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Seasonal influence on wing phenotypic plasticity in *Mansonia indiana* (Diptera: Culicidae) along the Thailand-Myanmar border

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Abstract. *Chaiphongpachara T, Sumruayphol S, Laojun S. 2025. Seasonal influence on wing phenotypic plasticity in* Mansonia indiana *(Diptera: Culicidae) along the Thailand-Myanmar border. Biodiversitas 26: 2253-2260. Mansonia indiana* (Diptera: Culicidae) is a vector of the nematode *Brugia malayi* that causes lymphatic filariasis in Southeast Asia. Thus, this study aimed to investigate the seasonal wing phenotypic plasticity of *M. indiana* collected along the Thailand-Myanmar border, employing landmark-based geometric morphometrics. Sampling was conducted from September 2021 to August 2022, encompassing three distinct seasons: the cool season (November-February), the hot season (March-May), and the rainy season (June-October). The Centroid Size (CS) ranged from 2.89 to 4.14 mm, with the cool season population recording the highest average CS at 3.68 mm and the rainy season population the lowest at 3.44 mm. Significant differences (p<0.05) in CS were observed between the cool and rainy season populations, as well as between the cool and hot season populations. Shape analysis revealed significant differences (p<0.05) across population pairs, underscoring the pronounced impact of seasonal influences on wing shape. Wireframe graphs indicated that landmarks 1, 12, and 18 exhibited high variation, suggesting a seasonal influence on wing structures. The unweighted Pair Group Method with Arithmetic Mean tree analysis, based on Mahalanobis distances, indicated that the cool-season population exhibited the most distinct shape. These findings indicate that variations in wing morphology may represent adaptive responses by mosquitoes to the varied environmental pressures of each season. Additionally, wing morphology influences flight efficiency, which is essential for effective host attacks and plays a crucial role in the transmission of filariasis to humans.

Keywords: Geometric morphometrics, insect ecology, mosquito, phenotypic variation, seasonal variation, Thailand-Myanmar border

INTRODUCTION

Phenotypic plasticity refers to the ability of organisms, including insects, to modify their phenotypes in response to environmental factors, thereby significantly contributing to both morphological diversity and species survival (Rodrigues and Beldade 2020; Ueno et al. 2023). Many insects adapt to environmental changes by altering their development to produce adaptive phenotypes (Deem et al. 2024). This developmental phenotypic plasticity is highly beneficial, enabling organisms to adjust to varying environmental conditions quickly)Deem et al. 2024). The significance of phenotypic plasticity in adaptive evolution, at both microevolutionary and macroevolutionary scales, is increasingly recognized due to a deeper understanding of its underlying mechanisms and evolutionary implications (Halali et al. 2024). Additionally, seasonal variation plays a crucial role in the study of phenotypic plasticity in insects. Seasonal environmental heterogeneity, characterized by rapid and cyclical changes, imposes diverse selective pressures on populations. This variability affects the evolutionary adaptations of species that produce multiple generations annually)Rodrigues and Beldade 2020; Ueno et al. 2023).

Mosquitoes are critical to medical and public health as vectors that transmit pathogens to humans (Yee et al. 2022). *Mansonia indiana* is notably significant, primarily transmitting the filarial nematode *Brugia malayi* in Southeast Asia (Wharton 1962; Abdulloh et al. 2024). Wharton (1962) reported that *M. indiana* from Malaysia and Indonesia were susceptible to *B. malayi* infection. In Thailand, *B. malayi* triggered a serious epidemic in the southern region (Rojanapanus et al. 2019). Due to rigorous control measures, the incidence of the disease has significantly decreased, and the country has gained international recognition for its management (Meetham et al. 2023). Despite this success, the disease's resurgence remains a concern in Thailand, particularly as outbreaks persist in neighboring countries, such as Myanmar (Rojanapanus et al. 2019; Meetham et al. 2023). Sarataphan et al. (2002) showed that *M. indiana* can still transmit *B. malayi* to humans, even in non-endemic areas. Consequently, studying these mosquito species in border regions is crucial to monitoring and mitigating the risk of mosquito-borne diseases due to cross-border outbreaks.

The phenotypic plasticity of *Mansonia* mosquitoes plays a crucial role in promoting and maintaining diversity across heterogeneous environments (Laojun et al. 2024). Climate conditions, such as habitat temperature, have been shown to impact mosquito larval development, resulting in significant variability in the overall phenotypic quality of adults, including their morphometric properties (i.e. shape, size, asymmetry) and other life-history traits, such as the vector's capacity to transmit pathogens to humans (Demirci et al. 2012; Hidalgo et al. 2015; Chaiphongpachara and Laojun 2019). However, data on *M. indiana* remain scarce. Additionally, *Mansonia* mosquitoes exhibit adaptations to cyclical environmental changes driven by seasonal variations (Abdulloh et al. 2024; Laojun et al. 2024). A recent study by Laojun et al. (2024) on the physiological variation of *Mansonia* mosquito wings in central Thailand revealed that seasonal changes have a significant influence on wing shape. Assessing the phenotypic plasticity of these mosquitoes in response to seasonal influences is vital for understanding their adaptation mechanisms (Abdulloh et al. 2024; Dennington et al. 2024; Laojun et al. 2024), particularly in the Thailand-Myanmar border area, a critical zone for disease surveillance. However, verifying rapid seasonal phenotypic plasticity within mosquito populations is complex and requires modern tools for precise investigation.

Geometric Morphometrics (GM) is a robust technique that applies multivariate statistical analyses to size and shape variables, utilizing Cartesian landmark coordinates to differentiate between species and population components (Chaiphongpachara et al. 2022; Galindo-Malagón et al. 2022; Laojun et al. 2023; Aupalee et al. 2024; Yeo et al. 2024(. Currently, this technique is used to investigate the phenotypic plasticity of various mosquito species in areas under surveillance for mosquito-borne diseases (Lorenz and Suesdek 2020). Therefore, this study aimed to explore the seasonal wing phenotypic plasticity of *M. indiana* collected along the Thailand-Myanmar border using landmark-based geometric morphometrics. The results enhance our understanding of how seasonal factors influence wing phenotypic plasticity in *M. indiana*. They provide essential information for comprehending their temporal physiological adaptations across the cool, hot, and rainy seasons.

MATERIALS AND METHODS

Ethics statement

An ethics permit was required and obtained prior to the mosquito sampling for this study. The research was conducted with the approval of the Suan Sunandha Rajabhat University Institutional Animal Care and Use Committee (IACUC 64-002/2021), Thailand.

Sample collection and identification

Mosquitoes were collected from two locations along the Thailand-Myanmar border, both known for a high prevalence of mosquito-borne diseases: Huai Nam Nak Village (13°22'28.9" N, 99°16'29.4" E) in Ratchaburi Province and Bong Ti Lang Village (14°06'36.2" N, 98°59'52.5" E) in Kanchanaburi Province. Both locations are in Western Thailand)Figure 1). Sampling occurred from September 2021 to August 2022, encompassing all three local seasons: the cool season (November-February), the hot season (March-May), and the rainy season (June-October). This seasonal division is based on previous studies from the region (Chatpiyaphat et al. 2021; Chaiphongpachara et al. 2024). Climate parameters for the study period are presented in Table 1. For sample collection, ten BG-Pro traps, CDC-style (BioGents, Regensburg, Germany), baited with dry ice as a carbon dioxide source, and BG-lure cartridges (Biogents, Germany) were used. After collection, the samples were euthanized at -20°C and transported to the laboratory of the College of Allied Health Sciences, Suan Sunandha Rajabhat University's Samut Songkhram Campus, Thailand, for further morphological identification.

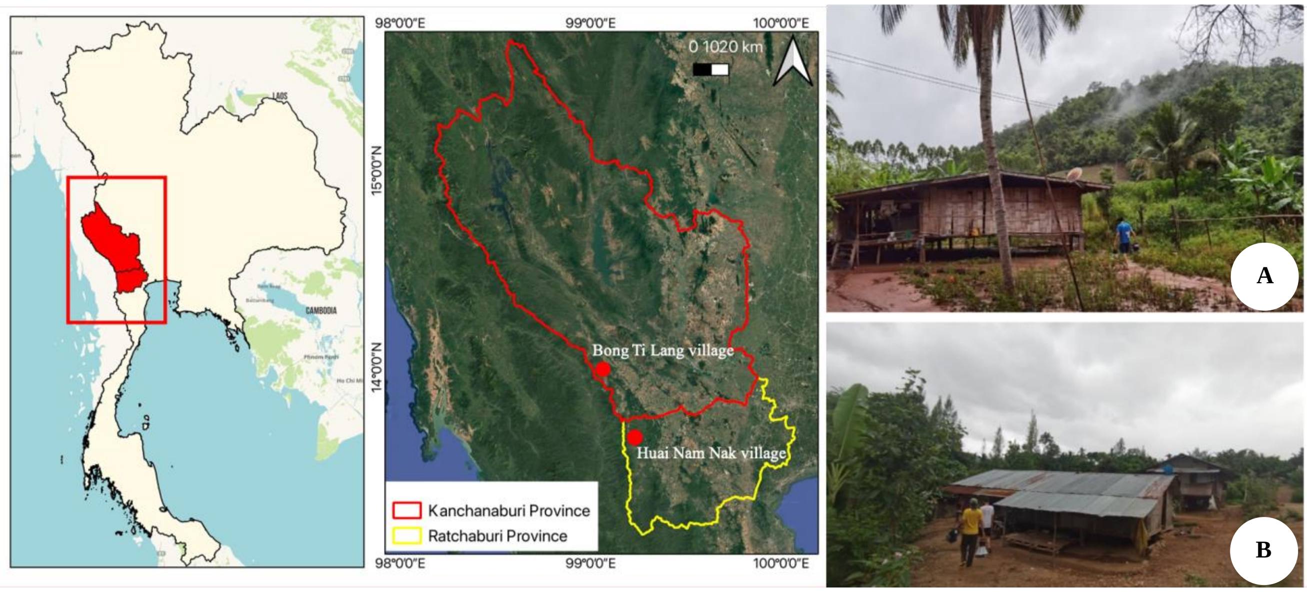


Figure 1. Location of two mosquito collection sites in Western Thailand. A. Bong Ti Lang Village (14°06'36.2" N, 98°59'52.5" E) in Kanchanaburi Province; B. Huai Nam Nak Village (13°22'28.9" N, 99°16'29.4" E) in Ratchaburi Province

Table 1. Average and Standard Deviation (SD) climate parameters by season at the study sites from September 2021 to August 2022. Climate data were obtained from the Meteorological Department of Thailand

Climate parameters	**Cool season (November-February)**		**Hot season (March-May)**		**Rainy season (June-October)**	
	Average	**SD**	**Average**	**SD**	**Average**	**SD**
Air pressure (hPa)	1012.13	0.58	1009.09	1.11	1007.76	0.76
Temperature (°C)	25.59	2.10	29.71	0.77	28.55	1.24
Total rainfall (mm)	20.01	38.82	106.70	64.90	147.16	92.56
Relative humidity (%)	70.54	7.93	72.77	5.32	78.24	6.28
Wind speeds (knots)	2.01	0.86	1.73	0.22	1.89	0.49

For the identification of *M. indiana*, we employed the illustrated keys to the mosquitoes of Thailand (Rattanarithikul et al. 2006). The specimens were examined under a Nikon SMZ 800N stereo microscope (Nikon Corp., Tokyo, Japan). The key distinguishing characteristics of *M. indiana* include a few white scales present on the scutum, which are scattered without forming a complete circle or a longitudinal stripe. In contrast, the post pronotum is characterized by thick, dense, white scales. Additionally, a few black scales may be scattered under the abdomen, though they may be absent in some specimens (Rattanarithikul et al. 2006).

Wing preparation

A total of 345 samples were identified as *M. indiana*, divided seasonally into 78 individuals for the cool season, 119 for the hot season, and 148 for the rainy season. After that, 100 *M. indiana* samples were selected for GM analysis based on two specific criteria: (i) the right wing must be intact and not torn; (ii) the landmark coordinates for analysis must be settable on the wing vein. Subsequently, the selected samples from each season were carefully dissected to remove the right wing, which was then placed on a microscope slide, fixed with Hoyer's medium, and covered with a microscope cover glass. The prepared wing slides were left at room temperature for about seven days to allow the slides and fixative to dry completely. After this period, the slides were photographed using a camera connected to a stereo microscope. Each wing image included a scale bar (1 mm) and was labeled with an ID number to avoid confusion during analysis.

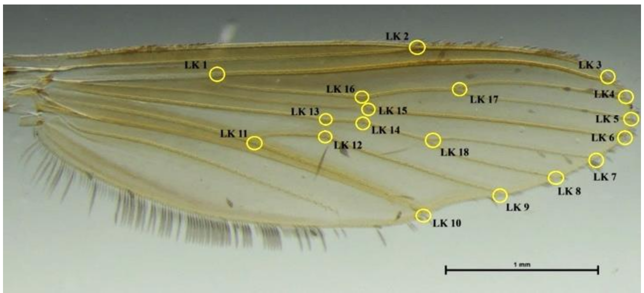


Figure 2. Locations of 18 landmarks (LK) chosen for geometric morphometric analysis of the wing of *Mansonia indiana*

In each wing image, the coordinates of 18 landmarks at the intersections of wing veins were digitized; the location of each landmark is depicted in Figure 2. These landmark positions were selected based on their proven effectiveness in previous studies of *Mansonia* mosquitoes that used the landmark-based GM method (Laojun et al. 2024). After the initial digitization of all wing images, 30 images, a representative sample of 10 per season, were randomly chosen for second digitization to assess the precision of the landmark digitization process. The precision of these measurements was evaluated using the repeatability index, as described by Arnqvist and Mårtensson (1998). If the precision was below 90%, the entire set of images was re-digitized to ensure accuracy in landmark placement.

Wing geometric morphometric analysis

To evaluate seasonal variations in wing size, we used the isometric estimator known as Centroid Size (CS), which is calculated by taking the square root of the sum of the squared distances between the center of the landmark configuration and each individual landmark. Variations in CS across the three seasons were visually depicted using a boxplot format. After that, the differences in CS among the three seasons were analyzed using one-way ANOVA, with the statistical significance of the results determined through a non-parametric procedure based on 1,000 random permutations. All statistical comparisons in this study were deemed significant at p<0.05.

Intraspecific variation assessments often reveal the relationship between wing size and wing shape variation, known as allometry, which can lead to biased results in shape analyses. Thus, estimating the allometric effect of wing size on wing shape is a crucial preliminary step before conducting shape analyses. This effect was estimated using multiple regression analysis, with Procrustes coordinates as the dependent variable and CS as the independent variable. The statistical significance of the allometric effect was determined through non-parametric permutation testing with 10,000 randomization permutations. When the relationship between wing size and wing shape variation was statistically significant (p<0.05), the residuals from the regression of shape on size, deemed allometry-free variables, were used to examine differences in shape without the size effect.

Subsequently, allometry-free variables were used as the output for Canonical Variate Analysis (CVA) to explore the degree of wing shape dissimilarity among seasonal populations. Differences in wing shape across the seasonal populations were analyzed using a permutation test (10,000 randomizations) based on Mahalanobis distances. To illustrate the relationships in wing shape among seasonal populations, an Unweighted Pair Group Method with Arithmetic Mean (UPGMA) tree was constructed from Mahalanobis distances. Additionally, the dissimilarity in wing shape among populations was estimated by a cross-validated reclassification test, where each individual was reclassified according to its similarity to the average shape of each seasonal group.

Software

Two GM software applications were used. The online platform XY Online Morphometrics (XYOM) version 3 (Dujardin and Dujardin 2019) was used to digitize landmarks and analyze wing size. MorphoJ version 1.07 (Klingenberg 2011) was employed to assess allometry, remove allometric effects, and conduct shape analysis. Additionally, PAST version 4.06 (Hammer et al. 2001) was used to construct the UPGMA tree.

RESULTS AND DISCUSSION

A total of 100 intact right-wing specimens, 35 from the cool season, 30 from the hot season, and 35 from the rainy season-were selected for GM analysis to assess seasonal variation. The repeatability analysis of the wing images demonstrated high precision in landmark digitization, achieving a repeatability score of 98% for shape with a measurement error of 2%. Consequently, the digitized image set underwent GM analysis without requiring any rework.

Wing size

Wing CS of *M. indiana* ranged from 2.89 to 4.14 mm. The population from the cool season recorded the highest average at 3.68 mm (SD: 0.22), while the population from the rainy season had the lowest at 3.44 mm (SD: 0.28) (Table 2). Figure 3 illustrates the variation in wing CS across seasonal populations. The rainy season population exhibited the widest range of intrapopulation variation, from 2.89 to 3.92 mm, whereas the hot season population displayed the narrowest range, from 3.34 to 3.69 mm. Significant differences ($p<0.05$) in CS were observed between the cool and rainy season populations, as well as between the cool and hot season populations (Table 2). Additionally, a cross-validated reclassification test for size among the three seasonal populations showed that the cool season population yielded the highest reclassification score of 65.7%, indicating distinct differences in wing size compared to other populations. In contrast, the hot season population had the lowest reclassification score of 13.3%, suggesting a more homogeneous size relative to other populations (Table 3).

Allometric effect

The regression of procrustes coordinates on CS revealed a highly significant difference ($p<0.05$), with allometry explaining 13.6% of the total shape variation. Consequently, the residuals from this regression, which represent allometry-free variables, were used for further analysis of shape.

Wing shape

The variation in wing shape among the three seasonal populations was visualized in a morpho-space derived from CVA (Figure 4). The CVA identified two canonical variates: canonical variate 1 (CV1), which accounted for 56.7% of the shape variation, and canonical variate 2 (CV2), which accounted for 43.3%. Together, both canonical variates comprised 100% of the total shape variation. The morpho-space from CV1 and CV2 indicated that the seasonal population groups overlapped partially but not completely.

Table 2. Statistical differences in wing Centroid Size (CS) of *Mansonia indiana* from three seasonal populations. Different superscript letters among populations indicate statistical significance ($p<0.05$). *n*: Sample size; Min: Minimum; Max: Maximum; SD: Standard Deviation

Season	*n*	Average CS (mm)	Min-Max	Variance	SD
Cool season	35	3.68^a	3.21-4.14	0.05	0.22
Hot season	30	3.54^b	3.34-3.69	0.01	0.11
Rainy season	35	3.44^b	2.89-3.92	0.08	0.28

Table 3. Cross-validated classification scores (%) for three seasonal populations of *Mansonia indiana*

Season	Size		Shape	
	No. of correctly assigned samples/No. of total observed samples	Cross-validated classification score (%)	No. of correctly assigned samples/No. of total observed samples	Cross-validated classification score (%)
Cool season	23/35	65.7%	21/35	60%
Hot season	4/30	13.3%	20/30	66.7%
Rainy season	21/35	60%	15/35	42.9%
Total cross-validated classification score	48/100	48%	56/100	56%

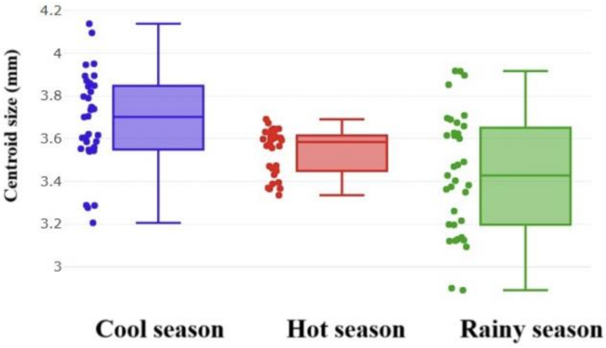


Figure 3. Variation in wing centroid size across three seasonal populations of *Mansonia indiana*

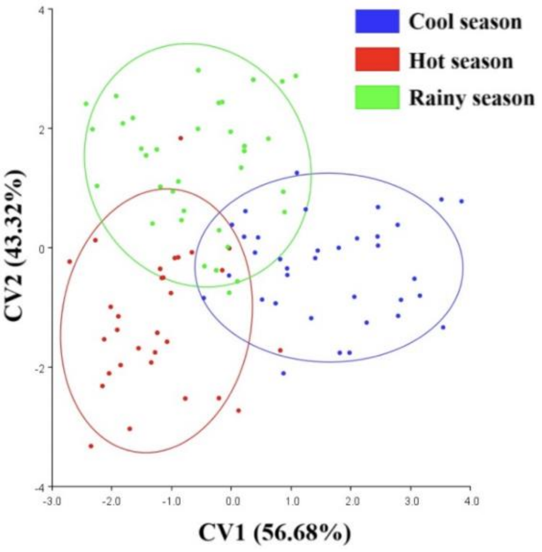


Figure 4. Morpho-space illustrating wing shape variation among three seasonal populations of *Mansonia indiana* along the first two canonical variate axes (CV1 and CV2) with 90% confidence ellipses. The numbers in parentheses indicate the percentage of variation accounted for by each canonical variate, summing to 100% of the total variation

Mahalanobis distances derived from the CVA for pairwise comparisons between seasonal populations revealed significant differences across all pairs (p<0.05; Table 4), with distances ranging from 2.69 (between the hot season and rainy season populations) to 3.02 (between the hot season and cool season populations). After Procrustes superimposition, an alignment was performed to highlight the variation in wing shape among the three seasonal populations (Figure 5). Wireframe graphs indicated that landmarks 1, 12, and 18 exhibited high variation, suggesting a seasonal influence on wing structures. Furthermore, a cross-validated reclassification test for wing shape among the three seasonal populations revealed that the hot season population achieved the highest reclassification score of 66.7%, highlighting significant shape variations compared to the other groups. Conversely, the rainy season population recorded the lowest score at 42.9%, indicating greater shape uniformity relative to other populations (Table 3). The UPGMA tree, which displayed phenetic relationships based on Mahalanobis distances to assess the similarity among all groups, is shown in Figure 6. The tree indicated that the cool-season population had the most distinct appearance compared to the other two populations.

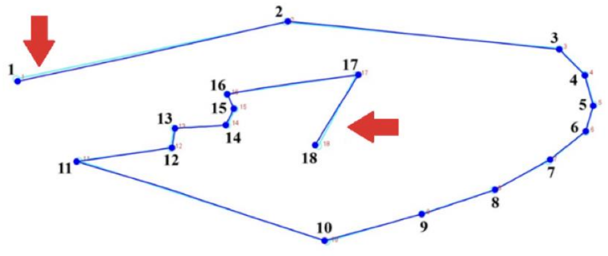
Discussion

Mansonia indiana is widely recognized as a major vector of the nematode that causes lymphatic filariasis in Thailand and other Southeast Asian countries (Abdulloh et al. 2024). Our study revealed variations in the wing patterns of this mosquito species along the Thailand-Myanmar border, which correspond with seasonal changes in climatic conditions. Annual weather patterns, characterized by variations in air pressure, temperature, rainfall, relative humidity, and wind speeds, create distinct patterns that are consistent across seasons (Ishaku et al. 2024; Kliengchuay et al. 2024). At our study sites, each season exhibited distinct climatic characteristics: the cool season featured relatively mild temperatures, averaging 25.6°C, with minimal rainfall (average of 20.01 mm) and moderate relative humidity (approximately 70.5%). The hot season was characterized by higher temperatures, averaging 29.7°C, with moderate rainfall (average of 106.70 mm) and slightly increased relative humidity (72.8%). Conversely, the rainy season was characterized by warm temperatures, averaging 28.6°C, high rainfall (an average of 147.16 mm), and the highest relative humidity of the year (78.2%). These climatic variations have a significant impact on the morphological variations in the wings of mosquitoes in the border areas of Thailand. This observation is consistent with previous research in Thailand, which has demonstrated that seasonal changes impact the isometric properties (size and shape) of mosquito vectors' wings (Chaiphongpachara et al. 2024).

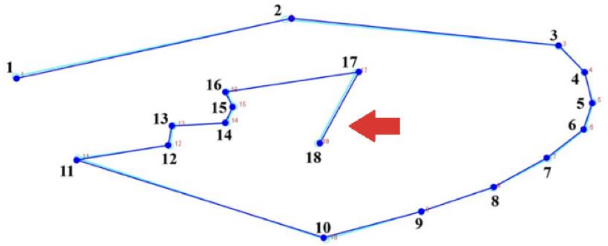
This study size analysis revealed that wings from the cool season population were significantly larger, averaging 3.68 mm, compared to those from the rainy and hot season populations, which averaged 3.44 mm and 3.54 mm, respectively (Table 2). These findings are supported by the results of a cross-validated reclassification test, in which the cool-season population's wing size achieved the highest score, indicating marked size differences compared to other populations. This is consistent with previous research on wing variation in three *Mansonia* mosquito species (*M. annulifera* (Theobald), *M. indiana*, and *M. uniformis* (Theobald)) in central Thailand, where larger wing sizes were observed during the cool season than in other seasons (Laojun et al. 2024). Numerous studies have identified temperature as the primary factor influencing insect wing size (Halim et al. 2022; Mesler and Mabry 2024; Nufio et al. 2025). Wing size, closely linked to body size, fitness, and trophic interactions, may diminish with rising temperatures, a phenomenon widely acknowledged as a universal ecological response to global warming (Wonglersak et al. 2020). Lower temperatures tend to slow developmental and metabolic rates in insects, potentially resulting in larger adult body sizes. Conversely, higher temperatures typically accelerate these rates, leading to smaller adult body sizes (Wonglersak et al. 2020).

Table 4. Significant differences in pairwise Mahalanobis distances among three seasonal populations of *Mansonia indiana*. An asterisk (*) denotes statistical significance ($p<0.05$) for the pair

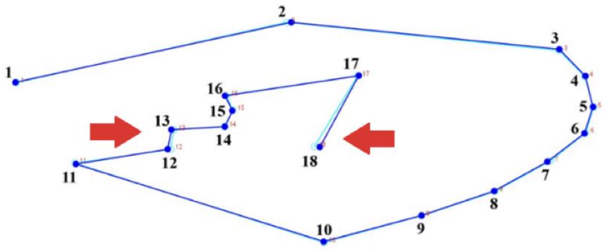
Season	Cool season	Hot season	Rainy season
Cool season	-		
Hot season	3.02*	-	
Rainy season	2.78*	2.69*	-



Cool season vs. Hot season



Cool season vs. Rainy season



Hot season vs. Rainy season

Figure 5. Aligned wing consensus after procrustes superimposition showing the shape variance based on canonical variable 1 among three seasonal populations of *Mansonia indiana*. The arrows indicate the landmarks most influential in wing variation

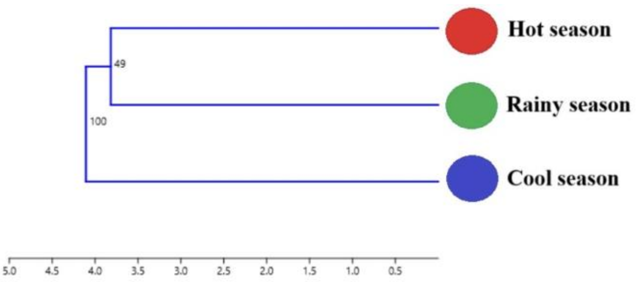


Figure 6. Unweighted pair group method with arithmetic mean tree displaying phenetic relationships based on Mahalanobis distances among three seasonal populations of *Mansonia indiana*

Despite these size trends being influenced by seasonal variations, the population during the hot season did not exhibit significant differences in wing size compared to the population during the rainy season. This similarity is likely due to the temperatures in the western part of Thailand during the hot (29.7°C) and rainy (28.6°C) seasons not being significantly different. Additionally, the hot season is influenced by the summer monsoons, which result in rainfall patterns similar to those of the rainy season. The climatic similarities between these two seasons may explain the lack of significant differences in wing sizes between the populations.

Shape analysis revealed significant differences across population pairs, underscoring the clear impact of seasonal influences on wing shape in all seasons. This aligns with previous studies that have reported the effects of environmental and seasonal weather factors on the wing shapes of mosquito vectors, including *Mansonia* species (Laojun et al. 2024). Similarly, Phanitchat et al. (2019) found that the wing shape of *Aedes albopictus* (Skuse) was most affected by lower temperatures in the Phachuab Khiri Khan strain. Our UPGMA tree assessment of seasonal wing shape patterns showed that the wing shapes of the hot and rainy season populations are more similar to each other than to the cool season population. This observation is consistent with research on other mosquito vectors, such as *A. albopictus* and *Culex tritaeniorhynchus* in Kanchanaburi, Western Thailand, where the rainy and hot season populations also displayed more similar wing shapes compared to the cool season population (Chaiphongpachara et al. 2024). These results from the shape analysis are consistent with those from wing size analysis, which indicated that the cool season had a more pronounced effect on the isometric properties of wings, including size and shape, than the other seasons.

Although the cross-validated reclassification scores further reflect these seasonal impacts, with the hot season population showing the greatest divergence in wing shape at 67%, followed by the cool season population at 60%, and the rainy season population at 43%, there is much overlap between the wing shapes of the hot and rainy season populations. This overlap results in the wing shape of the cool-season population being distinctly different from that of the other two seasonal populations.

Evaluation of the location of highly seasonal landmarks, based on aligned wing consensus after Procrustes superimposition, revealed significant variation in the mid-wing structure (landmarks 1, 12, and 18). This mid-wing structure plays a crucial role in controlling flight, suggesting that seasonal variations may significantly influence mosquito flight behavior as an adaptation to environmental pressures (Wootton 2020; Singh et al. 2021). Although differences in wing shape due to seasonal changes were observed, it remains unclear how these structural variations influence the transmission of pathogens by mosquito vectors. Nevertheless, these findings illustrated how seasonal climatic variations affect wing size and shape, enhancing our understanding of the mechanisms by which mosquitoes adapt to environmental stressors throughout the year.

In conclusion, this study analyzed the seasonal variations in wing phenotypic plasticity of *M. indiana* along the Thailand-Myanmar border, uncovering significant differences in wing size and shape across three seasonal populations. Phenotypic plasticity allows organisms to adjust to environmental variability by altering their behavior, morphology, or physiology without requiring genetic changes, a flexibility that is vital for survival in dynamic environments. This study revealed that the cool-season population exhibits larger sizes and more distinct wing shapes compared to those in the hot and rainy season populations. These variations in wing morphology likely represent adaptive responses by mosquito vectors to the diverse environmental pressures of each season, such as temperature fluctuations and changes in rainfall, which are crucial in shaping their phenotypic characteristics. Notably, the size of mosquitoes may influence the spread of pathogens, as larger bodies can potentially carry more pathogens. Additionally, a larger size is associated with longer adult lifespans in mosquitoes (Carvajal-Lago et al. 2021). Wing shape also affects flight performance (Wootton 2020; Singh et al. 2021), which is crucial for effective host attacks and plays a significant role in the transmission of filariasis to humans. Nevertheless, to fully understand how seasonal variation affects mosquito vectors within complex ecosystems, future studies should also account for additional factors such as geographic variation, land use change, pollution, and anthropogenic climate change.

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