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Thermal Constraints Drive Elevational Divergence in Mate-guarding Behaviour of Dragonflies and Damselflies (Odonata) in the Bhagirathi River Basin, Uttarakhand, India

Mate-guarding behaviour is a key reproductive strategy in Odonata, yet its variation across Himalayan elevational gradients remains poorly documented. This study examined mate-guarding behaviour in 53 species of dragonflies and damselflies observed across freshwater habitats of the Bhagirathi River Basin in Uttarakhand, Western Himalaya. Behavioural observations recorded copulation duration, guarding distance, ambient temperature and copulation success across multiple elevations. Results revealed substantial interspecific variation in mating investment, with prolonged copulation associated with higher reproductive success. Most dragonflies exhibited contact guarding, whereas damselflies showed a broader spectrum including spatial guarding strategies. These findings highlight the influence of thermal environments and behavioural investment on reproductive success in Himalayan odonate communities.

Key words: Odonata, Mate guarding, Bhagirathi basin, Western Himalaya, Reproductive ecology.

This study presents a comprehensive analysis of mate-guarding behaviour in 53 species of dragonflies and damselflies across the Bhagirathi River Basin, revealing how copulation duration, guarding strategies, and thermal conditions influence reproductive success along Himalayan freshwater elevation gradients.

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Introduction

Mate guarding is a common reproductive strategy in insects, particularly in Odonata, where males guard females during or after copulation to reduce sperm competition and ensure paternity (Corbet, 2004; Córdoba-Aguilar, 2009). In dragonflies and damselflies, guarding occurs either as contact guarding, where males remain attached to females in tandem during oviposition, or non-contact guarding, where males defend females from nearby perches.

Odonata research in India has a long history encompassing taxonomy, ecology, and distributional studies (Fraser, 1933, 1934, 1936; Prasad and Varshney, 1995; Dijkstra and Kalkman, 2012). Odonates are closely associated with freshwater ecosystems (Kalkman *et al*., 2007; Bried *et al*., 2020; Dijkstra *et al*., 2013) and respond strongly to environmental gradients such as temperature, hydrology, and habitat structure (Subramanian, 2005). Due to their ecological sensitivity and well-defined life histories, they are widely used as indicators (Subramanian and Babu, 2018; Uniyal *et al*., 2022) of freshwater ecosystem health and climate-driven ecological change (Kalkman *et al*., 2007; Bried *et al*., 2020).

Mountain systems such as the Western Himalaya exhibit steep environmental gradients that influence species distribution and life-history traits (Mani, 1974; Singh and Singh, 1992). Although odonate diversity in the Himalaya has been increasingly documented but their reproductive behaviours remain poorly studied (Subramanian and Babu, 2018; Kalkman *et al*., 2020; Kumar and Prasad, 1981). Previous studies from the Western Himalaya have documented diverse odonate assemblages associated with riverine and forested habitats (Uniyal *et al*., 2000; Kumar and Sharma, 2003). Recent studies have highlighted

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increasing threats to odonate populations due to habitat alteration, climate change, and anthropogenic pressures (Bried *et al*., 2020; Tang and Visconti, 2020).

The Bhagirathi River Basin in Uttarakhand (Fig. 1), a major headwater of the Ganga River, supports diverse freshwater habitats across a wide elevational range. These habitats provide breeding grounds for a rich assemblage of dragonflies and damselflies (Bhardwaj *et al*., 2016).

This study investigates mate-guarding behaviour across multiple odonate species in the Bhagirathi basin, examining variation among species and assessing how copulation duration and guarding distance influence reproductive success. The findings provide insights into

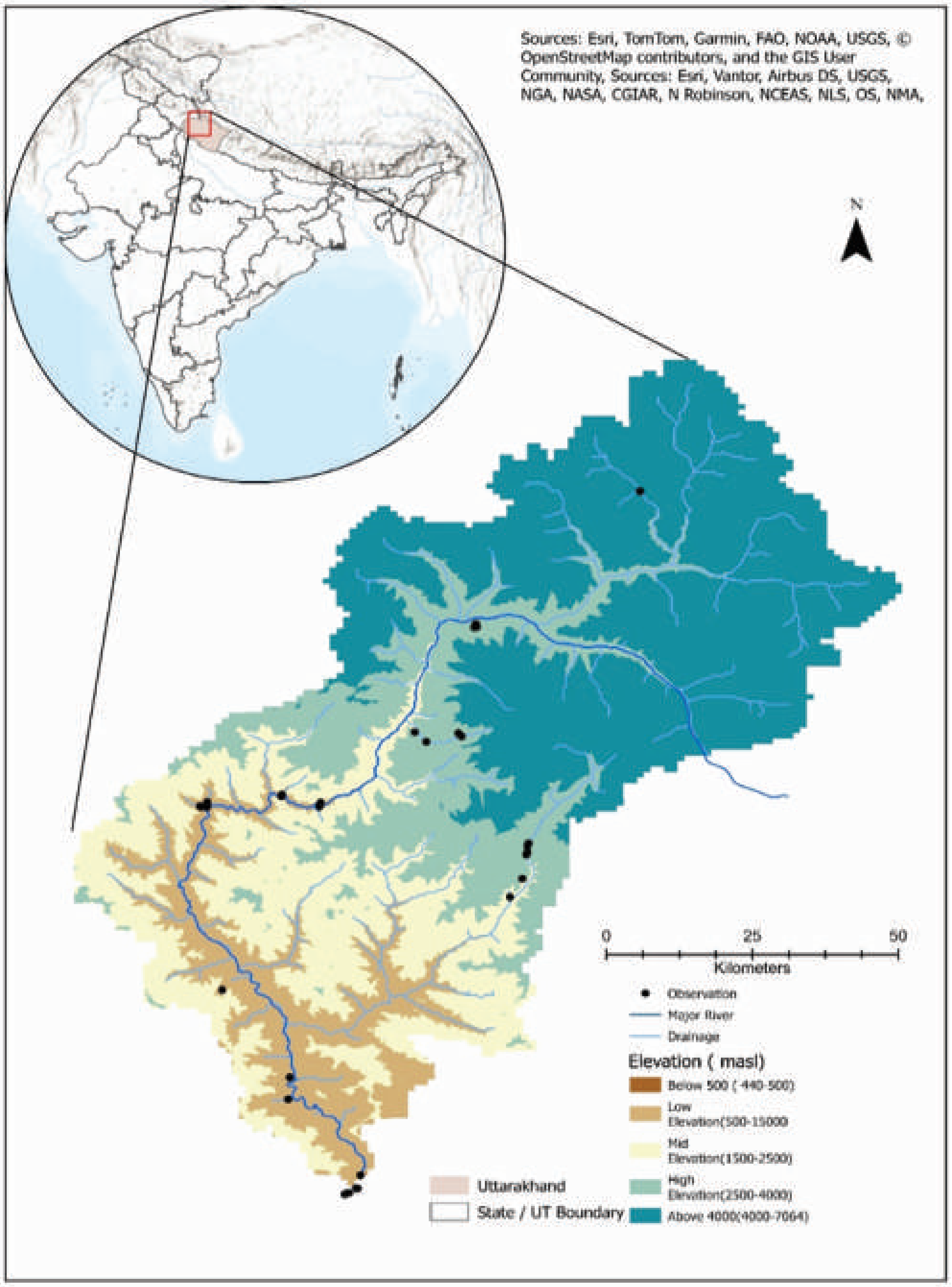

Fig. 1 : Elevation-Stratified study area and sampling locations in the Bhagirathi river basin for Mate-Guarding behaviour analysis in Odonata

the reproductive ecology of Himalayan odonates and contribute baseline information for freshwater biodiversity conservation.

Study Area

Habitat structure, hydrology, and vegetation composition are known to influence odonate assemblages and behaviour (Balzan, 2012; Husain, 2018). The study was conducted in freshwater habitats of the Bhagirathi River Basin, Uttarakhand (Fig. 1), India, in the Western Himalaya. Originating from the Gangotri Glacier, the basin spans a wide elevational gradient from alpine zones to subtropical foothills. Sampling sites included streams, riverbanks, forest wetlands, irrigation canals, and ponds across elevations. The region shows strong climatic seasonality with cold winters, monsoon-dominated summers, and marked temperature variation along elevation gradients, influencing the life cycles and breeding activity of odonates.

Material and Methods

Sampling period

The study was conducted in the Bhagirathi River Basin, encompassing diverse freshwater habitats such as streams, riverbanks, and riparian zones across elevational gradients (Plates 1 & 2). Field surveys were

Plate 1 : Representative aquatic habitats across elevation gradient—high-altitude meadow lakes **(A, B, D),** glacial river stream **(C),** and montane perennial streams **(E, F).**

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carried out from 2017 to 2019, covering multiple breeding seasons. Sampling was conducted during the pre-monsoon (March–June) and monsoon (July–September) periods, corresponding to peak emergence and reproductive activity of Odonata in montane ecosystems (Corbet, 2004). Maximum species richness and mating activity were observed during the pre-monsoon and early monsoon phases.

Species Identification and Selection

Fieldwork was conducted by a trained research team, with member's assigned roles including species identification, behavioural observation, and environmental data recording to ensure consistency and accuracy. Breeding behaviour of a total of 53 Odonata species were recorded, comprising 29 Anisoptera (Plates 3, 4, 5) and 24 Zygoptera (Plates 6, 7, 8). Species were selected based on observable mating behaviour, habitat representation, and adequate sample size.

Species identification was carried out using standard taxonomic keys, including The Fauna of British India, Odonata Volumes I–III and Dragonflies of India – A Field Guide. Identification was primarily based on visual observation and photographic documentation, supplemented by opportunistic capture–release using insect nets for difficult taxa (Fraser, 1933, 1934, 1936; Subramanian, 2005; De *et al.*, 2021). All individuals were released unharmed following identification.

Plate 2 : Representative aquatic habitats across elevation gradient—rocky river channel **(A),** reservoir **(B),** small hill stream **(C),** cascade stream **(D),** boulder-bed forest stream **(E),** and riparian meadow wetland **(F).**

Behavioural Observations

Field sampling was conducted using a belt transect approach along riparian habitats and water bodies to systematically record species presence and activity (Krebs, 1999). Transects of fixed width were surveyed, and all individuals encountered within the transect area were documented.

Following transect-based surveys, behavioural observations were conducted using focal animal sampling with continuous recording (Altmann, 1974). Individuals detected during transect walks were selected for detailed observation within defined focal zones of 5–10 m radius to minimize disturbance. Behavioural sequences were recorded from the initiation of tandem formation until completion of copulation or oviposition.

Copulation duration was measured using a digital stopwatch from tandem linkage to separation or oviposition completion. For each observation, species identity, copulation duration, guarding distance, ambient

Plate 3 : Mate-guarding and reproductive behaviours in Dragonflies- *Anax nigrolineatus* **(A–D):** non-contact guarding **(A),** contact guarding (tandem) **(B),** territorial attack posture with legs extended **(C),** and territorial hovering **(D);** *Orthetrum luzonicum*-copulation wheel position **(E);** *Cordulegaster brevistigma*—non-contact oviposition on a mossy rock **(F).**

temperature, copulation success, and number of observations were recorded. Mate-guarding behaviour was classified as contact guarding, non-contact guarding, or mixed guarding (Alcock, 1994; Córdoba-Aguilar, 2009).

Simultaneously, male territorial behaviour was documented, including perch defense, aggressive interactions (chasing and displacement), and territory occupancy duration. The association between territoriality and mating success was evaluated by recording whether mating events occurred within defended territories or non-territorial contexts, as territorial behaviour influences access to mates and oviposition sites (Alcock, 1994; Corbet, 2004).

(A) (B) (C) (D) (E) (F)

Plate 4 : Mate-guarding and reproductive behaviours in Dragonflies- *Orthetrum triangulare* **(A, B):** non-contact guarding while searching for oviposition site **(A)** and non-contact oviposition **(B);** *Sympetrum* hypomelas- copulation wheel position **(C);** *Aeshna petalura*- non-contact oviposition in aquatic vegetation **(D);** *Anax immaculifrons*-territorial guarding while searching for oviposition site **(E);** *Orthetrum pruinosum*-female with visible egg clutch **(F).**

Environmental Data Collection

Ambient temperature was recorded in situ during each behavioural observation using a handheld digital thermometer. Observations were conducted during peak activity hours (**0900–1500 h**) to minimize diel variation in behaviour (Corbet, 2004). Habitat features such as perch availability and proximity to water were also noted to support interpretation of territorial dynamics.

(A) (B) (C) (D) (E) (F)

Plate 5 : Mate-guarding and reproductive behaviours in Dragonflies- *Trithemis kirbyi* **(A, B):** male **(A)** and female **(B),** with stress-induced egg clutch release following capture of a copulated pair; *Sympetrum himalayanum* **(C, D):** female releasing egg clutch under handling stress during identification; *Orthetrum internum* **(E, F):** copulation **(E)** and non-contact guarding with territorial protection **(F).**

Data Analysis

Descriptive statistics (mean ± standard deviation) were calculated for all behavioural variables. Relationships among copulation duration, guarding distance, and copulation success were analysed using correlation and linear regression models. The effect of territorial behaviour on reproductive success was assessed by comparing mating success between territorial and non-territorial individuals. Comparative analyses were performed between Anisoptera and Zygoptera, and across mate-guarding categories. Data visualization included scatter plots, regression fits, and boxplots. All analyses were conducted using R (R Core Team, 2023).

Ethical Considerations

The study followed a non-invasive observational approach with minimal disturbance to natural populations. Capture–release methods were used only when necessary for species identification, and no specimens were collected or harmed during the study.

Plate 6 : Mate-guarding and reproductive behaviours in damselflies - *Indolestes cyaneus* **(A–C):** contact guarding while searching for oviposition site **(A),** exophytic oviposition **(B),** and endophytic oviposition **(C);** *Anisopleura lestoides* -copulation wheel position **(D);** *Ischnura forcipata* **(E, F):** copulation wheel **(E)** and exophytic oviposition **(F).**

Results and Discussion

Mate Guarding Strategies in Dragonflies (Anisoptera)

A total of 152 mating observations belonging to 29 species of dragonflies (Anisoptera) were recorded during the study. The observations revealed considerable interspecific variation in copulation duration, mate-guarding distance, ambient temperature, and copulation success, indicating diverse reproductive strategies among the observed taxa (Figs. 2 a, b, c and Table 1).

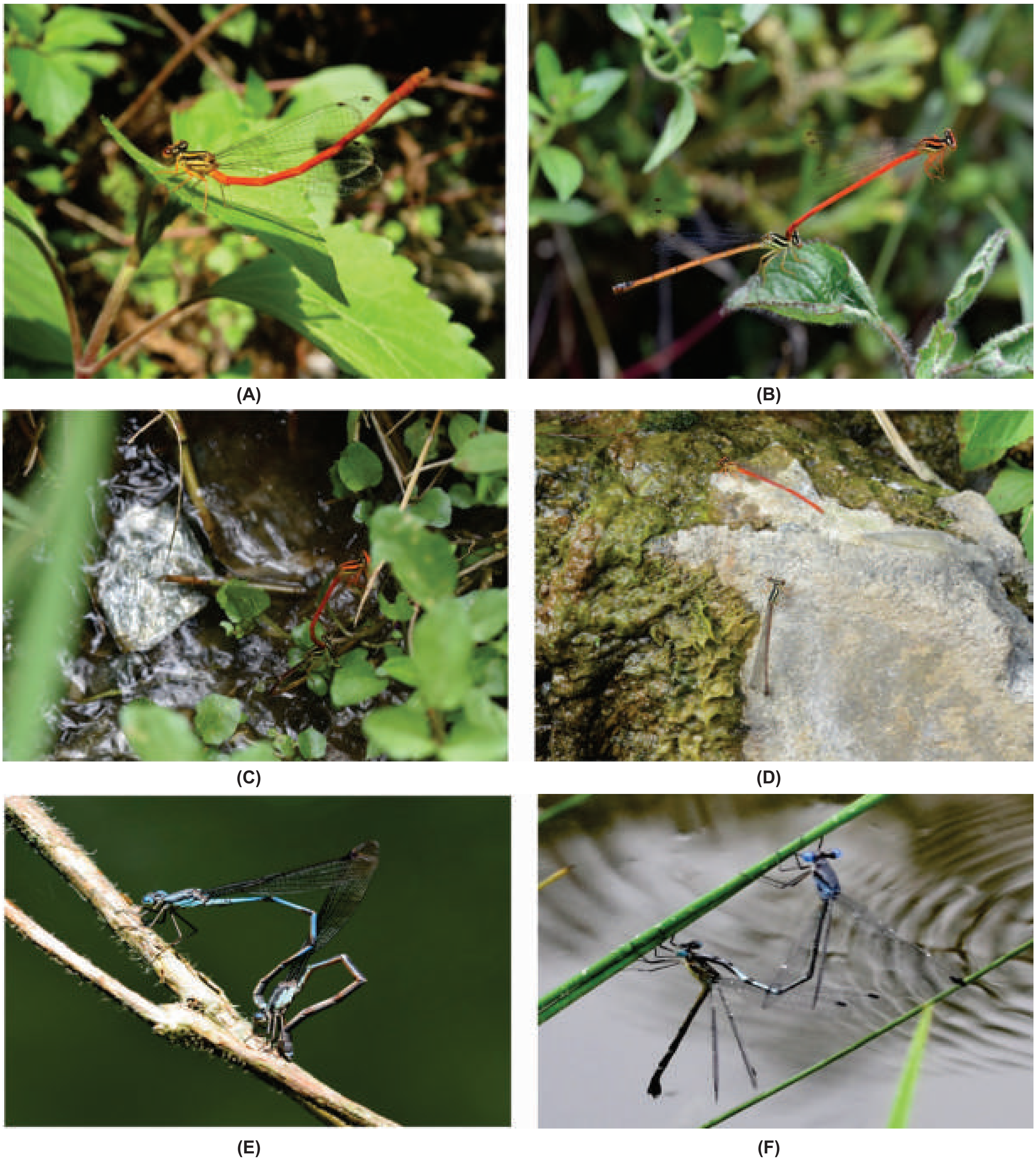
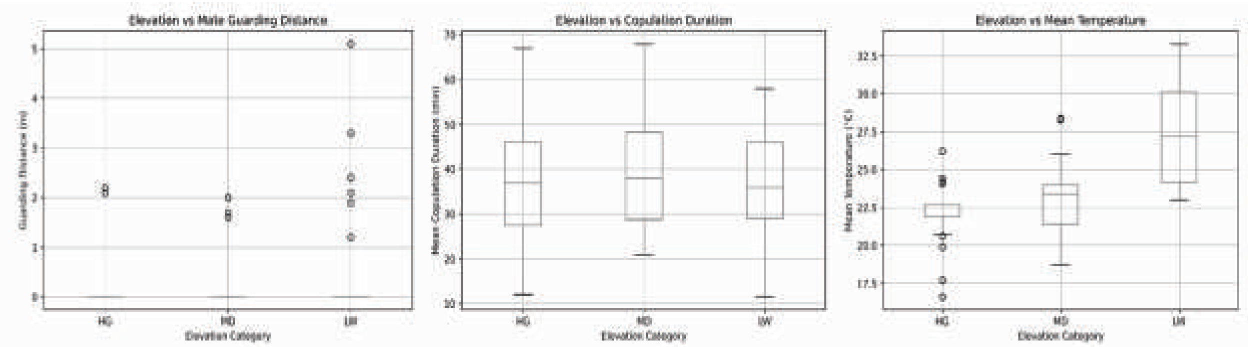


Plate 7 : Mate-guarding and reproductive behaviours in damselflies - *Calicnemia eximia* **(A–D):** territorial display by male **(A),** searching for oviposition site **(B),** contact oviposition in mountain drainage **(C),** and non-contact pair searching for oviposition site **(D);** *Indolestes cyaneus* - contact exophytic oviposition **(E);** *Lestes praemorsus* -contact exophytic oviposition **(F).**

Behavioural diversity in mate-guarding strategies has been widely reported across odonate taxa under varying ecological conditions (Alcock, 1994; Dijkstra *et al*., 2013; Thorp and Rogers, 2011). Variation in habitat structure and microclimatic conditions can significantly influence mating behaviour and territoriality in odonates (Balzan, 2012; Tang and Visconti, 2020). Copulation duration varied substantially among species, ranging from 15 minutes in *Brachythemis contaminata* to 52.00 ± 22.63 minutes in *Onychogomphus biforceps*. Several species belonging to the genus *Orthetrum* showed comparatively longer copulation durations, particularly *Orthetrum internum* (51.63 ± 4.82 min) and *Orthetrum triangulare* (47.00 ± 5.52 min). Intermediate durations

(A) (B) (C) (D) (E) (F)

Plate 8 : Mate-guarding and reproductive behaviours in damselflies - *Ceriagrion fallax*- contact guarding **(A);** *Ischnura rufostigma* **(B, C):** endophytic oviposition **(B)** and exophytic oviposition **(C);** *Ischnura forcipata*- contact endophytic oviposition **(D);** *Megalestes major* - use of high tree perches during territorial conflict while searching for oviposition sites **(E);** *Lestes praemorsus* - contact guarding with endophytic oviposition disturbed by a nearby male **(F).**



(a) (b) (c)

Fig. 2 : Elevational variation in mate-guarding behaviour and temperature in Dragonflies (a,b,c)

Table 1 : Summary of mate-guarding behavioural parameters across observed Anisoptera species.

Species ID	Genus	Species	Sample Size (n)	Duration (min)	Distance (m)	Temp. (°C)	Copulation success (%)
OD01	*Anax*	*nigrofasciatus*	16	27.88 ± 12.38	0.64 ± 1.39	24.74 ± 2.18	73.94 ± 19.29
OD02	*Aeshna*	*petalura*	24	36.08 ± 15.72	0	21.77 ± 3.31	89.00 ± 15.44
OD03	*Ictinogomphus*	*rapax*	17	39.88 ± 6.62	0	29.12 ± 2.07	93.53 ± 7.82
OD04	*Anisogomphus*	*bivitattus*	1	26	0	22.4	79
OD05	*Onychogomphus*	*biforceps*	2	52.00 ± 22.63	0	25.20 ± 2.55	77.00 ± 14.14
OD06	*Paragomphus*	*lineatus*	1	48	0	33.3	77
OD07	*Anotogaster*	*basalis*	3	38.00 ± 1.00	0	22.63 ± 1.24	89
OD08	*Cordulegaster*	*brevistigma*	2	26.50 ± 0.71	0	20.65 ± 0.07	81.5 ± 17.68
OD09	*Acisoma*	*panorpoides*	1	16	0	31.6	67
OD10	*Brachythemis*	*contaminata*	1	15	0	29.7	79
OD11	*Crocothemis*	*servilia*	2	19 ± 0	1.2 ± 1.70	28.15 ± 1.06	86 ± 11.31
OD12	*Orthetrum*	*pruinosum*	6	38.17 ± 5.75	0	27.25 ± 1.50	78.17 ± 2.79
OD13	*Orthetrum*	*sabina*	1	36	0	33	82
OD14	*Orthetrum*	*glaucum*	2	32 ± 8.49	0	32 ± 1.41	83.5 ± 0.71
OD15	*Orthetrum*	*internum*	8	51.63 ± 4.82	0	22.7 ± 0	87.75 ± 2.49
OD16	*Orthetrum*	*luzonicum*	1	38	0	26 ± –	76
OD17	*Orthetrum*	*taeniolatum*	2	40.5 ± 2.12	0	24.85 ± 2.05	75.5 ± 0.71
OD18	*Orthetrum*	*triangulare*	18	47.00 ± 5.52	0.17 ± 0.60	24.18 ± 0.70	75.83 ± 8.49
OD19	*Sympetrum*	*hypomelas*	8	29.75 ± 4.37	0	19.76 ± 1.33	77.38 ± 3.77
OD20	*Sympetrum*	*fonscolombii*	3	31.00 ± 1.00	0.70 ± 1.21	24.2 ± 1.00	79 ± 1.00
OD21	*Sympetrum*	*commixtum*	1	32	0	26.2	81
OD22	*Sympetrum*	*speciosum*	3	34.33 ± 1.53	2.17 ± 0.06	17.7 ± 0	83 ± 1.00
OD23	*Pantala*	*flavescens*	12	43.92 ± 11.87	0	23.78 ± 1.43	87.58 ± 4.49
OD24	*Potamarcha*	*congener*	1	40	3.3	33.3	67
OD25	*Tramea*	*virginia*	3	40.33 ± 8.74	0	21.4 ± 0	86 ± 0
OD26	*Trithemis*	*aurora*	2	41.50 ± 7.78	0	28 ± 0	76.5 ± 0.71
OD27	*Trithemis*	*festiva*	3	31 ± 8.08	0	25.53 ± 2.97	78 ± 1.00
OD28	*Trithemis*	*kirbyi*	2	34 ± 18.38	0	26.1 ± 5.66	79 ± 14.14
OD29	*Palpopleura*	*sexmaculata*	7	32.43 ± 5.50	0	27.24 ± 4.01	75.71 ± 3.20

were recorded for species such as *Aeshna petalura* (36.08 ± 15.72 min), *Pantala flavescens* (43.92 ± 11.87 min), and *Trithemis aurora* (41.50 ± 7.78 min). The observed differences in copulation duration indicate varying levels of behavioural investment during mating among dragonfly species.

Mate-guarding distance showed relatively lower variation compared with copulation duration. Most species displayed contact guarding behaviour, with guarding distances recorded as 0 m, indicating that males remained physically attached to females during oviposition. However, a few species exhibited limited non-contact guarding behaviour. For instance, *Potamarcha congener* showed the highest guarding distance (3.3 m), while *Sympetrum speciosum* (2.17 ± 0.06 m) and *Crocothemis servilia* (1.2 ± 1.70 m) also exhibited moderate guarding distances. These observations suggest that although contact guarding is the predominant strategy in dragonflies, some species adopt spatial guarding tactics.

Copulation success also varied among species, ranging from 67% in *Acisoma panorpoides* and *Potamarcha congener* to 93.53% in *Ictinogomphus rapax*. High success values were also observed in *Aeshna petalura* (89.00 ± 15.44%), *Anotogaster basalis* (89%), and *Pantala flavescens* (87.58 ± 4.49%). Ambient temperature during mating observations ranged between 17.7 °C and 33.3 °C, reflecting the wide environmental conditions under which reproductive behaviour occurred.

Behavioural analysis

Variation in reproductive success among species

Substantial variation in reproductive success was observed among the studied species (Figs. 3, 4, 5). Several taxa achieved success rates above 85%, while others showed comparatively lower reproductive outcomes. Species exhibiting relatively longer copulation durations generally demonstrated higher copulation success, suggesting that increased behavioural investment during mating may enhance reproductive outcomes. For example, species such as *Ictinogomphus rapax*, *Aeshna petalura*, and *Pantala flavescens* showed comparatively higher reproductive success values.

Relationship between copulation duration and reproductive success

Regression analysis revealed a moderate positive relationship between copulation duration and copulation success (Fig. 7). Species with longer copulation durations tended to achieve higher reproductive success, indicating that prolonged mating may increase sperm transfer efficiency or reduce the likelihood of interference by rival males. Similar behavioural patterns have been documented in several Odonate species where prolonged copulation contributes to improved fertilization success (Corbet, 2004; Córdoba-Aguilar, 2009; Thompson, 1990).

Mate-guarding distance and reproductive success

The relationship between mate-guarding distance and copulation success was comparatively weak (Fig. 6). Although a few species exhibited extended guarding distances, these did not consistently correspond with higher reproductive success. This suggests that spatial separation during guarding may not strongly determine mating outcomes in dragonflies. Instead, close physical association between males and females during oviposition appears to be a more common reproductive strategy within Anisoptera.

Behavioural strategy landscape of mate guarding

Integration of copulation duration and guarding distance revealed distinct behavioural patterns among species (Fig. 8). Most species clustered within a region characterized by short guarding distances and moderate copulation durations, indicating a predominant contact-guarding strategy. However, a few species displayed higher behavioural investment, characterized by longer copulation durations combined with moderate guarding distances. These patterns suggest that dragonfly species may adopt different reproductive tactics depending on ecological and behavioural constraints.

Mate-guarding strategy framework

The integrated mate-guarding strategy framework combining guarding distance, copulation duration, and reproductive success further highlighted the importance of behavioural investment in mating outcomes (Fig. 9). Species exhibiting longer copulation durations generally achieved higher reproductive success, as illustrated by larger bubble sizes representing higher reproductive success values. This pattern suggests that temporal investment during mating may play a significant role in determining reproductive success among dragonflies.

Correlation among behavioural variables

Correlation analysis among behavioural traits showed that copulation duration had the strongest

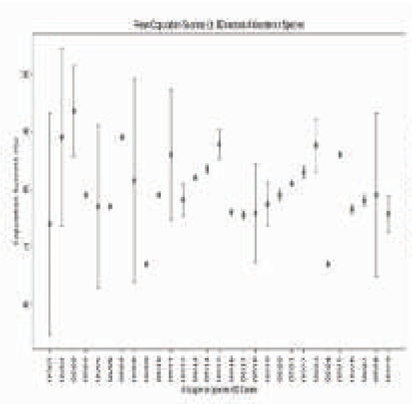


Fig. 3

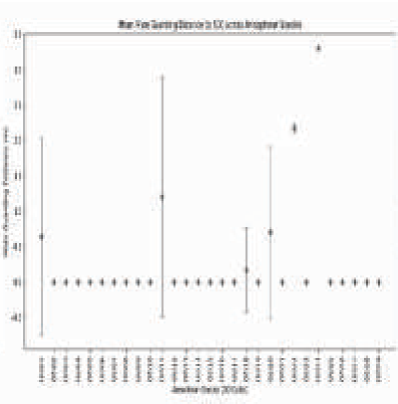


Fig. 4

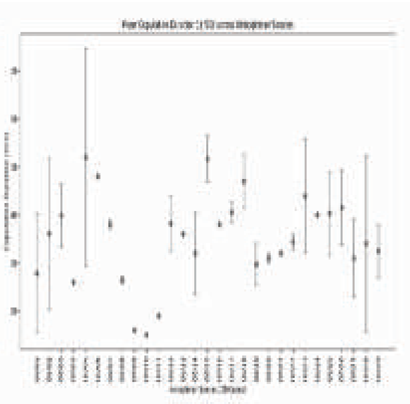


Fig. 5

Fig. 3-5 : Copulation success (%) across Anisopteran species (Mean ± SD), and its relationship with copulation duration and mate-guarding distance across species

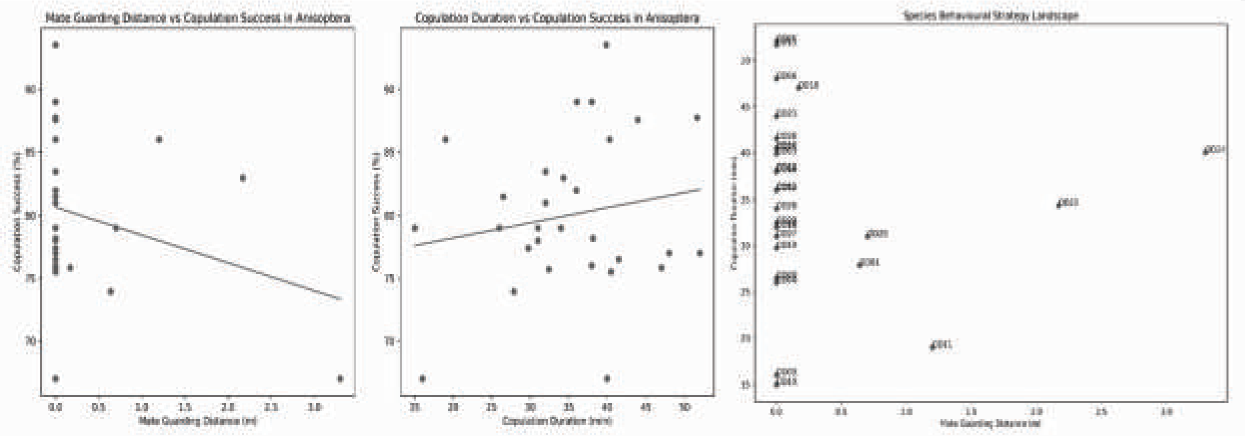


Fig. 6 Fig. 7 Fig. 8

Fig. 6-8 : Behavioural strategy landscape of *Zygopteran* species based on guarding distance and copulation duration.

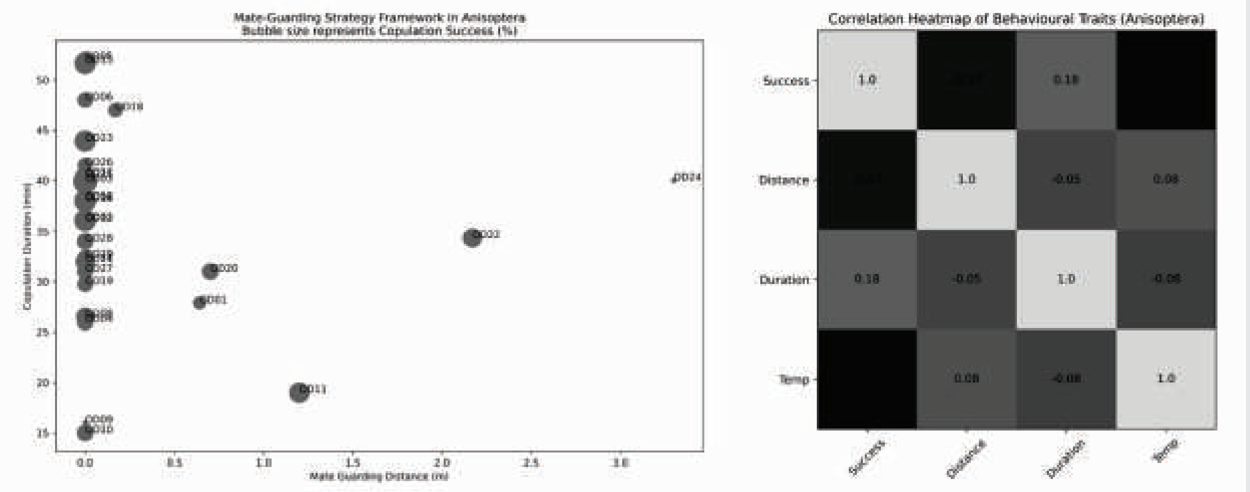


Fig. 9 Fig. 10

Fig. 9-10 : Mate-guarding strategy framework in *Zygoptera* integrating guarding distance, copulation duration, and copulation success &Correlation heatmap showing relationships among behavioural variables.

positive association with copulation success (r ≈ 0.56) (Fig. 10). Guarding distance exhibited only a weak relationship with reproductive success, while ambient temperature showed minimal influence on behavioural variables within the observed range. These findings indicate that reproductive success in dragonflies is influenced more strongly by behavioural investment during copulation than by spatial guarding behaviour.

Overall behavioural pattern

Overall, the results indicate that variation in mate-guarding strategies among dragonfly species is primarily structured along gradients of copulation duration and guarding distance. Reproductive success was more strongly associated with prolonged mating duration than with guarding distance, suggesting that temporal investment during copulation plays a more critical role in determining mating success. The diversity of guarding behaviours observed among species reflects multiple behavioural strategies that may have evolved in response to ecological pressures and reproductive competition, highlighting the adaptive significance of mate-guarding behaviour in dragonfly reproductive ecology.

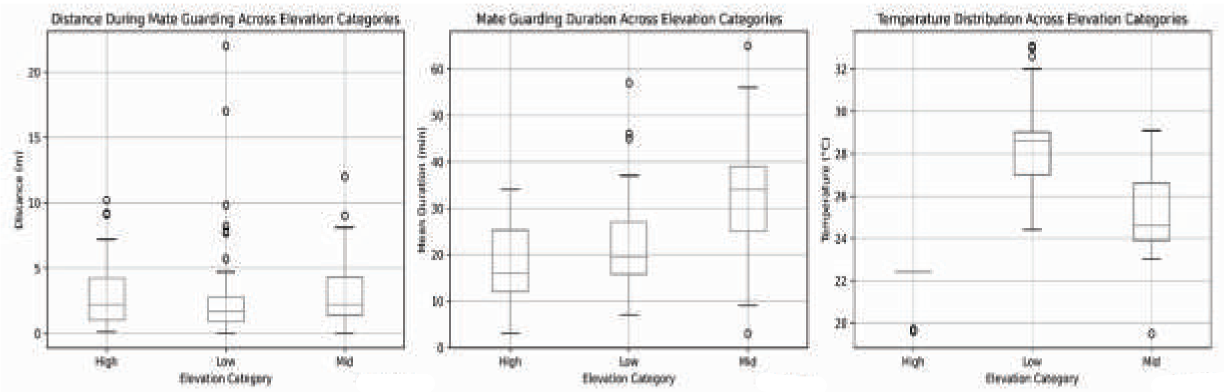
Mate-guarding behaviour in Damselflies (Zygoptera)

A total of 185 mating observations belonging to 24 species of damselflies were recorded across different seasons and elevations. The observations revealed substantial interspecific variation in copulation duration, mate-guarding distance, ambient temperature, and copulation success, indicating diverse reproductive strategies within the assemblage (Figs. 11 a, b, c and Table 2).

Copulation duration varied widely among species, ranging from 14.64 ± 4.21 minutes in *Agriocnemis*

Table 2 : Summary of mate-guarding behavioural parameters across observed *Zygoptera* species.

Species ID	Genus	Species	Sample Size (n)	Duration (min)	Distance (m)	Temperature (°C)	Copulation Success (%)
OD30	*Agriocnemis*	*Pygmaea*	11	14.64 ± 4.21	0.00 ± 0.00	28.93 ± 1.07	73.82 ± 9.21
OD31	*Ischnura*	*Aurora*	7	19.71 ± 8.60	0.71 ± 0.21	29.09 ± 3.41	59.71 ± 3.64
OD32	*Ischnura*	*Senegalensis*	9	15.00 ± 3.04	0.88 ± 0.19	27.07 ± 1.60	66.22 ± 8.87
OD33	*Ischnura*	*Forcipata*	1	16	1	26.6	52
OD34	*Ischnura*	*Rufostigma*	1	17	0.9	26.6	64
OD35	*Ischnura*	*Rubilio*	2	16.00 ± 0.00	0.90 ± 0.00	26.60 ± 0.00	55.00 ± 1.41
OD36	*Pseudagrion*	*Decorum*	3	16.00 ± 1.00	1.33 ± 0.55	28.60 ± 0.00	66.67 ± 2.08
OD37	*Pseudagrion*	*Rubriceps*	15	22.93 ± 7.50	3.63 ± 2.46	27.88 ± 1.33	64.87 ± 12.67
OD38	*Ceriagrion*	*Coromandeliaum*	7	25.57 ± 8.98	3.66 ± 0.98	25.46 ± 4.35	72.86 ± 6.06
OD39	*Lestes*	*Praemorsus*	21	26.62 ± 10.79	5.48 ± 5.30	27.05 ± 1.62	60.48 ± 21.40
OD40	*Indolestes*	*Cyaneus*	33	17.97 ± 9.51	2.94 ± 3.27	22.40 ± 0.00	77.12 ± 14.76
OD41	*Megalestes*	*Major*	13	30.38 ± 12.42	4.45 ± 2.70	24.39 ± 1.50	82.31 ± 9.03
OD42	*Copera*	*Vittata*	1	57	3.3	32.6	89
OD43	*Calicnemia*	*Eximia*	3	56.33 ± 8.74	0.87 ± 0.65	24.13 ± 1.37	77.33 ± 10.26
OD44	*Anisopleura*	*Lestoides*	8	36.63 ± 5.11	2.48 ± 3.52	24.30 ± 0.56	80.25 ± 9.89
OD45	*Anisopleura*	*Comes*	3	40.00 ± 1.00	1.40 ± 0.10	22.43 ± 2.00	76.00 ± 11.00
OD46	*Bayadera*	*Indica*	2	43.50 ± 0.71	1.50 ± 0.14	23.20 ± 0.00	64.50 ± 3.54
OD47	*Neurobasis*	*Chinensis*	4	35.00 ± 0.82	6.75 ± 3.08	31.10 ± 1.73	55.25 ± 13.10
OD48	*Drepanosticta*	*Carmichielli*	2	45.50 ± 0.71	3.20 ± 0.00	26.90 ± 0.00	95.00 ± 2.83
OD49	*Libellago*	*Lineata*	2	23.50 ± 0.71	0.15 ± 0.07	25.40 ± 0.00	72.50 ± 7.78
OD50	*Rhinocypha*	*Quadrimaculata*	17	16.94 ± 5.48	1.98 ± 0.87	27.54 ± 1.38	68.59 ± 19.46
OD51	*Rhinocypha*	*Biforata*	3	28.33 ± 7.23	3.43 ± 0.05	28.93 ± 0.29	80.00 ± 6.56
OD52	*Rhinocypha*	*Trifasciata*	12	28.00 ± 4.22	2.61 ± 0.49	28.17 ± 1.02	76.08 ± 15.44
OD53	*Rhinocypha*	*Unimaculata*	6	26.50 ± 2.51	1.82 ± 0.37	27.17 ± 0.75	72.00 ± 18.11



(a) (b) (c)

Fig. 11 a,b,c : Elevational variation in mate-guarding behaviour and temperature in Damselflies

pygmaea to 56.33 ± 8.74 minutes in *Calicnemia eximia*, indicating considerable differences in behavioural investment during mating. Mean mate-guarding distance ranged from 0 m in strictly contact-guarding species to 6.75 ± 3.08 m in *Neurobasis chinensis*, suggesting the presence of both contact guarding and non-contact guarding strategies within the studied taxa.

Copulation success also exhibited marked variation among species, ranging from 52% in *Ischnura forcipata* to 95% in *Drepanosticta carmichaeli*. Ambient temperature during mating observations ranged between 22.4 ± 0.0 °C and 32.6 °C, reflecting the broad environmental conditions under which reproductive behaviour occurred.

Behavioural analysis

Variation in reproductive success among species

Substantial variation in reproductive success was observed among species, with several taxa achieving success rates above 80%, while others exhibited comparatively lower reproductive outcomes. Species displaying longer copulation durations generally showed higher copulation success, suggesting that increased behavioural investment during mating may enhance reproductive outcomes (Figs. 12, 13 & 14).

Relationship between copulation duration and reproductive success

Regression analysis revealed a moderate positive relationship between copulation duration and copulation success (Fig. 15). Species with longer copulation durations tended to achieve higher reproductive success, indicating that prolonged mating may increase sperm transfer efficiency or reduce the likelihood of interference by rival males.

Mate-guarding distance and reproductive success

The relationship between mate-guarding distance and copulation success was comparatively weak (Fig. 16). Although some species exhibited extended guarding distances, these did not consistently correspond with higher reproductive success, suggesting that spatial separation during guarding may not strongly determine mating outcomes.

Behavioural strategy landscape of mate guarding

Integration of copulation duration and guarding distance revealed three distinct behavioural patterns among species (Fig. 17).

1. Contact-guarding strategy – species exhibiting short guarding distances and shorter copulation durations
2. Mixed guarding strategy – species with moderate guarding distances and intermediate durations
3. High behavioural investment strategy – species displaying long copulation durations combined with moderate guarding distances

These patterns suggest that species adopt different reproductive tactics depending on ecological and behavioural constraints.

Mate-guarding strategy framework

The integrated strategy framework combining guarding distance, copulation duration, and reproductive success further highlighted the importance of behavioural investment in mating outcomes (Fig. 18). Species exhibiting longer copulation durations generally achieved higher reproductive success, as illustrated by larger bubble sizes representing higher reproductive success values.

Correlation among behavioural variables

Correlation analysis among behavioural traits showed that copulation duration had the strongest positive association with copulation success (r ≈ 0.56). In

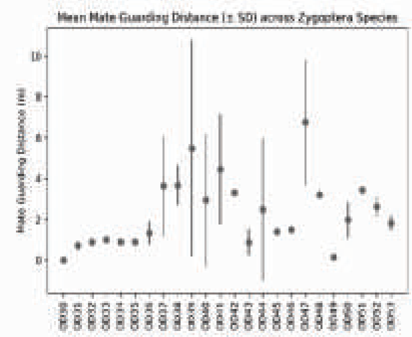


Fig. 12

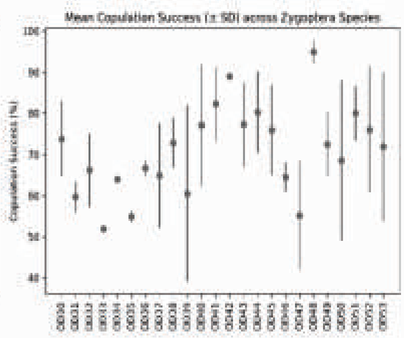


Fig. 13

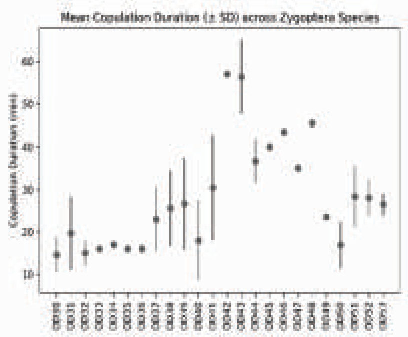


Fig. 14

Fig. 12-14 : Copulation success (%) across *Zygopteran* species (Mean ± SD), and its relationship with copulation duration and mate-guarding distance across species.

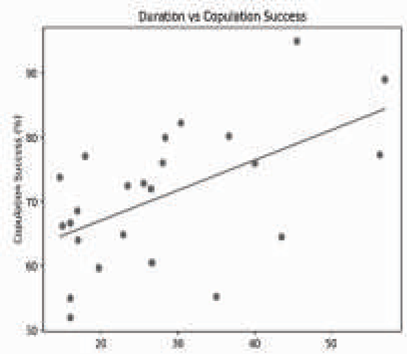


Fig. 15

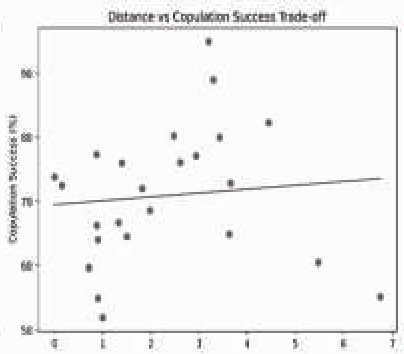


Fig. 16

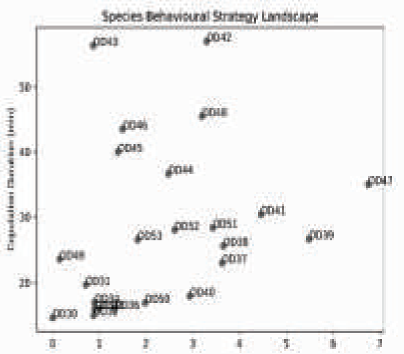


Fig. 17

Fig. 15-17 : Behavioural strategy landscape of *Zygopteran* species based on guarding distance and copulation duration.

contrast, guarding distance exhibited only a weak relationship with reproductive success, while ambient temperature showed minimal influence on behavioural variables within the observed range.

Behavioural pattern

Overall, the results indicate that variation in mate-guarding strategies among *Zygopteran* species is primarily structured along gradients of copulation duration and guarding distance. Reproductive success was more strongly associated with prolonged mating duration than with guarding distance, suggesting that temporal investment during copulation plays a more critical role in determining mating success (Fig. 19).

The diversity of guarding behaviours observed among species reflects multiple behavioural strategies that may have evolved in response to ecological pressures and reproductive competition, highlighting the adaptive significance of mate-guarding behaviour in damselfly reproductive ecology.

Discussion

The present study provides one of the most comprehensive behavioural datasets on mate-guarding strategies in Himalayan odonates. Observations across 53 species revealed substantial interspecific variation in reproductive behaviour, highlighting the diversity of mating strategies within the assemblage.

One of the most consistent patterns observed in the study was the positive relationship between copulation duration and reproductive success. Species exhibiting prolonged copulation generally achieved higher reproductive success, suggesting that extended mating may enhance sperm transfer efficiency and reduce the likelihood of sperm competition. Similar findings have been reported in several odonate species where prolonged copulation plays an important role in paternity assurance (Corbet, 2004; Córdoba-Aguilar, 2009).

In contrast, mate-guarding distance showed relatively weak influence on reproductive success, indicating that spatial guarding behaviour may be less important than temporal investment in mating. Many dragonfly species displayed strict contact guarding during oviposition, which is consistent with previous observations that Anisopteran species often maintain tandem formation to prevent interference by rival males.

Damselflies, however, displayed greater behavioural diversity. Several species exhibited mixed or non-contact guarding strategies, with males maintaining short distances from ovipositing females rather than continuous physical contact. This behavioural flexibility may reflect differences in habitat structure, territorial behaviour, and mating competition among Zygopteran species.

The behavioural strategy landscape analysis further revealed that most species clustered within a region characterized by short guarding distances and moderate copulation durations, suggesting that contact guarding remains the dominant reproductive strategy across many Himalayan odonates. However, a subset of species exhibited higher behavioural investment characterized by prolonged copulation durations.

Environmental factors such as temperature and habitat structure likely influence these behavioural strategies. Odonates are ectothermic organisms, and reproductive activity is strongly influenced by ambient temperature and seasonal conditions (Kalkman *et al*., 2007). In montane ecosystems such as the Western Himalaya, environmental variability may therefore play an important role in shaping mating behaviour and reproductive investment.

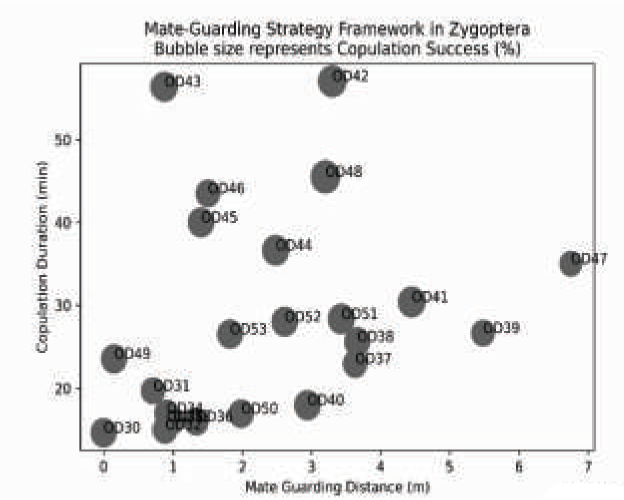


Fig. 18

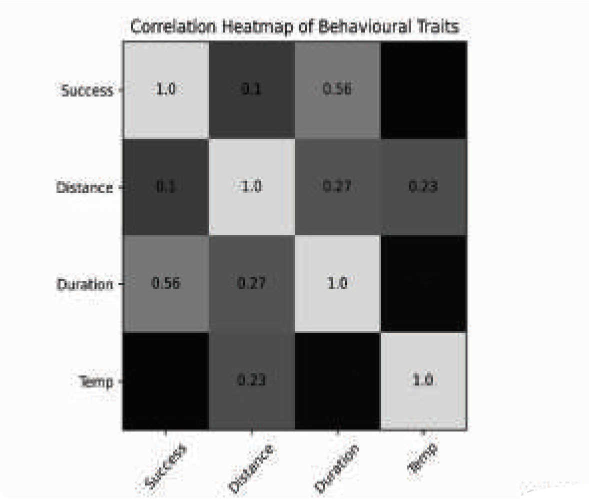


Fig. 19

Fig. 18-19 : Mate-guarding strategy framework in *Zygoptera* integrating guarding distance, copulation duration, and copulation success &Correlation heatmap showing relationships among behavioural variables.

Overall, the results highlight the adaptive diversity of mate-guarding strategies among odonates and emphasize the importance of behavioural ecology in understanding freshwater insect communities in Himalayan ecosystems.

Conservation and Management Implications

Freshwater ecosystems of the Western Himalaya are experiencing increasing pressures from climate change, hydropower development, river regulation, and land-use change (Singh and Singh, 1992). These disturbances can alter aquatic habitats and potentially affect odonate populations that depend on specific breeding environments.

Because reproductive behaviour in odonates is closely linked to habitat conditions and thermal environments, changes in freshwater ecosystems may disrupt mating systems and reduce reproductive success. Monitoring behavioural indicators such as mate-guarding strategies can therefore provide valuable early signals of ecological disturbance in freshwater habitats. (Das *et al*., 2016; Das and Uniyal, 2018, Das *et al*., 2020)

The Bhagirathi River Basin supports diverse odonate assemblages that play important ecological roles as predators of aquatic insects and as indicators of ecosystem health. Conservation strategies should prioritize the protection of natural riverine habitats, riparian vegetation, and wetland systems that support odonate breeding.

Maintaining environmental flows in Himalayan rivers and protecting freshwater microhabitats will be critical for sustaining odonate diversity and associated ecosystem functions in the region.

Conclusion

This study presents the first multi-species analysis of mate-guarding behaviour in dragonflies and damselflies from the Bhagirathi River Basin of the Western Himalaya. Substantial variation in copulation duration, guarding distance and reproductive success was observed among species.

Copulation duration showed the strongest positive relationship with reproductive success, indicating that behavioural investment during mating plays a key role in reproductive outcomes. While dragonflies predominantly exhibited contact guarding strategies, damselflies demonstrated greater behavioural diversity including spatial guarding tactics.

These findings contribute to the understanding of odonate reproductive ecology in Himalayan freshwater ecosystems and provide baseline behavioural data that may assist future biodiversity monitoring and conservation planning under changing environmental conditions.

भारत के उत्तराखंड राज्य में भागीरथी नदी बेसिन में ड्रैगनफ्लाई और डैम्सेलफ्लाई (ओडोनाटा) के साथी-संरक्षण व्यवहार में ऊंचाई के अनुसार भिन्नता का कारण ऊष्मीय अवरोध हैं।

शुवेंदु दास और वी.पी. उनियाल

सारांश

साथी की रक्षा करना ओडोनाटा प्रजाति में एक महत्वपूर्ण प्रजनन रणनीति है, लेकिन हिमालयी पर्वतमाला की विभिन्न ऊँचाइयों पर इसके विभिन्न रूपों का दस्तावेजीकरण अभी तक ठीक से नहीं हुआ है। इस अध्ययन में पश्चिमी हिमालय के उत्तराखंड स्थित भागीरथी नदी बेसिन के मीठे पानी वाले आवासों में पाई जाने वाली 53 प्रजातियों की ड्रैगनफ्लाई और डैमसेल्फलाई में साथी की रक्षा करने के व्यवहार का अध्ययन किया गया। व्यवहार संबंधी अवलोकनों में विभिन्न ऊँचाइयों पर संभोग की अवधि, रक्षा दूरी, परिवेशी तापमान और संभोग की सफलता को दर्ज किया गया। परिणामों से पता चला कि संभोग में निवेश में प्रजातियों के बीच काफी भिन्नता है, और लंबे समय तक चलने वाला संभोग उच्च प्रजनन सफलता से जुड़ा है। अधिकांश ड्रैगनफ्लाई संपर्क रक्षा प्रदर्शित करती हैं, जबकि डैमसेल्फलाई स्थानिक रक्षा रणनीतियों सहित एक व्यापक स्पेक्ट्रम दिखाती हैं। ये निष्कर्ष हिमालयी ओडोनाटा समुदायों में प्रजनन सफलता पर ऊष्मीय वातावरण और व्यवहारिक निवेश के प्रभाव को उजागर करते हैं।

References

Alcock J. (1994). Post insemination associations between males and females in insects: The mate-guarding hypothesis. *Annual Review of Entomology*, **39**: 1–21. https://doi.org/10.1146/annurev.en.39.010194.000245

Altmann J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, **49**: 227–267. https://doi.org/10.1163/156853974X00534

Balzan M.V. (2012). Associations of Dragonflies (Odonata) to Habitat Variables within the Maltese Islands: A Spatio-Temporal Approach. *Journal of Insect Science*,**12**(87): 1–18. https://doi.org/10.1673/031.012.8701

Bhardwaj M., Das S., Kala P. and Uniyal V.P. (2016). Bibliography on the butterflies and odonates of the Indian Himalayan Region. In: *Bibliography on the Fauna and Microflora of the Indian Himalayan Region*, Vol. **17**(2015–2016), Chapter 6. ENVIS – Wildlife and Protected Areas. https://doi.org/10.13140/RG.2.2.19649.35685

Bried J., RiesL., SmithB., PattenM., AbbottJ., Ball-DamerowJ., CanningsR., Cordero-RiveraA., Córdoba-AguilarA., De Marco JrP., DijkstraK-D, DolnýA., van GrunsvenR., HalsteadD., HarabišF., HassallC., JeanmouginM., JonesC., JuenL., KalkmanV., KietzkaG., MazzacanoC.S., OrrA., PerronM.A., Rocha-OrtegaM., SahlénG., SamwaysM., SiepielskiA., SimaikaJ., SuhlingF., Underhill L.and White E. (2020). Towards Global Volunteer Monitoring of Odonate Abundance. *BioScience*,**70**(10): 914–923. https://doi.org/10.1093/biosci/biaa092

Corbet P.S. (2004). Dragonflies. Behavior and Ecology of Odonata, revised edition. Cornell University Press, Ithaca, NY.

Córdoba-Aguilar A. (2009). *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research.* Oxford University Press, Oxford.

Das S., Bhardwaj M. and Uniyal V.P. (2016). *Wildlife Watch Series II: A user manual for monitoring Pied Paddy Skimmer (Neurothemis tullia)*. In Wildlife Watch in the Himalayan Region 2017–2018 (2nd ed.). Wildlife Institute of India, Chandrabani, Dehradun, Uttarakhand, India. https://doi.org/10.13140/RG.2.2.33071.12964

Das S. and Uniyal V.P. (2018). Wildlife Watch Series IV: A user manual for monitoring Red-veined Darter (*Sympetrum fonscolombii*). In: *Wildlife Watch in the Himalayan Region 2017–2018*, 4th ed. Wildlife Institute of India, Dehradun, India.

Das S., Thapa T., Uniyal V.P. and Gupta S.K. (2020). A systematic review on diversity and distribution of odonates (Insecta: Odonata) in the Indian Himalayan Region. In: *Proceedings of the 11th World Wilderness Congress*, Jaipur, India.

De K., Bhatt S., Singh A.P., Uniyal M. and Uniyal V.P. (2021). Checklist of Odonata (Insecta) of Doon Valley, Uttarakhand, India. *Journal of Threatened Taxa*,**13**(14): 20167–20173. https://doi.org/10.11609/jott.7518.13.14.20167-20173

Dijkstra K.D.B. and Kalkman V.J. (2012). Phylogeny, classification and taxonomy of Odonata. *Zootaxa*, **3478**: 1–12. DOI: 10.1007/s13127-012-0080-8

Dijkstra K.D.B., BechlyG., BybeeS.M., DowR.A., DumontH.J., FleckG., GarrisonR.W., HämäläinenM., KalkmanV.J., Karube H. and May M.L. (2013). The classification and diversity of dragonflies and damselflies (Odonata). *Zootaxa*,**3703**(1): 36–45. https://doi.org/10.11646/zootaxa.3703.1.9

Fraser F.C. (1933). *The Fauna of British India including Ceylon and Burma. Odonata Vol. I.* Taylor and Francis Ltd., London.

Fraser F.C. (1934). *The Fauna of British India including Ceylon and Burma. Odonata Vol. II.* Taylor and Francis Ltd., London.

Fraser F.C. (1936). *The Fauna of British India including Ceylon and Burma. Odonata Vol. III.* Taylor and Francis Ltd., London.

Hamalainen M. (1989). Odonata from Dehradun Valley (Uttar Pradesh, India) with notes on synonymy of some west Himalayan species. *Odontologica*,**18**(1): 13–20.

Husain A. (2018). Review on Odonate Diversity of Sahastradhara and Distribution Elsewhere in Dehra Dun and Uttarakhand. *BioBulletin*,**4**(1): 01–34.

Kalkman V.J., BabuR., BedjaničM., ConniffK., GyeltshenT., KhanM.K., SubramanianK.A., ZiaA. and OrrA.G. (2020). Checklist of the dragonflies and damselflies (Insecta: Odonata) of Bangladesh,Bhutan, India, Nepal, Pakistan and Sri Lanka. *Zootaxa*,**4849**(1): 001–084. https://doi.org/10.11646/zootaxa.4849.1.1

Kalkman V.J., Clausnitzer V., Dijkstra K., Orr A.G., Paulson D.R. and Tol J.V. Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia, **595***: 351-363.

Krebs C.J. (1999). Ecological Methodology. Benjamin/Cummings, Menlo Park.

Kumar A and Sharma G. (2003). Insecta: Odonata, pp. 11–13. In: Anon. (ed.). Wetland Ecosystem Series 5: Fauna of Asan Wetland (Dehra Dun Valley: Uttaranchal). Zoological Survey of India, Kolkata, 56pp.

Kumar A and Prasad M. (1981). Field ecology, zoogeography and taxonomy of Odonata of Western Himalaya, India. Records of the Zoological Survey of India, *Occasional Paper*,**20**: 1–118.

Mani M.S. (1974). *Ecology and Biogeography in India.* Dr. W. Junk Publishers, The Hague.

Prasad M. and Singh A. (1995). Odonata, pp. 195–215. In: Anon. (ed.). Fauna of Conservation Areas 5: Fauna of Rajaji National Park. Zoological Survey of India, Kolkata, 323pp.

Prasad M. and Varshney R.K. (1995). A check-list of the Odonata of India including data on larval studies. *Oriental Insects*, **29**(1): 385–428. https://doi.org/10.1080/00305316.1995.10433748

R Core Team (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Singh J.S. and Singh S.P. (1992). *Forests of Himalaya: Structure, Functioning and Impact of Man.* Gyanodaya Prakashan, Nainital.

Subramanian K.A. (2005). *Dragonflies and Damselflies of Peninsular India: A Field Guide.* Vigyan Prasar, New Delhi.

Subramanian K.A. and Babu R. (2018). Insecta: Odonata, pp. 227–240. In: Chandra, K., D. Gupta, K.C. Gopi, B. Tripathy and Kumar V. (eds.). Faunal Diversity of Indian Himalaya. Zoological Survey of India, Kolkata, 872pp.

Subramanian K.A. and Babu R. (2019). Dragonflies and damselflies (Insecta: Odonata of India), pp. 29–45. In: Ramani, S., P. Mohanraj & H.M. Yeshwanth (eds.). Indian Insects: Diversity and Science. CRC Press, London, 472pp.

Tang D.H.Y. and Visconti P. (2020). Biases of Odonata in Habitats Directive: Trends, trend drivers, and conservation status of European threatened Odonata. *Insect Conservation and Diversity*,**14**(1): 1–14. https://doi.org/10.1111/icad.12450

Thompson D.J. (1990). The effects of survival and wea ther on lifetime egg production in a model damsel y. Ecological Entomology 15, 455–482.

Thorp J.H. and RogersD.C. (2011). Dragonflies and Damselflies, pp. 191–197. In: Thorp, J.H. & D.C. Rogers (eds.). Field Guide to Freshwater Invertebrates of North America. Academic Press, Cambridge, Massachusetts, 274 pp. https://doi.org/10.1016/b978-0-12-381426-5.00021-1

Uniyal V.P., Mitra A. and Mathur P.K. (2000). Dragonfly fauna (Insecta: Odonata) of the Great Himalayan National Park, Western Himalaya. *Annals of Forestry*, **8**: 116–119.

Uniyal V.P., Gautam R.K., Kahera N.S., Purohit A., Sarkar I.D., Das S., Dey K., Chandra A., Sangela V. and Singh A.P. (2022). *Insect bioindicators along River Ganga*. Booklet, Wildlife Institute of India, Dehradun, India.

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