A Recent Outbreak of the Hawaiian Koa Moth, *Scotorythra paludicola* (Lepidoptera: Geometridae), and a Review of Outbreaks between 1892 and 2003[1]

William P. Haines,[2,3] *Mandy L. Heddle,*[4] *Patricia Welton,*[5] *and Daniel Rubinoff*[3]

Abstract: The koa moth, *Scotorythra paludicola*, is an endemic Hawaiian moth that undergoes sporadic outbreaks in koa forests in Hawai'i, causing vast defoliations of its host plant, *Acacia koa*. We studied one such outbreak that occurred on East Maui in 2003, in which approximately 16 km^2 of forest were defoliated. We collected adult moths and larvae, and recorded size-class distribution of larvae in defoliated regions. Larvae at a given site tended to be of a similar size class, suggesting that outbreaks were synchronous, and mean development time from first instar to adulthood was 42 days under laboratory conditions. Mortality of field-collected, laboratory-reared larvae due to disease was high (80%), making it impossible to quantify meaningful parasitism rates, but three non-native hymenopteran primary parasitoids were reared (the braconids *Meteorus laphygmae* and *Cotesia marginiventris*, and the ichneumonid *Hyposoter exiguae*). One ichneumonid hyperparasitoid, *Gelis* sp., was also reared. No native parasitoids were reared. We found no relationship between occurrence of five koa moth outbreaks on East Maui between 1920 and 2006 and annual or monthly precipitation or temperature during that period.

Sudden increases in population densities of herbivorous insects can be devastating to both managed and natural forest ecosystems, not only from the resulting defoliation but also through a cascade of trophic effects that can result in high tree mortality. Defoliation of forest trees during insect outbreaks can range in size from highly localized outbreaks of 1–3 km^2 (Piyakarnchana 1981, Kay 1982, Steinbauer et al. 2001) to over 500 km^2 of damage (Abbott 1990). The implications of such outbreaks can be severe, limiting the development of forest-based industries reliant on these trees and compromising the integrity of natural forest ecosystems.

Although tropical systems are generally considered to be more stable both with regard to climate and fluctuations in animal populations (Gray 1972, Wolda 1978), the impression of stability in tropical systems is misleading. For example, in the wet tropics, fluctuations in rainfall can have drastic effects on insect dynamics (Kirkpatrick 1957, Harvey and Mallya 1995). Tropical insect populations fluctuate annually (Wolda 1978), and outbreaks do occur, though they are relatively rarely reported (Fletcher 1967, Gray 1972, Piyakarnchana 1981, Harvey and Mallya 1995, Van Bael et al. 2004).

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[2] Corresponding author.

[3] Department of Plant and Environmental Protection Sciences, University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822.

[4] Center of Science and Mathematics Education: Opportunities for Success, Bowling Green State University, Bowling Green, Ohio 43403.

[5] Haleakalā National Park, Vegetation Management, Resources Management Division, Makawao, Hawai'i 96768.

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TABLE 1

Reports of Outbreaks by *Scotorythra* spp. across the Hawaiian Islands

Date Observed	Host Plant	Location	Species Responsible for Outbreak	Estimated Area Defoliated (km^2)[a]	Reference to Outbreak
1892	*A. koa*	Kona, Hawai'i	*S. paludicola*	NR	Perkins, pers. comm. in Swezey (1926)
1894–1895	*A. koa*	Haleakalā, East Maui	*S. paludicola*	NR	Perkins, pers. comm. in Swezey (1926)
1895	*A. koa*	Kīlauea, Hawai'i	*S. paludicola*	NR	Perkins, pers. comm. in Swezey (1926)
1895 or 1896	*A. koa*	Kona, Hawai'i	*S. paludicola*	NR	Perkins, pers. comm. in Swezey (1926)
1896	*A. koa*	Olinda Forest, East Maui	*S. paludicola*	NR	Perkins, pers. comm. in Swezey (1931)
1900	*A. koa*	Tantalus, O'ahu	*S. metacrossa* Meyrick, *S. rara* (Butler)	NR	Swezey (1926)
Before 1913	*A. koa*	Hawai'i Island	*S. paludicola*	NR	Perkins (1913)[b]
Jan. 1926	*A. koa*	Makawao Forest, East Maui	*S. paludicola*	NR	Swezey (1926, 1931)
Jan. 1946	*A. koa*	Makawao Forest and Kīpahulu, East Maui	*S. paludicola*	>0.8	Fullaway (1947*a*)
July–Aug. 1953	*A. koa*	Hawai'i Island	*S. paludicola*	5.2	Davis (1955)
Sept. 1971	*A. koa*	Makawao Forest, East Maui	*S. paludicola*	~0.4	Wong and Miyahira (1971)
Jan. 1977	*A. koa*	Makawao Forest and Halehaku, East Maui	*S. paludicola*	18.4[c]	Stein and Scowcroft (1984)
Oct. 1982	*Dodonaea viscosa* Jacq.	Mauna Loa, Hawai'i Island	*S. trapezias* Meyrick	NR	Mitchell and Davis (1985)
Aug. 2003 and Feb. 2004	*A. koa*	Kīpahulu and Makawao Forests, East Maui	*S. paludicola*	15.7	Most recent outbreak

[a] NR, extent of defoliation not reported

[b] Perkins wrote about an "earlier" outbreak on Hawai'i Island in his introduction to Fauna Hawaiiensis (1913) but did not supply a date or exact location for the outbreak. He was likely referring to one of the outbreaks he later wrote about to Swezey, but it is referenced here for a complete account of reported outbreaks.

[c] Although 18.2 km^2 of koa forest were reported to be severely defoliated, we consider this a likely error or overestimate, because Makawao Forest Reserve, which encompasses Stein's study site and much of the koa forest in the region, is only 8.5 km^2 in its entirety, and koa-dominated forest makes up less than half of the Reserve.

Scotorythra paludicola (Butler) (Geometridae: Ennominae), a specialist on the hardwood tree koa (*Acacia koa* A. Gray), is the most notable irruptive forest insect in Hawai'i. Endemic to the islands of O'ahu, Maui, and Hawai'i, *S. paludicola* occasionally experiences huge population explosions, causing defoliation of koa forests. Past outbreaks of *S. paludicola*, of which there have been at least 12 in the Hawaiian Islands (Table 1), were reported to cause as much as 35% mortality in koa forests (Stein and Scowcroft 1984). Regarding one of the earliest recorded outbreaks, Perkins (1913:cli) wrote, "native birds, attracted in thousands by the abundance of this, one of their favorite foods, were gorged to repletion, and the starving caterpillars formed writhing masses on the ground beneath the tall koa trees. The dropping of excrement from the trees on the dead leaves beneath made a rattling noise as of a hailstorm."

One such outbreak occurred between 2003 and 2004, when *S. paludicola* caused severe defoliation of nearly 16 km^2 of koa on East Maui, including parts of Haleakalā National Park, Kīpahulu Forest Reserve, and Makawao Forest Reserve (Figure 1). Defoliation is of grave concern for Hawai'i's forest ecosystems because koa is a dominant and defining tree in native mesic and wet forest throughout the Hawaiian Islands (Geesink et al. 1990), and constitutes approximately 2,500 km^2 of Hawai'i's natural and planted forests (Stein 1983). In economic terms, koa is the most valuable wood grown in Hawai'i and is one of the most highly prized woods in the world (Elevitch et al. 2006).

Despite the historical records of outbreaks of *S. paludicola*, very little is known about the life history of the moth, duration of life cycle, or the interactions between the moth, its natural enemies, and koa. Therefore, the environmental triggers for outbreaks of *S. paludicola* are unknown. Moths in the genus *Scotorythra* do not appear to exhibit seasonality, nor is there any apparent dormancy or diapause in *S. paludicola;* generations of larvae follow one another without a seasonal pause (Heddle 2003). This is typical of tropical rain forest species where food is available throughout the year, providing resources for continual breeding (Kirkpatrick 1957). Further, outbreaks do not appear to be periodic or cyclical; they have been reported at various intervals during the last century, and they do not usually occur simultaneously on multiple islands (Table 1).

The 2003–2004 outbreak allowed us to record the spread of defoliation by *S. paludicola* across the forests of East Maui. We supplemented these data with surveys of adult moths and larvae on koa, including parasitoids associated with *S. paludicola* during the outbreak. We also examined relationships between regional rainfall and temperature and the five known *S. paludicola* outbreaks in Makawao Forest over the past century.

MATERIALS AND METHODS

Monitoring Defoliation

Biologists at Haleakalā National Park (HNP) monitored the spread of defoliation in Kīpahulu Valley during regular service trips to the region by helicopter. Defoliated areas were mapped and digitized based on visual surveys by helicopter and on foot, with reference to landmarks and global positioning system (GPS)-mapped locations. HNP biologists conduct service trips by helicopter to various field camps in Kīpahulu Valley at least monthly, and after first observing defoliation there in mid-August 2003, HNP biologists visited defoliated regions during late August, early and late September, mid-October, early November, and early and mid-December. Healani, west of Kīpahulu Valley, was visited in January and December 2003 and January 2004. Although the defoliation was first noted there in January 2003, its importance was unclear at the time, and no attempt was made to map the defoliation on those visits.

In February 2004, the perimeters of defoliated areas of both Kīpahulu Valley and Makawao Forest were mapped during an areawide flyover, using a GPS (Trimble GeoXM) unit. Data were differentially corrected, and the resulting polygons were analyzed in ArcMap 9.1 (ESRI, Inc.). The spatial data from February 2004 are therefore the most accurate and measure the extent of defoliation near its maximum.

To measure extent of defoliation and recovery of trees, HNP vegetation management staff surveyed individual koa trees in 20 × 20 m plots along transects on the Upper Shelf and Healani beginning in December 2003. Initially, all trees > 1 cm basal diameter were surveyed, and a randomly chosen subset of trees in each plot was flagged to monitor on subsequent visits. For each tree, percentage of foliage remaining on branches was estimated, as well as the presence or absence of caterpillars, feeding damage, chlorotic phyllodes, epicormic growth (shoots arising from the main branch in response to injury), and true leaves. Transects were visited on the Upper Shelf in December 2003, January 2004, April 2004, and September 2004, and at Healani in February and May 2004.

Collections

To determine the identity of defoliating insects and associated parasitoids, we collected

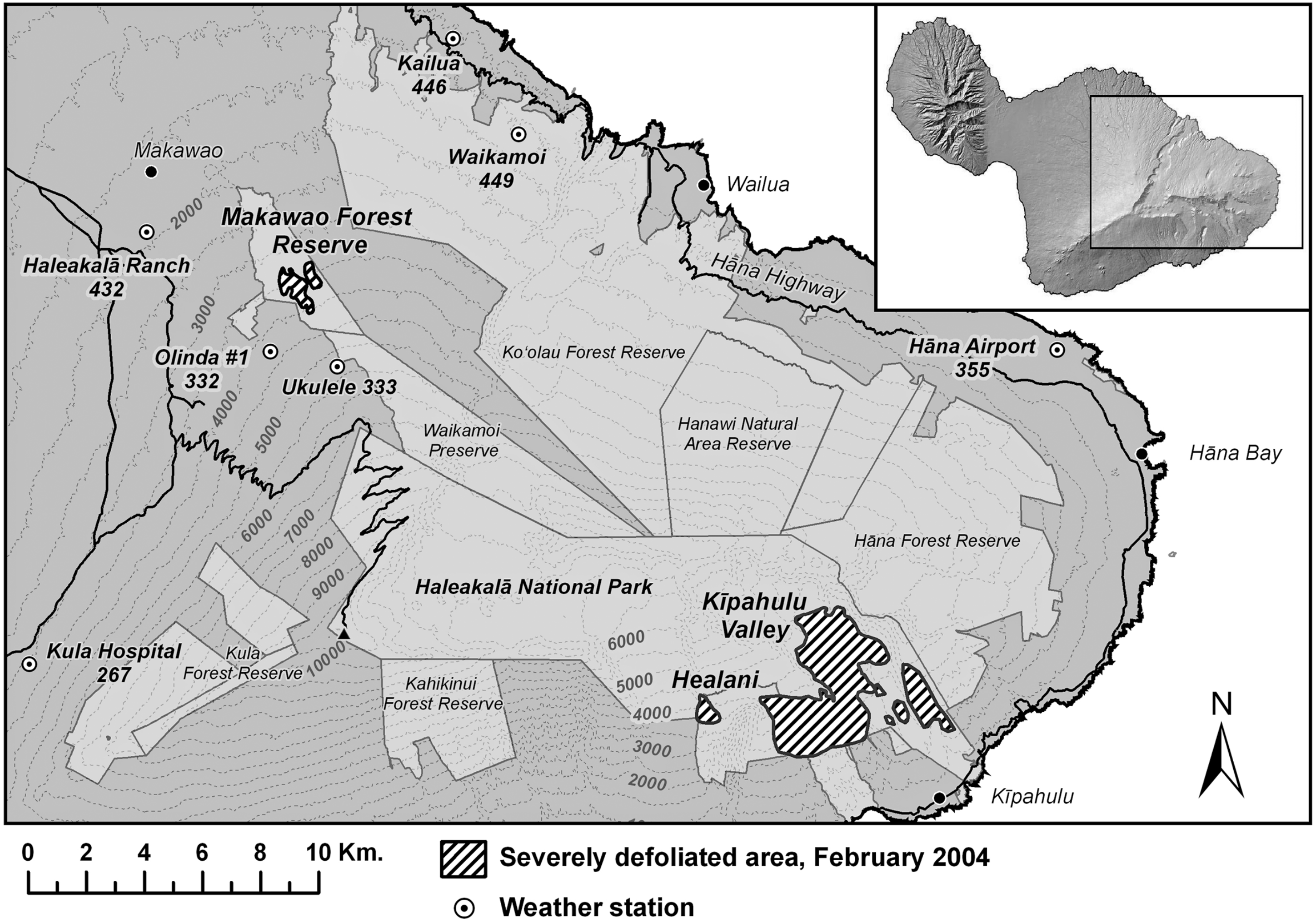


Figure 1. Near-maximum extent of koa defoliation on East Maui in February 2004, mapped by helicopter using GPS (global positioning system). Elevation contours are labeled as feet above sea level.

adult and larval insects in Kīpahulu Valley, at Healani, and in Makawao Forest Reserve. We visited Kīpahulu Valley on two occasions in 2004. Our first overnight visit to Kīpahulu Valley was 15–16 January 2004, when we surveyed koa trees for larvae and set three light traps and a blacklight sheet to collect nocturnal flying insects near Delta Camp. On 16 January 2004, we also surveyed koa trees during the daytime at Healani, west of Kīpahulu Valley. Our survey of the Healani area focused on larvae and observations of day-flying adults. We revisited Kīpahulu Valley 27–28 April 2004 and repeated the described sampling, but Healani was not visited.

We visited Makawao Forest Reserve five times during 2004. On 15 February, when the outbreak was first noted, larvae were observed but not collected. On 6–7 March, 29 March, 18 April, and 18 June 2004, larvae were collected and brought to the laboratory for rearing. A blacklight was used on 6–7 March and 18 June to attract adult moths to a sheet.

At all locations, we collected caterpillars by shaking branches from haphazardly selected trees onto a white, 1 m^2 "beating sheet." Search effort was not quantified or kept constant among collecting trips, so abundances of larvae collected on different days cannot be directly compared. All larvae observed were collected to determine size class, life cycle duration, and factors affecting larval mortality, particularly parasitoids. We also searched for pupae under bark and just below the soil surface, which was an effective strategy for Swezey (1927*a*) during a similar outbreak at Makawao Forest Reserve.

Larvae were brought to the laboratory and sorted into size classes based on head capsule widths as an estimate of larval age. Size classes corresponded to head capsule widths as follows: 1, 0.20–0.30 mm; 2, 0.45–0.60 mm; 3, 0.70–1.00 mm; 4, 1.00–1.40 mm; 5, 1.40–1.80 mm; 6, >1.80 mm. Larvae were reared individually on koa phyllodes in 30 ml (2 oz.) plastic cups at 23°C, with a small piece of moistened paper towel to maintain humidity. Development was monitored and recorded every 1 to 3 days. Any parasitoids that emerged were preserved and identified.

Rainfall and Temperature Data

We collated monthly rainfall data provided by the National Climatic Data Center (NCDC) (2008) for four East Maui weather stations: Haleakalā Ranch, 432; Olinda no. 1, 332; 'Ukulele, 333; and Waikamoi, 449. These stations are scattered around Makawao Forest (Figure 1). For all stations, observations extended from 1919 to 2006, with some months missing for each station (Haleakalā Ranch, 3 months; Olinda no. 1, 62 months; 'Ukulele, 5 months; Waikamoi, 7 months). To correct for differences in total rainfall between stations and between seasons, data were converted to deviations from long-term monthly averages for each station. Overall mean monthly deviations were then calculated across all stations for which data were available. Pearson correlations for data between sites were as follows: Haleakalā Ranch and Olinda no. 1 ($r = 0.69$, $P < .01$), Haleakalā Ranch and 'Ukulele ($r = 0.75$, $P < .01$), Haleakalā Ranch and Waikamoi ($r = 0.55$, $P = <.01$), Olinda no. 1 and 'Ukulele ($r = 0.68$, $P = <.01$), Olinda no. 1 and Waikamoi ($r = 0.40$, $P = <.01$), 'Ukulele and Waikamoi ($r = 0.48$, $P = <.01$).

Only three weather stations on East Maui had monthly summaries of daily temperature extending from 1919 to 2006: Hāna Airport, 354/355 (52 months missing); Kailua, 446 (118 months missing); and Kula Hospital, 267 (37 months missing) (NCDC 2008). These stations were not as close to our site as rainfall stations were. For our analyses, we used the monthly mean of daily maximum temperatures because this was the most highly correlated temperature variable among the three stations. As with rainfall data, monthly data for each station were converted to deviations from long-term monthly averages, then averaged across stations. Pearson correlations between sites for monthly mean maximum temperatures were: Hāna Airport and Kailua ($r = 0.47$, $P = <.01$), Hāna Airport and Kula Hospital ($r = 0.21$, $P = <.01$), Kailua and Kula Hospital ($r = 0.28$, $P = <.01$). Monthly mean maximum temperatures (averaged across sites) were negatively correlated with mean precipitation ($r = -0.22$, $P = <.01$).

Because rearing indicated that the life cycle of *S. paludicola* is completed within several months, we looked for any irregularities in rainfall or temperature within about a year of observed outbreak events. We explored the effect of precipitation and temperature on monthly and annual timescales. On a monthly scale, we plotted mean deviations from mean rainfall and mean maximum temperature for 3 yr preceding each outbreak and visually examined these plots for any common patterns among outbreaks.

On an annual scale, we performed logistic regression analyses (Minitab 14, Minitab, Inc, State College, Pennsylvania) with a binary response ("outbreak observed" or "no outbreak observed") and climate data as predictors. For each outbreak ($n = 5$), we calculated means of each variable for a 12-month period preceding the outbreak (e.g., for the outbreak observed in September 1971, we calculated average rainfall and temperature deviations for September 1970–August 1971). To represent conditions during nonoutbreak periods ($n = 81$), we used 12-month averages based on calendar years from 1919 to 2006, omitting any years that overlapped with the 12 months preceding outbreaks (1925, 1945, 1970, 1971, 1976, 2003, 2004). We started with a full model, which included the two climate variables (mean monthly rainfall deviation and mean monthly mean maximum temperature deviation) and an interaction term between the two. We then progressively removed nonsignificant predictor variables at the level $P > .10$. We also performed separate, nonparametric Mann-Whitney *U*-tests on the rainfall and temperature variables between the same outbreak and nonoutbreak periods.

RESULTS

Progress of the Outbreak

A time line of observations during the outbreak is presented in Table 2. The first signs of the most recent outbreak were observed in January of 2003, when HNP staff reported defoliation of mature koa trees in a small area at Healani, near Kaupō Gap (T. Bailey, pers. comm.). However, because Healani was not monitored between January and December 2003 (at which point a large area was completely defoliated), the early progress of defoliation at that site is unknown. In January 2004, trees were still defoliated at Healani, with no sprouted new growth.

In August 2003, HNP biologists noted signs of koa defoliation and an infestation of unidentified adult and larval Lepidoptera along the Central Pali, an inaccessible cliff separating the upper and lower shelves of Kīpahulu Valley (Figure 2), about 5 km ENE of the Healani site. In early September, crews visited the lower shelf and noted that the original defoliated area on the Central Pali had expanded and also included the tops of some ridges. By November the extent of noticeable defoliation had expanded considerably beyond the ridges and cliffs to the valley floors, and defoliated trees and large numbers of caterpillars were noted at several camps.

In koa, juvenile foliage and new growth is characterized by bipinnately compound true leaves. These are later replaced by leaflike phyllodes (flattened petioles), evidence of mature growth (Geesink et al. 1990). In Kīpahulu Valley recovery rates of trees were high, with nearly all defoliated trees putting out new growth within a matter of months. When HNP staff first monitored plots on the Upper Shelf of Kīpahulu Valley in December 2003 ($n = 99$ trees), the majority of trees (54%) retained less than 25% of their phyllodes, and only 7% of trees had true leaves or epicormic growth. By April 2004, consumption of phyllodes had increased but so had regeneration of new growth. Of the trees monitored on the Upper Shelf at that time ($n = 64$), 80% had less than 25% of their phyllodes (including 58% that had zero phyllodes remaining). However, 100% of trees showed some degree of epicormic growth or true leaves. By September 2004, trees had begun to regrow phyllodes, with 82% of all monitored trees ($n = 38$) having more than 25% of their phyllodes, and all trees continuing to also exhibit epicormic growth and true leaves.

When we visited the Lower Shelf in January 2004, most of the koa trees that had been

TABLE 2

Time Line of Observations for Most Recent Outbreak

Locality	Date	Observations
Healani	January 2003	Haleakalā National Park (HNP) staff report defoliation of koa.
Healani	January 2004	Hundreds of adult moths observed active in the daytime. No refoliation. Fewer larvae and fewer first instars than on the Lower Shelf of Kīpahulu Valley.
Kīpahulu Valley	August 2003	HNP employees report outbreaks and defoliation on the Central Pali. Adult moths were abundant and active at all hours at Ginger Camp and Dogleg Camp on the Upper Shelf.
Kīpahulu Valley	September 2003	HNP employees at two camps on the Lower Shelf report no moths, but the defoliation observed on the Central Pali in August had expanded.
Kīpahulu Valley	October 2003	HNP employees investigate outbreak at camps on Upper Shelf (same sites as in August 2003). Moths were again observed flying during the day and night. Severe defoliation had spread from Central Pali about halfway across the Lower Shelf and about 200 m onto the Upper Shelf.
Kīpahulu Valley	November 2003	HNP employees halfway across the Upper Shelf note a huge abundance of caterpillars at camp, on trees, and feeding on fallen phyllodes under trees. Trees had not yet been completely defoliated in the area.
Kīpahulu Valley	December 2003	HNP employees report that nearly all of the koa forest on the Upper Shelf and most of the koa on the Lower Shelf is defoliated. On the Upper Shelf, no caterpillars but some adult moths were observed. An abundance of caterpillars and moths, and defoliated koa were reported in Manawainui.
Kīpahulu Valley	January 2004	W.P.H. and D.R. visit the Lower Shelf (Delta Camp). Three light traps used to sample adults. Larvae collected in day and at night. Defoliation present but new leaves emerging. Mostly first-instar larvae. Over 100 moths collected in light traps, but no moths observed during the daytime. Many *Macaria abydata* observed.
Kīpahulu Valley	18 April 2004	Refoliation of young leaves and phyllodes. Very low abundance of *S. paludicola*. Only two specimens in light traps.
Kīpahulu Valley and Healani	February 2004	Extent of all visible defoliation is mapped using GPS via helicopter.
Makawao Forest Reserve	February 2004	Outbreak reported by W.P.H. Severe defoliation on Borges Ridge at about 1,090 m. Many late-instar larvae present on trees.
Makawao Forest Reserve	6–7 March 2004	Adult moths abundant. Few larvae apparent and those present were early instars. Many parasitoid cases observed (*Meteorus laphygmae*). Twelve larvae collected from foliage of varied age classes.
Makawao Forest Reserve	29 March 2004	Many larvae collected from Powerline Road. Around 50 larvae collected, mostly second instars.
Makawao Forest Reserve	18 April 2004	One hundred sixty larvae collected from Powerline Road and Borges Ridge. Mostly third instars.
Makawao Forest Reserve	June 2004	Light trap attracted five *S. paludicola* at most. Only two larvae collected from koa, both late instars. Refoliation of koa observed. Reports of defoliation at higher elevations (around 1,220 m).

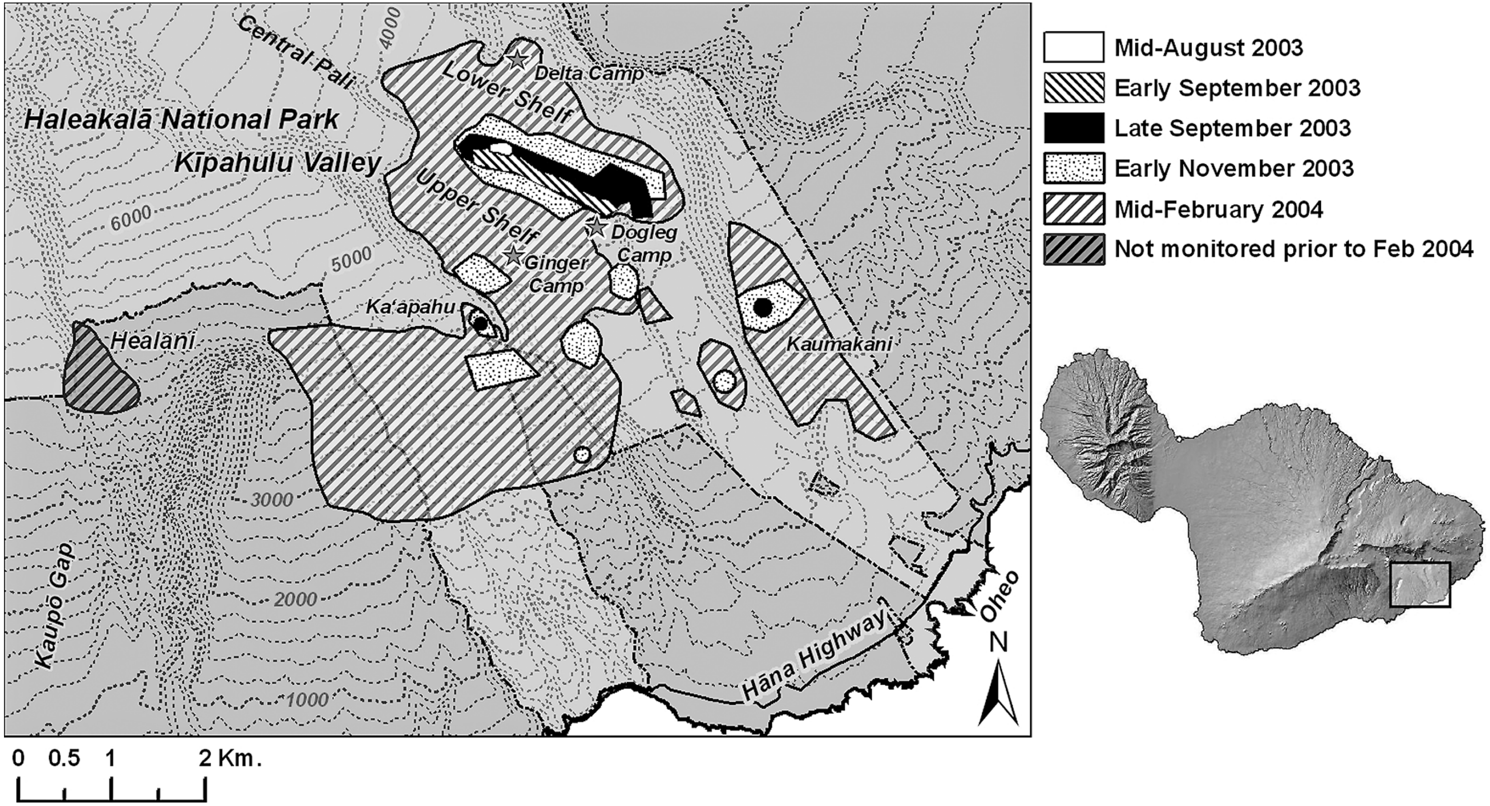


FIGURE 2. Spread of koa defoliation in Kīpahulu Valley between August 2003 and February 2004. The defoliation in Healani was not formally surveyed until the helicopter flyover in February 2004, although the first signs of defoliation were recorded at that site in December 2003. Elevation contours are labeled as feet above sea level.

completely defoliated in November were already putting out new true leaves from major stems, but many of the apical branches appeared to be dead. In April these previously denuded trees were observed producing phyllodes that appeared healthy and undamaged. Caterpillars were readily collected from foliage at that time and were still unusually abundant but not nearly as abundant as in earlier reports, when they had reached nuisance levels in several of the camps.

February 2004 marked the discovery of another defoliated site on the western slope of Haleakalā in Makawao Forest Reserve at about 1,040 m elevation, the same site as an outbreak in 1977 (Stein 1980, Stein and Scowcroft 1984) and probably previous outbreaks as well (Swezey 1926, Fullaway 1947*a*, Wong and Miyahira 1971). Caterpillars at that site appeared to have been active for some time before the discovery of the defoliation, and most koa trees in the area were estimated to be about 70% defoliated. We revisited Makawao four more times between March and June (Table 2), but the degree of defoliation there did not increase noticeably after February. In June 2004, we received reports from another researcher of active larvae and defoliation higher up from our collection site, at about 1,220 m elevation (J. T. Foster, pers. comm.). We suspect that this area had already been defoliated in February 2004 and was detected by the GPS helicopter flight at that time.

From GPS data taken via helicopter in February 2004 (Figure 1), we calculated that approximately 14.6 km^2 of koa forest in Kīpahulu Valley and approximately 1.1 km^2 in Makawao Forest were severely defoliated, for a total of at least 15.7 km^2 on East Maui. At that time, nearly all of the koa-dominated forest in these three regions had been affected by severe defoliation.

Without continuous monitoring, it is difficult to determine exactly when caterpillar populations returned to "normal" levels or to assign a specific "end" to the outbreak. The latest report of infestation-level populations of caterpillars was in December 2003 in Kīpahulu Valley (Manawainui), and HNP staff saw no expansion of defoliation after February 2004. In Makawao, caterpillar populations had decreased by June 2004, and although monitoring did not continue after that point, there were no reports of further defoliation or abundant caterpillars.

Two years later, in May 2006, a less-extensive outbreak of caterpillars was noted by HNP staff at two camps on the Upper Shelf of Kīpahulu Valley. In August 2006, monitoring of 72 koa trees on Upper Shelf transects showed that damage was less severe than in the 2003–2004 outbreak. About 90% of trees had visible caterpillar damage (P.W., unpubl. data), and about 6% of trees were completely defoliated, but two-thirds of the trees retained 50–100% of their phyllodes. About 90% of trees had also sprouted true leaves at that time (P.W., unpubl. data).

Size-Class Distribution and Development of Larvae

Field collections and observations are summarized in Table 2, and age classes of larvae from each site are summarized in Figure 3. Although our sampling was not quantitative and numbers of caterpillars collected should not be used as estimates of density, we observed marked differences in the abundance of larvae across the different locations at different times. Many newly hatched larvae were observed in January on the Lower Shelf (Delta Camp), and much feeding damage by first-instar larvae was observed, but by April we found few larvae in the same areas we searched in January, and the few we collected were of later developmental stages (Figure 3*A*). In January 2004 at the Healani site, the outbreak was characterized by an extreme abundance of moths, but it was difficult to find larvae, and those were early instars (Figure 3*B*). At that site, we observed recent defoliation of a few plants other than koa, including a completely denuded pūkiawe (*Leptecophylla tameiameiae* (Cham. & Schlechtend.): Epacridaceae), a native shrub. Although there was no direct evidence that this was due to *S. paludicola* feeding, the damage was consistent with caterpillar feeding, and the defoliated plants were beneath defoliated koa trees. Unfortunately, we were unable to

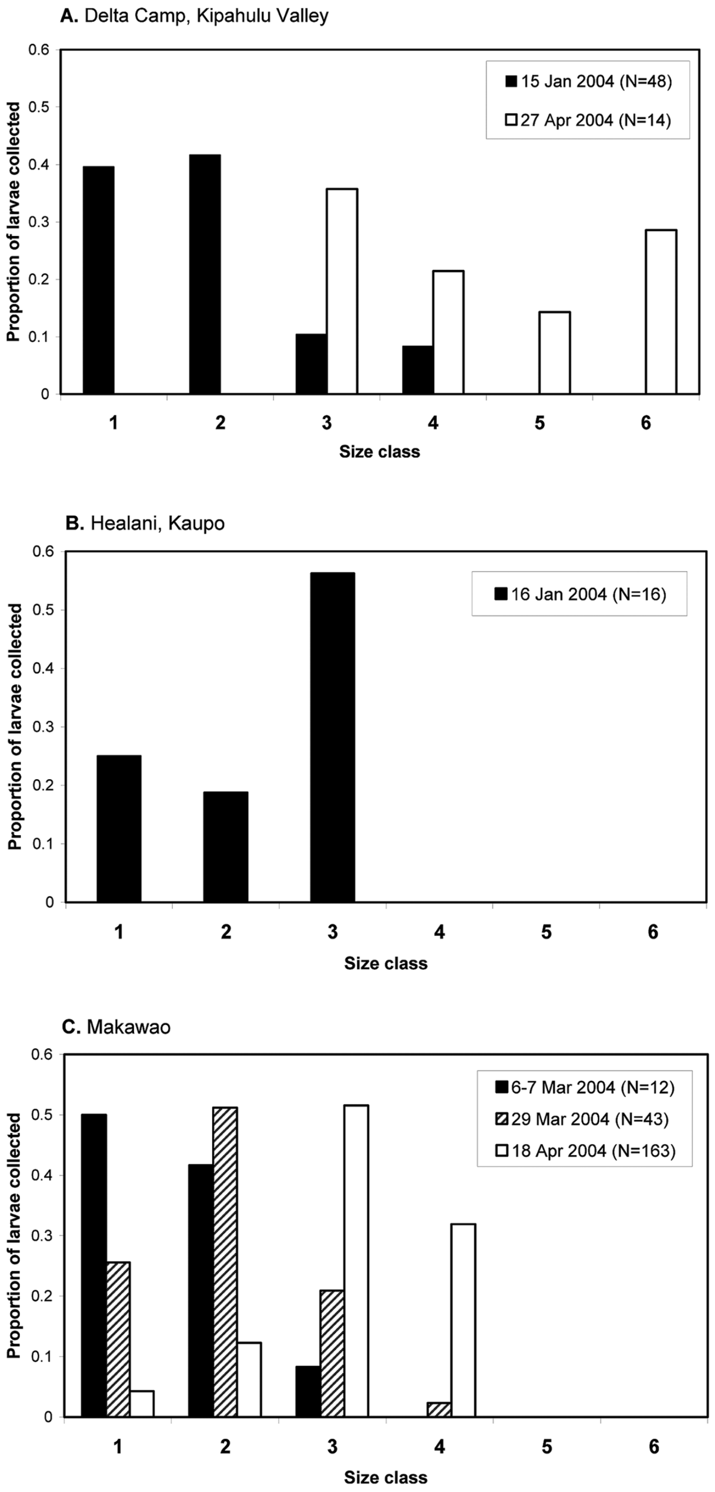


Figure 3. Size classes of *Scotorythra paludicola* larvae collected from koa at various times at (*A*) Kīpahulu Valley, (*B*) Kaupō, and (*C*) Makawao. Size classes are based on head capsule width as follows: 1, 0.20–0.30 mm; 2, 0.45–0.60 mm; 3, 0.70–1.00 mm; 4, 1.00–1.40 mm; 5, 1.40–1.80 mm; 6, >1.80 mm.

return to that site, so changes in the progression of the outbreak in that area were not recorded.

In Makawao Forest (Figure 3*C*), late-instar *S. paludicola* larvae were abundant during the first observations in February 2004, but larvae were not collected for rearing at that time. In early March, the population was dominated by early-instar larvae. During late March and April, intermediate-aged larvae were abundant. By June the population explosion seemed to have subsided, and only two larvae were collected from koa, both older larvae of approximately fourth or fifth instar.

Of the 47 larvae that were collected in the first instar, 16 completed development to adulthood in the laboratory. The mean development time from first instar to adulthood under laboratory conditions was 41.6 days (±0.84 SE, $n = 16$). Mean time spent as larvae (from first instar to pupation) under laboratory conditions was 29.1 days (±0.51 SE, $n = 8$).

Adult Moths

All estimates of adult moth abundance were qualitative, based either on unusual observations of large numbers of flying moths or on approximate numbers of moths collected in light traps during different visits. A variety of moths was collected in Kīpahulu and Makawao Forest, including *S. paludicola*, other species of *Scotorythra*, and large numbers of *Macaria abydata* Guenée. This alien geometrid moth feeds primarily on koa haole, *Leucaena leucocephala* (Lam.) (Fabaceae), a nonnative shrub. In all cases, numbers of *M. abydata* attracted to lights were equal to or greater than those of *S. paludicola*. Based on large numbers of adult *M. abydata* collected in light traps, we initially suspected that that moth might be contributing to the defoliation of koa. However, we did not find any caterpillars of that species during our sampling for *S. paludicola*.

In August 2003, crews at Ginger Camp and Dogleg Camp on the Upper Shelf of Kīpahulu Valley (south of the defoliation at the time) noted huge numbers of moths flying during the day and night. In October, the adult moth population appeared to have decreased considerably, although there were still large numbers of adults flying during the day. In January 2004 on the Lower Shelf (Delta Camp), no adults were observed during the daytime, but about 50 were attracted to a sheet with a black light, and about 100 were collected in three light traps. By April 2004, adults were no longer as abundant on the Lower Shelf, and we collected only two adult *S. paludicola* in light traps.

At Healani during January 2004, we observed hundreds of adult *S. paludicola*, usually nocturnal, flying and visiting pūkiawe flowers during the daytime throughout the area. Searching under rotting logs and in tree crevices for caterpillars and pupae also disturbed many moths.

In Makawao in early March, many adult *S. paludicola* were observed at the black light sheet, and while researchers were walking through the forest at night, dozens of *S. paludicola* could be seen at any given time flying in the understory. In June, abundance of adults was much lower, evidenced by no more than five adults at the black light and very few adults flying in the understory.

Parasitoids Reared

In Kīpahulu, Healani, and Makawao Forest, we found dozens of parasitoid pupal cases attached to koa twigs and phyllodes. Two species of primary parasitoid wasps were reared from these cases: the purposely introduced braconid *Meteorus laphygmae* Viereck and the accidentally introduced ichneumonid *Hyposoter exiguae* (Viereck). Both species produce distinctive pupal cases once the wasp larva has exited the caterpillar host. In a few instances, the nonnative secondary parasitoid (or hyperparasitoid) wasp, *Gelis* sp. (Ichneumonidae), was reared from field-collected cases of both *H. exiguae* and *M. laphygmae*.

Of the 296 *S. paludicola* larvae collected for the purposes of rearing, all but 60 died before emergence due to disease or other unknown mortality factors (Table 3). Of the remaining larvae, 48 successfully emerged as adult moths (Table 3). The remaining 12 larvae were par-

TABLE 3

Number and Fate of *Scotorythra paludicola* Larvae Collected in Kīpahulu, Healani, and Makawao during Outbreak Periods

Locality	Date	Larvae Collected	Died during Rearing	Survived to Adulthood	Parasitoids Emerged	*Meteorus laphygmae*	*Hyposoter exiguae*	*Cotesia marginiventris*
Kīpahulu Valley: Delta Camp	15 Jan 2004	48	37	8	3	2	0	0
Kīpahulu Valley: Delta Camp	27 Apr 2004	14	9	4	1	0	0	0
Kaupō: Healani	16 Jan 2004	16	7	7	2	1	1	0
Makawao Forest Reserve	6–7 Mar 2004	12	10	2	0	0	0	0
Makawao Forest Reserve	29 Mar 2004	43	31	11	1	1	0	0
Makawao Forest Reserve	18 Apr 2004	163	142	16	5	3	0	2
Total		296	236	48	12	7	1	2

TABLE 4

Results of Logistic Regression Analysis

Model	Predictor	Coefficient	SE Coefficient	*Z*	*P*
Full model	Constant	−3.00103	0.561661	−5.34	0
	Monthly rainfall deviation	−0.01661	0.012057	−1.38	.168
	Mean maximum temperature deviation	0.03684	1.10166	0.03	.973
	Mean max temp dev * Monthly rainfall dev	0.00218	0.026904	0.08	.935
Reduced model 1	Constant	−2.99446	0.553877	−5.41	0
	Monthly rainfall deviation	−0.01644	0.011806	−1.39	.164
	Mean maximum temperature deviation	−0.02402	0.806254	−0.03	.976
Reduced model 2	Constant	−2.99363	0.552819	−5.42	0
	Monthly rainfall deviation	−0.01646	0.011784	−1.4	.163

asitized by one of three species of wasp: *H. exiguae*, *M. laphygmae*, and the braconid *Cotesia marginiventris* (Cresson) (Table 3). All three of the parasitoid species reared are nonnative.

Rainfall and Temperature

We did not identify any patterns, on a monthly or annual scale, that would indicate an influence of rainfall or temperature on outbreaks since 1919. On an annual scale, logistic regression showed that outbreaks were clearly unrelated to both mean maximum temperature ($P = .976$) and the interaction between mean maximum temperature and rainfall ($P = .935$). Of the three predictor terms, rainfall came closest to predicting the outbreaks but was still nonsignificant at alpha level .10 ($P = .163$) (Table 4). Mann-Whitney *U*-tests also showed no significant differences in rainfall ($P = .166$) or mean maximum temperature ($P = .925$) between outbreak and nonoutbreak periods (Figure 4).

Plots of deviations in annual rainfall and temperature since 1919 showed no obvious patterns leading up to outbreaks (Figure 5). Looking more closely at each outbreak, deviations from mean monthly rainfall and maximum temperature for 3 yr before population explosions did not show consistent trends (Figure 6*A*–*E*). Although the current out-

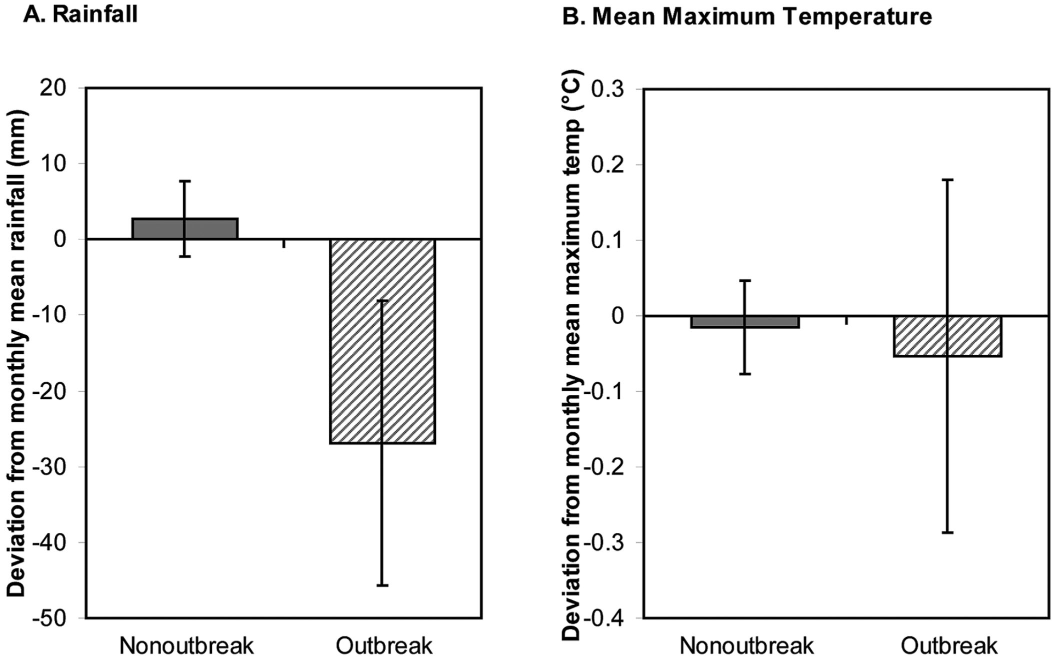


FIGURE 4. Average monthly deviations from (*A*) long-term mean rainfall (±SE) across four weather stations, and (*B*) mean maximum temperature (±SE) across three weather stations, during 12-month periods preceding outbreaks ($n = 5$, hatched bars) and nonoutbreak periods ($n = 81$, solid bars).

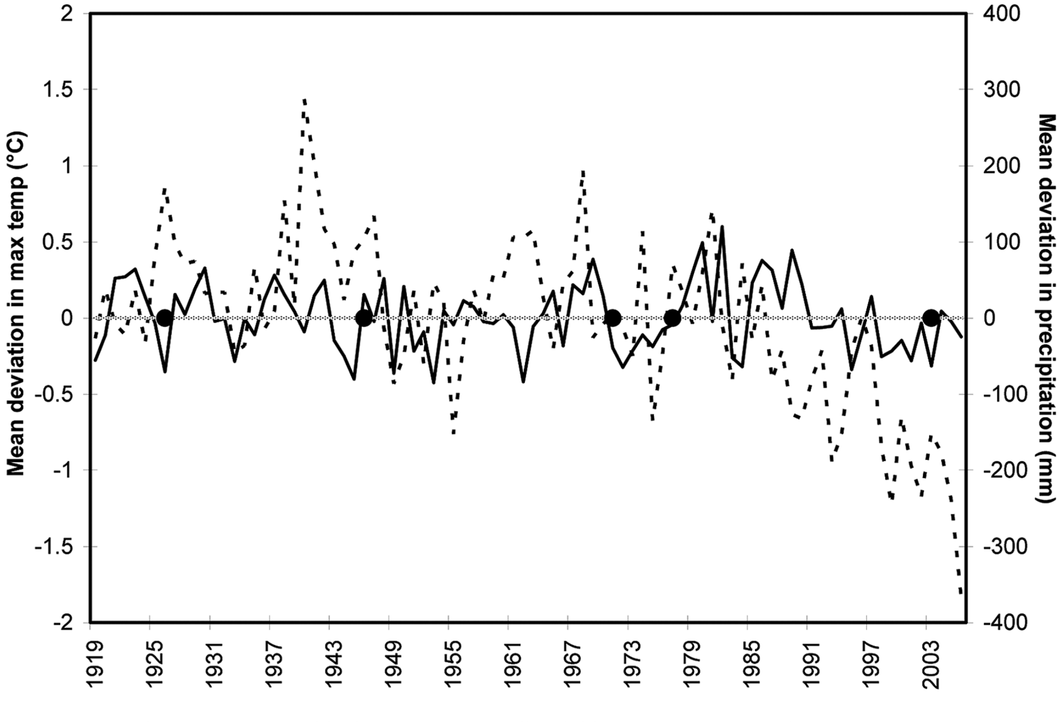
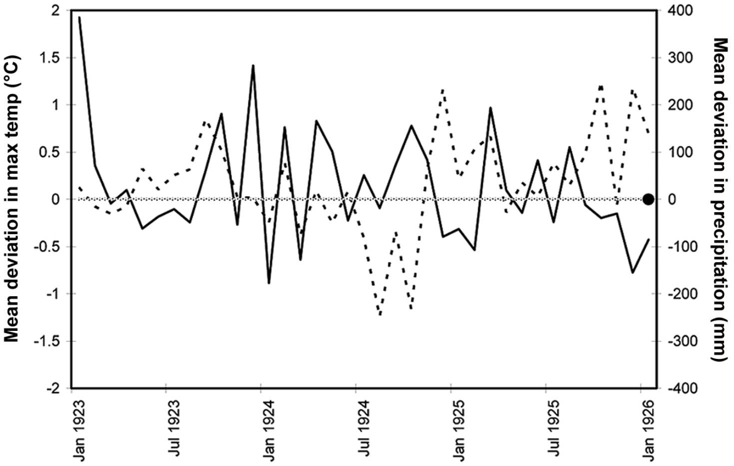
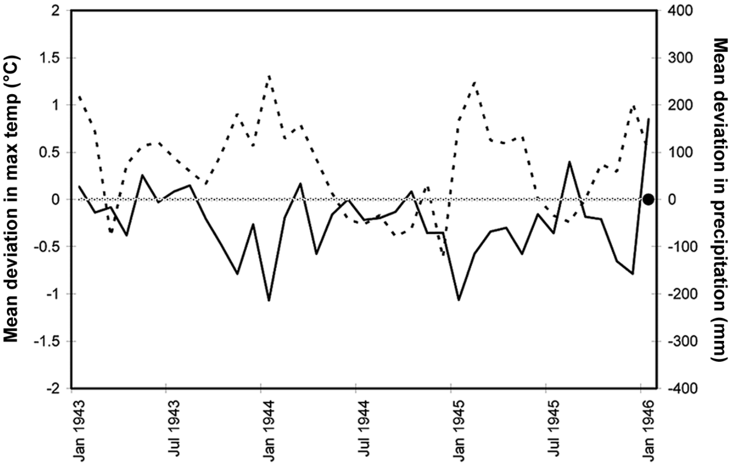


FIGURE 5. Yearly average of monthly deviations in rainfall (solid line, four stations) and mean maximum temperature (dashed line, three stations) for years 1919–2006. Circles indicate *S. paludicola* outbreaks in Makawao Forest.

A. Jan 1923 - Jan 1926



B. Jan 1943 - Jan 1946



C. Sep 1968 - Sep 1971

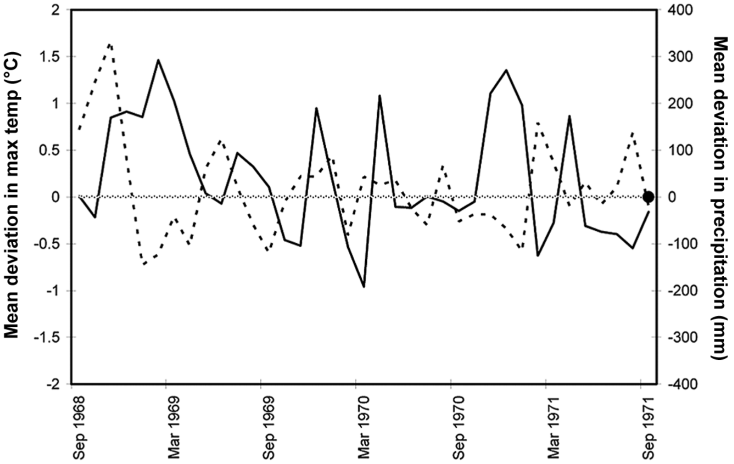


FIGURE 6 (*A–E*). Mean monthly deviations from long-term monthly rainfall (solid lines) and mean maximum temperatures (dashed lines) across four East Maui weather stations for 3 yr before recorded outbreaks of *S. paludicola* at Makawao Forest. Horizontal lines represent long-term monthly means (zero deviation) from 1919 to 2006. Solid circles indicate month when defoliation was first noted.

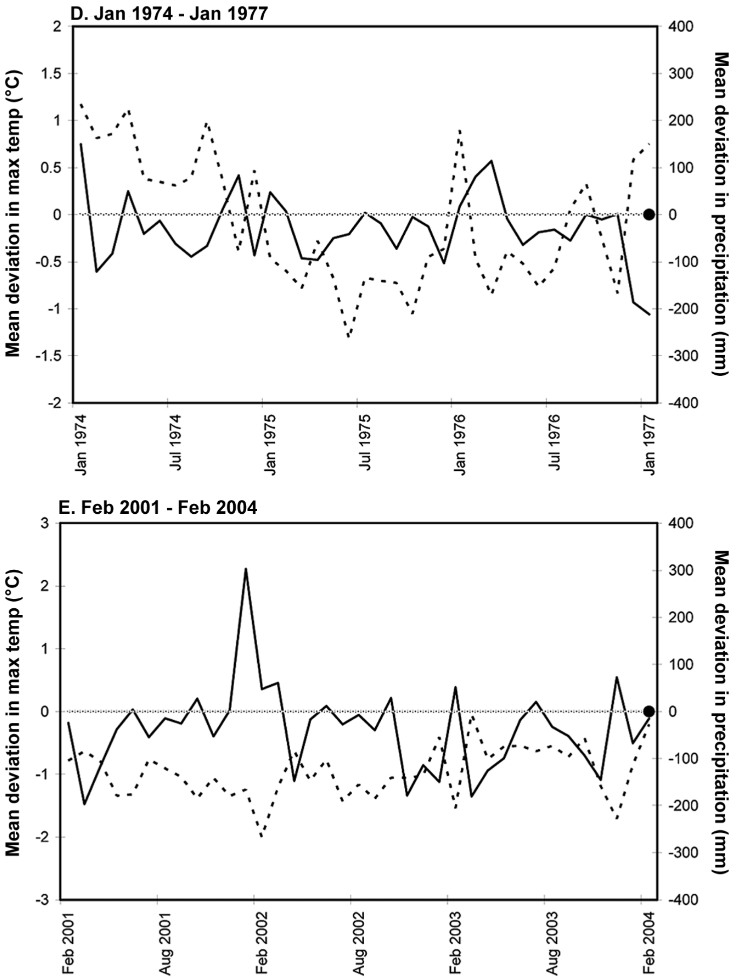


FIGURE 6. (continued)

break was preceded by 3 yr of generally lower than average rainfall and temperature (Figure 6*E*), rainfall and temperature preceding the other four outbreaks fluctuated erratically above and below the long-term monthly mean with no perceptible pattern.

DISCUSSION

General Characteristics of Outbreak

The recent defoliation by *S. paludicola* was first noted in early 2003 at Healani and progressed across East Maui from Kīpahulu to Makawao. These three regions represent the majority of koa-dominated forest on East Maui, because most of the surrounding native forest is dominated by ʻōhiʻa (*Metrosideros*). Our collections of larvae beginning in January 2004 suggest that generations of *S. paludicola* were synchronous within a localized area, because there was low variation in age classes within a site at any one time. This is consistent with Swezey's (1926) and Stein's (1981) observations during earlier outbreaks. However, our caterpillar collections generally occurred toward the tail end of the outbreaks, after the bulk of defoliation had already occurred, and if collections had been made at the onset of the outbreak, they may not have shown that pattern. Still, early observations of field crews indicated brief periods of very high caterpillar or moth abundance, suggesting synchronous, mass emergences.

Our rearing data allowed a rough estimate of life cycle duration in *S. paludicola*, but translating this to actual generation time in the field is problematic. Laboratory rearing temperatures were undoubtedly higher than natural conditions, and the 42 days observed in the laboratory was probably an underestimate of actual development time. The high mortality of laboratory-reared caterpillars may have worsened this underestimate, because the few caterpillars surviving to adulthood may have represented a more vigorous subset of the population. In other tropical moths in the subfamily Ennominae, the egg stage lasts less than a week, and mating and oviposition can occur within a few days of adult emergence (Palmer et al. 2007). Even if field development time is twice what we observed in the laboratory, we estimate a generation time of less than approximately 3 months. This is consistent with the field observations of Stein (1981), who estimated that larval feeding in Makawao began in January 1977, pupation occurred in February, and adult moths were noted in early March.

The time lag of several months to a year between observations of defoliation at Healani, Kīpahulu, and Makawao is puzzling and may be partly an artifact of the timing of site visits, because the early stages of defoliation in Makawao may have gone undetected before February 2004. It is also possible that population increases were triggered simultaneously at all sites but took longer to produce noticeable defoliation at the different sites due to differences in food availability, koa density, or other factors.

An alternative explanation is that a population explosion occurred in Healani, then spread by migration of adult moths to Kīpahulu Valley, then by subsequent migration to Makawao Forest. The forest on the northeastern slope of Haleakalā between Kīpahulu and Makawao is dominated by *Metrosideros* (ʻōhiʻa), and although koa does occur there, it is sparse and may not support outbreaks. Because population explosions appeared to be synchronous and long-distance dispersal is accomplished only by adult moths, we would expect a time lag of at least one life cycle before expansion into distant sites. This is consistent with the sequence of defoliation starting with Healani (January 2003), then Kīpahulu (August 2003), then Makawao (February 2004). However, this scenario implies a mass migration of moths between sites, which was not reported.

We observed some behaviors during the outbreak that are abnormal for *S. paludicola* during nonoutbreak periods. Although *S. paludicola* has never been recorded from pūkiawe (Heddle 2003), we presume that it was responsible for the defoliation of this and other plants in Healani, when starving caterpillars switched to alternative plants. This phenomenon was previously recorded in *S. paludicola* by Fullaway (1947*b*), who reported larvae feeding on the nonnative forestry trees *Lophostemon* and *Grevillea* during a 1946 outbreak on East Maui. A number of species of lepidopteran larvae, particularly during the later instars, are known to become less selective during population outbreaks (Rossiter 1987, Tuskes et al. 1996, Rieske and Townsend 2005). Diurnal activity of adult moths is another unusual behavior we observed in *S. paludicola*, which is typically nocturnal. Such expansion of flight periods during outbreaks is known in Saturniidae (Tuskes 1984, Schmid and Bennet 1988, Tuskes et al. 1996; D.R., pers. obs.) and may be a direct response to increased population densities.

Effects of Climate

We had reason to expect that *S. paludicola* outbreaks might be related to low levels of precipitation or high temperatures, because outbreaks of other forest Lepidoptera are associated with periods of drought (Mattson and Haack 1987, Van Bael et al. 2004). Droughts might create favorable conditions for insect herbivores through several mechanisms, including higher temperatures (resulting in more rapid growth and development of insects) and favorable nutrient concentration in stressed plant tissues, and unfavorable conditions for insect pathogens, such as fungi, bacteria, and viruses (Mattson and Haack 1987).

We did not find a significant relationship between recorded outbreaks of *S. paludicola* and either rainfall or maximum temperatures. Although annual rainfall was slightly lower preceding outbreaks than in nonoutbreak years (Figure 4*A*), this difference was nonsignificant. However, with only five data points for outbreaks on East Maui, we cannot be confident that a failure to show a significant relationship reflects a true lack of any effect. Nevertheless, there were many periods with low rainfall during which outbreaks were not recorded, and the outbreak in 1971 occurred after a 12-month period when rainfall was higher than the overall average (Figure 6*C*). We unambiguously failed to find an effect of mean maximum temperature preceding outbreaks or of the interaction between mean maximum temperature and rainfall.

It is possible that outbreaks are influenced by climatic factors other than rainfall or temperature, and our analyses would fail to detect such an influence. One factor that might influence *S. paludicola* outbreaks is wind. Winds in Kīpahulu Valley were reported to be unusually high during periods preceding the most recent outbreak (R. Kaholoa'a, 2004, pers. comm.), and defoliation was first noted on highly exposed cliffs and ridgetops. Of course, cliffs and ridges may differ from less-exposed areas in many factors unrelated to windiness, such as spatial isolation, tree density, and attractiveness as oviposition sites. However, high winds have been correlated with reduced parasitism rates in other Hawaiian caterpillars (Bess 1974), and wind should certainly be included in future studies on population fluctuations in *S. paludicola*. Unfortunately, long-term data on wind speeds were unavailable for our retrospective analysis.

Roles of Parasitoids, Predators, and Pathogens

There are many biotic factors that affect populations of *S. paludicola;* the most obvious of these are parasitoids and predators. However, because of the very high mortality due to disease and other factors (80% of all larvae collected), we cannot infer actual parasitism rates from our laboratory rearing. To do so would assume that parasitized larvae were not more or less likely to die before emergence than unparasitized larvae.

Pupal cases of *M. laphygmae*, the most commonly reared parasitoid in our study, were commonly observed on koa trees at all localities visited. *Meteorus laphygmae* is a highly generalized parasitoid first introduced to Hawai'i as a biological control agent against armyworm and other noctuid caterpillars in 1942 (Funasaki et al. 1988) and later reintroduced against *Macaria abydata* in 1975 (Nakao and Funasaki 1979). This species was documented attacking endemic Hawaiian caterpillars in upland native forest as early as 1947 (Swezey 1948) and has previously been reared from *S. paludicola* (Funasaki et al. 1988).

Although it may well be an artifact of low sample size and high mortality due to unknown causes, we reared no native parasitoids from larvae. Indeed, of the seven parasitoids previously reported from *S. paludicola*, only one, *Enicospilus lineatus*, is native (Table 5). During our surveys *Enicospilus* wasps, including *E. lineatus*, were collected in large numbers at black lights in Kīpahulu Valley (R. Kaholoa'a, 2004, pers. comm.). Although they were not reared from our field-collected larvae, we cannot conclude that they were not present in the population. These wasps attack late-instar larvae and emerge from moth pupae, in contrast to *M. laphygmae* and *H. exiguae*, which attack early-instar larvae. For this reason, it has been suggested that *Enicospilus* wasps might be preempted by nonnative parasitoids (Henneman and Memmott 2001), but this is unlikely to be true in the early stages of an outbreak, when there is an abundance of caterpillars, and parasitoid populations have not yet increased in response.

Parasitoids exert a limiting force in many insects, and a release from parasitism may trigger an outbreak (Morris 1959, Berryman 1987, 1995, 1996, Myers 1988). Likewise, increased parasitism rates, in response to increased caterpillar densities, often bring about the end of outbreaks by reducing caterpillar

TABLE 5

List of Insect Parasitoids and Predators Previously Known to Attack *Scotorythra* Larvae

Species	Order and Family	Reference
Native predators		
Odynerus nigripennis (Holmgren)	Hymenoptera: Vespidae	Williams (1927)
Oechalia pacifica (Stål)	Hemiptera: Pentatomidae	Davis (1955)
Oechalia grisea (Burmeister)	Hemiptera: Pentatomidae	Perkins (1913), Swezey (1926)
Native parasitoids		
Enicospilus lineatus (Cameron)	Hymenoptera : Ichneumonidae	Swezey (1926)
Nonnative parasitoids		
Hyposoter exiguae (Viereck)	Hymenoptera: Ichenuemonidae	Fullaway (1947*a*, *b*), Swezey (1927*b*), Swezey and Williams (1932)
Goniozus emigrates (Rohwer)	Hymenoptera: Bethylidae	Beardsley (1961)
Brachymeria obscurata (Walker)[a]	Hymenoptera: Chalcidae	Kirkaldy (1904)
Cotesia marginiventris (Cresson)[a]	Hymenoptera: Braconidae	Beardsley (1961)
Lespesia archippivora (Riley)[a]	Diptera: Tachinidae	Swezey (1926), Funasaki et al. (1988)
Meteorus laphygmae (Viereck)[a]	Hymenoptera: Braconidae	Funasaki et al. (1988)

[a] Biological control introduction.

populations to usual levels. More information on the biology of specific parasitoid wasps and their interactions with *S. paludicola* in nonoutbreak and outbreak periods is necessary to understand the role they play in the outbreaks.

Pathogens likely play a major role in this system and may well be a factor in the occurrence of outbreaks. Unidentified diseases accounted for most of the mortality observed in our field-collected larvae, but this was likely exacerbated by environmental conditions in the laboratory. Because we reared larvae in small cups with limited circulation and high humidity, observed disease rates are almost certainly much higher than what would be seen in the field. Future studies should benefit from rearing techniques that better approximate field conditions and diagnoses of pathogens causing diseases.

CONCLUSIONS

Identifying triggers for *S. paludicola* outbreaks will be a difficult undertaking, especially relying solely on data from previous outbreaks. Most observations of *S. paludicola* outbreaks, including our own, were opportunistic and were made some time after initial population explosions. It is difficult to determine exactly when an outbreak began, because defoliation may not have been noted until several months after it occurred. Without precise data from reports and with improving technology for aerial surveillance over the past 50 yr, it is difficult to compare the spatial extent of outbreaks across long timescales. Furthermore the definition of an outbreak has not been standardized and is not quantitative with regard to population density.

Most problematic in our analysis of climate data is the likelihood that outbreaks or extreme population fluctuations during the past century were never noted. Even during periods when there is no heavy defoliation of koa, these moths can be very common in the koa forests of Olinda (Swezey 1931) and Waikamoi (M.L.H., pers. obs.). In a casual survey conducted in 1997 over a period of several months in the Waikamoi region, hundreds of *S. paludicola* moths were collected in a bucket trap, during a period in which koa forest in the region was not being denuded (M.L.H., unpubl. data). Reports of specific outbreaks extend back only as far as 1892, although Perkins wrote that Hawaiians had observed these outbreaks before then, making it unclear whether the intensity or frequency of *S. paludicola* outbreaks has changed over the past centuries.

Understanding the dynamics of the *S. paludicola* outbreaks in Hawai‘i will require long-term research of both *S. paludicola* and the factors affecting its density. Factors keeping densities of organisms low during nonoutbreak periods are as meaningful as factors behind the occurrence of outbreaks (Tanhuanpaa et al. 1999), suggesting that we cannot determine causes for outbreaks by studying a system only during outbreaks. We recommend long-term monitoring of *S. paludicola* populations at a site such as Makawao Forest, which is easily accessible and has a long history of population explosions. Caterpillar populations can be monitored using quantitative sampling methods, coupled with laboratory rearing to measure parasitism rates. Adults could be monitored using light traps, flight-intercept traps, or even pheromone traps. This would allow a much more powerful analysis of the influence of climate and other factors on actual population fluctuations, in contrast to our own analyses, which necessarily treated outbreaks as a simple "yes or no" response. This is clearly an oversimplification of a dynamic system.

In other irruptive insects, an evolutionary approach has been informative, comparing irruptive species to related species that do not experience outbreaks (Hunter 1991, 1995, Price et al. 2005). Other species of *Scotorythra*, such as *S. aboricolans*, specialize on koa, yet outbreaks have never been observed in these species (Heddle 2003), but an outbreak on the native shrub *Dodonaea viscosa* has been observed in at least one other species (Mitchell and Davis 1985). Comparative studies of the biology of *S. paludicola* and these congeners may reveal traits correlated with extreme population fluctuations.

Koa forests have experienced dramatic changes over the past 100 yr, yet we understand little about subsequent impacts to ecosystem dynamics. Without knowledge of the organisms present at a given locality, their habitat preferences, and their community relationships, proper management of natural resources is impossible (Winston 1999). Long-term data on mortality factors and population fluctuations of *S. paludicola* and its parasitoids will shed much light on the broader dynamics of Hawai'i's koa forests, potential management strategies for the protection of threatened native forests, and the enhancement of koa as a commercial crop.

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