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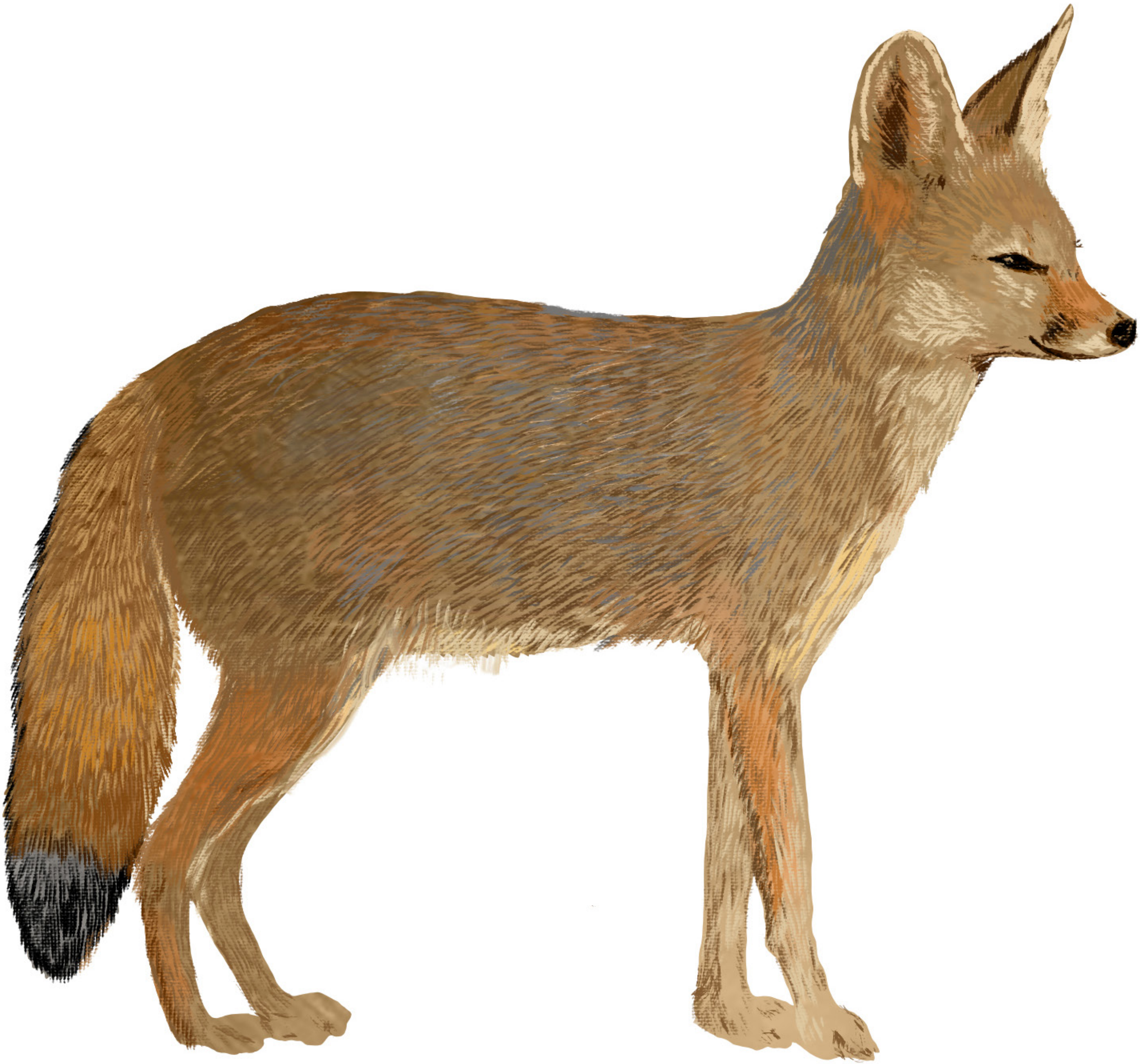

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COMMUNICATION

Preference and plasticity in selection of host for oviposition in Black Marsh Dart *Onychargia atrocyana* Selys, 1865 (Odonata: Zygoptera: Platycnemididae)

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Abstract: An experimental study was conducted in a natural pond to investigate host plant preference and plasticity in damselfly *Onychargia atrocyana*. The hypothesis was that this species has a host preference for oviposition and also sufficient plasticity to use other hosts in the absence of the preferred host. After mating, tandems were observed landing on plants in search of suitable oviposition substrates. The majority of landings occurred on *Alternanthera philoxeroides*, followed by *Colocasia esculenta* and *Commelina diffusa*. The frequency of landings on *A. philoxeroides* and *C. esculenta* was not significantly different, while landings on *C. esculenta* and *C. diffusa* did differ significantly. In the absence of emergent littoral plants, the damselflies exhibited plasticity in host preference and shifted ovipositional substrate by laying eggs on submerged areas of petioles of free-floating *Eichhornia crassipes*. Females of *O. atrocyana* exhibited a flexible oviposition strategy, transitioning from a combination of emergent and submerged oviposition to primarily selecting emergent oviposition in most cases. Additionally, they divided oviposition events into multiple phases when required to ensure successful reproduction. *E. crassipes* supported a higher rate of oviposition compared to other plants. A multiple regression analysis demonstrated that during submerged oviposition water temperature and pH were significant predictors of the duration of submergence.

Keywords: Damselflies, host preference, Marsh Dancer, natural pond, oviposition strategy, reproduction, water temperature.

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Author contributions: PKJ—designing and conducting field work, documentation, analysis and interpretation of results, preparation of initial manuscript. PHM—overall supervision, editing and reviewing the draft manuscript. TB—data analysis, interpretation and preparation of final manuscript which was approved by all the authors.

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INTRODUCTION

Odonates such as damselflies primarily rely on visual cues to find suitable places for laying their eggs (Wildermuth 1992). Damselflies that lay their eggs in plant tissue search for appropriate sites while in flight, then they land, choose an optimal location for inserting their ovipositor, and deposit the eggs (Martens 2001; Lambret et al. 2015a). Females are often selective when it comes to choosing an oviposition site (Martens 1992), which is influenced by specific stimuli, as noted by Martens (2001). Understanding this behavior is important, as ovipositional duration is correlated with clutch size (Martens 1992), which in turn determines brood size. The site of egg deposition holds valuable information regarding the habitat requirements and needs of both adult insects and their nymphs (Corbet 1999). The choice of oviposition location by an ovipositing parent is strongly influenced by oviposition site quality. These habitat characteristics are, in turn, influenced by water chemistry and the successional stage (Toivonen & Huttunen 1995; Pietsch 1996). The physico-chemical characteristics of the water in a given habitat play a crucial role in shaping the distribution patterns of damselflies (Ishizawa 2012; Sugiman et al. 2019; Mafuwe et al. 2021).

According to niche theory, the ecological requirements of an odonate species are influenced by both abiotic (physico-chemical environment) and biotic factors (Soberón & Peterson 2005). Factors like temperature (Hershey et al. 2010) and chemical properties such as pH (Gorham & Vodopich 1992; Rychla et al. 2011; Mafuwe et al. 2021) and TDS (Mafuwe et al. 2021) impact species presence and abundance. The presence of floating macrophytes is also crucial for determining odonate assemblages, as some taxa rely on them for oviposition (Schindler et al. 2003). A recent study by Cadena et al. (2023) further emphasized the impact of climate change on the diversity patterns of odonate groups, revealing clear spatial differences. Therefore, investigating the effects of water parameters such as temperature, pH, TDS, etc. is vital in understanding the reproductive strategies of odonates. These parameters provide valuable insights into the ecological dynamics of these organisms and help us comprehend the potential impacts of environmental changes on their reproductive behavior.

Onychargia atrocyana is a common damselfly found in India (Jana et al. 2021) and its reproductive behavior has been studied earlier by Jana et al. (2022). The selection of host plant substrate for oviposition is an important aspect in the reproductive success of damselflies that is not well understood in *O. atrocyana.* The aim of the present investigation is to identify the preferred host plant(s) for oviposition in natural environments, explore the plasticity of the species in shifting to other substrates in the absence of a preferred host, and also to assess the effect of changing water temperature, pH, and TDS on oviposition.

The confinement of this species to specific habitats vulnerable to alteration by human activities or natural processes is a significant conservation challenge. Safeguarding the species requires comprehending the reasons behind their persistence and exploring methods for their preservation or restoration. So, the findings can provide insight into the reproductive ecology of *O. atrocyana,* which might have great implications in the conservation and management of wetland ecosystems as well.

METHODS

The present study was conducted in a man-managed pond located at Madhabchak village (22.2650^{0}N, 87.5464^{0}E) in the Paschim Medinipur District of West Bengal, India. The pond was selected for its diverse aquatic vegetation, which included free-floating hydrophytes like *Spirodela polyrhiza* (L.) Schleid, *Pistia stratiotes* L., and *Eichhornia crassipes* (Mart.) Solms; submerged rooted-floating hydrophyte *Nymphaea alba* L.; and emergent littoral plants like *Alternanthera philoxeroides* (Mart.) Griseb., *Colocasia esculenta* (L.) Schott, and *Commelina diffusa* Burm.f. The identification of hydrophytes was after Cook (1996). To ensure equal surface areas for each vegetation type, separate patches of 1.22 x 1.22 m were set up in the pond, each representing a different plant type. These patches were chosen to have more than 95% coverage of the respective vegetation type. The standard procedure of visual estimation by the quadrat method (Jaccard 1901) was employed to record the percent coverage of hydrophytes within each patch. All observations were conducted during the period from 1 July to 15 September 2022, with observations taking place between 0600 h and 1600 h local solar time (IST).

Landing events of ovipositing pairs were assessed in undisturbed and clear weather conditions by direct observation. To avoid any misinterpretation regarding substrate choice, a 'positive' choice for substrate was considered when a female in tandem exhibited a backward descent behavior from the landing point to reach the submerged part of the plant, followed by palpation of the plant parts and the commencement of egg placement during the oviposition event, as described in Jana et al. (2022). A total of 136 landing events were observed, and 127 landings were taken into consideration for the calculation of the frequency of selecting a particular plant substrate for oviposition. From these, 112 cases were used to measure the clutch size, where females in tandem completed their egg-laying event in a single attempt without changing hosts.

To test the hypothesis that the species has a substrate preference for oviposition, a one-sample binomial test was employed. This test compared the observed landing events on specific plant substrates to an expected probability based on the null hypothesis that no substrate preference exists. A corresponding 95% Clopper-Pearson (exact) confidence interval was also calculated to evaluate the precision of the estimation. When the 95% confidence intervals for the two groups did not overlap it was assumed that there was a significant difference between them, indicating that the true population means were likely to be distinct as suggested by Lambret et al. (2015b). The duration of oviposition was measured with a mobile stopwatch in minutes. Number of eggs deposited was determined by counting eggs on substrate collected 24 h after oviposition under a binocular microscope. The rate of oviposition was calculated following Martens (1992) based on the first 12 cases.

To investigate plasticity and habitat shift from the preferred plant substrate to another substrate in the absence of preferred host plants, observations were also conducted in the same pond from 16 to 25 September 2022. After heavy rains in September, most of the emergent vegetation was submerged, except for *C. esculenta* and *A. philoxeroides*. Petioles of *C. esculenta* and apical parts of *A. philoxeroides* of the entire pond were cut just below the water surface and removed. The *E. crassipes* plants were taller than 0.25 m. To ensure the accurate identification of individual females and avoid potential bias from repeated observations, females were caught during the post-ovipositional rest and marked on the thorax with a permanent alphanumeric code using a red-colored marker after each observation. Based on the above- specified criteria, 30 oviposition events on *E. crassipes* were included in the statistical analysis.

A comprehensive study was conducted weekly to investigate the relationship between fluctuations in water temperature, pH, and total dissolved solids (TDS) with the duration of submerged oviposition.

A total of 32 oviposition events occurring between February and September 2022 were examined within a one-meter radius of the substrate. Water parameters were recorded with the help of a portable water analyzer (WQC-22A).

The submergence period data were exclusively collected during instances of oviposition on *A. philoxeroides*, as other plants were either regularly replaced or not consistently available throughout the year at the water level. Pearson correlation was used to assess the associations between water parameters and the duration of submerged oviposition. Additionally, a multiple regression analysis was performed to examine how well temperature, pH, and TDS predict the duration of the submergence period.

All statistical analyses, including the 95% Clopper-Pearson (exact) confidence interval, one-sample binomial test, Pearson correlation, and multiple regression analysis, were performed using SPSS version 26 (IBM Corp. 2019).

Throughout the study, utmost care was taken to ensure the well-being of the observed organisms. No harm was caused to any living organisms during the entire course of the research.

RESULTS

After mating, tandems of *O. atrocyana* landed on stems of *A. philoxeroides* and *C. diffusa* as well as on the petioles of *C. esculenta* in search of a suitable oviposition site. Then they started descending downwards to reach the water surface for oviposition and the female started probing the vegetation with her ovipositor for a suitable oviposition site. Of the 136 landings (Table 1), 51% landed on *A. philoxeroides* (n = 69), followed by *C. esculenta* (33%, n = 45) and *C. diffusa* (10%, n = 13). Landings were also observed on *E. crassipes* (5%, n = 7) and *P. stratiotes* (1%, n = 2) but egg-laying did not occur perhaps due to lack of suitable submerged plant parts available for palpation and insertion of eggs. Pairs were not observed to land on *S. polyrhiza* or *N. alba* for oviposition. Neither they were seen to palpate on leaves or deposit eggs on dead plants, which indicates that *O. atrocyana* prefers live stems and petioles for oviposition.

There were 127 successful landings where a female palpated after landing. The null hypothesis was that the proportion of *O. atrocyana* landings and palpation on each plant type was equal. The observed proportions of damselflies landing on *A. philoxeroides* and *C. esculenta* were 54% and 35%, respectively. When the confidence intervals were considered, the range for *A. philoxeroides* (45% to 63%) was higher than the range

Table 1. Aspects of oviposition in natural environment.

Types of hydrophytes	Plant	Frequency (%) of landing (n)	Palpated (Yes/ No)	Plant parts palpated	Clutch size. Mean ± SE (Range)	Rate of egg deposition (no. of eggs/m), Mean ±SE (range), n	Type of oviposition
Free- floating	*S. polyrhiza*	-	-	-	-	-	-
	P. stratiotes	1% (n = 2)	No	-	-	-	-
	E. crassipes	5% (n = 7)	No	-	-	-	-
Rooted- floating	*N. alba*	-	-	-	-	-	-
Emergent littoral	*A. philoxeroides*	51% (n = 69)	Yes	Stem	331 ± 8 (227–451)	23.54 ± 0.4 (21.4–26.8), 12	Emergent & submerged
	C. esculenta	33% (n = 45)	Yes	Petiole	430 ± 11 (342–577)	29.2 ± 0.7 (25–33.3), 12	Emergent & submerged
	C. diffusa	10% (n = 13)	Yes	Stem	288 ± 18 (189–416)	25.1 ± 1.2 (16.1–41.9), 12	Emergent & submerged

Table 2. Binomial test with confidence interval and p-value regarding preference for landing of *Onychargia atrocyana* on three hydrophytes.

Hydrophyte	No. of females landed & palpated	Observed proportion	Expected proportion	95% Clopper-Pearson (exact) confidence interval	Binomial p-value
A. philoxeroides	69	0.5433	0.333	45.3–63.2 %	0.375
C. esculenta	45	0.3543	0.333	27.2–44.4 %	0.001
C. diffusa	13	0.1024	0.333	5.6–16.9 %	0.000

for *C. esculenta* (27% to 44%) indicating its preference for *A. philoxeroides* (Figure 1, Table 2). The binomial p-value for landing and palpation (Table 2) also indicates that the proportion of landing on both *C. esculenta* and *C. diffusa* was significantly less as compared to those on *A. philoxeroides*.

In all 127 cases, the females went submerged, of which 15 cases involved the females in tandem ovipositing in multiple substrates. Out of the 127 successful landings, only 112 cases were selected to measure the clutch size, as these females completed their egg-laying in one attempt without switching their host. Among the different substrates, *C. esculenta* petioles exhibited the highest number of eggs laid, followed by *A. philoxeroides* and *C. diffusa*, as depicted in Figure 2 and Table 1. Likewise, the rate of oviposition was also maximum on *C. esculenta* petioles, averaging 29 eggs per minute, compared to other substrates, where it was 23 and 25 eggs per min on the stems of *A. philoxeroides* and *C. diffusa*, respectively, as shown in Figure 3. In all cases oviposition occurred in two phases – emergent and submergent.

In the absence of emergent littoral-associated plants, out of 30, 28 tandem (93%) landed on *E. crassipes,* and only two (7%) though initially landed on *P. stratiotes*, but due to want of oviposition they also landed ultimately on *E. crassipes* (Table 3). Thus, all the 30 tandems landed

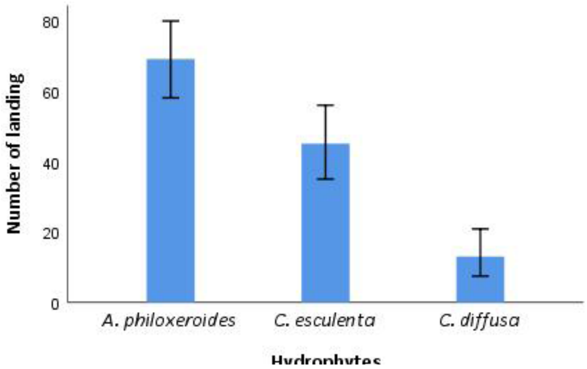

Figure 1. Preference as oviposition substrate by *Onychargia atrocyana* based on a number of landings in a natural habitat with 95% confidence limit.

on the upper portion of the inflated petiole and started backward descending movement, as they normally do. In doing so, females oviposited on the submerged parts of the base (Image 1) in a zigzag manner dragging their male partner all along. Submerged oviposition was seen in only 3% of cases. Moreover, in the absence of sufficient oviposition sites, females did not oviposit in a single attempt but divided the egg- laying process into multiple emergent egg- laying rounds, hopping from one petiole to the other. A female deposited on average 203 eggs in the first attempt which was roughly one- half of the total average number of eggs laid (368). The rate of

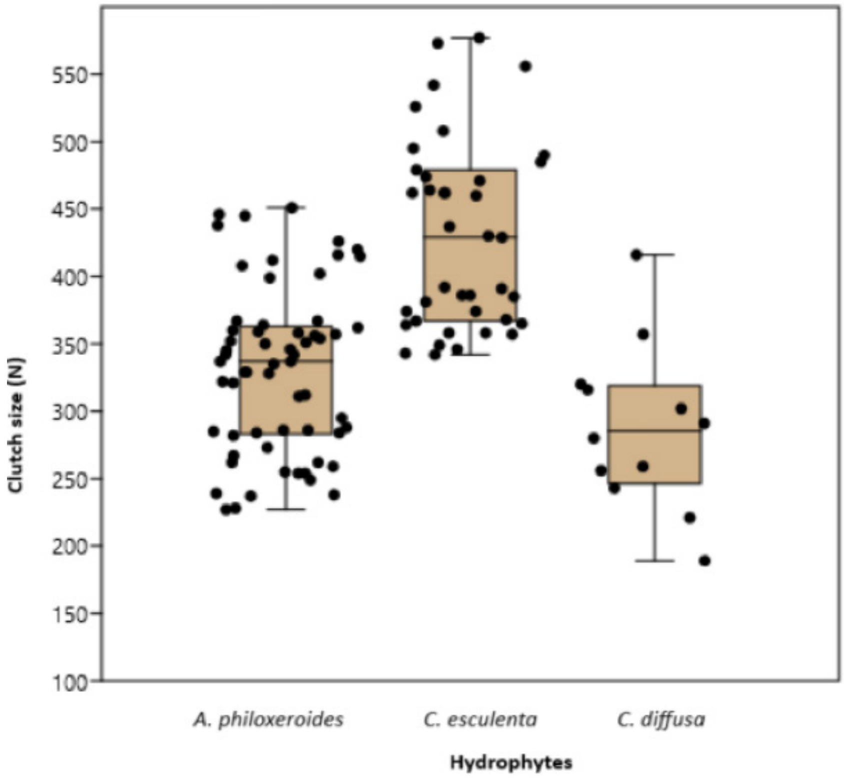

Figure 2. Clutch size of *Onychargia atrocyana* on different hydrophytes.

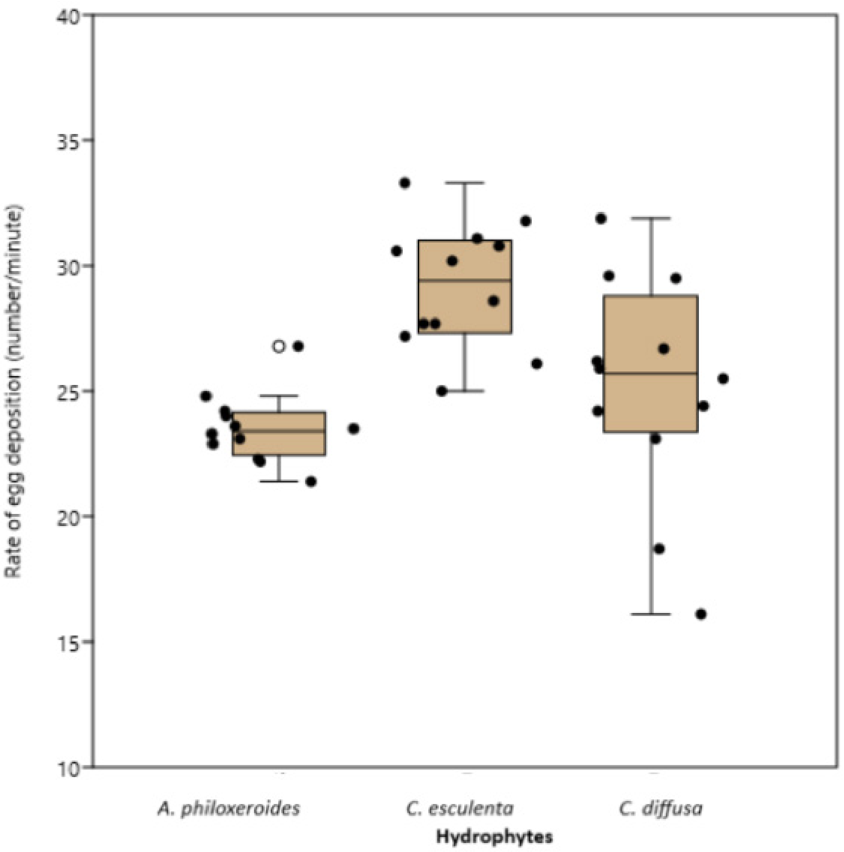

Figure 3. Rate of egg deposition of *Onychargia atrocyana* on different hydrophytes.

Table 3. Aspects of oviposition in an altered environment.

Types of plant	Name of plants	Frequency (%) of landing (n)	Palpated (Yes/No)	Plant Parts palpated	No. of eggs Mean ± SE (range), n	Rate of egg deposition (eggs/m), Mean ± SE (range), n	Type of oviposition
Free-floating	*E. crassipes*	93% (n = 28)	Yes	Petiole	Total eggs 368 ± 11 (198–465), 30		97% emergent & 3% submerged oviposition
					In 1st attempt 203 ± 8 (86–274), 30	31.6 ± 0.9 (26.5–37.3), 12	
	P. stratiotes	7% (n = 2)	No	-	-	-	-

Table 4. Pearson correlation between three water parameters and submergence ovipositional duration (SOD) of *Onychargia atrocyana*.

Factors	M ± SE (Range)	r			
		Temp	TDS	pH	SOD
Temp.	28.93 ± 0.38 (23.8–32.5)	-	0.861**	-0.822**	0.701**
TDS	232.5 ± 3.29 (198–278)	0.861**	-	-0.843**	0.550**
pH	6.64 ± 0.08 (5.2–7.6)	-0.822**	-0.843**	-	-0.380*
SOD	523.3 ± 10.8 (435–636)	0.701**	0.550**	-0.380*	-

** p <0.01 | *p <0.05.

egg deposition on *E. crassipes* during plasticity was on average 32 eggs/min .

Pearson correlation between temperature, TDS, and pH of the water was found to be strongly significant (p <0.01) with each other but the correlation between pH and the other two factors was negative. Likewise, submergence ovipositional duration (SOD) was also found to have a significant positive correlation with water temperature, and TDS but a negative correlation with pH (Table 4). It was also noted that submersion oviposition took place within a temperature range of 23.8–32.5 °C, a pH range of 5.2–7.6, and a TDS level ranging 198–278 ppm. The majority of submergent oviposition occurred within a narrower temperature range of 27.5–30.5°C, a pH range of 6.5–6.9, and a TDS level ranging 223–243 ppm (Figure 4a,b,c). An analysis of the multiple correlations reveals that the predictor water factors have a moderately strong positive relation with SOD (R = 0.783) and the R^2 value explains only 61% of the variability in the duration of submergence by the predictor variables. ANOVA, indicates that the overall regression model is strongly significant (F = 14.807, p <0.001). Results also suggest that temperature and pH are significant predictors of the duration of the submergence period while TDS is not (Table 5).

Table 5. Correlation between water parameters and SOD.

Water parameters	Standardized β	t	R	R^2	ANOVA (F)
Temperature	1.124	4.557**	0.783	0.613	14.807**
TDS	0.138	0.528			
pH	0.659	2.830*			

*p <0.01 | **p <0.001.

DISCUSSION

The findings presented in this study provide insights into the oviposition behavior of *O. atrocyana,* which exhibit its preference for *A. philoxeroides* and *C. esculenta* over other hydrophytes. *C. esculenta* petiole is used only during the rainy season when the water level in the pond rises. It is interesting to note that *O. atrocyana* has a preference for stems and petioles over other parts as oviposition sites. *Platycnemis subdilatata* Selys, 1849*,* a related species, on the contrary, prefers leaves of *Typha angustifolia* (Khelifa et al. 2016). Excessively high substrate stiffness may impede egg laying (Grunert 1995). The role of plant substrate stiffness in the selection of oviposition sites by endophytic zygopteran females has also been demonstrated by Matushkina and Gorb (2007). In *O. atrocyana*, choosing stem or petiole over

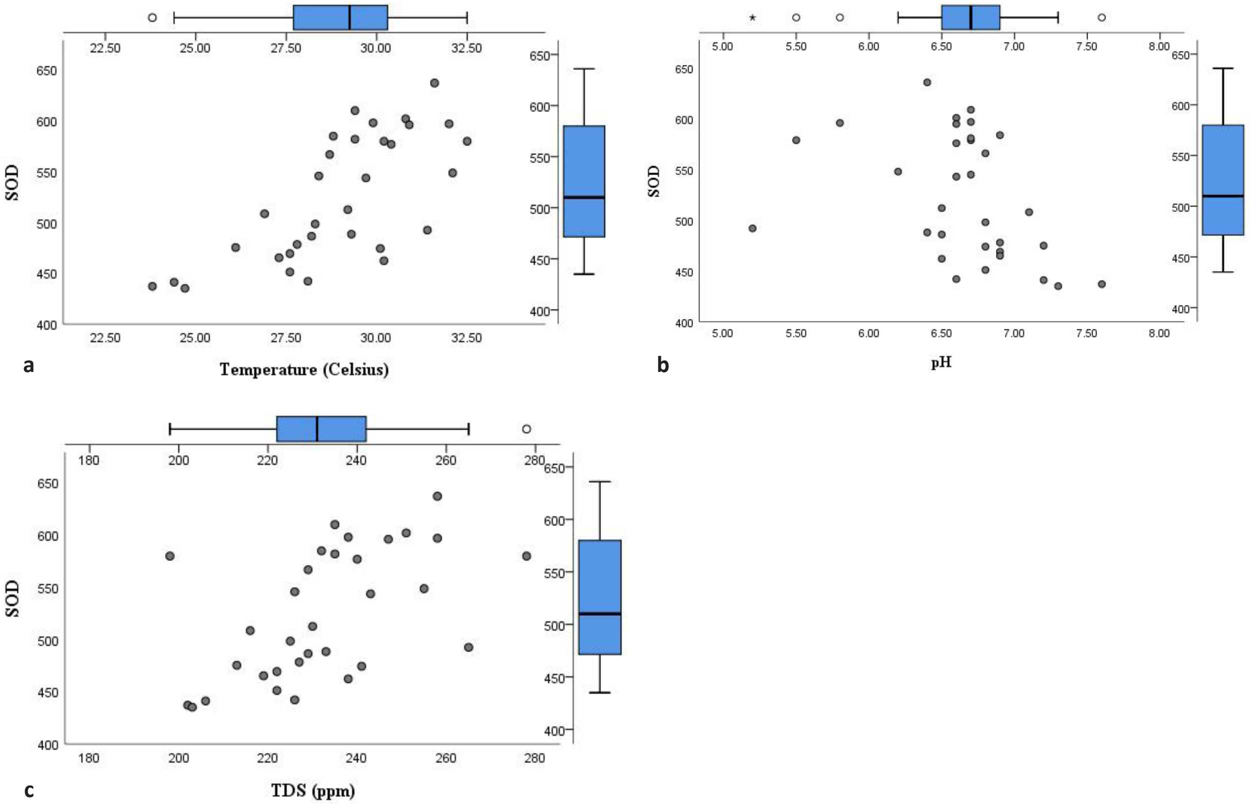

Figure 4. Regression plots showing the relationship between SOD and (a) water temperature, (b) pH, and (c) TDS.

Image 1. Eggs deposited by an *Onychargia atrocyana* female at the base of the petiole of *Eicchornia crassipes* during its first attempt.

the leaf as a substrate during submerged oviposition might be an effective anti-predator strategy as suggested by Harabiš et al. (2015) who opined that eggs near the water surface are more susceptible to parasitoids and showed higher mortality. The submerged oviposition strategy and selection of oviposition sites both may serve a protective function against abiotic stress like egg desiccation (Fincke 1986; Lambret et al. 2018) and might have evolved as a way to exploit additional oviposition sites in underwater substrates (Miller 1994) as well as to reduce sexual harassment during oviposition (Fincke 1986). The rate of egg deposition also varied among different plants. This suggests that the suitability of an oviposition site depends on the structural suitability of plant parts for the insertion of eggs.

The findings align with previous research by Martens (1992) and Lambret et al. (2015a), all of which have highlighted the influence of substrate characteristics on egg deposition rate. Lambret et al. (2015a) put forward a hypothesis suggesting that a higher egg deposition rate among adults offers advantages in terms of minimizing the duration of oviposition bouts. This reduction in oviposition duration serves to decrease the vulnerability of detection by predators and also leads to an increase in foraging time (Martens 2001). Consequently, a heightened rate of egg deposition on *E. crassipes* can be considered beneficial for *O. atrocyana.* In the absence of emergent plants, this species can shift its oviposition plant and substrate. It prefers the petioles of floating hydrophyte *E. crassipes* only in the absence of stemmed emergent hosts. This indicates habitat plasticity. The species displays remarkable habitat plasticity, as it shifts its oviposition plant and substrate in the absence of emergent plants, demonstrating adaptability in diverse environmental conditions. Females of *O. atrocyana* even alter their oviposition strategy, transitioning from a combination of emergent and submerged oviposition to predominantly selecting emergent oviposition (>96% of cases) and breaking oviposition events into multiple phases when necessary to ensure reproductive success. They quickly adjusted their choice toward an unusual host substrate. Also, such shifts in oviposition sites and changes in strategies are important aspects of their pre-ovipositional parental care which depends on the relative availability of oviposition sites. Though ovipositing tandems were not disturbed by the other conspecific males during emergent oviposition, there might exist undisclosed competition among ovipositing tandems, which could potentially be prevented in submerged oviposition as suggested by Rowe (1987).

In the present study water temperature and pH were identified as predictors of the SOD. These findings conflict with those of Sugiman et al. (2019) who found that in *Pseudagrion pruinosum* (Burmeister, 1839), TDS and water temperature were negatively correlated but pH had a positive correlation. In contrast, Mafuwe et al. (2021) found the distribution of adult and larval platycnemid damselflies was positively correlated with both pH and TDS. Martens (1992) found a minor influence of water temperature on oviposition in *Platycnemis pennipes* (Pallas, 1771) while Ishizawa (2012) observed a strong correlation between the onset of oviposition and ambient temperature, duration of oviposition exhibited a weak correlation with temperature in *Sympetrum frequens* (Selys, 1883). Purse & Thompson (2009), on the contrary, opined that habitat factors such as pH and water temperature were not reliable predictors of oviposition duration in *Coenagrion mercuriale* (Charpentier, 1840). Dolný et al. (2014) demonstrated that the type of submerged plants influences underwater oviposition in Lestidae. These contrasting findings suggest that different species of damselflies exhibit diverse responses to pH, TDS, and water temperature which warrant further research to understand the underlying mechanism.

In view of the present-day changing scenario of natural landscape, it is proposed that water bodies with small patches of *A. philoxeroides*, *C. diffusa*, *E. crassipes*, and *C. esculenta* be established which would not only provide suitable habitat for damselflies like *O. atrocyana* but also help in their conservation.

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