

Relationship between Lemon Emigrant Butterfly *Catopsilia pomona* (Lepidoptera: Pieridae) Population Dynamics and Weather Conditions in Khon Kaen Province, Thailand

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ABSTRACT.– The lemon emigrant butterfly *Catopsilia pomona* is one of the most common pierids in Southeast Asia. In this study, we examined the relationship between the weekly abundance of *C. pomona* and weather conditions to predict how this butterfly species might respond to climate change. We estimated the density of individuals in each life-history stage of *C. pomona* every week from November 2014 – October 2015 in Bueng Niam Subdistrict, Mueang Khon Kaen District, Khon Kaen Province by Pollard's walk. We built predictive models for the butterfly densities to investigate factors determining the densities and predicted effects of climate change on the butterfly population. Our models indicated that the egg and caterpillar densities exhibited a positive relationship with the densities of the previous week, whereas the adult densities did not. The butterfly densities were also associated with the air humidity in the caterpillar and adult stages and with the air temperature in the egg, caterpillar and adult stages. Moreover, the models predicted that climate change in the late 21st century will increase the abundance of and extend the oviposition period of *C. pomona*.

KEY WORDS: *Catopsilia pomona*, weather conditions, climate change, population dynamics, Khon Kaen Province

INTRODUCTION

Different species populations respond to climate change in different ways, such as tolerance to warming temperatures via phenotypic plasticity (e.g., acclimation, acclimatization, developmental adjustments) and microevolution (e.g., rapid evolution of phenology – Franks et al., 2007), dispersing locally to suitable microhabitats or regionally to newly suitable locations (Dawson et al., 2011). Some species may become locally extinct as they lose their habitable area due to a warming climate, whereas some thermophilic species may expand their distribution ranges or increase their abundances (Roy et al., 2001; Parmesan, 2006).

Butterflies are often used as models for predicting the effects of human-induced global changes in wildlife (Roy et al., 2001; Beaumont and Hughes, 2002; Parmesan and Yohe, 2003; Peterson et al., 2004; WallisDeVries et al., 2011) because butterfly populations are sensitive to ecosystem changes caused by humans, e.g., changes in land use (Ockinger et al., 2006; Forister, et al., 2010), habitat fragmentation (Krauss et al., 2003; Dover and Settele, 2009), and climate change (Parmesan et al., 1999; Wilson et al., 2007; Forister et al., 2010). As ectothermic organisms, butterflies are likely to be influenced by a warming climate, especially those in tropical regions, where the temperature change is large relative to the present temperature variability (Deutsch et al., 2008). However, for tropical

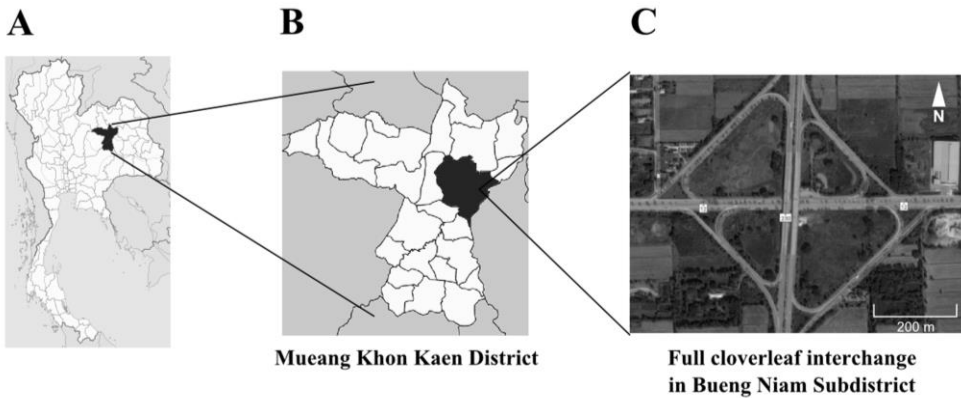


FIGURE 1. (A) The geographic map for Khon Kaen Province, (B) Mueang Khon Kaen District and (C) the satellite photo showing the study site at the full cloverleaf interchange between Thailand Route 12 (Maliwan Road – east-west direction) and Thailand Route 230 (Mueang Khon Kaen Ring Road – north-south direction) (Imagery © 2018 DigitalGlobe, Map data © 2018 Google).

terrestrial ecosystems, climate change has been less of a priority than in other ecosystems since it has been viewed as a less immediate threat than habitat degradation, logging and hunting (Corlett, 2012).

Catopsilia pomona is a medium-sized butterfly in the family Pieridae. This butterfly is one of the most common pierid butterflies in Southeast Asia (Corbet and Pendlebury, 1992). Its distribution range includes India, Sri Lanka, Southeast Asia, China, Taiwan and Australia (Orr and Kitching, 2010; Inayoshi, 2017). This butterfly has been recorded for its migratory habit in many countries, including Australia (Dingle et al., 1999; Orr and Kitching, 2010) and India (Ramesh et al., 2012). The caterpillar of this species feeds mainly on leaves of the family Fabaceae, including *Cassia bakeriana*, *C. fistula* and *C. garrettiana*, as well as on other plants such as *Senna siamea*, *S. alata*, *S. tora*, *Butea racemose* and *B. monosperma* (Robinson et al., 2010; Ek-Amnuay, 2012).

In Khon Kaen Province, many golden rain trees *Cassia fistula*, a larval host plant of *C. pomona* (Robinson et al., 2010; Ek-Amnuay, 2012), have been planted on streets and roads by the local municipality. Consequently, this butterfly is very abundant and can be observed almost year-round (pers obs). Furthermore, this butterfly exhibits an outbreak from April to June. During its outbreak, *C. pomona* caterpillars are often considered as nuisances to some people because they are frequently found in defoliating trees in large numbers and they sometimes invade houses and buildings. However, the butterfly is economically important in Khon Kaen and nearby areas because its caterpillars and pupae are used as food and are sold for between 200 to 250 baht per kilogram in local markets (Khoosakunrat, 2016).

The abundance of this species in Khon Kaen Province and its unique characteristics enabled us to record the abundances of all life history stages of this species. This approach gave us the opportunity to use *C. pomona* as a model species to study how a

species might respond to climate change in tropical areas. We estimated the weekly density in each stage from October 2014 to November 2015 and generated predictive models for the butterfly densities based on weather data. We utilized these models to predict butterfly densities under the warmer climate scenario predicted for the near future.

MATERIALS AND METHODS

Study site

This study was conducted in Bueng Niam Subdistrict, Mueang Khon Kaen District, Khon Kaen Province. The study site was located at the full cloverleaf interchange between Thailand Route 12 (Maliwan Road) and Thailand Route 230 (Mueang Khon Kaen Ring Road) in the eastern side of the Mueang Khon Kaen District (coordinates: 16.437421N, 102.916799E; altitude: 150 m). Within approximately 25 hectares of the study site, the Department of Highways has planted over 200 *C. fistula* trees along the roads and in the garden areas inside the interchange (Fig. 1).

Sampling methods

Twenty single species belt transects were established within the 25 hectares at the cloverleaf interchange to count the abundances of *C. pomona* based on the “Pollard Walk” butterfly survey method (Pollard, 1977; Pollard and Yates, 1993; van Swaay et al., 2012). Each transect was 50 meters in length and 5 meters in width. The transects laid along the roads or within the garden areas. We counted the number of adult butterflies by walking along each transect at a slow and constant pace. Each transect walk lasted 15 min on average. After that, we counted the number of eggs,

larvae and pupa on *C. fistula* trees within the transect. We conducted these surveys once a week between 9:00 and 14:00 on calm weather days from November 3, 2014 to October 31, 2015 (except one week between December 21 and December 27, 2014). During each week, all 20 transects were surveyed in a random order.

Weather data

Daily average air humidity (%), daily average air temperature (°C), rainfall (mm), water vapor (mm), and actual duration of sunshine (hours) were obtained from the Northeastern Meteorological Center – Upper Part (coordinates: 16.462667°N, 102.785872°E), which lies approximately 14 kilometers from the study site.

Butterfly density utilization

The program R (version 3.4.3) was used to perform all statistical analyses. To analyze changes in the individual densities of each butterfly stage and in the meteorological data, we used a Gompertz model for the log index (or first-order autoregressive scheme), with weather variables as covariates adapted from Roy et al. (2001) and Goulson et al. (2005). For a model with one weather variable, the butterfly abundance in a particular week is given by:

$$N_t = a + b_0 N_{t-1} + b_1 W \quad (1),$$

where N_t and N_{t-1} denote the \log_{10} of the butterfly density in week t and in the previous week ($t-1$), respectively, W denotes the value of the weather variable, and a and b are constants. In the equation, the butterfly density in the previous week represents the density-dependent effects.

The density in each week was calculated and the \log_{10} was transformed before analysis. For this transformation, we used a value of 0.1 instead of 0 for weeks in which

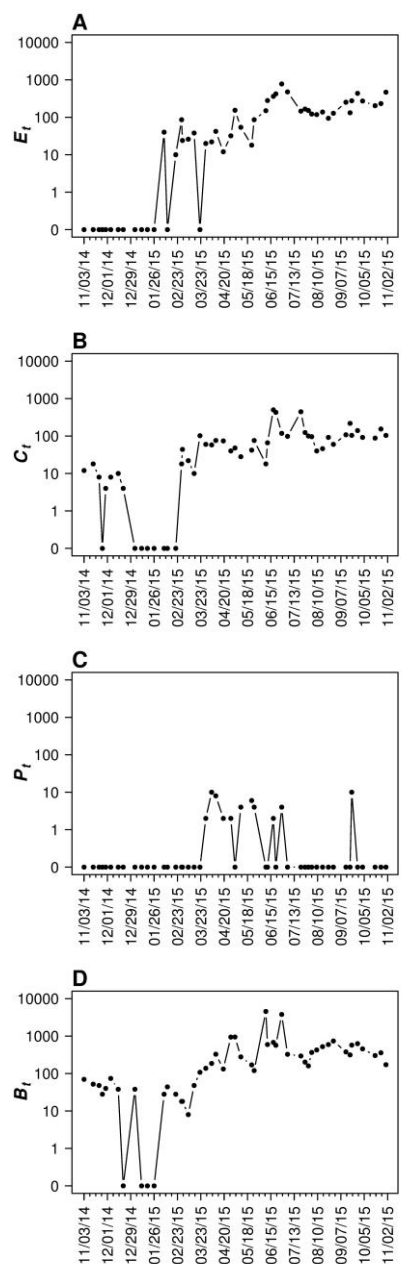


FIGURE 2. Weekly estimated densities (individuals per hectare) of each *C. pomona* life stage from November 2014 to October 2015 in the study site: (A) eggs (E_t), (B) caterpillars (C_t), (C) pupae (P_t) and (D) adult butterflies (B_t)

we did not find butterflies of any stages. The butterfly data from the first week were only

used to estimate the density in the second week. We built a predictive model for each

butterfly life history stage. The weather variables and the densities of the same butterfly stage in the previous week were screened by fitting each to the data for each stage of *C. pomona* using function *lm* in the program R.

The models were simplified using stepwise deletion (Crawley, 2013). Any variable that was statistically significant at the 10% level was kept in a new model to reduce the chances of missing its effects. The simplified model was compared with the previous model by using the function *anova* in the program R. If the previous model did not differ from the new simpler model as a description of the data at 5% statistical significance, the model simplification was accepted.

We tested the accuracy between the predicted population densities from the models and the observed population densities of each stage by using Pearson product-moment correlation. We also conducted a more stringent test for the predictive models based on Kleijnen et al. (1998) and Goulson et al. (2005), who posit that, if the model is accurate, there should be no statistically significant relationship when the differences between observed and predicted values are regressed against the sums of their values.

Butterfly density under a climate change scenario

To examine the probable effects of climate change on *C. pomona* density, we adopted the highest greenhouse gas concentration scenario (RCP8.5) for Southeast Asia to predict the population dynamics of the butterfly during the late 21st century in the Khon Kaen Province. We added 3 °C to the temperature data and 20% to the rainfall data of 2014-2015 to reflect the late 21st century climate (IPCC, 2014). The models for each *C. pomona*

stage were used to predict the effects of climate change. As the degree of change in air humidity due to climate change has not been reported, we did not include the possible effects of air humidity change in the model; however, air humidity was associated with *C. pomona* caterpillar and adult butterfly densities (see results).

RESULTS

Population dynamics of *Catopsilia pomona* in Khon Kaen province

In total, 3,233 eggs, 2,000 caterpillars, 27 pupae and 10,452 adult butterflies of *C. pomona* were counted between November 2014 and October 2015. The weekly estimated densities of each *C. pomona* stage are shown in Fig. 2. *Catopsilia pomona* eggs were first observed on February 15, 2015 (Fig. 2A). The highest egg density of 776 eggs per hectare occurred on June 28, 2015. The egg density remained relatively high (over 100 eggs per hectare in almost all weeks) from July to November 2015. *C. pomona* caterpillars were found in almost all weeks, except between January and February 2015 (Fig. 2B). The peak densities of the caterpillars occurred on June 18 (500 caterpillars per hectare) and July 21, 2015 (444 caterpillars per hectare). The pupae of this butterfly species were found only between March and September 2015 (Fig. 2C). The highest density of pupae was estimated to be 10 pupae per hectare. The adult butterflies were relatively low in density (<50 individuals per hectare) from December 2014 to February 2015 and were absent during four weeks between December 2014 and January 2015 (Fig. 2D). The butterfly density increased in March and remained high until November 2015, with two peaks at 4,542 and 3,786

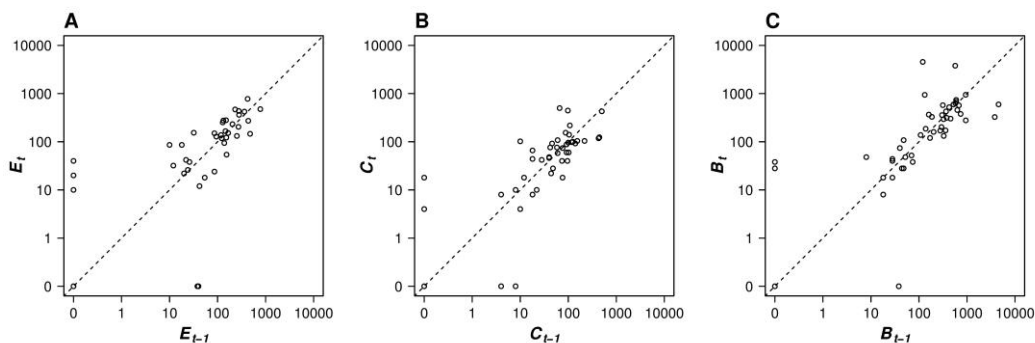


FIGURE 3. Correlation between the densities of *C. pomona* of the same life stage in week t and those in the previous week ($t-1$). The dashed line shows the case in which the density in week t is equal to the density in week $t-1$. The Pearson product-moment correlation coefficients (r) between these two values are as follows: $r = 0.83$ for the egg stage ($t = 10.27$, $df = 48$, $p = 1.04\text{e-}13$); $r = 0.84$ for the caterpillar stage ($t = 10.78$, $df = 48$, $p = 1.99\text{e-}14$); $r = 0.69$ for the adult butterfly stage ($t = 6.69$, $df = 48$, $p = 2.22\text{e-}08$): (A) the egg densities (E_t and E_{t-1}), (B) the caterpillar densities (C_t and C_{t-1}), and (C) the adult butterfly density (B_t and B_{t-1}).

individuals per hectare on June 9 and 28, 2015, respectively. In the remaining weeks, the density of adult butterflies never reached 1,000 individuals per hectare.

Association between weather and *C. pomona* density

We created regression models between the densities of each stage of *C. pomona* and weather conditions. The pupa stage was excluded from this analysis because it was not observed in most weeks and because its density was relatively low in comparison to other stages. In the models, the butterfly densities in the same stage in the previous week were considered to be covariates because the densities of each butterfly stage positively correlated with their respective densities in the previous week (Fig. 3). The models showed that the densities of *C. pomona* eggs could be predicted from the egg densities in the previous week and from air temperature, whereas the caterpillar densities could be predicted from the caterpillar densities in the previous week, air humidity and air temperature (Table 1A – density-dependent model). The egg and caterpillar densities in the previous week

were the most powerful predictor, and their densities were positively associated with those in the previous week. The adult butterfly densities were not significantly predictable by the densities in the previous week because the adult densities more varied between weeks than the other stages. They were, instead, best explained by air humidity and air temperature (Table 1B – density-independent model). For the adult butterfly model, air temperature was the most important predictor, and the model showed a generally positive correlation between density and air temperature. After model simplification, the following models were obtained to predict the density of *C. pomona* in each stage:

for eggs:

$$E_t = -1.46 + 0.72E_{t-1} + 0.07T \quad (2)$$

(Residual standard error = 0.78 on 47 degrees of freedom; $n = 50$; adjusted $R^2 = 0.69$; $F_{2,47} = 55.30$; $p = 4.49\text{e-}13$). The intercept and air temperature were retained in the model. although p -values for these

TABLE 1. Factors explaining the density of each stage of *C. pomona*. The most simplified models, after model simplification using stepwise deletion, are shown in the table. (A) density-dependent model; (B) density-independent model

(A) Stage	Factor	Estimate	Std. Error	t value	Pr(> t)
Egg (E_t)	(Intercept)	-1.46	1.16	-1.25	0.217
	E_{t-1}	0.72	0.10	7.20	4.03e-09
	temperature	0.07	0.04	1.51	0.138
Caterpillar (C_t)	(Intercept)	-4.65	1.07	-4.36	7.15e-05
	C_{t-1}	0.55	0.09	6.06	2.39e-07
	humidity	0.02	0.01	2.74	0.009
	temperature	0.13	0.03	4.66	2.73e-05
(B) Stage	Factor	Estimate	Std. Error	t value	Pr(> t)
Egg (E_t)	(Intercept)	-11.05	1.46	-7.58	1.08e-09
	humidity	0.06	0.01	5.24	3.72e-06
	temperature	0.28	0.04	7.07	6.32e-09
Caterpillar (C_t)	(Intercept)	-9.38	1.10	-8.57	4.35e-11
	humidity	0.06	0.01	6.03	2.61e-07
	temperature	0.25	0.03	8.40	7.79e-11
	rainfall	-0.04	0.02	-2.04	0.047
Butterfly (B_t)	(Intercept)	-7.46	1.09	-6.85	1.36e-08
	humidity	0.05	0.01	5.74	6.75e-07
	temperature	0.21	0.03	7.04	7.00e-09

E_t , C_t , and B_t are the \log_{10} of the densities of *C. pomona* eggs, caterpillars and butterflies (individuals per hectare) in week t , respectively and E_{t-1} , C_{t-1} , and B_{t-1} indicates the densities in the previous week ($t-1$).

factors were greater than 0.05 (Table 1A) because the simplified model was significantly worse than this model (*anova*: $p = 0.045$).

for caterpillars:

$$C_t = -4.65 + 0.55C_{t-1} + 0.02H + 0.13T \quad (3)$$

(Residual standard error = 0.51 on 46 degrees of freedom; $n = 50$; adjusted $R^2 = 0.79$; $F_{3,46} = 63.08$; $p = 2.48\text{e-}16$),

for butterflies:

$$B_t = -7.47 + 0.05H + 0.21T \quad (4),$$

(Residual standard error = 0.67 on 47 degrees of freedom; $n = 50$; adjusted $R^2 = 0.60$; $F_{2,47} = 38.08$; $p = 1.47\text{e-}10$),

where E_t , C_t , and B_t are the \log_{10} of the densities of *C. pomona* eggs, caterpillars and butterflies at week t , respectively, and E_{t-1} and C_{t-1} denote the egg and caterpillar densities in the previous week, respectively. H and T are air humidity and air temperature, respectively. The predicted densities from the models were closely correlated with the observed butterfly densities of three stages (Fig. 4 – solid line).

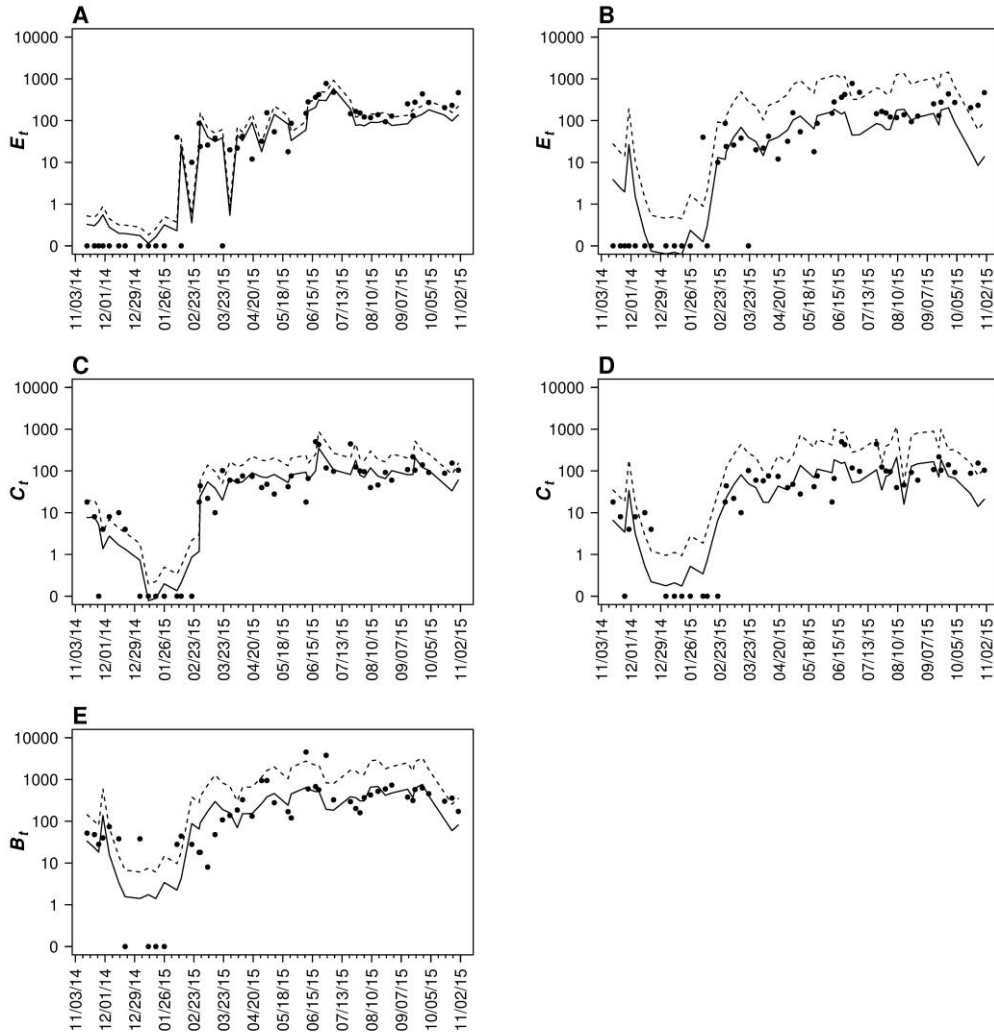


FIGURE 4. Graphs representing the actual weekly *C. pomona* densities (black points), predicted densities for 2014–2015 (solid lines) and predicted densities for the late 21st century under RCP8.5 (dashed lines): (A) the density-dependent model for egg densities (E_t); (B) the density-independent model for egg densities (E_t); (C) the density-dependent model for caterpillar densities (C_t); (D) the density-independent model for caterpillar densities (C_t); and (E) the density-independent model for adult butterflies densities (B_t).

When we did not include the densities in the previous week into the models, weather alone could provide significant predictive values for the egg and caterpillar densities, although their predictive power was decreased (Table 1B – density-independent model). It must be noted that the model for

adult butterflies remains unchanged because, in model (4), the butterfly density was already unassociated with the butterfly density of the previous week. The density-independent models for the egg and caterpillar densities are as follows:

TABLE 2. Pearson product–moment correlation coefficients between the predicted and observed densities for each butterfly stage: (A) density-dependent model; (B) density-independent model

(A) Stage	<i>t</i>	<i>df</i>	<i>p</i>	<i>r</i>
Egg	10.63	48	3.32e-14	0.84
Caterpillar	14.05	48	< 2.20e-16	0.90
(B) Stage				
Egg	8.56	48	3.23e-11	0.78
Caterpillar	10.05	48	2.17e-13	0.82
Butterfly	8.82	48	1.31e-11	0.79

for eggs:

$$E_t = -11.05 + 0.06H + 0.28T \quad (5)$$

(Residual standard error = 0.90 on 47 degrees of freedom; $n = 50$; adjusted $R^2 = 0.60$; $F_{2,47} = 35.84$; $p = 3.53\text{e-}10$)

and for caterpillars:

$$C_t = -9.38 + 0.06H + 0.25T - 0.04R \quad (6)$$

(Residual standard error = 0.63 on 45 degrees of freedom; $n = 50$; adjusted $R^2 = 0.70$; $F_{3,46} = 26.65$; $p = 2.28\text{e-}11$),

where R denotes rainfall. Notably, air temperature was the most powerful predictor for *C. pomona* egg and caterpillar density, with some effects of air humidity on eggs and some effects of air humidity and rainfall on caterpillars.

The predicted butterfly densities were closely correlated with the observed population densities for all stages (Table 2). A more stringent test for the predictive models indicated that only the density-dependent model for the caterpillars was accurate by showing no statistical significance of regression between the differences and the sums of the observed and predicted values ($F_{1,48} = 2.92$, $p = 0.094$). However, the other models did not pass this test at 5% statistical significance

(for model (2): $F_{1,48} = 5.10$, $p = 0.028$; for model (4): $F_{1,48} = 7.41$, $p = 0.009$; for model (5): $F_{1,48} = 7.87$, $p = 0.007$; for model (6): $F_{1,48} = 5.71$, $p = 0.021$) because the predictions tended to differ between observations where the eggs and butterflies were absent and where both densities peaked (Fig. 4 – compare between black points and solid line).

Effects of climate change on *C. pomona* populations

We used models (2) through (6) to predict the effects of climate change on *C. pomona* populations (Fig. 4A – 4E). The models predicted that a warming climate will lead to increases in density of all the *C. pomona* stages (Fig. 4 – dash line) because, in all the models, the densities of *C. pomona* were associated with air temperature. For the density-dependent model, the egg densities were predicted to increase on average by 58.89% in a warming climate, while, for caterpillars, the densities were predicted to increase on average by 151.06%. In the density-independent models, the effects of a warming climate on *C. pomona* egg and caterpillar densities were stronger than those of the density-dependent model, *i.e.*, the densities of eggs and caterpillars increased on average by 613.38% and 419.26%, respectively. The densities of adult

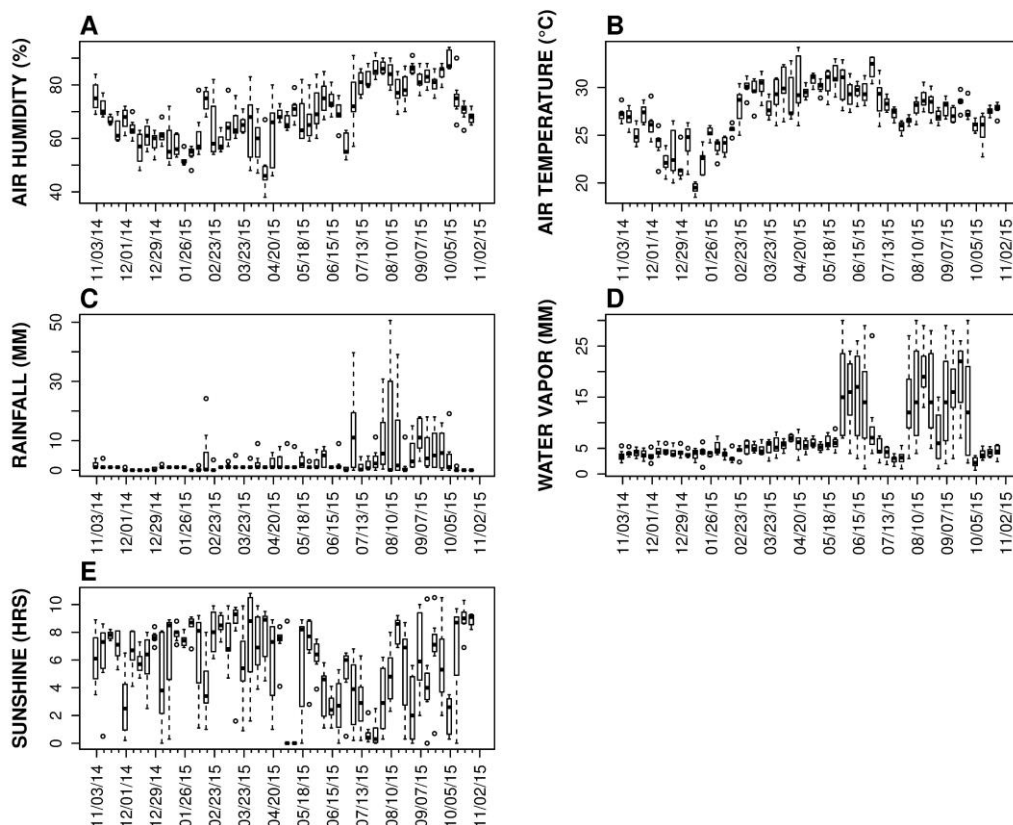


FIGURE 5. Variation of weather conditions at Thai Northeastern Meteorological Center (Upper Part), Khon Kaen Province in each week between November 2014 and October 2015: (A) daily average air humidity (%), (B) daily average air temperature (°C), (C) rainfall (mm), (D) water vapor (mm), and (E) actual duration of sunshine (hours)

butterflies were predicted to increase approximately 331.42% in the future climate. In addition, an extension of the oviposition period of *C. pomona* was predicted under a climate change scenario using model (5) (Fig. 4B).

DISCUSSION

In this study, we presented the weekly dynamics of each stage of *C. pomona*, from eggs to adult butterflies, in the field for a full year from November 2014 to October

2015 in Bueng Niam Subdistrict, Mueang Khon Kaen District, Khon Kaen Province, Thailand. We observed that *C. fistula*, planted as street trees in the study site, were used by *C. pomona* as oviposition sites and larval host plants. The butterfly dynamic appeared to be associated with local weather factors (air humidity, air temperature and rainfall).

Population dynamics of *C. pomona*

In the study site, all stages of *C. pomona* were absent during the winter (Fig. 2), which, in Khon Kaen, lasts from mid-October to mid-February, where air humidity,

air temperature and rainfall were low (Fig. 5), although the duration of absence varied among stages. In winter, the leaves of *C. fistula* are partly deciduous, and only old leaves remain on trees. Caterpillars of *C. pomona* might not survive in the winter due to a lack of young leaves, which are the preferred food of caterpillars. In 2015, the flowering *C. fistula* in the area was first observed around the middle of March after the weather grew warmer (Fig. 5B). After flowering, *C. fistula* developed young leaves. Adult *C. pomona* might adjust their oviposition behavior to correspond to the phenology of the larval host plant by avoiding laying eggs during winter months. For this reason, *C. pomona* eggs were not found until the end of February. This butterfly is likely to overwinter as adult individuals since the winter in Khon Kaen was generally mild (Fig. 5B). January 2015 was the coldest month in this study, with an average temperature of 22.6 °C and a peak low temperature of 11.6 °C on January 14, 2015. Although the temperature limit of this butterfly is unknown, some *C. pomona* adult butterflies should survive under the lowest temperature in winter. In comparison, another species of tropical butterfly *Bicyclus anynana* could survive short durations of exposure to temperatures below 0 °C (Fischer et al., 2010). However, we could not observe adult butterflies in four weeks from the end of December to the end of January in the study site, but we could observe adult butterflies in other areas. Most likely, in this period, lower temperatures might trigger adult butterflies to move away from the study site to find nectar sources, as we did not observe any nectar plants in the study site during the winter months. Butterflies require sugar from nectar, which is converted to lipid or glycogen and stored as energy for overwintering or migration

(Brower et al., 2006). We could observe *C. pomona* in the study site again at the beginning of February when the average temperature began to increase.

Khoosakunrat (2016) studied *C. pomona* development times in March 2015 at room temperature in Khon Kaen Province and found that *C. pomona* development, from egg to adult, was completed in 12 – 16 days (2-3 days in the egg stage, 5 – 7 days in the caterpillar stage and 5-7 days in the pupal stage). Thus, the first group of eggs laid in the end of February should develop into adult butterfly around the middle of March. Around March, the density of adult butterflies, eggs and caterpillars also began to increase, with peaks occurring in June. Adult butterflies continued to actively oviposit until October 2015. While the survival rate from eggs to caterpillars (estimated from the density of caterpillars divided by the density of eggs in the previous week) was relatively high (73.91%), the survival rate from caterpillars to pupae (estimated from the density of pupae divided by the density of caterpillars in the previous week) was very low (1.71%), and only several pupae were found in the study site. In comparison, in Tripura, India, the survival rate from eggs to pupae varied from 13.04% to 30.00%, depending on the weather factors, *i.e.*, humidity, temperature and rainfall (Choudhury and Agarwala, 2013). One reason for the low survival rate of caterpillars in our study might be biotic factors, as we noticed many animals prey on caterpillars in the study site, including birds (e.g., sparrows, bulbuls, tailorbirds, and mynas) and insects (e.g., mantids). In addition, local people might also collect caterpillars and pupae for food.

Since the study site was an open habitat, adult *C. pomona* might fly from other areas to the study site. The butterflies most likely

visited the study site mainly to lay eggs on *C. fistula* trees and left soon after oviposition due to the lack of nectar sources in the area. The migration of this butterfly was observed in June 2015 when the adult density was at its peak. On June 9, thousands of *C. pomona* flew from the Northeast toward the Southwest, while on June 28, they flew from the Southwest to the Northeast. In the remaining weeks, we did not observe such directional flight of the butterfly. It should be noted that the 2014–16 El Niño event occurred during our data collection period. In Thailand, the El Niño event caused below-average rainfall, high temperatures and prolonged dry weather (FAO, 2015). The 2014–16 El Niño event might have delayed migration of *C. pomona* in the Khon Kaen Province. In comparison, in 2017, we observed an earlier migration of *C. pomona*, from the end of April to the beginning of May.

Effects of weather conditions and climate change on *C. pomona* densities

As an ectotherm, *C. pomona* growth, development and survival might be affected by environmental factors. Our models indicated that the densities of all stages of *C. pomona* were positively associated with air humidity and air temperature (Table 1). Warmer temperatures and higher humidity should positively influence the number of *C. pomona* by shortening the generation time of the butterfly. This is because increasing temperatures can modify both the behavioral and physiological traits of butterflies, such as reducing development time, body mass, food intake, and immune activity, and increasing humidity can have positive effects on the development and immune functions of butterflies (Karl and Fischer, 2008; Choudhury and Agarwala, 2013; Fischer et al., 2014). Moreover, the survey studies of Choudhury and Agarwala (2013)

in Tripura, India showed that the average relative humidity and temperature showed strong positive correlations with the survival rate of *C. pomona* from egg to adult. In contrast to our study, Choudhury and Agarwala (2013) suggested that rainfall exhibits positive effects on caterpillar densities. However, the negative effect of rainfall on caterpillar densities in our result is in concordance with several studies showing that persistent or heavy rainfall can be deleterious to caterpillars, e.g., it can cause drowning of caterpillars, increasing the risk of diseases and infections such as fungi and viruses and can hinder caterpillar movements which affect the individual growth rate (Dennis and Sparks, 2007; Tamburini et al., 2013).

Previous studies predicted that some thermophilic insect species will increase their abundance under a warming climate (Roy et al. 2001; Goulson et al., 2005; Kwon et al., 2010). Our models also demonstrated that *C. pomona* respond positively to a warming climate by increasing in abundance of all stages and expanding the oviposition period. In addition, it is possible that the butterfly's generation time will shorten because of rising temperatures. With a prolonged oviposition period and a shorter generation time, *C. pomona* might have more generations per year and be able to increase its population size. Nevertheless, our prediction would be accurate only if the larval host plants changed their phenology to match that of the butterfly. However, the effects of a warming climate on *C. fistula* and other larval host plants of *C. pomona* are unknown. If the host plants respond to climate change by advancing their flowering or lengthening their growing season, as have been observed in some species (reviewed in Parmesan, 2006), the population of *C.*

pomona would increase more than expected based on the models. Otherwise, climate change might lead to temporal mismatch between *C. pomona* and its host plants, which would result in negative fitness consequences in this butterfly species (Visser and Both, 2005). Positive responses of *C. pomona* to a warming climate might have other consequences, which we did not include in this study, e.g., range and elevation shift. Climate change will possibly allow for the range expansion of *C. pomona* to higher latitudes and/or higher elevations as have been reported in other butterfly species (Warren et al., 2001; Hickling et al., 2006).

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