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Morphological and colour pattern associations of male mate location behaviour in central Indian butterflies

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ABSTRACT

Many ecological studies have documented mate location behaviour in relation to morphology for temperate butterflies. However, to what extent morphology and mate location behaviour are similarly associated in tropical, subtropical and temperate region butterflies is unknown; no study has yet been undertaken of mate location behaviour in relation to morphology in Indian butterflies. The male mate locating behaviour of 70 butterfly species has been recorded; 23 exhibited both perching and patrolling behaviour, 31 are strict perchers, 16 solely patrol, 22 display male territorial defence and nine establish aggregations (leks). We tested two issues relating morphology to mate location behaviour: 1. Perching and patrolling males differ in morphology. 2. Perching and patrolling males differ in wing colour. It was found that, within species, individual perching males have shorter bodies, greater wing spans and greater weight than patrolling males, and that within and between species perching males are duller/paler in colour than patrolling males. The reasons for these distinctions are discussed and are considered to relate to the different activities of perchers and patrollers, the former significantly associated with territorial defence.

KEYWORDS: body length, body weight, Lepidoptera, morphology, perching, patrolling, territorial defence, wing span

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INTRODUCTION

Most animals face the difficult task of finding mates to reproduce successfully. Variation in visually-cued mate location behaviour in insects has been widely classified into the wait or seek dichotomy [1-3]. Perching and patrolling are the two basic methods used by male butterflies for locating mates [4-7]. Both strategies have probably evolved in response to the particular way in which larval and adult resources are distributed [8, 9]. Perching is typically associated with the concentration of a resource, consumer resource (i.e. host plant, nectar source) or utility resource (i.e. sunspots, ‘peaks’ in the landscape) [9, 10]. In contrast, patrolling males typically seek females over wider areas, often using linear features such as stream banks and ridges on hills as flyways [11]. This behaviour is probably more favourable when resources are patchy and females are scattered over resource patches [12].

In addition to perching and patrolling, mate locating behaviours also include territorial defence, lekking and landscape associations (e.g. hilltopping). Territoral behaviour involves contact as well as mutual non-contact manoeuvres during aerial interactions in which two or more males circle or hover near each other for a period of time before one male ‘gives up’ and is chased from the site [13-16]. In *Pararge aegeria*, it was initially observed that the resident male prevailed in these contests over site ownership [13]. Several researchers then focused on the extent to which certain physical and/or physiological characteristics, including body size and flight morphology and wing patterns, also influence contest success [17-20]. In lekking, males assemble to form aggregations at specific sites, such as tree tops, in wait for females. Landmarks figure prominently in mate location. The males, while hilltopping, move to distinct topographic peaks (hilltop) in order to obtain mates adopting either perching or patrolling [21] and occasionally forming aggregations [22]. Lekking also occurs on minor landforms (e.g. gravel piles, *Lasiommata megera*; [23]) and resource patches (e.g. nectar bushes, *Ochlodes venata*; [24]).

It has also been demonstrated that perching and patrolling species differ morphologically, both in dimensions and colouration [25]. This is expected as the energy and flight abilities demanded by both modes of male searching behaviours are quite different [25, 26]. For example, perching species invest relatively more resources into their thorax than patrolling species [25]. Thoracic mass is predominantly muscle, whereas the abdominal mass includes diverse organs, and contributes most to the overall body length in butterflies [27].

Variation in mate locating behaviour has been shown to exist not only between but also within butterfly species [5, 23]. Such differences can be permanent or change over time (i.e. daily or seasonally), and several factors influence the proportions of males exhibiting each searching behaviour at any point [26]. For example, darker males of *Pararge aegeria* are more likely to patrol than paler ones, which were mainly territorial perchers [28]. It was suggested that paler males occur as a response to overheating in sunny territories while darker males are able to warm faster and remain for longer periods under shadier conditions [26].

It is evident that the components that explain different mate location behaviours and exploitation of different encounter sites are still far from being understood. Data have rarely been collected on numerous species occurring in the same area or occupying the same or neighbouring biotopes. The objective of this study is to fill a gap by extending our knowledge on mate location behaviour and resource use to tropical environments, biotopes within the urban environment of Nagpur, India. From current knowledge of mate location behaviour, it is possible to generate firm hypotheses linking male mate location behaviour to butterfly morphology and colouration.

Here we report the mate locating behaviours of 70 butterfly species of central India. We examined the morphology and colouration of butterfly males in order to test whether such traits vary with mate searching behaviour in much the same way as found in temperate species. In particular we ask whether (1) perching males have bigger bodies (greater body lengths), greater wing spans and weights than patrolling males, (2) dull/pale coloured males preferably adopt perching behaviour for mate location. In addition, we determine whether (3) territorial males are mostly perchers, as the additional energy expenditure and speed required in defence is likely to affect morphology.

MATERIALS AND METHODS

Study sites and survey

The field study was conducted in and around Nagpur, central India (20° 99' N, 79° 99' E) by one of us (ADT; data are available from the first author) as part of a wider study on butterfly diversity of Nagpur City. Observations on mate location behaviour in five butterfly families (Hesperiidae, Papilionidae, Pieridae, Lycaenidae and Nymphalidae) were carried out on 70 of 145 butterfly species occurring at Nagpur between 1 June 2006 and 31 May 2008 as part of two systematic surveys investigating butterfly habitats and behaviour. The study was based on extensive Pollard transect records over six sites [29] and behavioural observations on individuals obtained from complete areal cover of the same sites (Table 1). In the tropical climate of Central India butterfly species abundance rises with the onset of the monsoon in June, reaches a peak in early

Table 1. Sites near Nagpur where behavioural data were collected.

S. N.	Site name	Habitat description
1	Seminary Hills (north-west Nagpur)	Natural forest vegetation. *Tectona grandis* (Teak) is the dominant tree species with *Lantana camara* as dominant weed (67 ha).
2	Satpuda botanical Garden (west Nagpur)	Hill and lake county (Futala Lake) with mixed vegetation comprising ornamental, fruit plants, scrub, grassland; some part with natural forest dominated with *Lantana* spp., (25 ha).
3	Agricultural Land, Bull Rearing Center (west Nagpur)	Vegetation mixed cultivated fodder plants (e.g. Barseam and Jawar), wild forest plantation, scrub and grassland for grazing (44 ha).
4	RTM Nagpur University Campus and Laxmi Narayan Institute of Technology (LIT) Campus (west Nagpur)	Vegetation is mixed; ornamental plants near buildings, natural plantations in some areas, the rest of the area with scrub and extensive grasslands (89 ha).
5	Ambazari garden and bare land at Lake Side (west Nagpur)	Flowering plants, forest, scrub and grassland (6 ha).
6	Sides of National Highway (south Nagpur)	Flowering plants (2 ha).

October and starts declining in February or March. Temperature ranged from 10 to 45°C and relative humidity from 10 to 95%.

Variables and measurements

Observations on mate location behaviour were made during behavioural observations carried out systematically over the sites. Individual male butterflies were observed for short periods (10 seconds to several minutes) and scored for one or more of several behaviours: patrolling, perching, territorial defence and lek aggregation. Male butterflies were classed as patrolling when mate searching (interacting with other insects, especially conspecifics, involving prolonged inspections and attempted mating) was conducted in continuous flight, and as perching when males rose to inspect passing insects from settled basking or resting positions (perches). Males were regarded as engaging territorial defence when interactions with other insects, especially conspecific males, involved aggressive encounters (i.e., horizontal chases, spirals and physical contact). Lek assembly was recorded when male aggregations occurred in close proximity on vegetation and other structures, the males responding to intruding butterflies particularly conspecific females. In this way, the definition of lekking coincides with the traditional definition to the extent that it is considered to be a gathering of males, of certain animal species, for the purposes of competitive mating display, but excluding levels of defence.

For the morphological study, butterfly male specimens, five each for perchers and patrollers, were collected for measurement in the laboratory and subsequently released without harm. Measurements were made of body length, wingspan and total weight [29]. The direct measurements were made using a graduated, stereoscopic dissecting microscope. Wingspan was determined by measuring the distance between the two wing tips (apices) and body length was measured from the area between the eyes (vertex) to the end of the abdomen [31]. The total weights (body wet weight) of butterflies were measured on a digital balance (Mettler portable electronic balance; in mg). All measurements were repeated to ensure precision but, with priority given to the rapid and safe release of butterflies, no study was made of the level of precision. In addition, individuals of each species were categorized according to their hind and forewing ventral colour into three categories: 1 dull/pale, 2 normal and 3 bright/dark based on the surveyor’s personal experience with samples of the species. The butterflies were released at the capture location after taking measurements.

Statistical analysis

To determine whether males with different searching behaviour also diverge morphologically, two types of analyses were carried out. First, body length, wing span, weight and colouration were compared between patrolling and perching males within species that exhibited both behaviours. Absolute comparisons were made using the paired t test (variables normalized). Relative differences (direction of differences between pairs of species) were made using the Sign test and the Wilcoxon Matched Paired test. Second, similar comparisons were carried out within genera where males of species exhibited both behaviours. As numbers of species were small, a conservative approach to absolute comparisons was applied using Mann-Whitney and Kruskal-Wallis ANOVA tests for comparisons between two or more species, respectively, whereas direction of differences was determined again by Sign test and the Wilcoxon Matched Pairs test. Correlations are Spearman rank correlations (r_s). Analyses were conducted in STATISTICA 9 (Statsoft Inc.) and significance adopted at $P < 0.05$.

RESULTS

We observed male mate locating behaviour in 70 of 145 species of butterflies recorded in the Nagpur area (Table 2). Among the 70 butterfly species, 23 exhibited both perching and patrolling behaviour, 31 invariantly perched and 16 invariantly patrolled. Territorial defence in males was observed in 22 of these species. Males formed aggregations (leks) in only nine of these species (Table 2). Leks were found in the canopies of trees (e.g. *Papilio demoleus*, *Catopsilia pomona*, *Tirumala limniace*, *Danaus chrysippus, Euploea core*) and on vegetation and other structures

Table 2. Mate locating behaviour of central Indian butterfly species.

Scientific name	Mate location behaviour			
	Lek assembly	Perch	Patrol	Territorial defence
Papilionidae				
Pachliopta aristolochiae			+	
Pachliopta hector			+	
Graphium doson		+	+	+
Graphium agamemnon			+	
Papilio demoleus	+	+	+	+
Papilio polytes		+	+	
Pieridae				
Catopsilia pomona	+	+	+	+
Catopsilia pyranthe		+	+	
Eurema brigitta		+	+	
Eurema laeta		+		
Eurema andersonii			+	
Eurema hecabe	+	+	+	
Eurema blanda			+	
Delias eucharis		+		
Cepora nerissa		+		
Anaphaeis aurota		+		+
Colotis etrida			+	
Pareronia valeria		+		+

Table 2 continued..

Scientific name	Mate location behaviour			
	Lek assembly	**Perch**	**Patrol**	**Territorial defence**
Melanitis leda	+	+		
Melanitis phedima		+		
Lethe europa			+	
Mycalesis perseus		+		
Mycalesis mineus		+		
Mycalesis subdita		+		
Charaxes polyxena		+		
Phalanta phalantha		+	+	+
Neptis columella		+		
Neptis jumbah		+		
Neptis hylas		+	+	
Limenitis procris		+		
Euthalia nais		+		
Byblia ilithyia		+		
Ariadne ariadne		+		
Ariadne merione			+	
Junonia hierta			+	+
Junonia orithya		+		+
Junonia lemonias		+	+	+
Junonia almana		+		+
Junonia atlites			+	
Junonia iphita		+		+
Hypolimnas bolina		+		+
Hypolimnas misippus		+	+	+
Tirumala limniace	+	+	+	+
Danaus chrysippus	+	+	+	+
Danaus genutia		+		
Euploea core	+	+	+	+
Lycaenidae				
Castalius rosimon			+	
Tarucus nara		+	+	
Leptotes plinius		+	+	+
Everes lacturnus		+		
Actolepis puspa		+	+	
Anthene emolus			+	
Anthene lycaenina		+		
Psuedozizeeria maha			+	
Zizeeria karsandra			+	
Zizina otis		+		

Table 2 continued..

Scientific name	Mate location behaviour			
	Lek assembly	Perch	Patrol	Territorial defence
Zizula hylax		+	+	
Chilades laius		+		
Chilades laius		+		
Chilades parrhasius		+	+	
Chilades pandava	+	+	+	+
Freyeria trochylus			+	
Euchrysops cnejus		+	+	
Catochrysops strabo			+	+
Lampides boeticus		+		
Prosotas nora	+	+		
Hesperiidae				
Spialia galba		+		
Telicota ancilla		+	+	+
Parnara naso		+		+
Pelopidas mathias			+	
Borbo cinnara		+	+	+
Baoris farri		+		
Caltoris kumara		+	+	

(e.g. *Tirumala limniace*, *Danaus chrysippus*, *Euploea core, Chilades pandava, Prosotas nora, Eurema hecabe, Melanitis leda*).

Across species there is a close correlation among morphological variables of body length, wing expanse and weight (Spearman r_s = 0.91 to 0.93, P < 0.0001, N = 70 species).

Comparisons within species

There is a clear tendency for individuals belonging to the same species that perch, rather than patrol, to be heavier (Sign test Z = 4.17, Wilcoxon Z = 3.50, P = 0.001), to have greater wing expanses (Sign test Z = 3.20, Wilcoxon Z = 3.23, P = 0.0005) but to have shorter body lengths (Sign test Z = 2.92, Wilcoxon Z = 2.37, P = 0.018) (n = 23 pairs tested) (Table 3). Individual tests within species (n = 5 each for perchers and patrollers) exacted significant differences for 14, nine and 14 species respectively for body length, wing expanse and body weight. For body length, 11 of the 14 significant comparisons indicated that patrollers have longer bodies than perchers, eight of nine comparisons indicated greater wing expanses for perchers than patrollers, and 13 of 14 comparisons heavier perchers than patrollers. The exceptional species for which this pattern was reversed were *Euchrysops cnejus*, *Hypolimnas misippus* and *Papilio polytes* (body length) and *Graphium doson* (for wing expanse and weight). Even so, significant absolute differences occur between patrollers and perchers for one measurement only, wing expanse (paired t test, log transformed data, body length t = 1.82, P = 0.08; wing expanse t = -2.62, P = 0.016 with perchers > patrollers; weight t = -0.95, P = 0.35; n = 23 pairs of species tested).

Nineteen of 23 species, which engage both mate location behaviours (perch and patrol), patrol and are significantly darker/brighter in mean wing colour (Sign test Z = 4.59, Wilcoxon Matched Pairs test, Z = 4.20, P < 0.0001, n = 23 pairs; means determined from n = 5 individuals for each species

Table 3. Comparison of mate location behaviour (patrollers, perchers) for average body measurements in butterflies from central India (Nagpur).

Species	Body length (mm)		Wing expanse (mm)		Weight (mg)		Body length (mm)		Wing expanse (mm)		Weight (mg)	
	PA	PE	PA	PE	PA	PE	Z	P	Z	P	Z	P
Graphium doson	17	17.2	74.8	57	244.8	123.2	-1.24	0.21	-2.63	0.009	-2.63	0.009
Papilio demoleus	26.4	25.3	82.6	84.8	324	328.2	-2.47	0.01	-1.97	0.049	-1.92	0.05
Papilio polytes	22.6	24.1	89.2	88.6	189.8	192	-2.74	0.006	-0.21	0.83	-0.95	0.34
Catopsilia pomona	22.6	19.1	61.2	67.6	142.8	155.2	-2.67	0.008	-1.68	0.10	-1.57	0.15
Catopsilia pyranthe	22.7	21.6	61.2	63	142.8	155.2	-2.67	0.008	-1.27	0.21	-1.57	0.12
Eurema brigitta	23.4	12.7	21.2	26.4	19.2	22.6	-2.65	0.008	-2.63	0.009	-2.45	0.01
Eurema hecabe	13.4	13	31.1	31.2	18.6	20	-2.3	0.02	-0.43	0.67	-1.74	0.08
Phalanta phalantha	17.8	17.3	44	49.8	71	83.6	-1.75	0.09	-2.1	0.03	-2.62	0.008
Junonia lemonias	14.7	14.6	45.8	45.6	74.8	79.8	-0.45	0.65	-2.34	0.02	-2.12	0.03
Hypolimnas misippus	20.6	24.5	83.8	83.8	267	280.4	-2.64	0.008	0.00	1.00	-1.47	0.14
Tirumala limniace	26.9	25.8	80.8	85.4	365.8	371	-2.74	0.006	-1.78	0.08	-1.48	0.14
Danaus chrysippus	27.1	26.7	71.2	74.2	145.8	150.6	-1.39	0.17	-1.81	0.07	-1.16	0.25
Euploea core	26.2	25.9	85.2	90	233.2	241.2	-1.34	0.18	-1.82	0.07	-0.11	0.92
Tarucus nara	9	8.9	22.6	24.4	10.88	11.6	-1	0.32	-2.39	0.02	-2.39	0.02
Leptotes plinius	9	8.7	24.4	25.4	11.24	12.2	-1.06	0.29	-1.17	0.24	-2.63	0.009
Actolepis puspa	11.9	11.7	32	33.6	32.4	34.8	-0.78	0.44	-1.62	0.11	-2.28	0.02
Zizula hylax	7.8	7.3	17.6	19.5	6.22	6.8	-2.15	0.03	-1.49	0.14	-2.48	0.01
Chilades pandava	10.5	9.7	30.4	32.8	18.28	19.1	-2.3	0.02	-2.27	0.02	-1.17	0.24
Chilades parrhasius	9.2	8.7	25.8	29.6	16	17.2	-2.15	0.03	-2.13	0.03	-2.13	0.03
Euchrysops cnejus	9.7	10.3	29.8	31.4	15.5	16.7	-2.15	0.03	-1.7	0.09	-2.46	0.01
Telicota ancilla	13.8	13.7	32.6	34.8	112.4	122.4	-0.24	0.81	-1.8	0.07	-2.26	0.02
Borbo cinnara	15.9	14.1	30.2	32.4	71.4	73.8	-2.79	0.005	-2.39	0.02	-2.02	0.04
Caltoris kumara	19.5	18.2	36	37.8	91.2	93.6	-2.67	0.008	-1.27	0.21	-2.04	0.04

PA, patroller; PE, percher.

Table 4. Comparison of wing colour[1] for different mate-location behaviours in species displaying both behaviours.

Species	Colour (mean)		Mann-Whitney U test	
	Patrollers	Perchers	Z	P
Graphium doson	2.8	1.2	-2.68	0.007
Papilio demoleus	2.4	1.6	-1.90	0.058
Papilio polytes	2.8	1.6	-2.46	0.014
Catopsilia pomona	2.4	1.4	-2.15	0.030
Catopsilia pyranthe	2.4	1.2	-2.46	0.014
Eurema brigitta	2.8	1.2	-2.68	0.007
Eurema hecabe	2.8	1.8	-2.43	0.015
Phalanta phalantha	2.8	1.8	-2.43	0.015
Junonia lemonias	2.2	1.8	-1.34	0.180
Hypolimnas misippus	2.8	1.4	-2.55	0.011
Tirumala limniace	2.8	1.6	-2.46	0.014
Danaus chrysippus	2.8	1.2	-2.68	0.007
Euploea core	2.8	1.2	-2.68	0.007
Tarucus nara	2.2	1.8	-1.34	0.180
Leptotes plinius	2.6	1.2	-2.55	0.011
Actolepis puspa	2.8	1.2	-2.68	0.007
Zizula hylax	2.6	1.2	-2.55	0.011
Chilades pandava	2.8	1.4	-2.55	0.011
Chilades parrhasius	2.8	2.4	-1.23	0.221
Euchrysops cnejus	2.2	1.2	-2.43	0.015
Telicota ancilla	2.8	1.4	-2.55	0.011
Borbo cinnara	2.8	1.2	-2.68	0.007
Caltoris kumara	2.4	1.2	-2.46	0.014

Based on n = 5 individuals for each species; [1]colour coding: 1 dull/light, 2 normal, 3 dark/bright.

and behaviour category) (Table 4). Absolute differences between species are also significant (t = 13.39, P < 0.0001, n = 23 pairs of species) (Fig. 1).

Comparison within genus

Relative differences between species belonging to a single genus have been carried out using the means for species (based on n = 5 individuals for each of species and behaviour). Only five genera could be compared (i.e. *Ariadne, Anthene*, *Junonia*, *Neptis* and *Eurema*). No relative differences were found for body measurements (Z < 1.0, P > 0.35), but significant relative differences occur for wing colour (Wilcoxon Matched Pairs test Z = 2.02, P = 0.043, patrolling species brighter/darker than perching species).

Different species within the same genus displaying different modes of mate location (perching and patrolling) differ for absolute measures of morphology. But, the differences are not consistent. In *Anthene* (i.e. *Anthene emolus* (Patroller) and *A. lycaenina* (Percher) (Lycaenidae) (Mann Whitney U, Z = -2.23, P = 0.026, n = 5 for each species), the patroller is heavier, whereas in *Ariadne* (i.e. *Ariadne ariadne* (Pe) and *A. merione* (Pa) (Nymphalidae) (Mann Whitney U, Z = -2.63, P = 0.009), the percher is heavier. *Junonia*, *Neptis* and *Eurema* species (five, four and three species respectively) all differ for mate location behaviour types and morphology, for body length in all genera, and for wing expanse and weight for the last two genera (Kruskal-Wallis > 9, P < 0.01, N = 5

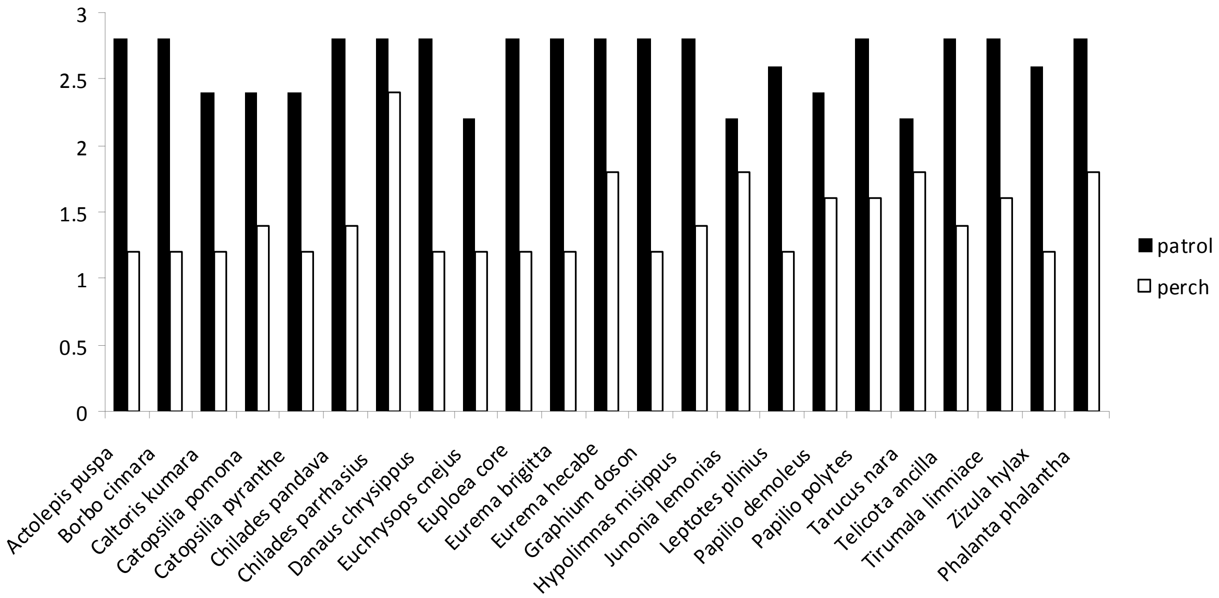

Figure 1. Comparison (means) of mate location behaviour (patrollers, perchers) for dorsal wing colour within central Indian (Nagpur) butterflies (n = 23). Wing colour range: dull/pale = 1, medium = 2 and bright/dark = 3.

Table 5. Comparison of mate location behaviour (patrollers, perchers) for average body measurements for species in three butterfly genera from central India (Nagpur).

Species	Behaviour	Body length	Wing expanse	Weight	Wing colour
Eurema laeta	PE	11.8†	30.6	20	1.6†
Eurema andersonii	PA	13.2†	32	20.2	2.4†
Eurema blanda	PA	12.9†	29.8	19	2.8†
Neptis columella	PE	21.4	68.8	118	1.4†
Neptis jumbah	PE	18.6‡	65.2‡	119.0‡	1.2†
Neptis hylas	PA	15.0‡	43.0‡	55.0‡	2.4†
Neptis hylas	PE	14.5‡	43.0‡	55.0‡	1.2†
Ariadne ariadne	PE	17.6	50.2	51.8‡	2.4
Ariadne merione	PA	16.9	51.4	43‡	1.8
Junonia hierta	PA	19.4‡	47.0‡	90.6‡	2.4†
Junonia orithya	PE	15.2‡	42.8‡	76.4‡	1.4†
Junonia almana	PE	17.1‡	51.6‡	77.6‡	1.4†
Junonia atlites	PA	17.0‡	52.0‡	77.4‡	1.8†
Junonia iphita	PE	21.5‡	63.0‡	97.0‡	1.2†
Anthene emolus	PA	11.4	27.8	13.3†	2.8‡
Anthene lycaenina	PE	11.6	26	12.52†	1.4‡

Anthene is in the Lycaenidae, *Ariadne, Junonia* and *Neptis* are Nymphalidae and *Eurema* Pieridae; PA, patroller; PE, percher. Significance of taxonomic distinctions from Mann-Whitney U test and Kruskal Wallis ANOVA; ‡ $P < 0.01$, † $P < 0.05$.

for each species) (Table 5). Thus, *Eurema* species differ in body length with the perching species having a significant shorter body length than the two patrolling species, but in *Junonia* perching species have both shorter and longer body lengths than patrolling species.

Absolute comparisons of species within genera for wing colour produced significant differences for four out of five genera (Table 5). For *Anthene*, *Junonia*, *Neptis* and *Eurema*, patroller species were darker than perching species (Mann-Whitney U and Kruskal-Wallis ANOVA, P = 0.01 to 0.03). However, in *Ariadne* the perching species (*Ariadne ariadne*) is brighter than the patrolling species (*Ariadne merione*) (Z = -1.69, P = 0.09).

Territoriality

There was a significant positive association between species engaged in territorial defence and perching (Spearman r_s = 0.27, P = 0.016) and a negative one with patrolling (r_s = -0.30, P = 0.007). The only exception of a species that did not include perching in its behavioural repertoire was *Catochrysops strabo,* a patroller but territorial in nature (Table 2).

DISCUSSION

Among butterflies there is a vast range in morphology and wing colour patterning. These differences potentially relate to contrasts in resource use, biotopes and biomes occupied as well as to different functions (i.e. sex, adult and juvenile feeding, thermoregulation and predation) [32, 33]. Distinctions are typically evident between different butterfly families and likely relate to different hostplant-habitat conditions during evolution [10, 34]. It is unsurprising, then, that differences occur that are related to distinctions in modes of male and female mate location behaviour - perching, patrolling, territorial defence and lek assembly [35]. In this study of butterflies in the urban tropical regime of Nagpur, India, distinct morphological and wing colour differences are found at two taxonomic levels related to perching and patrolling mate location behaviours. First, within species, there are consistent differences in body length, wing expanse, weight and wing colour between patrolling and perching individuals. Second, this same distinction is also found for wing colour amongst closely related species that either patrol or perch. However, there is no systematic difference across species in size (morphology) for mate location behaviour. In essence, this means that although perching and patrolling behaviour has a biological impact on an individual's morphology and pattern, these activities are not limited by morphology or pattern, nor act as major delimiters of morphology and pattern. Other activities (i.e. herbivory, predation, thermoregulation) associated with distinct resources and environments present potentially more important factors in determining species' morphology and, to a lesser extent, wing colour patterns.

Even so, within species, perchers are distinct from patrollers in morphology and colour pattern. Perchers are shorter, heavier, and duller coloured but have greater wing spans than patrollers. There is an important link with activity that lies at the root of these differences. Perchers, in intercepting mates and intruders (i.e. other males, non conspecifics) tend to be more active than patrollers. Interception involves a burst of energy and often extended periods of fast, combative energy-burning flight [24]. The link is strongly supported by the significant positive correlation of perching with territorial defence and the negative association with patrolling. Many patrolling species use energy-conserving gliding flight, by comparison. In these circumstances, larger wings improve lift off and flight capacity, and a shorter body improves manoeuvrability, also reducing the target for predators while stationary (perching). The fact that perchers have shorter bodies but are heavier indicates a greater investment in thoracic muscles, improving flight capacity. These differences between individuals suggest an advantage to shorter, heavier males with larger wings and more powerful flight muscles in the competition for mates. The duller colour very likely relates to predation and thermoregulation. Perching is a sit and wait tactic; females make themselves known by soliciting mating and flying towards perch areas (territorial sites). Patrolling, in contrast, is a seek strategy, depending more on both sexes being apparent (conspicuous) to one another [10]. Perching in suitable spots for passing females renders individual males vulnerable to predation and overheating in sun spots, in which case, duller colours (that absorb less heat) provide better protection than brighter ones. It is evident that distinctions for these behaviours (perch, patrol) are more important for wing colour than differences in morphology, as the colour pattern distinction occurs across species as well as within species.

The current findings for a tropical location support a number of observations, but not all, made in temperate contexts. It has long been known that body and wing attributes are allometrically related [36, 37] and that morphological and colour pattern distinctions exist between patrollers and perchers in the same species [17, 25]. In Nagpur butterflies, high positive correlations between body length, weight and wing span have been previously reported in relation to nectar feeding [30]. What is interesting in this study is that selection for mate location morphology within species is counter-intuitive in relationship to these morph attribute correlations. Within species, although there is selection for greater body weight and wing span in males that are perching, selection has operated to *reduce* body length. There has to be a good reason for the systematic reduction in body size for a number of species, especially as larger bodies might well be thought to correlate with increased number and larger spermatophores. One potential trade-off is that occurring between increased thorax musculature and body mass. It would be expected that such a trade-off in morphology does not affect spermatophore status as females are unlikely to select males with relatively poor reproductive resources. The existence of a trade-off in morphology is perhaps suggested by species which do *not* follow this pattern of relationships but differ significantly in a counter direction, i.e. perchers are longer, not shorter, bodied (e.g. *Euchrysops cnejus*, *Hypolimnas misippus* and *Papilio polytes*). It would be interesting to see if these individuals better adopt intermediate strategies, able to both perch and patrol more successfully than those with more orthodox morphology and wing colour.

Regarding conflict in trade-offs for butterfly morphology, an unknown issue is the extent to which species are plastic for the morphological and wing colour traits examined. Certainly, regarding variation in dorsal wing colour, numerous examples exist of seasonal phenotypic plasticity [38]. One question then is why darker males do not seem to take up unoccupied sunlit patches (perches). For numerous species (n = 23) in this study, as for the vast majority of *Pararge aegeria*, males could be classified as either perchers or patrollers [13, 14, 17, 28, 31]. But, males of several butterfly species freely switch between territorial perching and patrolling behaviour depending on conditions and the density of conspecific males at encounter sites [23, 28, 31, 39]. In these situations, the balance of perchers and patrollers depends on opportunities governed by population density as well as landscape and resource attributes that benefit one or the other strategy at any location. There may also be a phenotype-dependent probability for perching or patrolling, and practicing one strategy for longer periods could improve experience and therefore increase efficiency of, and consequentially inertia for, a specific mate location strategy. Wickman and Wiklund [14] provided evidence for learning, as some males avoided successfully defended sunlit patches if they were unable to win contests with the local males. There is also the question of female choice, important for male colour evolution [40]. There is clearly much yet to discover about the interaction of butterfly morphology and wing pattern with mate location strategies [37]. This study records exceptions to the general findings, and answers to these unexpected findings can only be accessed by more detailed studies of their mate location strategies and comparison with congeners that follow the 'rules'. The Nagpur study has identified a set of relationships, and raised issues, that are worthy of more detailed investigation.

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