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Contributed Paper

Application of Agriculture-Developed Demographic Analysis for the Conservation of the Hawaiian Alpine Wekiu Bug

JESSE EIBEN* AND DANIEL RUBINOFF†

*College of Agriculture, Forestry and Natural Resource Management, University of Hawaii at Hilo, 200 W. Kawili Street, Hilo, HI 96720, U.S.A., email eiben@hawaii.edu

†Department of Plant and Environmental Protection Science, University of Hawaii at Manoa, 3050 Maile Way, Gilmore Hall 310, Honolulu, HI 96822, U.S.A.

Abstract: *Insects that should be considered for conservation attention are often overlooked because of a lack of data. The detailed information necessary to assess population growth, decline, and maximum range is particularly difficult to acquire for rare and cryptic species. Many of these difficulties can be overcome with the use of life table analyses and heat energy accumulation models common in agriculture. The wekiu bug (*Nysius wekiuicola*), endemic to the summit of one volcanic mountain in Hawaii, is a rare insect living in an environmentally sensitive alpine stone desert, where field-based population assessments would be inefficient or potentially detrimental to natural and cultural resources. We conducted laboratory experiments with the insects by manipulating rearing temperatures of laboratory colonies and made detailed observations of habitat conditions to develop life tables representing population growth parameters and environmental models for wekiu bug phenology and demographic change. Wekiu bugs developed at temperatures only found in its environment on sunny days and required the thermal buffer found on cinder cones for growth and population increase. Wekiu bugs required approximately 3.5 months to complete one generation. The bug developed optimally from 26 to 30 °C, temperatures that are much higher than the air temperature attains in its elevational range. The developmental temperature range of the species confirmed a physiological reason why the wekiu bug is only found on cinder cones. This physiology information can help guide population monitoring and inform habitat restoration and conservation. The wekiu bug was a candidate for listing under the U.S. Endangered Species Act, and the developmental parameters we quantified were used to determine the species would not be listed as endangered or threatened. The use of developmental threshold experiments, life table analyses, and degree day modeling can directly inform otherwise unobservable habitat needs and demographic characteristics of extremely rare insects.*

Keywords: degree day model, Hawaii, life table, Lygaeidae, Mauna Kea, *Nysius wekiuicola*

Aplicación de Análisis Demográfico de Desarrollo Agrícola para la Conservación del Insecto Weiku Alpino Hawaiano

Resumen: *Los insectos que debieran ser considerados para conservación a menudo son ignorados debido a la carencia de datos. La información detallada necesaria para evaluar el crecimiento poblacional, declinación y rango máximo de distribución es particularmente difícil de obtener para especies raras y crípticas. Muchas de esas dificultades pueden ser superadas con el uso de análisis de tablas de vida y modelos de acumulación de energía calórica comunes en agricultura. El insecto wekiu (*Nysius wkiuicola*), endémico de la cima de un volcán en Hawái, es un insecto raro que vive en un desierto alpino rocoso ambientalmente sensible, donde las evaluaciones poblacionales basadas en campo serían ineficientes o potencialmente perjudiciales a recursos naturales y culturales. Realizamos experimentos de laboratorio con los insectos mediante la manipulaciones de temperaturas en colonias e hicimos observaciones detalladas de las condiciones del hábitat para desarrollar tablas de vida representando los parámetros de crecimiento poblacional y modelos ambientales para los cambios fenológicos y demográficos. Los insectos weiku desarrollados en temperaturas encontradas solo en*

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su ambiente en días soleados y requirieron el búfer térmico de los conos de ceniza para crecer e incrementar la población. Los insectos weiku requirieron aproximadamente 3.5 meses para completar una generación. El insecto se desarrolló óptimamente entre 26 y 30° C, temperaturas que son mucho más altas que la temperatura que alcanza el aire en su rango altitudinal. El rango de temperatura de desarrollo de la especie confirmó una razón fisiológica por la que el insecto solo se encuentra en conos de ceniza. Esta información fisiológica puede ayudar al monitoreo de la población y proporcionar información para la restauración y conservación del hábitat. El insecto wiku fue un candidato para ser enlistado en el Acta de Especies en Peligro de E.U.A, y los parámetros que cuantificamos fueron utilizados para determinar que la especie no fuera enlistada como en peligro o amenazada. El uso de experimentos de umbrales de desarrollo, análisis de tablas de vida y modelos de grados-día puede proporcionar información sobre otras necesidades de hábitat y características demográficas de insectos extremadamente raros que de otra manera no serían observadas.

Palabras Clave: Hawái, Lygaeidae, Mauna Kea, modelo de grados-día, *Nysius wekiuicola*, tabla de vida

Introduction

Conservation of insects and other small invertebrates is often hampered by a lack of field-based ecological data concerning seasonality and abundance, and this lack of data may lead to incorrect management actions (Samways & Grant 2007). It is impossible to assess the individual conservation status of millions of potentially threatened species with field and laboratory observations (New 1999). Thus, we need a shortcut to infer relevant data to inform conservation of species already singled out as conservation priorities. Accumulation of indirect data from demographic models based on laboratory rearing and microclimate data may be an effective way to understand the ecological parameters of small or cryptic insects of conservation concern. Common tools for modeling population growth in insect pests could be important in conservation. Statistics such as life tables, which detail key aspects of the life history, reproductive potential, and survival, can be combined with degree day (DD) models, in which thermal energy accumulation calculations are used to define temperature dependent developmental rates, to offer essential ecological data for conservation of cryptic species (Allen 1976; Cesaraccio et al. 2001). These analyses may be repurposed to inform and guide conservation actions, and many aspects of agricultural entomology research have direct, but underappreciated, relevance to conservation biology and other nonpest applications. Use of developmental thresholds outside of agriculture are not common in entomology; some examples include the use of DD modeling in forensic entomology (Catts & Goff 1992; VanLaerhoven 2008), phenological studies of firefly emergence (Faust & Weston 2009), comparing shade and sunlight microclimate effects on development time (Bryant et al. 2002) and phenology of life stages (Koda & Nakamura 2010) of nonpest butterflies. Koda and Nakamura (2010, 2012) provide an interesting precedent for the use of DD models in studying threatened Japanese butterflies. Developmental times for larvae reared at different temperatures were compared to ambient temperatures and used to estimate the insect's phenology as a guide to limit mortality by mowing grassland habitat when caterpillars are less likely to be present. Their results suggest that degree models may be a viable method for estimating the presence of different life stages based on widely available weather data each year. These papers suggest that understanding developmental thresholds and reproductive potential under various conditions may apply as directly to the conservation of insects as it does to their suppression as pests.

The wekiu bug (*Nysius wekiuicola*) is a flightless carnivorous scavenger endemic to the upper reaches of the dormant Mauna Kea volcano, on the Island of Hawaii. As an insect of conservation concern due to threats from the development of astronomy facilities, tourism, invasive species, and climate change, ecological data detailing the species' habitat requirements are needed (U.S. Fish and Wildlife Service 1999). Understanding how habitat conditions affect population growth is essential for informed management decisions. Yet, due to the bug's rarity, secretive nature, and harsh environmental conditions on the mountain, assessing the status of wekiu bug populations through direct observation is impractical, as evidenced by the vast variability in relative density numbers from ongoing live-trap monitoring (Englund et al. 2002; Preston et al. 2012). Wekiu bugs only occur between 3415 m and the mountain summit at 4205 m, in the alpine stone desert biome. The main nutrient input to the summit ecosystem comes from aeolian deposition of arthropods and debris blown up from lower elevations (Ashlock & Gagné 1983; Howarth 1987). The rock-cinder areas where wekiu bugs occur is subject to dramatic temperature extremes (from −15 °C to 47 °C); daily fluctuations in their microhabitat are caused by solar heating and intense solar radiation typical of high-elevation tropical latitudes. Portions of volcanic cinder rock occupied by wekiu bugs are regularly covered with snow from December through May. The depth and frequency of snowfall is highly variable, and this snowfall has been implicated in the survival of the wekiu bug because the snow is a water source and a frozen storage reservoir for their arthropod prey (Ashlock & Gagné 1983; Englund et al. 2002). Wekiu bugs can survive below 0 °C (Duman & Montgomery 1991), but how they can do this is unknown (Ziegler 2002). Because of the variability in depth and composition of the rock substrate within and between cinder cones and the drastic fluctuations in wekiu bug trap captures within cinder cones and throughout the year (Porter & Englund 2006; Eiben & Rubinoff 2010), a detailed analysis to understand how the wekiu bug survives and reproduces within the alpine desert habitat is necessary.

We created a DD accumulation model quantifying wekiu bug development time throughout its thermal thresholds and created a life table showing survival and reproduction across temperatures. We believe our results can be used to model population increases in the field more realistically than field observations, and the understanding of generation time our results provide may support management decisions and outcomes. Because the wekiu bug is secretive and difficult to observe, a DD model aids in creating efficient population assessments to simplify field logistics and survey efficiency. For example, we hope to guide population monitoring efforts to coincide with breeding seasons and help explain observed periods of maximum and minimum abundance.

Methods

Insects

We adapted published trapping methods and selected wekiu bug and microhabitat survey locations near known continuous (6 years) high relative density wekiu bug habitat areas (Howarth et al. 1999; Brenner 2002; Porter & Englund 2006). Our trap design and survey method is fully described in Eiben and Rubinoff (2010). We collected wekiu bugs near the summit of Mauna Kea (WGS84, N19 49.427 W155 28.538; 1 April 2007) to establish the first captive breeding program for the species. The laboratory colony was started with 30 live wekiu bugs (9 female and 7 male adults and 14 nymphs) in April 2007, and the colony was supplemented with 20–30 wild caught bugs 4 times during 2007–2009 (4 August 2007, 30 March 2008, 15 August 2008, and 23 April 2009).

Field Data Collection

We recorded the temperatures experienced by wekiu bugs on Mauna Kea in 3 ways. We deployed 2 different types of HOBO (Onset, Cape Cod, MA) data sensors and loggers (U23-002 and U12-008), manually recorded the temperatures (air and different depths of substrate) when placing traps (Supporting Information), and recorded the spot temperature with an infrared thermometer on the substrate where wekiu bugs were observed. During 7 field trips (Table 3 and Supporting Information), we installed 3 temperature data loggers near the base of the southeast slope of the cinder cone at the center of Mauna Kea, Puu Hau Oki (WGS84, N19 49.427 W155 28.538), where a consistent high-density population of wekiu bugs occurs. The 3 sensors simultaneously recorded the microhabitat conditions at the surface of the rock tephra, 5–8 cm below the surface, and at the ash layer and cinder tephra interface 20–30 cm below the surface for the duration of every field trip. Opportunistic, but detailed, observations of wekiu bug behavior were made during field trips.

Laboratory Rearing and Experimental Design

Wekiu bugs were reared in the laboratory in a series of 3 VWR cold temperature environmental chambers (model 2015, Sheldon Manufacturing, Cornelius, OR, U.S.A.) with 14:10 light (GE Ecolux F40SP41-ECO T12 40 watt, 48 in fluorescent tube, General Electric Company, Fairfield, CT, USA) scheduled at different temperature regimes including 8, 22, 24, 26, 28, 30, 32 °C and split day and night conditions of 24 and 11 °C, 30 and 11 °C, 32 and 11 °C, and 30 and 26 °C. We also conducted a paired experiment comparing *Drosophila melanogaster* as a food source with a variety of wild caught insects to assess any influence of the laboratory diet on life table parameters. The ambient relative humidity in the chambers was approximately 15%–25%, though the relative humidity in the rearing containers increased after daily provision of drinking water. Drinking water dried naturally by the next day; this helped prevent fungal growth (100% to 15–25% daily change in humidity). We reared multiple cohorts of 14–60 wekiu bugs per trial to determine nymph stadia growth (see Table 1 for exact sample sizes) and reared slightly more bugs (Table 2) for longevity and survival experiments because only death was recorded (not instar progression), allowing for more insect rearing with less effort. See Supporting Information for details on rearing wekiu bugs.

Statistical Analyses

We analyzed the developmental times of nymphs under the 9 temperature conditions using analysis of variance (ANOVA) (Minitab 14 2004) with Tukey pairwise comparisons. To determined survival of wekiu bugs at all temperature conditions we used a series of Kaplan–Meier curves created with the R programming language v. 2.15.03 (Kaplan & Meier 1958; R Core Team 2013). We used the survdiff function in the R Survival package to test log-rank differences of survival rates under the 9 temperature conditions (R Core Team 2013; Therneau 2013). We tested for significant differences for each pair of temperature conditions with the survdiff function with a Bonferroni corrected confidence level for multiple comparisons for a total of 36 comparisons (Table 2). We also recorded descriptive statistics of development and

Table 1. Life table statistics for the Wekiu bug at constant and varying temperatures and with different food sources.

Temp °C	*n*	*Number died as nymphs (% mortality)*	*Mating pairs*	*Mean eggs laid (SD)*	*Mean eggs batch (SD)*	*Mean eggs per day (SD)*	*Mean hatched eggs per day (SD)*	*Gross reproductive rate (GRR) (female eggs)*	*Net reproductive rate (Ro) (female eggs)*	*Generation time (T) (days)*	*Doubling time (DT) (days)*	*Intrinsic rate of increase (rm) (females /female/day)*
22	*20*	*16 (80)*	*0*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
24	20	9 (45)	6	49.00 (9.18)	7.67 (5.02)	1.78 (0.29)	0.33 (0.24)	24.50	2.11	82.12	76.29	0.009
26	60	15 (25)	21	66.86 (60.02)	30.8 (40.21)	1.97 (1.49)	0.88 (1.04)	33.43	11.01	50.09	14.47	0.048
28	20	5 (25)	7	75.71 (32.52)	36.71 (29.71)	3.34 (1.21)	1.50 (1.24)	37.85	13.77	48.16	12.73	0.054
30	30	27 (90)	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
32	30	26 (87)	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
24/11	14	4 (29)	17	8.41 (12.32)	1.35(5.58)	0.17 (0.26)	0.02(0.08)	4.25	0.48	226.53	NA	-0.003
30/26	40	12 (30)	10	76.30 (61.69)	42.20 (33.05)	3.29 (1.88)	1.79 (1.37)	38.15	15.4	39.6	10.04	0.069
32/11	15	5 (33)	4	85.83 (15.24)	25.67 (5.57)	2.17	0.77	42.92	8.6	60.14	19.37	0.036
Diet comparison[a]												
Fly 30/11	15	5 (33)	4	90 (44.4)	22.25 (15.8)	2.48 (0.19)	0.83 (0.58)	45	7.45	60.90	21.02	0.033
FP 30/11	15	7 (46)	4	77.5 (29.0)	32.5 (6.36)	1.53 (0.07)	0.67 (0.15)	38.75	8.77	62.78	20.04	0.035

[a] *Lab reared D. melanogaster (Fly) versus diverse field collected insect prey (frozen and thawed) (FP).*

Table 2. Results (χ^2, p) of wekiu bug Kaplan–Meier survival curve comparisons at all temperature conditions. Temperature (°C).

Temperature, °C (n)	*22*	*24*	*26*	*28*	*30*	*32*	*24 and 11*	*30 and 26*
22 (20)	-	-	-	-	-	-	-	-
24 (17)	16.6, <0.0013[a]	-	-	-	-	-	-	-
26 (60)	5.4, 0.020	16.4, <0.0013[a]	-	-	-	-	-	-
28 (20)	0.5, 0.491	5.8, 0.016	2,0.159	-	-	-	-	-
30 (30)	22.5, <0.0013[a]	40.5, <0.0013[a]	46.9, <0.0013[a]	26.9, <0.0013[a]	-	-	-	-
32 (30)	18.1, <0.0013[a]	40.5, <0.0013[a]	44.9, <0.0013[a]	26.7, <0.0013[a]	0.4, 0.534	-	-	-
24 and 11 (66)	0.3, 0.582	4.8, 0.0284	1.1, 0.295	1, 0.318	6.4, 0.011	3.5, 0.061	-	-
30 and 26 (40)	6.5, 0.039	22.8, <0.0013[a]	26.3, <0.0013[a]	6.3, 0.0122	33, <0.0013[a]	31.3, <0.0013[a]	0,0.890	-
32 and 11 (45)	2.1, 0.148	10.7, <0.0013[a]	0, 0.856	0, 0.866	31.5, <0.0013[a]	27.8, <0.0013[a]	0.6, 0.426	8.9, 0.003

[a] *Significant differences assessed with a Bonferonni confidence level correction for multiple comparisons (36 comparisons)* ($p = 0.001389$).

reproductive capacities of wekiu bugs (Minitab 14 2004). The 8 °C temperature condition was excluded from analyses because the environmental chamber could not reliably hold this temperature.

Minimum developmental thresholds and the rate of development were calculated using a simple linear regression, $\overline{y} = a + bx$, where $\overline{y}$ is the reciprocal of mean number of days for development in a stage and x is temperature (°C). The minimum threshold was estimated as the x intercept of the developmental rate at each stage.

The intrinsic rate of increase (rm), net reproductive rate (Ro) (1:1 sex ratio), mean generation time (Tc), and population doubling time (Td) were calculated using standard methods (Birch 1948).

DD Accumulation Calculation

The DD accumulation required for each stage (C) was estimated as $C = D(T - K)$, where K is the theoretical minimum temperature threshold for development, T is the experimental temperature, and D is the mean days to develop in a given stage.

To determine the average daily temperature under day and night alternating temperature regimes in the temperature chambers (day and night: 24 and 11 °C, 32 and 11 °C, 30 and 26 °C), we used a weighted average with 14 h at the high temperature and 10 h at the minimum temperature or the weighted average at the calculated minimum developmental threshold per stage, whichever was higher. This standard correction was to ensure no negative values for development in calculations ($T - K$) because insects do not regress in development at temperatures below the minimum threshold.

A model of field-based DD accumulation was created using a continuous microhabitat temperature data set collected on Mauna Kea from April to July 2007. These months are typically the months of highest recorded wekiu bug relative densities and activity (Eiben & Rubinoff 2010). The temperature for every hour interval was recorded at 3 substrate depths in the microhabitat.

The accumulated DDs were calculated using the maximum hourly temperature found at any substrate depth, then limited by the wekiu bug upper developmental temperature threshold because we calculated the theoretical fastest possible development time. In this way, we assumed wekiu bugs seek the most favorable temperatures for rapid development. This hour interval was used to calculate the daily DD accumulation of each month as per the previously stated equation, [$C = D(T - K)$].

The maximum accumulated DDs observed in the substrate were also compared with 4 DD accumulation models commonly used in agriculture. The commonly applied DD models used in population growth estimation and pesticide application timing for agricultural pests are based on upper and lower developmental thresholds of the insect and different options for estimating daily total energy accumulation on the basis of only 2 observed temperatures; typically a maximum and minimum daily air or soil temperature. To compare estimated temperature profiles and energy accumulation with our observed temperatures in wekiu bug habitat, we used sine, double sine, triangle, and double triangle methods (Lindsey & Newman 1956; Baskerville & Emin 1969; Allen 1976; Sevacherian et al. 1977). We used the online DD calculator, Calculate Degree Days, (http://www.ipm.ucdavis.edu/WEATHER/ddretrieve.html, accessed August 2011) to create the 4 model type outputs from our temperature data from 1 April through 31 July 2007.

Finally, the linear regressions of the substrate temperature, as a function of the ambient air temperature (from our simultaneously recorded air temperature data), and the microhabitat substrate temperatures were used to determine if the ambient temperature data commonly used in DD modeling calculations for insects could be used to model wekiu bug growth. Use of ambient temperature as a proxy for the microhabitat temperatures would be much easier because microhabitat information represents a much more limited data set that is much harder to measure. We fit regression lines to the data with Microsoft Excel (Excel 2013). Data from a pyrometer recording solar radiation on the Mauna Kea summit (Schöck et al. 2009) was used to demonstrate the effect of solar radiation on heating of the microhabitat.

Results

Life Table Parameters

Minimum developmental thresholds were approximately as follows: egg stage = 13 °C, 1st instar = 11 °C, 2nd instar = 12 °C, 3rd instar = 15 °C, 4th instar = 16 °C, and 5th instar = 17 °C. The overall minimum threshold for 1st–5th instar development when total nymph development was tallied was 15.35 °C (Fig. 1).

Increasing temperatures generally decreased development time to reach adulthood (Fig. 1, Supporting Information). All stage-specific developmental times at different temperatures were significant: 1st instar, df = 8, $f = 154.3$, $p < 0.01$; 2nd instar, df = 8, $f = 210.51$, $p < 0.01$; 3rd instar, df = 8, $f = 161.07$, $p < 0.01$; 4th instar, df = 8, $f = 237.9$, $p < 0.01$; 5th, df = 8, $f = 385.12$, $p < 0.01$; and total duration of nymph stages, df = 8, $f = 895.38$, $p < 0.01$. The diet fed to wekiu bugs had no perceptible effect on development (t test, df = 14, $t = -1.35$, $p > 0.05$) (Table 1). Wekiu bugs fed *D. melanogaster* took 37.2 (0.87 SE, $n = 15$) days to develop to an adult after hatching, and bugs fed a diversity of wild caught insects required 39 (1.02 SE, $n = 15$) days.

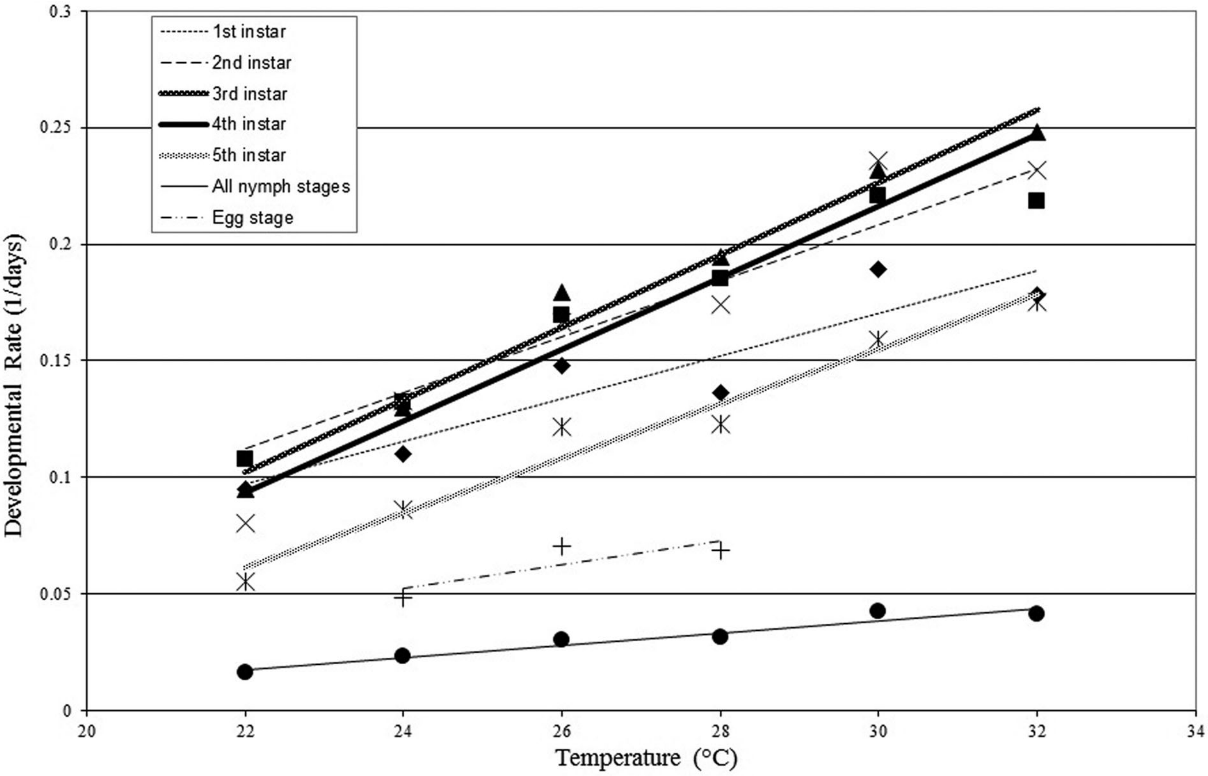

Figure 1. Developmental rates of immature wekiu bugs under different temperature regimes.

The sex ratio for wekiu bugs reared in all experimental temperature conditions was 51.53% male and 48.47% female ($n = 196$). A χ^2 test showed no difference from a 1:1 sex ratio (df = 1, $\chi^2 = 0.184$, $p > 0.05$), thus a sex ratio of 50% was used for population increase metrics.

Wekiu bugs died rapidly at constant temperatures above 30 °C (Fig. 2, Table 2, & Supporting Information). At the simulated natural habitat temperature regime of 32 and 11 °C, wekiu bugs did not die more rapidly than at other temperatures, indicating that high temperatures for part of the day are, at least, tolerable. Wekiu bugs held at low temperatures survived for hundreds of days if they could successfully molt to late instars (Fig. 2 & Supporting Information).

The intrinsic rate of increase for wekiu bugs across the range of temperatures examined varied from no successful reproduction at 22, 30, and 32 °C, to a slightly negative growth rate at 24 and 11 °C ($rm = -0.0003$). The rest of the temperature conditions had positive growth rates ($rm = 0.009$ to 0.069). The measurable fecundity of wekiu bugs was lowest at their laboratory developmental temperature of 24 °C. Wekiu bugs did not survive long enough to reproduce at 22, 30, or 32 °C. Fecundity was highest at 26, 28 °C, and the high dual temperature conditions of 30 °C and 26 °C (Table 1).

At the lowest laboratory temperature of 8 °C, field caught adult wekiu bugs survived for an average of 46 d ($n = 11$), and the 2 field caught nymphs kept at this temperature survived for 25 d and 91 d without molting. Three of the 11 adults were females, and no eggs were laid during this trial. All females were observed mating at least once, with one pair observed mating for 20 consecutive days.

The DDs required to complete each life stage are shown in Supporting Information. Generally, the 1st and 5th instars demonstrated greater DD accumulation for transition to the next life stage than the intermediate stages. The egg stage showed approximately 200 DDs to hatch, the most for any life stage. Approximately, 622 DDs are required for wekiu bugs to complete a generation.

The number of hours each month for the 4 months (April, May, June, and July 2007) that the temperature at 3 microhabitat depths was above the minimum threshold and above the maximum threshold for growth (Table 3) demonstrated the extreme variability in temperatures found near the summit of Mauna Kea within which wekiu bugs are found.

The maximum monthly DD accumulation possible for wekiu bugs in the substrate based on observed conditions was 160 in April, 180 in May, 192 in June, and 174 in July 2007 (Supporting Information). Therefore, one generation would take approximately 3.5 months during the summer to accrue 621.9 DD. The 4 common DD accumulation models used in pest population

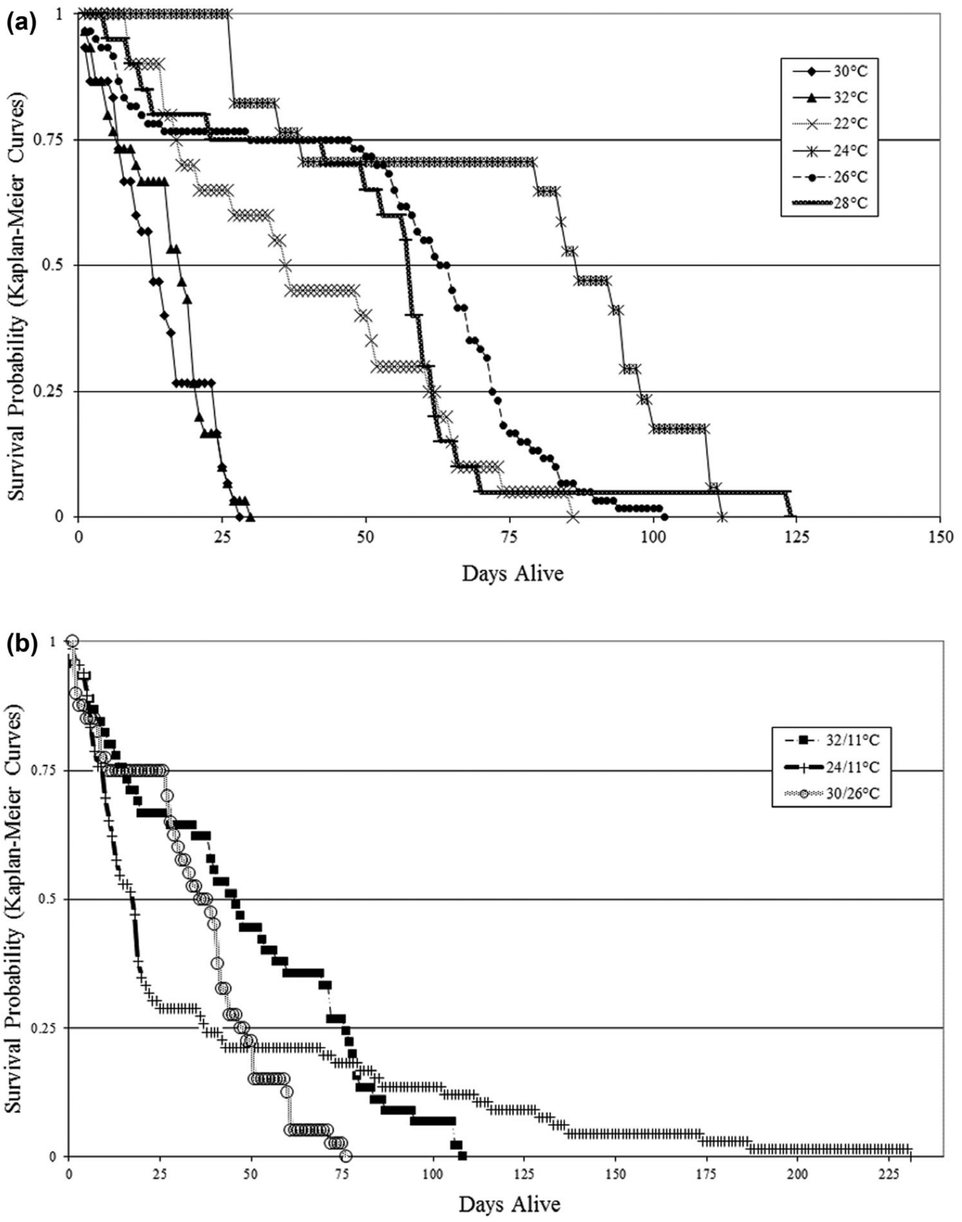

Figure 2. Survival probabilities of wekiu bugs under (a) constant and (b) fluctuating day-night cycle temperature regimes.

modeling in agricultural systems underestimated the amount of thermal accumulation by 13%–20% (Supporting Information). Solar irradiance had a strong positive relationship with the rock substrate in wekiu bug microhabitat (Fig. 3 & Supporting Information). The DD accumulation calculated with microhabitat temperatures and solar input showed a stronger relationship than the comparison of the DD accumulation and air temperature (Fig. 3). The solar irradiance measured hourly on Mauna Kea from 28 to 30 March 2007, when there was concurrent data between all 3 data measurement devices, had a strong relationship with microhabitat substrate temperature and DD accumulation (Fig. 3 & Supporting Information).

Discussion

Life History, Population Growth, and Demography

Wekiu bugs have a narrow range of developmental temperatures that are not well matched to the measured air temperatures in their environment. Insects that actively thermoregulate manipulate their exposure to environmental conditions and survive in climates where ambient temperatures would be otherwise fatal (Crawford 1981). Many insects thermoregulate (Heinrich 1995), and wekiu bugs need access to microhabitats to survive and reproduce. While we could not experimentally manipulate the ambient temperatures wekiu bugs experience in their habitat, we demonstrated a robust model of

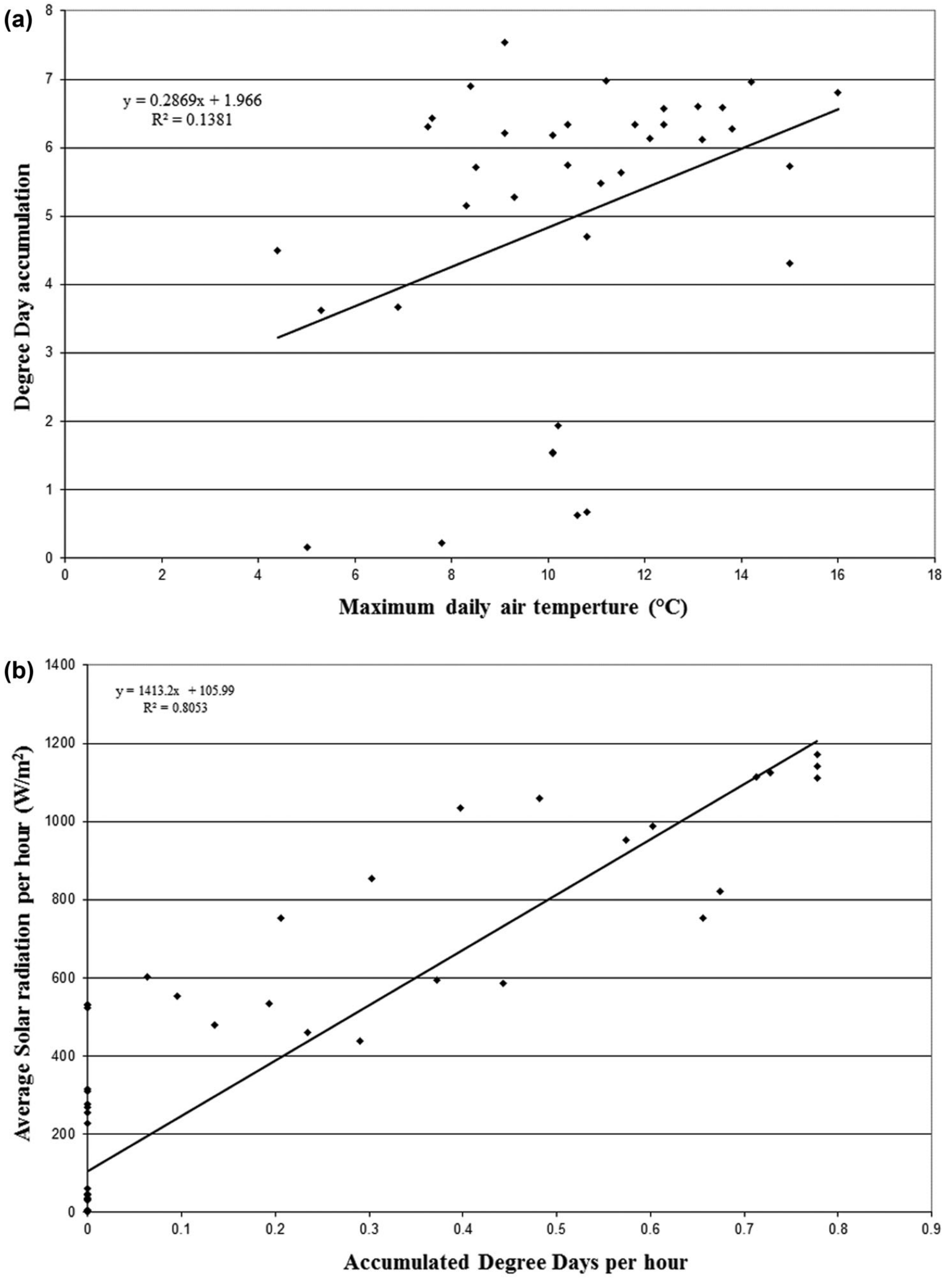

Figure 3. Relationship between wekiu bug (a) degree day (DD) accumulation and daily air temperature and (b) hourly (DD) accumulation and hourly solar radiation.

growth and development at a suite of temperatures in captivity. Wekiu bugs develop fastest at temperatures typical of low elevation members of their genus (Usinger 1942; Kehat & Wyndham 1972), yet the ambient air temperatures that wekiu bugs encounter are below their minimal developmental threshold (Table 3 & Supporting Information), which demonstrates the importance of comparing laboratory and ambient temperature regimes before applying models of thermal development. Koda and Nakamura (2010, 2012) provide a pertinent example of how DD models can be used to estimate phenology in rare insects, but their work differs from our study in several significant ways. All their estimates relied on lab conditions at constant temperatures, and they did not directly measure habitat temperature profiles or variation where the caterpillars occur to validate the differences in temperatures assumed between dry riverbed habitats. For many cryptic species, daily temperature fluctuations have significant impacts on development times and behavior. Wekiu bug habitat may represent an extreme example of these fluctuations, but threatened taxa may frequently be vulnerable due to finite and specific habitat characteristics, so models that most accurately estimate actual environmental conditions may be crucial. Further, Koda and Nakamura (2012) acknowledge that they did not ground truth their temperature data, which are based on national meterological averages for cities. Mauna Kea provides a clear example of the importance of using in

Table 3. **Microhabitat temperatures (°C) relating to wekiu bug inhabited cinder cones.**

	Air temp. °C		*Substrate surface*		*Substrate subsurface*		*Substrate ash layer*		*Total hours of thermal accumulation*	
Month	*mean daily max UKIRT, CFHT (1991–2006)*[a]	*mean daily min UKIRT, CFHT (1991–2006)*[a]	*mean daily max (SE) (2007)*	*mean daily min (SE) (2007)*	*mean daily max (SE) (2007)*	*mean daily min (SE) (2007)*	*mean daily max (SE) (2007)*	*mean daily min (SE) (2007)*	*above min threshold of 11.34 °C (2007)*	*above max threshold of 30 °C (2007)*
April	6.5, 5.3	−2.2, −1.4	36.2 (0.90)	−7.4 (0.49)	17.1 (0.35)	−0.5 (0.27)	8.4 (0.23)	3.8 (0.19)	283	115
May	7.8, 6.2	−1.1, -0.5	38.2 (0.62)	−5.9 (0.51)	19.5 (0.32)	0.95 (0.26)	10.1 (0.18)	5.3 (0.16)	323	139.5
June	9.9, 7.8	0.3, 1.1	38.5 (0.91)	−5.4 (0.53)	21.7 (0.35)	1.6 (0.24)	11.3 (0.15)	6.6 (0.11)	347.75	150
July	9.3, 7.6	0.1, 0.7	34.5 (1.0)	−3.9 (0.43)	18.6 (0.65)	1.6 (0.22)	9.8 (0.23)	5.5 (0.21)	327	123.75

[a] *Temperature stations are affixed to 2 separate telescopes at approximately 4200 m. United Kingdom Infrared Telescope (UKIRT), Canada, France, Hawaii, Telescope (CFHT) (from Couto da Silva 2006).*

situ microhabitat measurements to compare actual temperature fluctuations experienced by the insects with those provided in the lab. In the case of the Wekiu bug, weather service temperature measurements can be up to 30 °C different from temperatures which the insect is experiencing in the rock substrate, on both the high and low end. This discrepancy is likely to be substantial in alpine or otherwise exposed habitats (e.g., deserts, plains, intertidal zones) and may be crucial to understanding an insect's ecology and survival.

An arctic relative of the wekiu bug, *Nysius groenlandicus* (Zetterstedt), is a high-latitude species that prefers higher ambient temperatures (30 °C) and is found in higher densities on south-facing dry slopes. Such thermoregulatory behavior minimizes development time in this univoltine species during the cold and short summer (Bocher & Nachman 2001). This habitat preference supports the thermoregulation requirements we observed in the laboratory. We know of no specific temperature dependent physiological reason wekiu bugs could not survive at lower elevations, so the lower elevation bound of approximately 3415 m may be associated with avoiding competition and predation from lower elevation species which cannot survive on the summit. Because the wekiu bug comes from a recent lineage of herbivores (lygaeid seed bugs) (Ashlock & Gagné 1983), it does not have an effective means of capturing live prey (i.e., raptorial legs or stout mouthparts); thus, the nightly freezing temperatures present throughout their range likely plays an important role in subduing food.

Our DD model for growth in 2007 offers indirect evidence regarding the phenology and thermoregulatory ecology of these insects, data which would be virtually impossible to collect directly in the field. On the surface, the model and data suggest that only one full generation could have occurred during the period for which continuous microhabitat temperature records are available (April to July 2007). However, we collected nymphs and adults at a approximately 50% ratio in late March 2007, demonstrating a cohort must have been born prior to our intensive microhabitat temperature data collection. Because the wekiu bug requires approximately 3.5 (relatively warm and sunny) months per generation to accumulate the DD thermal constant of approximately 622 DD, we not only know they must thermoregulate, but we also can predict they have 3 generations per year based on field data and laboratory trials.

Throughout the summer and fall we found a diversity of wekiu bug stadia, likely from overlapping generations (Eiben & Rubinoff 2010). The few wekiu bugs we captured in early spring were likely representatives of a long-lived and slowly developing over-wintering cohort, which mate and lay eggs in late spring as more sunlight warms the microhabitat and melts snow. The low temperature field simulation (24 °C and11°C) supports our field observation of mostly adult wekiu bugs surviving the colder winter months (Fig. 2). We cannot rule out reproductive diapause in the wekiu bug because the physiological ability is known in other *Nysius* (Wei 2008), but due to the diversity of ages attracted to baited traps throughout the year, a winter stage-specific (egg, nymphal, or adult) hibernation diapause is unlikely. While egg diapause from the winter or fall is possible, no eggs were laid or hatched in captivity when the females were cooled below 22°C (22 °C and 8 °C), again indirectly offering important ecological information on insect behavior and phenology.

A compelling finding of our study is that fluctuating temperature conditions resulted in higher survival and faster growth rates than would be expected under a simple linear model. Specifically, the split temperature condition of 30 °C and 26 °C had the highest intrinsic rate of increase and was higher than both of the steady temperatures of 30 °C or 26 °C. Also, the split 32 °C and 11 °C condition had a higher intrinsic rate of increase than the 32 °C showed on the simple linear model. This same phenomenon has been shown in many agricultural pests (Liu & Meng 2000; Reji & Chander 2008; Wu et al. 2009), though its cause is still unclear. Wekiu bugs are likely adapted to grow best in the fluctuating environmental temperatures they experience in the field. The ability to predict the population growth of this unique species for management decisions and actions hinges on the availability of this relevant growth model and the accuracy and availability of temperature data on Mauna Kea for ground truthing in the wekiu bug habitat range.

Management Challenges and Data Needs

The largest temperature data set available for the summit of Mauna Kea in wekiu bug habitat areas is limited to 2 data loggers mounted on telescopes many meters above the ground. These temperature sensors are recording a different thermal regime than the tephra layers where the wekiu bug occurs and show very little average temperature variation within and between months (Couto da Silva 2006), including average air temperatures that were always below the wekiu bug minimum developmental threshold. Further, generalized models of DD accumulation (single sine, double sine, single triangle, and double triangle, Supporting Information) underestimated the potential for energy accumulation on the basis of only the maximum and minimum substrate temperatures in the models.

The weaker relationship between the air temperature and the substrate temperature reinforces the problem with using commonly applied air temperature data for creating DD accumulation predictions of population growth in the wekiu bug and likely many other species that use microhabitats. Based on our results, the vast temperature data set (1980s-present, Couto da Silva 2006) that might have been used to correlate past wekiu bug trapping rates (1984–2011) with climate conditions on Mauna Kea is likely irrelevant without further correlation analyses between the relevant ground and air temperatures. This result exemplifies some of the challenges in assessing and collecting relevant data for threatened invertebrate population modeling.

Our data for wekiu bug optimal developmental thresholds and the temperature range on the summit of Mauna Kea suggest that the wekiu bug must actively thermoregulate to maintain body temperatures within its functional limits, to develop and reproduce, and that this thermoregulation is restricted to the cinder cone rock tephra due to the thermal buffer it provides. These insects are habitat specialists, and the necessary cinder cone habitat comprises only about 12 km^2 in their elevation range. Application of the techniques used here could have broad relevance to the conservation of many other small or cryptic taxa for which direct observation of habitat characteristics is impossible or impractical. Agriculturally based DD models and relevant field data can reveal essential conservation parameters and assist in the conservation of obscure and cryptic taxa.

This study was part of a larger body of research that provided data for the U.S. Fish and Wildlife Service (USFWS) to make a decision on whether to list *N. wekiuicola* as an endangered or threatened species (U.S. Fish and Wildlife Service 2011). By creating a model of temperature dependent growth and reproduction, we have defined physiological parameters that explain why the wekiu bug is only found in certain areas. The USFWS concluded that there is enough wekiu bug habitat protected and that past fluctuations in observed wekiu bug numbers were not indicative of a declining population (U.S. Fish and Wildlife Service 2011).

However, the future of the wekiu bug is still uncertain, due to global climate change and increased human impacts on its limited habitat; fortunately, there is a continuing commitment to monitor and protect the species. Two land management authorities (Office of Mauna Kea Management at the University of Hawaii, Hilo, and Hawaii State Natural Area Reserve System) are responsible for the stewardship of land on which the wekiu bug depends and use the most current monitoring data to conserve the unique summit ecosystem of Mauna Kea. We have created a life table and DD model for wekiu bug population growth that assists in the evaluation of current habitat quality and use and aids in ongoing habitat restoration efforts by efficiently monitoring wekiu bug population establishment in restored habitat.

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Supporting Information

Wekiu bug survival and developmental times (Appendix S1), wekiu bug rearing conditions (Appendix S2), survival confidence intervals (Appendix S3), and Kaplan-Meier survival curves (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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