<table>
<thead>
<tr>
<th>Title</th>
<th>Population dynamics of Armigeres subalbatus (Diptera: Culicidae) across a temperate altitudinal gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author(s)</td>
<td>Chaves, Luis Fernando; Imanishi, Nozomi; Hoshi, Tomonori</td>
</tr>
<tr>
<td>Citation</td>
<td>Bulletin of Entomological Research, 105(5), pp.589-597; 2015</td>
</tr>
<tr>
<td>Issue Date</td>
<td>2015-10</td>
</tr>
<tr>
<td>URL</td>
<td><a href="http://hdl.handle.net/10069/35829">http://hdl.handle.net/10069/35829</a></td>
</tr>
<tr>
<td>Rights</td>
<td>© Cambridge University Press 2015</td>
</tr>
</tbody>
</table>

長崎大学学術研究成果リポジトリ

NAOSITE: Nagasaki university’s Academic Output SITE
Population dynamics of *Armigeres subalbatus* (Diptera: Culicidae) across a temperate altitudinal gradient

Luis Fernando Chaves¹,²,*, Nozomi Imanishi¹ and Tomonori Hoshi¹

¹Institute of Tropical Medicine (NEKKEN), Nagasaki University, Sakamoto 1-12-4, Nagasaki 852-8523, Japan

²Programa de Investigación en Enfermedades Tropicales (PIET), Escuela de Medicina Veterinaria, Universidad Nacional, Apartado Postal 304-3000, Heredia, Costa Rica

*Author for correspondence, Phone: +81-95-819-7809; Fax: +81-95-819-7812; email: lchaves@nagasaki-u.ac.jp

Short Title: Population dynamics of *Armigeres subalbatus*
Abstract

Understanding the impacts of weather fluctuations, and environmental gradients, on the abundance of vectors is fundamental to grasp the dynamic nature of the entomological risk for disease transmission. The mosquito *Armigeres subalbatus* (Coquillet) is a common vector of filariasis. Nevertheless, its population dynamics have been relatively poorly studied. Here, we present results from a season long study where we studied spatio-temporal abundance patterns of *Ar. subalbatus* across the altitudinal gradient of Mt. Konpira in Nagasaki, Japan. Spatially, we found that abundance of adult *Ar. subalbatus* decreased with altitude and increased in areas where the ground was rich in leaf litter. Similarly, adult activity was observed only when relative humidity was over 65%. Temporally, we found that peaks in abundance followed large rainfall events. Nevertheless, this mosquito was under significant density dependence regulation. Our results suggest that *Ar. subalbatus* population peaks following large rainfall events could reflect the recruitment of individuals that were dormant as dry eggs. We did not find a clear signal of temperature on abundance changes of this mosquito, but only on its phenology. Since ground cover seemed more critical than temperature to its spatial distribution, we propose that this mosquito might have some degree of autonomy to changes in temperature.

Key-Words: Schmalhausen’s law, Ricker model, filariasis, density-dependence, forcing
Introduction

Mosquitoes have been widely studied because of their role as vectors of several pathogens affecting humans and animals (Silver 2008). Mosquito population dynamics are of particular interest because mosquito abundance shapes the entomological risk of vector-borne disease transmission (Dye 1990). Specifically, vectorial capacity, the ability of a pathogen to be propagated by the action of insect vectors, linearly increases with vector-abundance (Garrett-Jones 1964). Thus, the risk for disease transmission can be both spatially (Kitron 1998) and temporally (Chaves et al. 2011) linked to vector abundance. Nevertheless, a detailed knowledge of factors regulating the abundance of mosquitoes, such as density-dependence and the impact of weather changes over a heterogenous landscape, have been relatively poorly studied for species other than dominant vectors (Chaves and Koenraadt 2010), with few exceptions (Yang et al. 2008a, Hoshi et al. 2014a). Studies of mosquitoes over altitudinal gradients, in the context of climate change, allow to simultaneously evaluate mosquito abundance over the gradient of temperatures associated with elevation (Eisen et al. 2008), where, in general, temperature decreases with altitude. Similarly, information about mosquitoes with minor, or without any, medical importance is fundamental to understand possible evolutionary constraints on the response of mosquitoes, and the diseases they transmit, to climate change (Chaves and Koenraadt 2010).

The mosquito *Armigeres subalbatus* is a vector of filarial worms with medical importance, *Brugia pahangi* (Muslim et al. 2013) and with veterinary importance, *Dirofilaria repens* (Lee et al. 2007). *Ar. subalbatus* has also been found infected with Japanese Encephalitis Virus, JEV (Tanaka et al. 1979) and has been incriminated as a JEV vector in settings without rice fields (Chen et al. 2000). Regarding bloodfeeding, it has been reported that this mosquito was able to experimentally feed on humans, mice, chickens and reptiles, but not amphibians (Miyagi 1972), thus reinforcing the view that this mosquito can transmit zoonotic pathogens (Chaves et al. 2010).

The mosquito *Ar. subalbatus* is widely distributed in Asia (Tanaka et al. 1979, Amerasinghe and Munasingha 1988a, b) and has been observed across altitudinal gradients (Zea Iriarte et al. 1991), yet no detailed study has assessed its population
regulation. Studies on the natural history of *Ar. subalbatus* have shown that its larvae are common in nutrient enriched water (Senior-White 1925, Barr and Chellappah 1964), including septic tanks (Moriya et al. 1967), especially with high ammonia concentration (Rajavel 1992b), and the nutrient enriched water can be clear or turbid (Amerasinghe and Munasingha 1988b). This mosquito also colonizes bamboo stumps (Kurashige 1963), artificial containers (Zea Iriarte et al. 1991) and treeholes (Tsuda et al. 1994). Overwintering occurs in the larval stage (Mogi 1996), and larvae seem to enter diapause because of a synergistic interaction between low temperature and short day length (Oda et al. 1978). It has also been suggested, based on laboratory observations, that dry conditions may lead to egg diapause (Barr and Chellappah 1964). The phenology of adults also seems to be strongly seasonal, with latitudinal variation. For example, in Taiwan adult *Ar. subalbatus* were absent from mosquito traps during January and February (Sun 1964), at the higher latitude of Shandong province, China from November to early May (Zhang et al. 1992). At the even higher latitude of Kyoto, Japan adult mosquitoes have been only observed from August to October (Nakata and Ito 1955). Rainfall has been suggested as an important factor for *Ar. subalbatus* population changes, with significant adult abundance increases during and after high rainfall (Amerasinghe and Munasingha 1988a). Here, we present results from a season long study of *Ar. subalbatus* abundance patterns in Mt. Konpira in Nagasaki, Japan. We asked what factors of the landscape where correlated with *Ar. subalbatus* abundance across the altitudinal gradient of Mt. Konpira, and whether its population dynamics were under density dependence regulation while accounting for potential impacts of weather changes on its abundance.

**Materials and Methods**

*Study site*: Larval and adult mosquitoes were biweekly sampled across 27 locations in Mt. Konpira (Fig. 1). Mt. Konpira is located in Nagasaki city, northwest Kyushu, western Japan (Fig. 1). Nagasaki has a temperate seasonal climate, with 4 well defined seasons. Temperature in the winter (from December to February) rarely drops below 0 °C and snowfall is minimal, often absent. By contrast, the summer (mid July to mid September) has both high relative humidity, above 65%, and temperature, above 27 °C (Isida 1969).
Our sampling locations in Mt. Konpira followed those of a previous study in the same area, ranging from 109 to 330 m in altitude (Zea Iriarte et al. 1991). The sampling setting consisted of three radial transects, across an altitudinal gradient, joined at a middle point (Fig. 1). Our sampling locations were mainly located across a secondary forest, with diverse types of dominant vegetation according to the Japanese Ministry of the Environment (available at http://www.vegetation.biodic.go.jp/), but there were some urban sites in the periphery of all the sampling locations (Fig. 1). Exact coordinates for each sampling location were measured with a Garmin Oregon 650 GPS (Garmin Ltd, KS, USA), which was also used to measure the site altitude, in m. The altitude measures were compared with those from an ASTER digital elevation model, DEM, for Mt. Konpira (available at http://gdem.ersdac.jspacesystems.or.jp/), and given the low disagreement between the two measurements, we employed the DEM data in our analysis. At each sampling location we characterized the canopy cover in May 25th 2014 by following a standard methodology (Frazer et al. 2001) where 4 photographs were taken with a fisheye ball lens located at ground level within a 1.5 m radius of a focal tree, i.e., a tree where an ovitrap was located. For the photos we used a EOS 40D camera (Canon Co., Tokyo, Japan) that had attached a normal lens (EF-S17-85mm F4-5.6 IS USM; Canon Co., Tokyo, Japan) and a 180° fisheye lens (Nordward optronics 0.25X Super fisheye lens 180° G2; Revel Royal Inc, Aichi, Japan), which allowed to take hemispherical photos. The images were subsequently analyzed with the gap light analysis mobile application for android tablets (http://gap-light-analysis-mobile-app.android.informer.com/) to determine the average and S.D. of canopy cover for each sampling location. We also quantified the ground cover by sampling twelve 2.5 m long transects radiating from each focal tree. Each transect had an approximate angular separation of 30°. We categorized each transect as: grass, leaf litter, bush, trees, concrete and terrace, based on the dominant group type among those 6 categories. A matrix with the percent of transects in each category at each sampling point was then analyzed with principal components analysis (Chaves et al. 2011), and the 1st principal component (Table S1) was then used as a ground cover index.

**Mosquito Sampling:** To sample immature mosquito stages we made "ovitraps" (Zea Iriarte et al. 1991) by using 350 ml Coca-Cola® cans painted black with an acrylic spray
paint (Kanpe Hapio Co., Ltd., Osaka, Japan) inside and outside. We made one 5 mm opening to both hold the can to a tree, using a cord, and to drain excess water above 280 ml. All traps were uniformly set at 1.2 m above the ground level. We selected this height given that previous reports indicated that *Ar. subalbatus* preferentially oviposits in containers around this height (Amerasinghe and Alagoda 1984). Ovitraps were filled with rain water collected during April 2014 and were set in May 18th, and then biweekly surveyed from June 1st until November 29th of 2014. During each survey we determined the presence of 1st to 3rd instar mosquito larvae of any species, and we counted the number 4th instar larvae of *Tripteroides bambusa* Yamada and *Ar. subalbatus*, due to their easy identification in the field (Tanaka et al. 1979), and removed all other 4th instar larvae and all pupae for laboratory rearing and identification of emerged adults (Hoshi et al. 2014a).

Adult mosquitoes were sampled using a sweep net (36-cm diam; Model 61-1B; Shiga Insect Co., Tokyo, Japan), a common tool to sample adult mosquitoes (Hoshi et al. 2014b). Sampling started at sunrise. We selected this sampling time given previous reports that indicated this mosquito is active at sunrise (Berlin et al. 1975). Also sweep nets are appropriate to sample this mosquito, which is predominant at ground level (Tsuda et al. 2003). The use of sweep nets was standardized by staying at a fixed point within a 2.5 m radius from the focal tree where the ovitraps were set up. After arriving to a sampling location the net was swept around the body of the person sampling for 2 minutes, after this time period the person sampling stopped for 1 min and then swept the net for another 2 min. During each sampling session the order of the sampling locations was determined randomly in order to avoid any possible bias due to sampling the same locations always at the same time. Adult mosquitoes were biweekly sampled between May 4th and November 15th of 2014. We selected a biweekly sampling to have a sampling interval that coincided with the pre-adult developmental time of *Ar. subalbatus* (Weathersby 1962). Similarly, we started to collect mosquitoes in May, given that in Shandong Province, China, at the same latitude of Nagasaki, adult mosquitoes have only been caught after May 10th (Zhang et al. 1992).
Weather Variables: At each sampling session we recorded the air temperature and relative humidity using a portable O-230 thermohygrometer (Dretec Co., Saitama, Japan). The water temperature in the ovitraps was measured using an AD-5617WP infrared thermometer (A&D Co., Tokyo, Japan). Data on daily records for rainfall from May 1st 2014 to December 1st 2014 were obtained for Nagasaki city from the Japanese Meteorological Agency Website (http://www.jma.go.jp/jma/index.html). For the analyses we employed the cumulative amount of rainfall on the 14 days prior to the mosquito sampling. The weather station is located within a 5 km radius from our study site.

Mosquito identification: Fourth instar larvae and adult mosquitoes were identified using the taxonomic key of Tanaka et al (1979). Voucher specimens are available in the Entomological Collection in the Institute of Tropical Medicine of Nagasaki University, Japan and in the Mosquito Collection in the Walter Reed Biosystematics Unit – Smithsonian Institute, Washington DC, USA.

Statistical analysis: Larvae data of *Ar. subalbatus* were not analyzed given that we found them at two localities, once at one site, inside a vacant lot bordering a prickly forest, and two times at another other site, inside an area whose vegetation was dominated by acorns (Fig. 1).

To detect spatio-temporal clusters, i.e., hotspots, of *Ar. subalbatus* adults, we employed an elliptical cluster detection mode in a SCAN spatio temporal Poisson model (Kulldorff and Nagarwalla 1995, Kulldorff et al. 2005). We constrained the maximum cluster size up to 50% of the samples while scanning the whole study site. We chose the elliptical shape over a circular one given that our sampling followed transects (Kulldorff et al. 2006). For statistical inference we employed 999 Monte Carlo simulations. We then proceeded with a spatial analysis of *Ar. subalbatus* abundance in Mt. Konpira, Nagasaki. We fitted Poisson generalized linear models (Faraway 2006) to the total abundance per site. The total abundance per site was obtained by adding the abundance through the 14 biweeks of sampling at each sampling location (Fig. 1). We started by building a model that included elevation (m), mean and S.D. canopy openness (%), mean, S.D. and kurtosis of temperature (°C) and relative humidity (%), and the ground cover index. This model was simplified by a combined backward-
elimination and forward-addition algorithm (Kuhn and Johnson 2013) that minimized the Akaike Information Criterion (AIC). Briefly, AIC is a model selection criterion that weighs the trade-off between the goodness of fit in a model and the number of parameters, and the best model is chosen by minimizing the difference between a function of a model log-likelihood and the number of parameters (Kuhn and Johnson 2013). Moran’s I test (Venables and Ripley 2002) was employed to test the spatial independence of residuals in the model selected as best, in order to ensure that inferences from the best Poisson generalized linear model were sound (Chaves 2010).

For the temporal analysis of *Ar. subalbatus* abundance we generated a 14 observations adult abundance time series, given the absence of adult mosquitoes during May 4th 2014. The time series was generated by adding the biweekly records across the 27 sampled sites per sampling session. We used this time series for some preliminary time series statistical analysis. We estimated the autocorrelation (ACF) and partial autocorrelation (PACF) functions to describe the patterns of temporal autocorrelation in *Ar. subalbatus* abundance (Chaves et al. 2012, Chaves et al. 2013). The ACF presents the correlation of a time series with itself through different time lags, while PACF shows a similar profile that only considers the correlation between consecutive time lags (Shumway and Stoffer 2011). We also estimated the cross correlation functions (CCFs), i.e., the temporal correlation function between two time series for different time lags (Shumway and Stoffer 2011), between the *Ar. subalbatus* abundance time series and Rainfall, Temperature and Relative Humidity. We estimated the 95% confidence limits, CL, of the ACFs, PACFs and CCFs to test if the correlations departed from what would be expected by random, with only correlations outside the 95% CL being considered statistically significant (Shumway and Stoffer 2011). Then, we proceeded to study of the density-dependence regulation of *Ar. subalbatus* adults. We started by plotting the per-capita growth rate (*r*) of this mosquito as function of its total adult abundance (*N*). The per-capita growth rate is defined by (Turchin 2003):

\[ r = \ln(N_t) - \ln(N_{t-1}) \]  

(1)

Based on the results from this preliminary analysis, we fitted the Ricker model to the *Ar. subalbatus* time series data. The Ricker model has been widely used to study mosquito
populations (Yang et al. 2008a, Yang et al. 2008b, Hoshi et al. 2014a) and is defined by the following equation:

\[ N_t = \lambda_0 N_{t-1} \exp(-bN_{t-1}) \]  

(2)

Where \( \lambda_0 \) is the intrinsic rate of population growth and \( b \) is a density-dependence coefficient (Turchin 2003). When \(-b<0\), it can be affirmed that a population undergoes density-dependent regulation (Turchin 2003). Further details about this model are presented elsewhere, including its derivation (Turchin 2003, Mangel 2006) and several stochastic versions (Melbourne and Hastings 2008).

To fit the models to our data we assumed biweekly adult counts had a negative binomial (NegBin) distribution, given our observations had a variance larger than their mean, i.e., they were over-dispersed (Bolker 2008). This assumption for the model presented in (2), when also assuming the model has an observation error, i.e., without feedback on future states (Bolker 2008), coincides with the assumption that mosquito abundance follows a negative binomial environmental stochastic Ricker model (Melbourne and Hastings 2008):

\[ N_t \sim \text{NegBin}(\text{mean} = \lambda_0 N_{t-1} \exp(-bN_{t-1}), \text{overdispersion} = k) \]  

(3)

Which implies stochasticity affects individuals, in this case *Ar. subalbatus* mosquitoes, independently of their density. We also fitted the model assuming stochasticity was demographic, i.e., a function of mosquito density (Melbourne and Hastings 2008):

\[ N_t \sim \text{NegBin}(\text{mean} = \lambda_0 N_{t-1} \exp(-bN_{t-1}), \text{overdispersion} = kN_{t-1}) \]  

(4)

We expanded the model presented in (2) to account for the potential impacts of weather variables (WV) on the dynamics, as follows:

\[ N_t = \lambda_0 N_{t-1} \exp(-bN_{t-1} + \gamma W_{V_{t-\ell}}) \]  

(5)

Where \( \gamma \) is a coefficient for the impact of a WV at any time lag \( \ell \). The lag \( \ell \) for the WVs was estimated with the CCFs previously described. To incorporate the forcing of
equation (5) into equations (3) and (4), we simply changed the mean of the negative
binomial to the following:

\[ \text{mean} = \lambda_0 N_{t-1} \exp(-b N_{t-1} + \gamma WV_{t-z}) \] (6)

To fit the model presented in (3) and its forced version (6), we employed a
negative binomial generalized linear model (Faraway 2006), using the natural logarithm
of \( N_{t-1} \) as an offset, and \( N_{t-1} \) and \( WV_{t-z} \) as covariates. Nevertheless, to fit the model
presented in (4) and its forced version (6), we wrote an R function that is available as a
supplementary online material (Appendix S1). We computed the AIC of the models for
comparison.

All statistical analysis were implemented with the statistical software R version
3.2.0, with the exception of the SCAN cluster analysis that was performed with
SaTScan version 9.3.1.

Results

We collected a total of 114 adults and 21 4th instar larvae of \emph{Ar. subalbatus}
during the duration of our study (Fig. 1). Adults of \emph{Ar. subalbatus} were present through
all the land cover uses and vegetation types that we sampled, and were only absent
from one of the points that we sampled (Fig. 1). The average (± S.D.) number of adults
per sampling location was 4.22 ± 2.35, ranging from 0, i.e., a place where \emph{Ar. subalbatus}
was never detected, to 9 individuals (Fig. 1). Fig. 1 also shows that adults of
\emph{Ar. subalbatus} were clustered across the northernmost sampling locations, which were
all inside an area of the forest dominated by acorns.

The best spatial model showed that elevation and ground cover (Table 1) were
the best covariates explaining the spatial patterns of \emph{Ar. subalbatus} abundance. The
lack of significance for the Moran’s I index (Table 1) indicates spatial independence in
the residuals, thus fulfilling the assumptions for a sound statistical inference (Chaves
2010). Fig. 2 clearly shows how the number of adult \emph{Ar. subalbatus} decreased with
elevation and increased with the ground cover index, where positive values indicate a
dominance of leaf litter over bushes and/or concrete (Table S1 online only), while negative values indicate an abundance of bushes and/or concrete over leaf litter.

Temporal patterns of *Ar. subalbatus* (Fig. 3) showed that its abundance peaked during the 5th, 7th and 9th sampling biweek, i.e., July 12th, August 9th and September 6th respectively, reaching a maximum of 34 individuals (Fig. 3A). From the 13th biweek of sampling we did not catch any *Ar. subalbatus*. The average (± S.D.) number of adults per sampling biweek was 8.14 ± 10.23. In general, *Ar. subalbatus* abundance time series had temporally independent observations, as indicated by the lack of significant lags in its ACF (Fig. 3B) and PACF (Fig. 3C). Regarding fluctuations in the weather variables, it can be seen that peaks in mosquito abundance (Fig. 3A) overlapped with those of rainfall (Fig. 3D), but not those of temperature (Fig. 3E) nor relative humidity (Fig. 3F), nevertheless, these two last factors seem to be related with the presence of adult mosquitoes, which were only captured when their values were high. CCF analysis showed that *Ar. subalbatus* abundance was significantly associated with rainfall without a temporal lag (Fig. 3G), but not with temperature (Fig. 3H), nor with Relative Humidity (Fig. 3I).

As expected in a population undergoing density-dependent regulation (Fig. 4) we found that the per capita growth rate of *Ar. subalbatus* decreased with its population size.

Estimates of the environmental negative binomial Ricker model (Table 2) outperformed those of the demographic one (Table S2, online only). Table 2 shows the fit considering the forcing by rainfall was better, i.e., with a lower AIC, than an autonomous model. The effect of rainfall on the density dependent regulation of *Ar. subalbatus* (Fig. 5) was to increase the number of mosquitoes, nevertheless, in all cases the abundance of *Ar. subalbatus* was under a strong density dependence, with the per capita growth rate diminishing with adult abundance in all instances.

**Discussion**

We found that temporal changes in adults of *Ar. subalbatus* were autonomous from changes in temperature and relative humidity. Nevertheless, these two factors may
be important for the phenology of *Ar. subalbatus* adult activity, since we only found the
species when temperatures were above 14 °C and relative humidity above 65%. In fact,
we found that phenology of adults of *Ar. subalbatus* at our study site was similar to
observations at a similar latitude in China, where adult mosquitoes were only observed
from May to October (Zhang et al. 1992). Moreover, our spatial model indicated that
abundance of *Ar. subalbatus* adults decreased with altitude, further supporting that
temperature might be important to the phenology and distribution of this mosquito, as
suggested by observations across different latitudes (Nakata and Ito 1955, Sun 1964,
Zhang et al. 1992) and studies on its overwintering (Oda et al. 1978). However, spatially
we also found that adults of *Ar. subalbatus* were more common on grounds with
abundant leaf litter, suggesting that organic matter necessary for enriching potential
larval habitats (Senior-White 1925, Rajavel 1992b) is a factor that might modulate
habitat use by adults. This ground cover also resembles the habitats where this
mosquito has been found transmitting filarial worms (Muslim et al. 2013). Therefore,
ground cover might be important to understand landscape heterogeneities in pathogen
transmission risk by *Ar. subalbatus*.

The positive impact of rainfall on adult *Ar. subalbatus* abundance can be related
to two aspects of its biology: (i) under dry conditions, eggs can enter diapause (Barr and
Chellappah 1964) and (ii) the low variability in oviposition above the water surface,
where more than 75% of the eggs were within a “threshold” of 16 mm above the
waterline (Amerasinghe and Alagoda 1984), suggest that any rainfall above the
oviposition “threshold” has the potential to synchronously trigger egg hatching in *Ar.
subalbatus* larval habitats, which can lead to an eventual “outbreak” or sudden large
change in mosquito abundance (Chaves et al. 2014), as we observed in our study site,
a pattern also observed in Sri Lanka (Amerasinghe and Munasingha 1988a).
Unfortunately, the scarcity of larval samples did not allow us to connect any potential
changes in larval density with adult abundance. However, a previous study (Rajavel
1992a) suggests that at high larval density *Ar. subalbatus* keeps its numbers in check
by cannibalizing larvae, especially if *Ar. subalbatus* does not co-occur with other
mosquito species, and in that regard we can mention that we found 4th instar larvae of
*Ar. subalbatus* only co-existing with larvae of *Tp. bambusa*, the most common and
abundant mosquito in our ovitraps, following a similar pattern also observed by Zea Iriarte et al. (1991) in our study area. However, we were unable to assess any potential interaction between these two species given the scarce Ar. subalbatus larval data that we collected.

Our results clearly indicate that there is density dependence regulation in Ar. subalbatus. The density dependence parameter $b$ in the Ricker model was negative as expected under density dependence regulation (Turchin 2003), and in congruence with patterns observed in several mosquitoes (Makiya 1973, 1974, Yang et al. 2008a, Yang et al. 2008b, Chaves et al. 2012, Hoshi et al. 2014a). However, although rainfall can transiently increase the number of adults, population growth still decreases with population abundance, highlighting the importance of density dependence regulation. It is also interesting to note that for the autonomous environmental stochastic Ricker model, the natural logarithm of the intrinsic rate of population growth parameter, i.e., $\ln(\lambda_0) = 1.98$, was close to the threshold value for weather independent oscillations, a.k.a., bifurcations, which is $\ln(\lambda_0) \geq 2$ (Mangel 2006). Nonetheless, when considering rainfall it became clear that any potential periodicities likely reflected rainfall patterns. Finally, we can conclude that population dynamics of adult Ar. subalbatus follows Schmalhausen’s law, the prediction that systems are more sensitive to environmental variables more unpredictable around their mean (Chaves and Koenraadt 2010, Chaves et al. 2012). Rainfall, the only weather variable associated with abundance changes in Ar. subalbatus adults, undergoes less extreme changes in its mean behaviour than temperature or relative humidity at our study site, which although more extreme, have a more predictable pattern of change and seem to impact Ar. subalbatus phenology, but not its abundance dynamics.

Acknowledgements

We thank Sai Zaw Min Oo, Dr. Hanako Iwashita and Prof. Mark Wilson (The University of Michigan) for their help measuring the ground cover and canopy openness at each sampling point. Trang T. T. Huynh also kindly helped us measuring diverse aspects of the sampling locations and with the larval surveys. Ms. Junko Sakemoto provided valuable administrative help.
Figure Legends

**Fig. 1** Map of sampling locations. The inset figure shows the location of Mt. Konpira in Nagasaki, Japan. Contour lines indicate the elevation. The inset legend indicates the land use types and vegetation cover, and there is also a guide to the total abundance of *Armigeres subalbatus* adults and 4th instar larvae sampled during May to November 2014. A dashed red line indicates a significant spatio-temporal cluster.

**Fig. 2** Spatial patterns of *Armigeres subalbatus* abundance. Dot size is proportional to abundance of *Ar. subalbatus*, ranging from 1 to 9, as function of ground cover and altitude. The grey gradient indicates the abundance estimated with the model presented in Table 1.

**Fig. 3** Temporal patterns of *Armigeres subalbatus* abundance. (A) Time series of *Ar. subalbatus*, TSAS, biweekly abundance from May 18th to November 15th 2014. (B) Auto-Correlation function, ACF, of TSAS, (C) Partial ACF, PACF, of TSAS. Time series of weather variables: (D) Rainfall, (E) Temperature and (F) Relative Humidity, RH. Cross-Correlation functions between TSAS and: (G) Rainfall, (H) Temperature and (I) RH.

**Fig. 4** Per capita population growth rate (*r*) of *Armigeres subalbatus* as function of its density, (*N*<sub>t-1</sub>), in Mt. Konpira, Nagasaki, Japan.

**Fig. 5** Temporal Abundance of *Armigeres subalbatus* (*N*<sub>t</sub>) as function of its previous abundance (*N*<sub>t-1</sub>) and Rainfall. In the plot dots are proportional to the biweekly abundance of *Ar. subalbatus* (*N*<sub>t</sub>), which ranged from 1 to 34. The grey gradient indicates the expected number of *Ar. subalbatus* according to the Ricker model forced by Rainfall (for parameters see Table 2).
Table 1 Parameter estimates for the best spatial Poisson Generalized Linear model explaining *Armigeres subalbatus* abundance across an altitudinal gradient. This model was selected by a combined backward-elimination and forward-addition algorithm, from a model that included elevation (m), mean and S.D. canopy openness, mean, S.D. and kurtosis of temperature (°C) and relative humidity (%), and a ground cover index. The AIC of the starting model was 124.05, and the AIC for the model presented here is 111.25.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>2.46</td>
<td>0.45</td>
<td>5.496</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>-0.0051</td>
<td>0.0020</td>
<td>-2.521</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Ground Cover</td>
<td>0.124</td>
<td>0.032</td>
<td>3.881</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Moran’s I</td>
<td>-0.0652</td>
<td>-</td>
<td>-</td>
<td>0.574</td>
</tr>
</tbody>
</table>

*Statistically significant (P<0.05)
Table 2 Parameter estimates for the negative binomial environmental stochastic Ricker model fitted to the time series of Armigeres subalbatus biweekly abundance. Models were fitted with (Forced) and without (Autonomous) rainfall as covariate. AIC stands for the Akaike Information Criterion.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Forced</th>
<th>Autonomous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intrinsic rate of population growth ($\lambda$)</td>
<td>2.17, 1.08, 2.01, *</td>
<td>7.37, 2.75, 2.68, *</td>
</tr>
<tr>
<td>Density dependence coefficient ($\hat{\beta}$)</td>
<td>-0.12, 0.03, -4.50, **</td>
<td>-0.15, 0.03, -5.38, **</td>
</tr>
<tr>
<td>Rainfall coefficient ($\hat{\gamma}$)</td>
<td>0.0054, 0.0020, 2.70, **</td>
<td>- , - , -</td>
</tr>
<tr>
<td>Negative binomial overdispersion ($\hat{k}$)</td>
<td>2.68, 1.53, -</td>
<td>1.43, 0.66</td>
</tr>
<tr>
<td>AIC</td>
<td>74.44</td>
<td>78.00</td>
</tr>
</tbody>
</table>

NS = not significant (P > 0.05), **Statistically significant (P < 0.001), *Statistically significant (P < 0.05)
References


Figure 3

(A) Time series plot of N with peaks at various time points.
(B) Autocorrelation function (ACF) plot showing periodicity.
(C) Partial autocorrelation function (PACF) plot indicating significant lag.
(D) Graph of Rainfall giving seasonal patterns.
(E) Temperature graph showing fluctuations over time.
(F) Relative Humidity (RH) graph depicting variability.
(G) Cross-correlation function (CCF) plot for rainfall and N.
(H) CCF plot indicating potential correlation between temperature and N.
(I) CCF plot for RH and N showing lack of significant correlation.
Figure 4

\[ r = \ln(N_t) - \ln(N_{t-1}) \]
Table S1 Principal Component Analysis for the estimation of a ground cover index

<table>
<thead>
<tr>
<th>Ground Cover</th>
<th>Comp.1</th>
<th>Comp.2</th>
<th>Comp.3</th>
<th>Comp.4</th>
<th>Comp.5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrace</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-0.2</td>
<td>0.979</td>
</tr>
<tr>
<td>Grass</td>
<td>0</td>
<td>0</td>
<td>-0.764</td>
<td>0.458</td>
<td>0</td>
</tr>
<tr>
<td>Tree</td>
<td>0</td>
<td>0.122</td>
<td>-0.255</td>
<td>-0.829</td>
<td>-0.178</td>
</tr>
<tr>
<td>Bush</td>
<td>-0.390</td>
<td>-0.730</td>
<td>0.334</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Leaf Litter</td>
<td>0.836</td>
<td>0</td>
<td>0.294</td>
<td>0.113</td>
<td>0</td>
</tr>
<tr>
<td>Concrete</td>
<td>-0.381</td>
<td>0.671</td>
<td>0.39</td>
<td>0.221</td>
<td>0</td>
</tr>
<tr>
<td>% Variance</td>
<td>0.738</td>
<td>0.196</td>
<td>0.033</td>
<td>0.027</td>
<td>0.005</td>
</tr>
<tr>
<td>Cumulative Variance</td>
<td>0.738</td>
<td>0.935</td>
<td>0.968</td>
<td>0.995</td>
<td>1.000</td>
</tr>
</tbody>
</table>
Table S2 Parameter estimates for the negative binomial demographic stochastic Ricker model fitted to the time series of *Armigeres subalbatus* biweekly abundance. Models were fitted with (Forced) and without (Autonomous) rainfall as covariate. AIC stands for the Akaike Information Criterion.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>S.E.</th>
<th>z</th>
<th>P</th>
<th>Estimate</th>
<th>S.E.</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intrinsic rate of population growth ($\lambda$)</td>
<td>1.57</td>
<td>0.83</td>
<td>1.88</td>
<td>NS</td>
<td>5.40</td>
<td>2.25</td>
<td>2.39</td>
<td>*</td>
</tr>
<tr>
<td>Density dependence coefficient ($b$)</td>
<td>-0.10</td>
<td>0.02</td>
<td>-4.18</td>
<td>**</td>
<td>-0.13</td>
<td>0.02</td>
<td>-5.69</td>
<td>**</td>
</tr>
<tr>
<td>Rainfall coefficient ($j$)</td>
<td>0.0054</td>
<td>0.0021</td>
<td>2.51</td>
<td>*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Negative binomial overdispersion ($k$)</td>
<td>0.56</td>
<td>0.39</td>
<td>-</td>
<td></td>
<td>0.27</td>
<td>0.14</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>AIC</td>
<td>79.32</td>
<td></td>
<td>81.89</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

NS = not significant (P>0.05), **Statistically significant (P<0.001), *Statistically significant (P<0.05)
### Appendix S1

### R functions to fit the Stochastic Ricker Model

### Time Series

Armigeres subalbatus abundance at \( t+1 \) (biweeks 2-12)
\[
n_{t+1} = (4, 7, 5, 34, 1, 17, 5, 25, 9, 1, 4)
\]

Armigeres subalbatus abundance at \( t \) (biweeks 1-11)
\[
n_t = (2, 4, 7, 5, 34, 1, 17, 5, 25, 9, 1)
\]

Cumulative bi-weekly rainfall before \( t+1 \)
\[
RR = (34.5, 29.0, 197.5, 376.5, 34.0, 301.0, 73.0, 188.0, 43.5, 68.5, 53.5)
\]

### Calling a library with the Negative Binomial Generalized linear model fitting function

library(MASS)

### Fitting the environmental stochastic Ricker model as a Neg-Bin GLM (Autonomous)

\[
rglmnba = \text{glm.nb}(n_{t+1} \sim \text{offset}(\log(n_t)) + n_t)
\]

### Calling the model summary (to see parameter estimates)

summary(rglmnba)

### Fitting the environmental stochastic Ricker model as a Neg-Bin GLM (Forced by Rainfall)

\[
rglmnbF = \text{glm.nb}(n_{t+1} \sim \text{offset}(\log(n_t)) + n_t + RR)
\]

### Calling the model summary

summary(rglmnbF)

### Likelihood functions

### Calling a library with convenient functions to fit Maximum likelihood models

library(bbmle)

### Function to fit the environmental stochastic Ricker model (Autonomous)

\[
\text{renva} = \text{function}(\lambda_0, b, \kappa)\
\begin{align*}
&n_{t+1} = n_t \\
&\text{nt} = \text{nt} - \sum(d\text{nb}inom(n_{t+1}, \mu=(\lambda_0 \times \text{nt} \times exp(-1 \times b \times \text{nt})), size=\kappa, log=\text{TRUE}))
\end{align*}
\]

### Fitting the model

\[
\text{fitrenva} = \text{mle2}(\text{renva}, start=list(\lambda_0=7.37, b=0.15, \kappa=1.43))
\]

### Calling the model summary

summary(fitrenva)

### Function to fit the environmental stochastic Ricker model (Forced by Rainfall)

\[
\text{renvF} = \text{function}(\lambda_0, b, \kappa, g)\
\begin{align*}
&n_{t+1} = n_t \\
&\text{nt} = n_t - \sum(d\text{nb}inom(n_{t+1}, \mu=(\lambda_0 \times \text{nt} \times exp(-1 \times b \times nt + g \times RR)), size=\kappa, log=\text{TRUE}))
\end{align*}
\]

}
### Fitting the model

`fitrenvF=mle2(renvF,start=list(lambda0=2.1714, b=0.115, kappa=2.678, g=0.0054))`

### Calling the model summary

`summary(fitrenvF)`

### Function to fit the demographic stochastic Ricker model (Autonomous)

```r
dema <- function (lambda0, b, kappa){
  nt1<-nt1
  nt<-nt
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(1*b*nt)),size=kappa*nt,log=TRUE))
}
```

### Fitting the model

`fitrdema=mle2(dema,start=list(lambda0=5.4005, b=0.1314215, kappa=0.2724))`

### Calling the model summary

`summary(fitrdema)`

### Function to fit the demographic stochastic Ricker model (Forced by Rainfall)

```r
demF <- function (lambda0, b, kappa, g){
  nt1<-nt1
  nt<-nt
  RR<-RR
  -sum(dnbinom(nt1, mu=(lambda0*nt*exp(-1*b*nt+g*RR)),size=kappa*nt,log=TRUE))
}
```

### Fitting the model

`fitrdemF=mle2(demF,start=list(lambda0=1.5716, b=0.0979, kappa=0.5574, g=0.00536))`

### Calling the model summary

`summary(fitrdemF)`