

Uranotaenia novobscura ryukyuna (Diptera: Culicidae) Population Dynamics Are Denso-Dependent and Autonomous From Weather Fluctuations

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ABSTRACT Larvae of the mosquito *Uranotaenia novobscura ryukyuna* Tanaka et al., have been reported in tree-holes, bamboo stumps, and artificial water containers. So far, no study has addressed the role that density dependence and weather fluctuations could have played in the abundance of this nonvector mosquito. A year-long study was conducted on the population dynamics of this mosquito using oviposition traps in Okinawa, Japan. Time series analysis and the Ricker population model were used to analyze the association between mosquito density and population growth and fluctuations in relative humidity, temperature, and rainfall. Our results suggest that *Ur. novobscura ryukyuna* has stable denso-dependent dynamics, which are autonomous from weather fluctuations. Our results were opposite to patterns observed in other subtropical mosquito species, whose population dynamics might be partially driven by weather fluctuations, thus highlighting the diversity of responses that mosquitoes can have to changing environments.

KEY WORDS Okinawa, Ricker model, climate change, population regulation, oviposition trap

Mosquitoes are ubiquitous across ecosystems. Their life history involves ontological niche shifts during development (aquatic larvae and terrestrial adults). Mosquitoes are recognized as an irritating nuisance pest worldwide (commonly biting humans), and some species have medical and veterinary importance because of their role as pathogen vectors (Silver 2008). These characteristics render mosquitoes as important and interesting insect taxa in nature. Moreover, mosquito development is temperature dependent (Taylor 1981), and biological changes associated with warmer temperatures may play a role in the exacerbation of the diseases they transmit under climate change (Reisen et al. 2010). For example, in temperate areas, the transmission (or mosquito nuisance) season can be lengthened by changes in mosquito overwintering, given that the mosquito overwintering duration can be shortened, or even disappear, in warmer temperatures (Mogi 1996, Reisen et al. 2010). In tropical areas, extremely hot temperatures can underlie mosquito outbreaks by driving changes in the denso-dependent regulation of mosquito population size (Chaves et al. 2012). The latter is very important because mosquito population regulation is still poorly understood, espe-

cially in species with unknown vectorial roles. In that sense, the study of mosquito population regulation remains valuable for both understanding the ecological impacts of global warming on insects and exploring changes in disease transmission related to mosquito population dynamics (Chaves and Koenraadt 2010).

Ecology of mosquitoes in the genus *Uranotaenia* Lynch Arribalzaga is among the most poorly studied across mosquito taxa in general, especially the role that density dependence and weather fluctuations could have in their population abundance. The genus *Uranotaenia* comprises various species that have a relatively small size when compared with other Culicinae mosquitoes in the adult stage (Tanaka et al. 1979, Toma and Miyagi 1986). *Uranotaenia* spp. larvae have been primarily collected from stable permanent, that is, unlikely to dry, or semipermanent, that is, that become dry with a low probability, aquatic habitats (Hinman 1935), which include crab holes (Mogi et al. 1984), treeholes, bamboo stumps (Sota et al. 1994), leaf axils, pitcher plants and artificial containers (Toma and Miyagi 1981), and wetlands (Chambers et al. 1979). Adults have been observed feeding predominantly on reptiles and amphibians (Miyagi et al. 2010), a pattern confirmed by mosquito bloodmeal analysis (Fyodorova et al. 2006, Hamer et al. 2009, Tamashiro et al. 2011). Species are gonotrophically concordant, with eggs oviposited in clutches that form floating rafts (Hinman 1935; Dampf 1943; Chapman 1964, 1970; Miyagi et al. 2010). It has been widely recognized that *Uranotaenia* spp. mosquitoes are dif-

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difficult to sample, especially in the adult stage (Hinman 1935, Dampf 1943, Lane 1943, Toma and Miyagi 1981). By contrast, the sampling of immature stages can be relatively easier, especially because larvae tend to aggregate in stable aquatic habitats (Hinman 1935, Sota et al. 1994). *Uranotaenia* spp. presence is also a potential indicator of environmental quality. An earlier study showed mosquitoes of the genus *Uranotaenia* disappeared with urban development in Mexico (Dampf 1943) and were less abundant, or absent, in highly urbanized sectors of cities in Japan (Moriya 1974) and the United States (Chaves et al. 2011b).

Here, we study the population dynamics of the Ryukyu Chibika, *Uranotaenia novobscura ryukyuana*, a mosquito subspecies endemic to the Ryukyu archipelago, Japan. This subspecies has been captured in only 6 of the 18 Ryukyu islands where mosquito fauna has been extensively sampled, and it is absent from the main Japanese archipelago, Taiwan, and Continental Asia (Toma and Miyagi 1990). The larvae of this species primarily inhabit treeholes and artificial containers (Toma and Miyagi 1981). Previous observations across several habitats showed relatively low variability in the abundance of *Ur. novobscura ryukyuana* larvae sampled at irregular intervals in Northern Okinawa Island (Toma and Miyagi 1981). Thus, we postulate the hypothesis that population growth in this species is denso-dependent. To quantitatively test this hypothesis, we systematically collected data on the Chibika abundance in Okinawa Island biweekly. We used standardized traps to quantify the impact that weather variables could have on the fluctuations of this species and used the data to fit the Ricker model of denso-dependent population growth. We found that Chibika mosquito population dynamics were autonomous from weather fluctuations and regulated in a denso-dependent fashion.

Materials and Methods

Study Location. Mosquitoes were collected at the University of the Ryukyus campus, southern Okinawa Island, Japan (127° 77' E, 26° 26' N).

Mosquito Sampling. From 28 April 2007 to 1 March 2008, larvae and adult mosquitoes were collected biweekly using oviposition traps and light traps, respectively. A biweek sampling period was chosen to coincide with the larval developmental time of *Uranotaenia* spp. mosquitoes (Belkin and McDonald 1956; Chapman 1964, 1970; Miyagi et al. 2010) because such time span is desirable for discrete time population modeling purposes (Turchin 2003). Six oviposition traps were made using black plastic buckets (15 by 20 cm, 3.53 liters; Daiso Co., Hiroshima, Japan) filled with rain water (2.5 liters), and were placed on the ground near vegetation in a forest preserve, a farm, and a water reservoir shore, with two oviposition traps per site. The buckets had two holes (1 cm in diameter) at 15 cm in height to avoid overflowing in the event of rainfall. Although oviposition traps are commonly used to attract gravid females to lay eggs (Chaves and Kitron 2011, Nguyen et al. 2012), in our study, they

were used to let the larvae develop for subsequent sampling and identification of mosquito species (Moriya 1974). In each sampling session, the water content in each one of the six oviposition traps was sieved, and the filtered water was returned to the oviposition traps. The length of this procedure averaged 20 min per trap and was performed in the mornings starting at 9 a.m. and normally ending at 11 a.m. The sieving and conservation of water was done to preserve the microbial communities that might be involved in resource transformation or can serve as food to container mosquitoes (Chaves et al. 2011a, Nguyen et al. 2012). The mosquito larvae from each ovitrap were collected in vials and transported to the laboratory for counting (censusing) and identification. During each sampling session, a total of two light traps (model MC 8200, Ishizaki Electric Mfg. Co. LTD., Tokyo, Japan) were operated from 4:00 p.m. to 8:00 a.m., placed 1.5 m above ground level and on the same location, one trap in the farm and the other in the forest.

Mosquito Identification. Larvae and adult mosquitoes were identified using the taxonomic key by Toma and Miyagi (1986). After a preliminary identification, larvae were counted and fed with dried yeast (1.0 g/liter) and reared to adults in a room with a controlled temperature (27–28°C) for species identification. A dark spot in the wing base was used as the main diagnostic character for *Ur. novobscura ryukyuana* (Tanaka et al. 1979). Voucher specimens are available in the Entomological Collection in the Institute of Tropical Medicine of Nagasaki University.

Weather Variables. Data on daily records for relative humidity, rainfall, and temperature (maximum, mean, and minimum) from 1 April 2007 to 31 March 2008 were obtained for the city of Naha, Okinawa Island, Japan (127° 77' E, 26° 26' N) from the Japanese Meteorological Agency Web site (<http://www.jma.go.jp/jma/index.html>), a location within a 9-km radius from the study site.

Statistical Analysis. Adult Ryukyu Chibika data were not analyzed given the scarcity of collected individuals. For the median larval Ryukyu Chibika time series, we estimated the autocorrelation (ACF) and partial autocorrelation (PACF) functions with the aim of diagnosing possible patterns of temporal autocorrelation in mosquito abundance (Chaves et al. 2012). In brief, ACF is a profile of the correlation of the time series with itself through different time lags and PACF is the correlation between consecutive time lags (Shumway and Stoffer 2000). We used the median number of larvae as a robust estimator of abundance, given the absence of this species from one of the oviposition traps during the study period (Ranta et al. 2006). We also estimated the cross correlation functions (CCFs) between larval Ryukyu Chibika abundance and the biweekly mean relative humidity, temperature (mean, minimum, and maximum), and rainfall (cumulative and daily SD for 14-d period). The CCF is the temporal profile of correlations between two time series for different time lags (Shumway and Stoffer 2000). The significance of the correlations de-

pected in the ACFs, PACFs, and CCFs were subsequently evaluated by testing if correlations were significantly different from what could be expected by random (Shumway and Stoffer 2000). To this end, 95% CL, the confidence limits of the correlations that can be expected to arise by random, were estimated, and any correlation contained between these 95% CL was considered spurious (Shumway and Stoffer 2000). After the descriptive time series analyses, we studied the possibility of density-dependent regulation on the larval Ryukyu Chibika population dynamics. First, we plotted the per-capita growth rate (r) of this mosquito as a function of the median larval abundance (N_t). The per-capita growth rate (Turchin 2003) is defined by:

$$r = \ln(N_{t+1}) / \ln(N_t)$$

Based on the results from the qualitative analysis, we fitted the Ricker model to the mosquito time series. The Ricker model is one of the most widely studied discrete-time density-dependent population models (Turchin 2003, Mangel 2006) and is defined by the following equation:

$$N_{t+1} = \lambda_0 N_t \exp(-bN_t) \quad [1]$$

where the parameter λ_0 is the intrinsic rate of population growth and b is the density-dependence coefficient. A formal test of density-dependence in a population can be done through the estimation of parameter b , which supports density dependence when the following condition holds $-b < 0$ (Turchin 2003). A detailed derivation of the model is presented by Turchin (2003). The mathematical properties of the model and its equilibria are presented by Mangel (2006). An extended discussion of the dynamic stochastic behavior of the Ricker model is presented by Melbourne and Hastings (2008), showing the versatility of this model to test more refined hypothesis about density-dependence, beyond the goals of this study. For example, tests for the presence of demographic and environmental stochasticity in density-dependent population regulation (Mangel 2006, Bolker 2008). We estimated the model parameters by maximum likelihood (Bolker 2008). For the estimation, we used a combination of numerical optimization methods, first globally searching plausible parameter values with the simulated annealing algorithm and then refining the estimation with the Nelder-Mead algorithm as described by Chaves et al. (2012). For parameter estimation, we assumed that stochasticity in our larval counts was just observational and not related to dynamic stochastic processes (Bolker 2008). We assumed larval counts had a negative binomial (Neg-Binom) distribution, where our observations were over dispersed, with a variance larger than the mean (Mangel 2006):

$$N_t \sim \text{NegBinom} \left(\begin{array}{l} \text{mean} = N_t, \\ \text{overdispersion} = k \end{array} \right) \quad [2]$$

where the variance ($\text{VAR}(N_t)$) is given by:

$$\text{VAR}(N_t) = N_t (1 + N_t/k) \quad [3]$$

We also estimated parameters assuming that larval counts followed a Poisson distribution, where our observations had a variance equal to the mean (Mangel 2006):

$$N_t \sim \text{Poisson}(\text{mean} = \text{VAR}(N_t) = N_t) \quad [4]$$

Finally, we compared the two models employing the Akaike Information Criterion, which considers the trade-off between the likelihood and the number of parameters employed when evaluating the model goodness-of-fit and which is minimized by the best model (Shumway and Stoffer 2000).

Results

We collected a total of 9,988 Ryukyu Chibika mosquitoes. Adults were scarce, amounting to 72 individuals in total, from 46 trap-nights, where a trap-night is defined as a sampling session with light traps. By contrast, 9,916 larvae were collected in the same period over a total of 138 sampling sessions. The average abundance (mean \pm SE) of adult mosquitoes was 1.57 ± 0.27 per trap-night, ranging from 0 to 21 individuals. The average abundance of Ryukyu Chibika larvae was 71.86 ± 13.11 , ranging from 0 to 791 individuals per oviposition trap census. Larvae were absent from one oviposition trap, during the observation period, located in the farm where water was likely polluted as suggested by the presence of the southern house mosquito *Culex quinquefasciatus* Say (Nguyen et al. 2012). Figure 1a shows that adults had a population peak close to 20 individuals per trap-night in the first week of sampling (April 2007) that abruptly plummeted to a value that varied between 2 and 0 individuals per trap-night during the rest of the study. By contrast, if we ignore the first observations in Fig. 1a, the median larval population reached a stable population of $\approx 80-90$ individuals per trap night. After the second sampling session, we observed larvae from all instars. During our study period, relative humidity was consistently high, and with low variation (Fig. 1b), temperature showed a seasonal peak from June to August, rounding to 30°C on average (Fig. 1c). Cumulative rainfall and the variability within a biweekly period showed a pattern having transient peaks approximately every 2 mo (Fig. 1d) and had a higher variability than relative humidity (Fig. 1b) but did not show a marked seasonality like temperature (Fig. 1c). The ACF (Fig. 1e) and PACF (Fig. 1f) of the Ryukyu Chibika larvae time series showed that observations were not autocorrelated, that is, independent through time. The CCFs showed that larval abundance was independent of changes in relative humidity (Fig. 1g), temperature, either mean (Fig. 1h), maximum (Fig. 1i) or minimum (Fig. 1j), and rainfall, either cumulative (Fig. 1k) or its variability (Fig. 1l). For the ACF, PACF, and CCFs, the inference of independence is based on the observation that correlations were not different from what is expected by random, with all correlations for all time lags contained within the dashed lines that define the 95% CL of associations

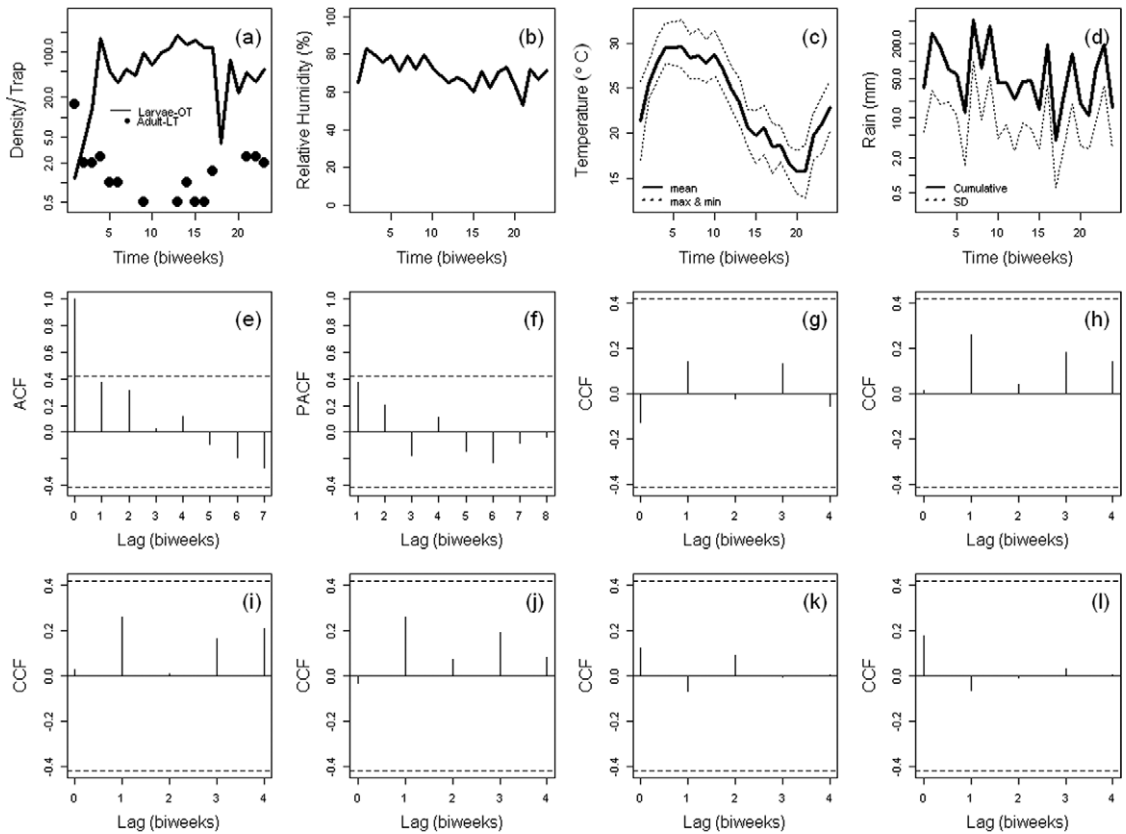


Fig. 1. Data time series and correlation functions of (a) Ryukyu Chibika mosquito, *Ur. novobscura ryukyuana*, biweekly median density per oviposition trap, OT, and light trap, LT. Week 1 corresponds to 28 April 2007; (b) biweekly mean relative humidity, RH; (c) biweekly mean, maximum, and minimum temperature; (d) biweekly cumulative rainfall and SD of daily rainfall for 14 d; (e) N_t autocorrelation function, ACF; (f) N_t partial autocorrelation function, PACF; (g) cross correlation function, CCF, between N_t and RH; (h) CCF between N_t and mean temperature; (i) CCF between N_t and maximum temperature; (j) CCF between N_t and minimum temperature; (k) CCF between N_t and cumulative rainfall for 14 d; and (l) CCF between N_t and the standard deviation of daily rainfall for 14 d. In panels (a) and (d), the y-axis is on \log_{10} scale. In panels (b) to (d), week 1 corresponds to 14 April 2007. In panels (e) to (l), the dotted lines indicate the 95% CL within which the correlation functions are not different from what is expected by random.

that can emerge by random. Here, we also want to stress that an ACF of 1 at lag 0 (Fig. 1e) is not in contradiction with temporal independence. By definition, an ACF at lag 0 is the correlation of a time series with itself, which is expected to always be 1 because of the perfect correlation (Shumway and Stoffer 2000).

The per-capita growth rate of the Ryukyu Chibika decreased with density (Fig. 2) as expected under a strong denso-dependent regulation. Parameter estimates for the Ricker model (Table 1) were similar under the negative binomial and the Poisson distribution, especially for the density dependence coefficient b , where $-b < 0$, thus supporting denso-dependent population regulation in the Ryukyu Chibika. This latter point is illustrated in Fig. 3, where the deterministic skeleton, that is, model iterations in the absence of any process stochasticity (Mangel 2006), of both models converge to a value of ≈ 100 larvae per oviposition trap, that is, 0.04 larvae/ml in 2500 ml in the oviposition traps. Nevertheless, model fitting for the

negative binomial model was considerably better than that for the Poisson model as inferred by the large difference in their AIC (Table 1). Also, the negative binomial model can replicate the time series observations more successfully, as illustrated by sample simulations from the Poisson and negative binomial models (Fig. 3).

Discussion

Our data strongly suggest that population dynamics of immature *Ur. novobscura ryukyuana* on Okinawa Island is regulated in a denso-dependent manner. Both the inspection of the per-capita growth rate as a function of larval density and the successful fitting of the Ricker model robustly support this proposition. In that sense, our results are qualitatively similar to the observations made for the Ryukyu Chibika by Toma and Miyagi (1981), where minimal fluctuations were observed during 3 yr of irregularly spaced observations in northern Okinawa. Similar patterns of denso-de-

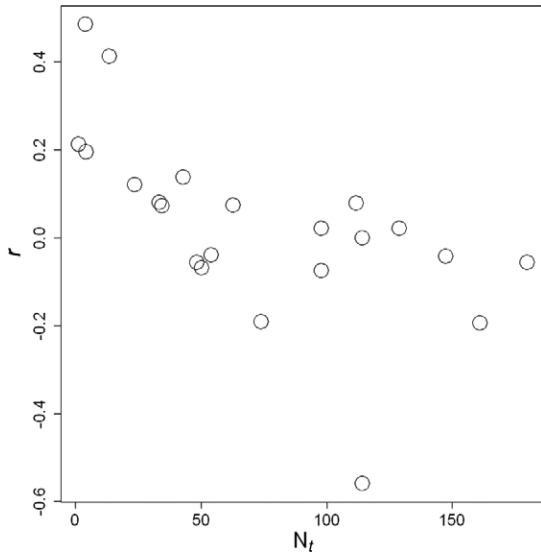


Fig. 2. Per capita population growth rate, $r = \ln(N_{t+1}) / \ln(N_t)$, of the Ryukyu Chibika mosquito, *Ur. novobscura ryukyuana*, as a function of its median density per oviposition trap (N_t).

pendency have been observed for immature *Ur. novobscura* Durrier, the form of the species present in the main Japanese archipelago (Tanaka et al. 1979), where this species consistently had high levels of intraspecific crowding in bamboo stumps and treeholes (Sota et al. 1994). The lack of significant correlations between the abundance of immature Ryukyu Chibika and the weather factors we explored further support the preponderance that density-dependence could have on the Ryukyu Chibika abundance regulation. However, it can also reflect the relative stability of weather factors around optimal conditions for the development of this mosquito. For example, in temperate environments, the recruitment of adult individuals from larvae of *Ur. novobscura* seemed to be modulated by temperature, which was negatively correlated with the time to pupation from fourth instar larvae (Mogi 1996). Nevertheless, the autonomy from the changing environment in the Ryukyu Chibika abundance contrasts with patterns observed in other Culicinae mosquitoes in subtropical environments. For example, larvae of the Asian tiger mosquito *Aedes albopictus* (Skuse) in southern (Toma et al. 1982) and northern Okinawa (Toma and Miyagi 1981), the

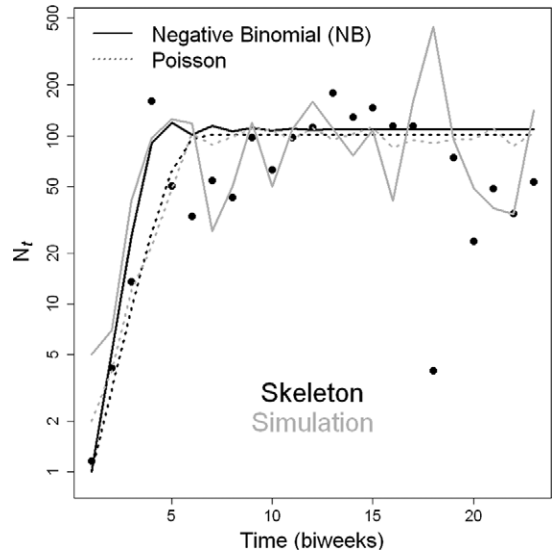


Fig. 3. Model fits and simulations for the Ricker model applied to the Ryukyu Chibika mosquito, *Ur. novobscura ryukyuana*. Black dots are the collected data. Solid and dotted lines show the fits for negative binomial and Poisson models, respectively. Black lines correspond to the deterministic skeleton and gray lines show a simulation output for each model. The y-axis is on Log_{10} scale.

Ryukyu eka *Culex ryukyuensis* Bohart in northern Okinawa (Toma and Miyagi 1981), and the southern house mosquito *Cx. quinquefasciatus* in southern Texas (Hayes 1975, Hayes and Hsi 1975) fluctuate with temperature, highlighting a diversity of abundance patterns in response to weather changes in immature Culicinae mosquitoes.

Another interesting aspect of immature *Ur. novobscura ryukyuana* population dynamics is the convergence to a fixed stable point, as expected when the natural logarithm of the intrinsic rate of population growth ($\ln(\lambda_0)$) is below 2.00, the threshold value above which endogenous oscillations are generated in the Ricker model (Mangel 2006). In other words, the density of the Ryukyu Chibika converges to a stable, primarily constant, density that corresponds to the carrying capacity estimated by the model. Stability is a common pattern observed in other mosquito species (Yang et al. 2008, Chaves et al. 2012) and other insects and animal species (Hassell et al. 1976, Ellner and Turchin 1995, Kendall et al. 1998).

Table 1. Parameter estimates for the Ricker model applied to the Ryukyu Chibika mosquito, *Ur. novobscura ryukyuana*, assuming larval counts had a negative binomial or poisson distribution

Parameter	Meaning	Estimate (95% CI)	
		Negative binomial	Poisson
$\hat{\lambda}_0$	Intrinsic rate of population growth	5.257 (3.117, 9.681) ^a	3.136 (2.804, 3.451) ^a
\hat{b}	Density dependence coefficient	-0.015 (-0.021, -0.009) ^a	-0.011 (-0.012, -0.010) ^a
\hat{k}	Negative binomial overdispersion	1.480 (0.816, 2.496) ^a	—
AIC	Akaike information criterion	240	1046

^a Statistically significant ($P < 0.05$).

The scarcity of adults in our samples is similar to what has been observed for *Uranotaenia* spp. mosquitoes in other subtropical environments around the globe. For adult mosquitoes, to the best of our knowledge, the longest systematic study was carried out on *Uranotaenia syntheta* Dyar and Shannon in Mexico City, Mexico, showing that in >4 yr of weekly observations, this species was predominantly abundant over the winter season (Dampf 1943), an observation also made over one season for *Uranotaenia sapphirina* Osten-Sacken in Fort Jackson, LA (Hinman 1935). This is an interesting phenomenon as it might reveal a synchronous behavior in *Uranotaenia* sp. mosquitoes, probably related to dispersal as observed in other insects (Southwood 1962) and that deserves further study.

Finally, our data clearly suggest the denso-dependent regulation of immature Ryukyu Chibika populations on Okinawa Island. The scarcity of adult samples calls for further studies on the causes of what seems to be annual synchronous events in adult activity.

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