. Patrick. 2012. *Butterflies of the South Pacific*. Dunedin: Otago University Press.

Rasband, W. S. 1997–2015. *ImageJ*. Bethesda, MD: U.S. National Institutes of Health. http://imagej.nih.gov/ij/.

Rausher, M. D. 1981. "Host Plant Selection by *Battus philenor* Butterflies: The Roles of Predation, Nutrition, and Plant Chemistry." *Ecological Monographs* 5: 1–20.

Rausher, M. D. 1983. "Alteration of Oviposition Behavior by *Battus philenor* Butterflies in Response to Variation in Host-Plant Density." *Ecology* 64: 1028–34.

Reich, P. B. 1995. "Phenology of Tropical Trees: Patterns, Causes, and Consequences." *Canadian Journal of Botany* 73: 164–74.

Root, R. B. 1973. "Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica oleracea*)." *Ecological Monographs* 43: 95–124.

Tennent, W. J. 2006. "A Checklist of the Butterflies of Melanesia, Micronesian, Polynesia and Some Adjacent Areas." *Zootaxa* 1178: 1–209.

Thompson, J. N., and O. Pellmyr. 1991. "Evolution of Oviposition Behavior and Host Preference in Lepidoptera." *Annual Review of Entomology* 36: 65–89.

Veldtman, R., M. A. McGeoch, and C. H. Scholtz. 2007. "Fine-Scale Abundance and Distribution of Wild Silk Moth Pupae." *Bulletin of Entomological Research* 97: 15–27.

Weseloh, R. M. 2012. "Predation by *Calosoma sycophanta* L. (Coleoptera: Carabidae): Evidence for a Large Impact on Gypsy Moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), Pupae." *The Canadian Entomologist* 117: 1117–26.

Whistler, W. A. 2004. *Rainforest Trees of Samoa: A Guide to the Common Lowland and Foothill Forest Trees of the Samoan Archipelago*. Honolulu, HI: Isle Botanica.

Zimmerman, E. C. 1958. *Insects of Hawaii. Vol. 7, Macrolepidoptera. Honolulu*, Vol 7. Honolulu, HI: University of Hawaii Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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