

## Interspecific Variation in Morphology, Behavior, and Ecology among Three Praying Mantid Species *Tenodera attenuata* Stoll, 1937, *Mantis religiosa* Linnaeus, 1758, and *Sphodromantis transcaucasica* Stoll 1937 from District Mirpurkhas, Sindh, Pakistan

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### ABSTRACT

Mantids (Mantodea: Mantidae) are vital predatory insects in agroecosystems, yet their distribution and morphological variation remain poorly understood in Pakistan. This study aimed to address this knowledge gap by collecting (275) individuals of three mantid species including *Tenodera attenuata*, *Mantis religiosa*, and *Sphodromantis transcaucasica* from seven major Taluka's of district Mirpurkhas between May and November 2022-2023. Morphological traits, including body and pronotum length, were measured, and sex was determined via genitalia and abdominal segmentation. One-way ANOVA revealed significant differences in total body length between males and females ( $F = 3234.10$ ,  $P < 0.001$ ) and among species ( $F = 3419.33$ ,  $P < 0.001$ ). Notably, *Mantis religiosa* had the smallest body size, while *Tenodera attenuata* had the largest, followed by *Sphodromantis transcaucasica*. These variations likely reflect ecological adaptations, such as reproductive strategies, prey selection, and habitat preferences. This study provides essential baseline data on mantid distribution, morphology, and ecological significance in Mirpurkhas, highlighting their potential as biological control agents in local agroecosystems and contributing to our understanding of mantid diversity.

## INTRODUCTION:

Insects are the little things that run the world (Wilson, 1987). Sindh, located in the Oriental region, significantly contributes to Pakistan's agricultural industry due to its extensive moderate climate (Sadaf Soomro & Riffat Sultana *et al.*, 2024). Mirpurkhas, a district in Sindh (25°33'02 N and 069°00'11 E), is a key agricultural area spanning 331,655.11 ha. The district comprises six sub-divisions (talukas): Digri, Hussain Bux Mari, Jhuddo, Kot Ghulam Muhammad, Mirpurkhas, and Sindhri (Rashid Saraz *et al.*, 2023). Although the region is home to many insects, most are pests that cause significant economic losses. However, some insect groups, like the order Mantodea (praying mantids), include important predatory species. The name "Mantodea" originates from the Greek word for "prophet," coined by German entomologist Hermann Burmeister. The order is commonly referred to as "mantes" in Latin and "mantis" in Greek (Shar *et al.*, 2025). Praying mantids are a diverse group of about 2500 carnivorous predatory insects that are primarily found in warm, humid tropical and subtropical regions around the world, with sporadic occurrences in colder climates (Greyvenstein *et al.*, 2020; Otte *et al.*, 2020; Fatimah *et al.*, 2021; Anderson, 2022).

Praying mantids (order Mantodea) exemplify remarkable morphological and ecological adaptations. Previous studies on oothecae (egg cases) in the Mirpurkhas District revealed significant interspecific variations in size, shape, and texture, indicating adaptations to local environmental conditions (Khokhar *et al.*, 2022). Building on these findings, this study investigates adult morphological variation, feeding behavior, and habitat associations of sympatric mantid species in the same region. Notably, coexisting mantid species often exhibit distinct morphological, behavioral, and habitat-use adaptations, suggesting diverse niche specialization despite similar climatic and faunal conditions.

Recent research in Sindh has further highlighted species-level diversity, with an updated description of six mantid genera, including four new regional records (Sadaf Fatima *et al.*, 2024). Two mantids species reported from district Tharaparkar, Sindh, *Archimantis latistyla* (Serville, 1838) and *Mantis noblis* (Brunner, 1878) by; (Mirza *et al.*, 2023)

This study compares the morphological, behavioral, and ecological features of three sympatric mantid species co-occurring in Mirpurkhas, Sindh. Our goal is to elucidate the differences in appearance and behavior among these species despite their shared habitat. Although mantid diversity is well-documented in various regions, comparative studies between Asian and Mediterranean genera are scarce. Most research has focused on single-species descriptions or faunistic checklists, with limited exploration of interspecific variations in morphology, behavior, and ecology. In Pakistan and surrounding areas, studies have primarily emphasized taxonomy and distribution, highlighting the need for comprehensive research on resource allocation and coexistence of sympatric mantid species in similar environments.

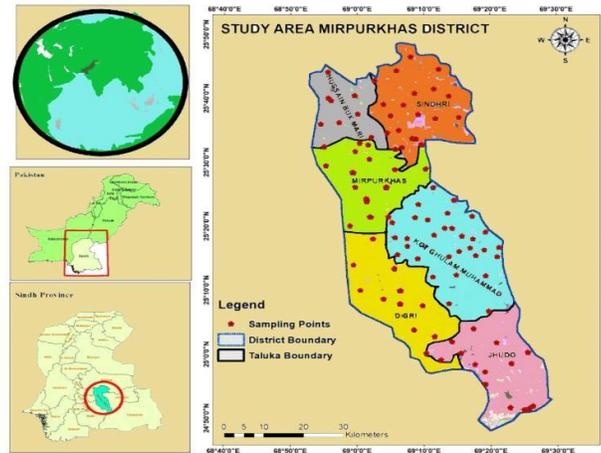
## MATERIALS AND METHODS

### STUDY AREA

The Mirpurkhas District in Sindh, Pakistan, where this study was conducted, is characterized by fertile alluvial soils and a semi-arid climate, making it agriculturally significant. The district supports diverse cropping systems, including rabi season crops like barley, gram, wheat, and onions, and kharif season crops like rice, cotton, sugarcane, and chilies (Brohi *et al.*, 2020). Mango groves are also prevalent, particularly in Sindhri and Kot Ghulam Muhammad talukas. The district comprises seven talukas with varying vegetation and land use: Mirpurkhas, Jhudo, Sindhri, Hussain Bux, Digri, and Kot Ghulam Muhammad. These

talukas offer a range of microhabitats, from semi-desert areas and scrub to irrigated fields and orchards, supporting diverse mantid populations. The environmental heterogeneity is marked by intense agriculture in central

regions like Mirpurkhas and Digri, transitional zones in Jhudo and Sindhri, and agro-industrial activities in Kot Ghulam Muhammad. ( Fig: 01 )



**Fig: 01.** District Mirpurkhas (Sindh, Pakistan) showing distribution of the sampling sites across various talukas.

### Cropping Patterns and Ecological Potential for Mantids

The diverse farming practices in Mirpurkhas District's seven talukas impact native mantid species. Specifically:

Mirpurkhas and Digri: Irrigated crops (wheat, gram, onion, rice, sugarcane) support *Tenodera attenuata* with lush vegetation.

Hussain Bux Mari and Kot Ghulam Muhammad: Mixed agriculture and orchards/gardens provide diverse prey and cover for *Mantis religiosa*.

Jhudo and Sindhri: Semi-arid scrub vegetation suits *Sphodromantis transcaucasica*, a thermophilic, open-habitat species.

### Sampling Duration and Localities

Field sampling was carried out throughout the Mirpurkhas District during the Rabi and kharif cropping seasons, from May 2022 to November 2023. Ten representative localities were surveyed in major talukas, including Jhudo, Shujaabad, Sindhri (Mataro Khaskheli

village), Hussain Bux Mari (Bair Mori and Ghulam Qadir Mari villages), Mirpurkhas (Dolat Lagari, Khadim Hussain Shah), and Kot Ghulam Muhammad (central Kot Ghulam Muhammad village).

*Tenodera attenuata* is the most widely dispersed species, found in almost all talukas, and 105 individuals were collected throughout the study period. With 94 specimens reported from the talukas of Mirpurkhas, Shujaabad, Hussain Bux Mari, Jhudo, Kot Ghulam Muhammad, and Sindhri, *Mantis religiosa* was the next most prevalent. With only 76 individuals, *Sphodromantis transcaucasica* was rather uncommon and mostly found in the talukas of Sindhri, Jhudo, Kot Ghulam Muhammad, and Hussain Bux Mari.

These collections show the semi-arid agroecosystem of Mirpurkhas' spatial heterogeneity as well as species-specific habitat requirements. (Table: 01)

**Table: 01 Sampling duration, localities, and number of specimens of three mantid species collected from Mirpurkhas District, Sindh, Pakistan (May 2022 – November 2023).**

Species Name	Talukas / Villages (Collection Sites)	Sampling Period	No. of Specimens Collected
<i>Tenodera attenuata</i> (Stoll, 1937)	Mirpurkhas taaluka (Dolat Lagari); Sindhri (Mataro Khaskheli village); Hussain Bux Mari (Bair Mori & Ghulam Qadir Mari villages); Kot Ghulam Muhammad taaluka (Kot Ghulam Muhammad village – center of taluka); Jhudo taluka	May 2022 – Nov 2023	105
<i>Mantis religiosa</i> (Linnaeus, 1758)	Mirpurkhas taaluka (Khadim Hussain Shah village, Mataro Khaskheli); Shujaabad; Hussain Bux Mari (Bair Mori village); Jhudo; Kot Ghulam Muhammad; Sindhri Taluka	May 2022 – Nov 2023	94
<i>Sphodromantis transcaucasica</i> (Stoll, 1937)	Sindhri; Jhudo; Kot Ghulam Muhammad; Hussain Bux Mari talukas	May 2022 – Nov 2023	76
<b>Total</b>	—	—	<b>275</b>

The collected specimens from these representative sites were subsequently examined to compare their morphological characteristics, behavioral patterns, and habitat associations.

#### **Morphological and Behavioral Analysis**

In order to document morphological traits such total body length, pronotum length, dominant coloration, prey size ratio, reproduction courtship behavior, and habitat correlations, collected mantid specimens were viewed under a stereomicroscope. External genitalia and abdominal segmentation were used to establish sex.

With an accuracy of  $\pm 0.01$  mm, the body length of mantid specimens was measured with a digital Vernier caliper. In accordance with established procedures, measurements were made from the head's anterior border to the tip of the abdomen. Male and female body length data were subjected to one-way Analysis of Variance (ANOVA) in order to investigate morphological variations between species. Resting posture, prey capture

behavior, and habitat preference were the main topics of behavioral observations that were documented both in the wild and in a lab setting. For documentation and species comparison, photos were obtained. Through the use of known taxonomic keys and literature, morphological identity was verified.

#### **Habitat associations**

Repeated field observations at each sampling location were used to determine the habitat relationships for each species. Microhabitat factors, such as crop structure, canopy cover, vegetation type, and exposure to sunlight or shade, were noted for each specimen or group that was examined. In order to determine species-specific preferences and ecological patterns throughout the district, the abundance of each species was then correlated with the type of habitat (such as irrigated cropland, orchard, fallow field, or scrubland). As explained below, the collected morphometric, behavioral, and habitat data were combined for statistical and comparative analysis (Table: 02).

Species names	<i>Tendodera attenuata</i>		<i>Mantis religiosa</i>		<i>Sphodromantis transcaucasica</i>	
Sex of Specie	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE
Body length (mm)	78.40	79.25	45.25	48.75	48.25	51.75
Pronotum length (mm)	28.75	29.15	13.75	15.00	15.15	16.75
Dominant coloration	Tan and brown with pale hind wings	Tan & pale green sometimes transparent	Brown & pale green	Brown & green	Brown and green	Brown & green
Prey size ratio	Prefers relatively large prey (crickets, small grasshoppers); capable of overpowering prey up to half its own body length.	Takes large prey relative to size (grasshoppers, small beetles, moths).	Medium prey preference (flies, small crickets); tends to hunt actively.	Captures larger prey than male; capable of subduing insects up to 2/3 body length	Large and powerful predator; capable of catching prey nearly equal to own body size.	Very large prey ratio; captures grasshoppers, moths, even small vertebrates on occasion.
Reproduction courtship behavior	Males approach cautiously; courtship involves rhythmic antennae movements; sexual cannibalism occasionally observed after mating.	Often stationary during courtship; may show aggressive response toward males before copulation.	Males perform slow approach with abdomen bending; high risk of sexual cannibalism; visual signaling common.	Stationary and receptive posture during male approach; cannibalism frequent after copulation.	Males display wing-flicking and vibration; cannibalism rare compared to other species.	Females may respond to male movements with foreleg display; cannibalism infrequent.
Habitat	live and feed upon the bushes		commonly found in the old bushes and grasses		commonly found upon small plants and some time on the ground and rarely come at the places where at night search light shines	
NOTES/REMARKS	Robust body medium large size		Elongated and medium-large size		Bulky and wide Medium-large body size	

**Table 02. Comparative morphometric characteristics of three mantid species collected from Mirpurkhas District, Sindh, Pak.**

### Data Analysis

Microsoft Excel was used to compile the data from the morphometric measurements, and descriptive statistics (mean  $\pm$  SD) were used for analysis. To identify interspecific variation, ANOVA was used to compare morphological traits, such as the total body length of male and females of each of the three species that were recorded. We compared ecological observations for species abundance and richness across several talukas and environments. GPS coordinates gathered from every sampling location were used to create distribution maps.

### Results

### Morphological Variation in Body Length among Species

To evaluate interspecific differences, the body length measures of male and female mantids were compared. Body length differences among the three species under study were shown to be statistically significant using Analysis of Variance (ANOVA) male specimens:  $F(2, 17) = 3234.10, p < 0.001$ ; female specimens:  $F(2, 17) = 3419.33, p < 0.001$ ). Males in Species 1 had the longest average body length ( $78.77 \pm 0.57$  mm), followed by Species 3 ( $48.69 \pm 0.63$  mm) and Species 2 ( $45.64 \pm 0.67$  mm). Likewise, Species 1 had the highest female body lengths

(79.64 ± 0.75 mm), while Species 3 and Species 2 had smaller mean lengths (mean ±

SD) of 50.83 ± 0.44 mm and 47.86 ± 0.44 mm, respectively (See Table: 03 & Table: 04)

**Table: 03 ANOVA results summary (Males):**

\*ss= sum of squares, df=degrees of freedom, MS= mean square (MS = SS ÷ df),

F=F-Statistic (Higher F = greater likelihood that group means are significantly different.)

P-value= Probability value (p < 0.05 means the differences between groups are significant),

F crit= critical F value (If F > F crit, the null hypothesis (no difference between groups) is rejected)

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	4022.148	2	2011.074	3234.104	1.71 × 10 <sup>-20</sup>	3.68232
Within Groups	9.3275	15	0.6218			
Total	4031.475	17				

F-value = 3234.104 — this is much larger than the critical value (F crit = 3.682), meaning there is a very strong difference between the groups (species).

- P-value ≈ 0 (1.7e-20) — this is effectively zero, indicating the difference in body length among the

**Table: 04 ANOVA results summary (Females)**

Source of Variation	SS	Df	MS	F	P-value	F crit
Between Groups	3698.763	2	1849.382	3419.328	1.13E-20	3.68232
Within Groups	8.112917	15	0.540861			
Total	3706.876	17				

ANOVA results for females are also highly significant and consistent with the male data. Here's what they show:

- P-value = 1.13 × 10<sup>-20</sup>, which is far less than 0.05, confirming statistically significant differences in body length between the three mantid species.
- The F-value (~3419) is much greater than the critical F-value (~3.68), again confirming strong evidence against the null hypothesis of no difference.

three species is highly statistically significant.

- Variance within groups is very small compared to variance between groups, meaning individuals within the same species are similar, but species differ sharply.

- Variances within groups are low, meaning the data is consistent and reliable.

**Behaviors of Predation and Feeding**

*T. attenuata* targeted comparatively larger prey (prey–predator size ratio = 0.35) than *M. religiosa* (≈ 0.25) and *S. transcaucasica* (≈ 0.22), according to feeding observations. *M. religiosa* used a more adaptable stalking strategy, while *T. attenuata* used quick ambush strikes. The capturing movements of *S. transcaucasica* were vigorous but slower.

As in other mantids, prey detected mainly by vision and captured using their raptorial forelegs (Fukudome & Yamawaki, 2016).

### **Courtship and Reproductive Behavior**

The ways that each species courted varied greatly. *T. attenuata* made quick, straightforward attempts at mating, but *M. religiosa* engaged in frequent antennal and foreleg displays during the longest courtship duration. Male *S. transcaucasica* exhibited strong territorial hostility before copulation. In 25% of reported mating encounters, female

*M. religiosa* were found to engage in sexual cannibalism. Pre-copulatory cannibalism has been observed in several species of predatory invertebrates (Elgar, 1992) but is most commonly reported in praying mantids (Barry *et al.* 2009; Walker and Holwell, 2015; AM Fisher *et al.*, 2020)

### **Habitat Preference and Distribution**

Clear microhabitat segregation was shown via habitat analysis. Tall crop fields and humid vegetation zones were home to *T. attenuata*, mixed agricultural margins and gardens were home to *M. religiosa*, and open, sun-exposed scrublands with sparse vegetation were home to *S. transcaucasica*. This pattern was mirrored in the distribution across talukas, with *S. transcaucasica* predominating in Sindhri and *T. attenuata* in Digri. Although the three species' distributions generally overlapped somewhat, they all had distinct preferences for particular microhabitats within the Mirpurkhas agro-ecological mosaic. Their widespread ecological adaptation and their significance as natural biological control agents are indicated by their prevalence in both cultivated and uncultivated areas. The trends observed in mantid diversity across Mirpurkhas align with the ecological relationships previously reported by (Memon *et al.*, 2025), reinforcing the influence of habitat variation on species composition and distribution.

### **Discussion**

In habitats with tall foliage, *T. attenuata's* bigger body size and longer pronotum probably improve vision range and predatory efficiency, while *S. transcaucasica's* compact morphology might provide thermoregulatory benefits in hot, open areas. Species differences in predatory behavior point to behavioral partitioning that reduces competition across species. A predator-prey relationship is not always stable and can be reversed by ontogenetic changes in body size (Woodward and Hildrew, 2002). The

relevance of morphological and behavioral plasticity in Mantodea evolution is supported by reports of similar adaptive divergence in South Asian species (Fatimah *et al.*, 2024) and Mediterranean mantid assemblages (Battiston *et al.*, 2010).

Differences in agricultural systems might be partially blamed for the observed variations in species abundance among talukas. *T. attenuata* thrived in tall irrigated crops like rice and sugarcane in Mirpurkhas and Digri, but *S. transcaucasica* thrived in semi-arid scrub and fallow fields in Sindhri and Jhudo. Given its wide ecological tolerance, the generalist *M. religiosa* was probably sustained by the mosaic of garden and cultivated habitats in Hussain Bux Mari and Kot Ghulam Muhammad. The coexistence of sympatric mantid species in semi-arid Mirpurkhas is facilitated by niche differentiation, as seen by distinct habitat connections. Earlier studies indicated that color changes in *M. religiosa* are influenced by the substrate at the time of moulting (James, 1944; Ergene, 1952), while later work related these changes to humidity, temperature, and light intensity (Jovancic, 1960; Lopez, 1998). Such environmental plasticity supports the species' wide ecological tolerance.

The three mantid species exhibit substantial morphological divergence, as evidenced by the notable variances in body length. While smaller sizes in Species 2 and Species 3 may represent adaptations to various microhabitats or prey availability, larger body sizes in Species 1 may give ecological advantages such as improved prey capture efficiency or competitive supremacy. These differences in size may potentially have an impact on predator avoidance and reproductive tactics. Analogous research in Mantodea has documented comparable interspecific variations in body size associated with behavioral adaptations and habitat preferences (e.g., Maxwell & Frinchaboy, 2016; Oufiero,

2020). Sexual selection, resource partitioning, and habitat structure are examples of selective pressures that can lead to morphological divergence and influence the evolutionary paths of species. Additional studies that include more characteristics and ecological factors would assist elucidate the morphological patterns. These results emphasize the importance of conserving mantid populations as natural regulators of pest species in agro ecosystems.

### **Conclusion**

Distinct morphological, behavioral, and habitat traits show adaptive divergence.

Sympatric mantid species coexist by niche differentiation.

Findings provide baseline data for ecological and conservation studies in Sindh.

The ANOVA confirms that the male body lengths of the three mantid species differ very significantly. The difference is not subtle but clear and statistically robust.

The ANOVA revealed a statistically significant variation in female body length among the three mantid species, indicating that interspecific differences are strong and well supported.

The ANOVA confirmed that male body lengths among the three mantid species differed very significantly ( $p < 0.001$ ). Similarly, female body lengths also varied significantly, confirming strong interspecific differences.

### **Conflict of interest:**

The authors declare no conflict of interests.

### **Data Availability**

All data and materials are present in the manuscript.

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