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# Male mate location behaviour and encounter sites in a community of tropical butterflies: taxonomic and site associations and distinctions

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Male mate location behaviour and encounter sites have been studied in 72 butterfly species at Nagpur, India, and related to taxonomy, morphology, habitat and population parameters. Species can be placed in three broad classes of mate location behaviour: invariant patrolling, invariant perching, and perch-patrol, the latter associated with increasing site fidelity, territorial defence and male assemblages. Significant taxonomic differences occur, closely related species tending to share mate location behaviours. Morphological differences are found with heavier and larger butterflies displaying greater site fidelity and territorial defence, and differences occur between individuals of species which both perch and patrol. Invariant patrolling is particularly associated with tracks through vegetation, host plant-track distributions, and high female to male numbers observed on transects; invariant perching is linked more to edge features than patrolling, and to lower population counts on transects. Species which perch-patrol, defend territories and establish male assemblages are associated with more complex vegetation structures, and have encounter sites at vegetation edges, landforms and predictable resource (host plant) concentrations. Attention is drawn to the importance of distinctive mate encounter sites for the conservation of butterfly species' habitats.

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## 1. Introduction

A resource-based view of habitats for arthropods, as for other organisms, points to the existence of crucial resources and conditions in habitats other than consumer requirements, that is, the occurrence of larval host plants and adult nectar sources for phytophagous insects (Dennis *et al.* 2003, 2006a; Dennis 2010). Mate location and encounter sites form one of a number of essential non-consumer resource types within habitats (mating systems, Emlen and Oring 1977; birds, Burton 1985; Short 1993; mammals, Reichard

and Boesch 2003). Among arthropods, butterflies have proved useful model organisms for testing many ideas in conservation biology, especially differential resource exploitation. The availability of suitable mate location sites forms a key resource for butterflies as for other organisms in which different sites are found to relate to distinctive behaviour. However, compared to data on consumer resources, comparatively little is known about mate location sites and behaviour (Emlen and Oring 1977; Odendaal *et al.* 1985; Bradbury 1985; Dennis and Shreeve 1988; Rutowski 1991). Even so, an increasing number of case studies and

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reviews have identified distinctive behaviours and contrasting circumstances (encounter sites) among species used in temperate locations (Rutowski 1991; Wickman 2009).

Among butterflies, four distinctive male mate location behaviours have been identified, referred to as perching, patrolling, territorial defence and lek assembly (Shields 1967; Baker 1972, 1984; Scott 1974; Davies 1978). In patrolling, males actively seek females, whereas in perching they await the arrival of females soliciting courtship (Baker 1972). Territorial activity is a measure of the preparedness of males to defend an area, distinct from fidelity to an area or site; in butterflies territorial encounters often involve physical contact (Wickman and Wiklund 1983; Dennis and Williams 1987; Kemp and Wiklund 2001). In lek assembly, sites are at a premium, aggregations of males occur in close proximity and females choose among several males. These mate location behaviours are by no means mutually exclusive or always clear cut. Species that perch may well also patrol (e.g. *Lasiommata megera* L., Satyrinae, Dennis 1982-83; *Pararge aegeria* L. Satyrinae, Merckx and Van Dyck 2005) as well as engage in territorial defence and partake in assemblies. Fidelity and territorial defence describe continua and not rigid categories. Even so, there are still outstanding issues in mate location behaviour; a prominent one is the relative influence of ecology and phylogeny in mate location behaviour (Scott 1974; Ehrlich 1984). Certainly, different mate location behaviours have repeatedly arisen within different butterfly taxa (families) (Dennis and Shreeve 1988).

Identifying ecological, morphological and population dynamic correlates of mate location behaviour among butterfly communities still remains an outstanding task (Dennis and Shreeve 1988; Rutowski 1991). A prime objective for conservation is to identify environmental (landscape; resources) links for encounter sites and mate location behaviour at encounter sites that differ among species. The key issue for the distribution of encounter sites is the distribution of receptive females. Primarily, this has suggested to be pupation sites (Rutowski 1991; Wickman 2009); exceptions are considered to be found in long-lived species that defer mating and/or mate repeatedly, but even then it is argued that males mating with virgin females will be at an advantage owing to rapidly depleting finite male contributions at mating (Rutowski 1991). As pupation sites are typically on or near larval host plants, receptive females are suggested to be found most frequently near to host plants (Rutowski 1991). But, it is likely that this depends on at least three aspects of the geography of early stages: (i) the distribution of host plants (i.e. their dispersal in biotopes, abundance, density, clumping, and apparency), (ii) the loading of eggs on host plants and (iii) selectivity for a range of host plant qualities by egg laying females. For example only a fraction of host plant cover is ever exploited

by butterflies for egg laying and larval development (Dennis 2010). For a number of reasons associated with these factors, the distribution of eclosing receptive females may be unpredictable to males searching for mates. In such situations, other resources may become important (i.e. adult nectar resources, especially when compact; local climate influences on heat and light; edge situations or hill tops) any, or all, of which have the capacity to increase the density of individuals and enhance encounter rates between the sexes (Dennis and Shreeve 1988). Dennis and Shreeve (1988) pointed out that there is no simple cue for mate location encounter sites and behaviour. They later drew attention to several prominent factors in understanding any aspect of butterfly behaviour, as for arthropod behaviour in general (Dennis *et al.* 2003; Dennis 2010). First, any specific resource use cannot be understood in exclusion of other resource exploitation, including enemy avoidance; females remaining near host plant sites after eclosion and mating are likely to be harassed by males using host plant mate location cues. Second, morphological adaptations can place limitations on activities in individuals; wing and body dimensions are affected not just by different mate location behaviours but also by adult feeding (Porter *et al.* 1992; Corbet 2000; Tiple *et al.* 2009), aposematism and predator escape (Chai and Srygley 1990; Marden and Chai 1991) and migration between resource zones (Baker 1969; Dennis 1992; Cook *et al.* 2001; Merckx and Van Dyck 2002). Third, behaviour patterns are subject to temporal changes in populations; the distribution of receptive females may follow strict diurnal and seasonal patterns, often linked to changes in environmental conditions, which influence not just behaviour but probable encounter sites (Gilbert and Singer 1975). Finally, behaviour patterns may vary regionally in response to changing resource distributions (Dennis 2010).

It is evident that the components that explain different mate location behaviours and exploitation of different encounter sites are still far from being understood. Although data are accumulating on mate location activity and resource use (*see* Rutowski 1991; Shreeve 1992; Wicklund 2003; Wickman 2009), our knowledge of mate location in butterflies remains incomplete or inaccurate and rarely have data been collected on numerous species occurring in the same area or occupying the same or neighbouring biotopes. Data on mate location behaviour and encounter sites in tropical regions is extremely limited. The objective of this study is to contribute to our knowledge on butterfly mate location behaviour and resource use in tropical environments, biotopes within the urban environment of Nagpur, India. In particular, the study investigates mate location behaviour in butterflies in relation to encounter sites (i.e. biotopes, landmarks), relative population size, and morphology including individual conspicuousness (size).

## 2. Methods

### 2.1 Study site 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 72 of 145 butterfly species occurring at Nagpur between 1 June 2006 and 31 May 2008 as part of a survey investigating butterfly habitats and behaviour. The study was based on extensive Pollard transect records over six sites (Pollard and Yates 1993) and ecological and behavioural observations on individual butterflies obtained from complete areal cover of the same sites (table 1). For the Pollard transects, the six sites were divided into three transect sections (each 500 m long); the sites differ in biotopes (vegetation structure) and in resources for butterflies (i.e. occurrence of larval host plants, flowering nectar plant

species and physical structures used for mate location). The relative abundances of butterfly species (27,700 individuals, minimum 15, maximum 1575 individuals per species) distinguished where possible by sex, were obtained from the Pollard transect records taken within confined bounds (5 metre box) walked at a steady pace (Tiple *et al.* 2009). Species difficult to identify on the wing were captured and subsequently released. In independent surveys, observations were made of mate location behaviour, nectar (flowering) plant use (Tiple *et al.* 2009), abundance of larval host plants and the areal cover of distinct biotopes on transect sections (percentage cover of bare ground, short herb/grasses, tall herbs, shrubs, preclimax woodland, climax forest).

### 2.2 Variables and measurements

Observations on mate location behaviour were made during behavioural observations carried out systematically over the sites (mean number  $\pm$  standard error of individuals per species observed:  $33.9 \pm 3.8$ ). Individual male butterflies were observed for short periods (10 seconds to several

**Table 1.** Sites for data collection in Nagpur City, India

Sites at Nagpur	Description of sites
Site 1 Seminary Hills (S1-S3) (north-west Nagpur)	Natural forest type vegetation. <i>Tectona grandis</i> (Teak) is the dominant tree species with <i>Lantana camara</i> as dominant weed (67 ha). BG 11.7, HS 23.3, HT 15.0, SH 30.0, PCF 5.0, CF 0.0.
Site 2 Satpuda Botanical Garden (B1-B3) (west Nagpur)	Hill and lake country (Futala) with mixed vegetation comprising ornamental, fruit plants, scrub, grassland; some part with natural forest dominated with <i>Lantana</i> sp. (25 ha). BG 8.3, HS 18.3, HT 31.7, SH 31.7, PCF 5.0, CF 5.0.
Site 3 Agricultural Land, Bull Rearing Center (L1-L3) (west Nagpur)	Vegetation is mixed; cultivated fodder plants (e.g. Barseam and Jawar), wild forest plantation, scrub and grassland for grazing (44 ha). BG 3.3, HS 25.0, HT 45.0, SH 23.3, PCF 3.3, CF 0.0.
Site 4 RTM Nagpur University Campus and Laxmi Narayan Institute of Technology (LIT) Campus (U1-U2) (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). BG 8.3, HS 28.3, HT 33.3, SH 25.0, PCF 1.7, CF 0.0.
Site 5 Ambazari garden and bare land at Lake Side (A1-A3) (west Nagpur)	Ornamental, flowering plants, forest, scrub and grassland (6 ha). BG 13.3, HS 25.0, HT 25.0, SH 30.0, PCF 3.3, CF 3.3.
Site 6 Sides of National Highway (R1-R3) (south Nagpur)	Ornamental flowering plants along the roadside and along an accompanying track (2 ha). BG 3.3, HS 18.3, HT 35.0, SH 43.3, PCF 0.0, CF 0.0.

Biotopes: Sere 1 BG bare ground dominant, screes, slopes with scarce herbs/grasses; sere 2 HS short herbs/grasses; 3 HT tall herbs/grasses and scattered shrubs; sere 4 SH shrubs and invading trees; 5 PCF pre-climax forest; 6 CF climax forest with regeneration patches. Cover (%) for different biotopes (vegetation classes) given as average for the three sections at each site.

minutes) and scored for one or more of several behaviours: patrolling, perching, site fidelity, territorial defence and lek aggregation. Mate location behaviour was identified by the occurrence of perching and/or patrolling; individuals that could not be so classed were not scored for mate location behaviour. 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). The survey technique did not allow accurate identification of the territorial area defended, and the measure was one of occurrence or absence of notable aggression at encounters. 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. Site fidelity or tenacity was not timed but divided simply into two categories, based on returns and the repeated occurrences of individuals at specific sites during the same or on subsequent visits: 1 low, seconds to a few minutes; 2 high, few minutes up to a day or more. From these data individual butterfly species could then be classed for five binary coded behavioural variables (patrol, yes/no; perch, perch, yes/no; site fidelity, low or high; territorial defence, territorial or not; lek assemblage, presence or absence of male assemblages). (Supplementary table 1).

The locations (transect sections) used for these activities were also recorded and placed into one or more of the following binary coded 'landscape structure' categories (patch of bare ground; area of short herbs/grasses; tracks through tall herbs, shrubs and other taller vegetation; shrub edges; wood edges; rock faces [including walls]; stream banks; hilltops). The binary scores are also summed to give a measure of landform association (MLela), distinguishing species that use few or many distinct landforms for mate location. A similar coding was established for biotopes or seres (sere 1, bare ground, screes and sparse herbs; sere 2, short herbs/grass; sere 3, tall herbs with invading shrubs; sere 4, shrubs and scattered trees; sere 5, preclimax forest; sere 6, climax forest). Binary scores for biotopes were summed into open seres (seres 1 to 3) and closed seres (seres 4 to 6). Mate location behaviour (perch and/or patrol) of butterfly species was scored (presence/absence; multiple classification) for use of these landscape structures and biotopes.

Observations on nectar plants used were obtained during transect recording and from an independent survey (*see Tiple et al.* 2009). Data were collected on the number of nectaring events by different species on 20 plants. Butterfly larval host plants were identified and recorded for transect sections using the following simple ranked abundance score categories: 0 absent, 1 rare, 2 frequent, 3 abundant. Larval host plant resources for butterfly species were also scored by the first author (ADT) for dispersion (1 scattered [dispersed], 2 clumped [aggregated], 3 both), life form (four ranked size categories: 1 short herb/grass, 2 tall herb, 3 shrub, 4 tree/climber) and characteristic distributions for the following edge sites and landmarks (track edges through herbs; track edges through shrubs and forest; shrub edges; wood edges; rock faces and walls; hilltops; stream banks; all binary coded and summed to give an overall measure of host plant landform affiliation (HPela), the reasoning as for MLela above. Butterfly host plant use was scored for egg laying (1 one or two eggs per egg laying visit, 2 small batch <10 eggs per visit; 3 large batch of 10 to 100 eggs per visit). Butterfly species were also scored for host plant predictability (conspicuously clumped and/or distributed in relation to landform features) by the field recorder (ADT; binary score: 1 unpredictable, 2 predictable) as a further measure of host plant conspicuousness. Those plants difficult to identify in the field were preserved by making dry herbarium sheet specimens including all details of the plants for further identification. These herbarium specimens were identified in consultation with Prof. K H Makde and Dr N M Dongerwar, Department of Botany, RTM Nagpur University, Nagpur and other renowned taxonomists.

For the morphological study, five butterfly specimens of each sex identified as perchers or patrollers were collected for measurement in the laboratory and subsequently released without harm. Measurements were made of body length, wingspan and total weight (*see Tiple et al.* 2009) and means established for each species; higher taxa (families) have already been demonstrated to differ significantly for body and wing morphology variables (Tiple *et al.* 2009). 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 (Van Dyck *et al.* 1997). The total weights (body wet weight) of butterflies were measured on a digital balance (Mettler portable electronic balance; in mg). Two indices were calculated: wing loading index (body weight/wingspan) and proboscis index (proboscis length/body length), the latter measure obtained in a previous study (Tiple *et al.* 2009). 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.

### 2.3 Objectives and hypotheses

The following specific hypotheses are tested:

1. There are discrete types of male mate location behaviour. Invariant patrolling is expected to emerge as distinct behaviour from perching, territorial defence and lek assembly (Scott 1974; Dennis and Shreeve 1988).
2. Lower and higher taxa differ significantly in the frequency of male mate location behaviours (Dennis and Shreeve 1988).
3. Significant associations link butterfly morphology and male mate location behaviours. Specifically, species which have high wing loading are expected to perch, engage in territorial defence and establish leks (Wickman 2009).
4. Habitual species' biotope occupancy influences male mate location behaviours. Specifically, patrolling is expected to be more frequent in open seres, and perching, accompanied by territorial defence and lek assembly, more frequent in closed seres (Dennis and Shreeve 1988).
5. Different male mate location behaviours are expected to relate to different landscape features used as encounter sites. Specifically, perching behaviour, territorial defence and lek assembly are expected to be associated with more edge features than patrolling activity (Dennis and Shreeve 1988).
6. Different male mate location behaviours are expected to relate to distinctions in resource use (Rutowski 1991). Specifically, patrolling is expected to relate more closely to scattered unpredictable host plants and use of a wider array of nectar sources, whereas perching, territorial defence and lek assembly are expected to relate more closely to concentrated, predictable host plants and limited array of nectar sources (Baker 1972; Scott, 1974; Rutowski 1991; Tiple *et al.* 2009).
7. Population parameters significantly influence different male mate location behaviours. Specifically, it is expected that higher female to male numbers (as a surrogate for recipient females) encourages more frequent patrolling, whereas relatively more males than females leads to perching, territorial defence and lek assembly (Shields 1967; Scott 1974; Ehrlich 1984).

### 2.4 Analyses

Analysis has been conducted on a species (rows) x attributes/variables (column matrix). Apart from taxonomic groupings

(butterfly families, categories), transects counts and butterfly morphology (interval ratio scale), variables are scored on binary or ranked scales. Relationships between behavioural repertoires and predictor variable suites have been examined using multiple correspondence analysis (MCA). Mate location behaviours have been kept distinct as recommended by Rutowski (1991). Potential predictors for different mate location behaviours have been entered as active variables and mate location behaviours and taxa (families) entered as supplementary to analysis. The minority of variables not in binary format have been reduced to a binary form for multiple correspondence analysis; this has been undertaken by collapsing numbers of attributes for ranked variables and by dividing distributions at the mean for continuous variables. Coding used is recorded in the legends to figures where necessary. Significance of direct associations within MCA plots is reported as Kendall's tau ( $\tau$ ). Kendall's tau is equivalent to the phi coefficient, or  $\sqrt{\chi^2/N}$ , applied to categorical or binary data (Siegel 1956). Comparisons have applied suitable tests for data type and distribution, the chi test, Fisher exact test, the Kruskal-Wallis ANOVA by ranks and sign test.

Relationships among taxa (species) for male mate location behaviours have been examined using SAHN cluster analysis (unweighted pair-group average method based on Euclidean distances ( $d$  or Sokal's  $\delta_{jk}$  (Sneath and Sokal 1973: 124) and non metric scaling. The relationship between butterfly morphology, butterfly taxa and mate location behaviour has been investigated using logit regression and principal components analysis (PCA) based on normalized variables. For logit regression, the influence of family (categorical variable) has been tested against morphology in a forwards stepwise model with behaviour scored in a binary format. For PCA, butterfly species are distinguished for taxa and behaviour in the first two principal components axes for the morphology variables.

No exhaustive phylogeny exists for the 72 butterfly species in this study but we were able to find comparable mitochondrial cytochrome c-oxidase (COI) gene data for cytochrome oxidase subunit I in 29 Papilionidae, Pieridae and Nymphalidae species (Supplementary table 3). Sequences have been aligned by ClustalW and genetic distances have been calculated by DNADIST 3.5 using default options. Possible correlations between distance matrices of genetic and behavioural characteristics have been tested by Mantel tests using zt software (Bonnet and Van de Peer 2002). Taxonomic relationships at generic level have been assessed directly on Euclidean distances (Mann-Whitney  $U$  test) for the suite of mate location behaviours between pairs of species distinguished as congeneric or not.  $P$  values have been derived using a Monte Carlo routine based on 10,000 iterations.

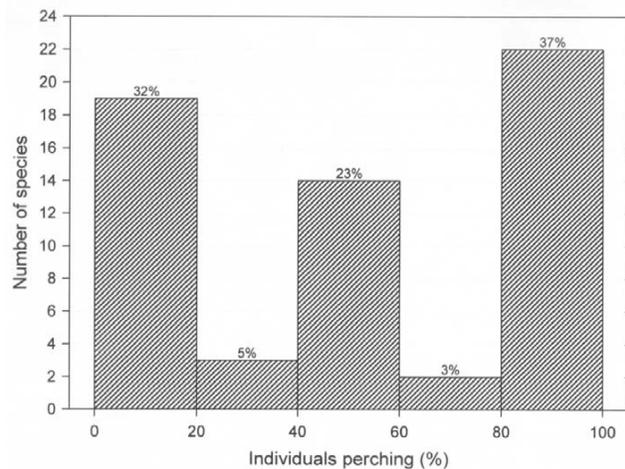
Analyses have been conducted in Statistica (Statsoft Inc., Tulsa, OK, USA, version 7.1) and SPSS 15.0 (SPSS Inc. Illinois, USA). Significance is adopted at  $P < 0.05$ . Although Bonferroni corrections are frequently applied for multiple tests this increases the risk of ignoring real relationships (Moran 2003) of value in research such as the current explorative study of mate location behaviours; as such, they are not applied but are reported for readers to make their own judgements about relationships. Significant associations ( $P < 0.05$ ) are reported in Supplementary table 2. It is possible that numbers on transects are affected by the relative conspicuousness of species. As wing span of species at Nagpur varies enormously, wing span is regarded as one possible measure of conspicuousness of butterflies to recorders (Dennis *et al.* 2006b). The relationship between population numbers and numbers of individuals observed for mate location behaviour is affected by their conspicuousness. In a regression of normalized transect counts (males, females, total, numbers of males observed in mate location behaviour; log transformed) against wing span, no significant relationship was found ( $r < 0.16$ ,  $P > 0.20$ ); the inference is that any increase in conspicuousness does not result in greater numbers being observed.

### 3. Results

#### 3.1 Associations among mate location behaviours

The distribution of the percent of individuals perching produced a tri-modal distribution (figure 1). Two of the modes describe invariant perchers and invariant patrollers; the third mode describes perch-patrollers, species equally distributed for perching and patrolling. Using the algorithm  $0.5 - |(\alpha - 50)/100|$  where  $\alpha$  is percent perching, describing a scale from invariant perchers or patrollers (0, min) to an equal number of males observed perching and patrolling (0.5, max), a significant correlation was found with numbers of males observed (Kendall  $\tau$  0.56,  $P < 0.0001$ ). As this relationship indicates that perch-patrol frequency is sensitive to the number of observations and because conditions of observation were not determined for each observation, species observed to both perch and patrol were deemed to be perch-patrollers regardless of perching frequency.

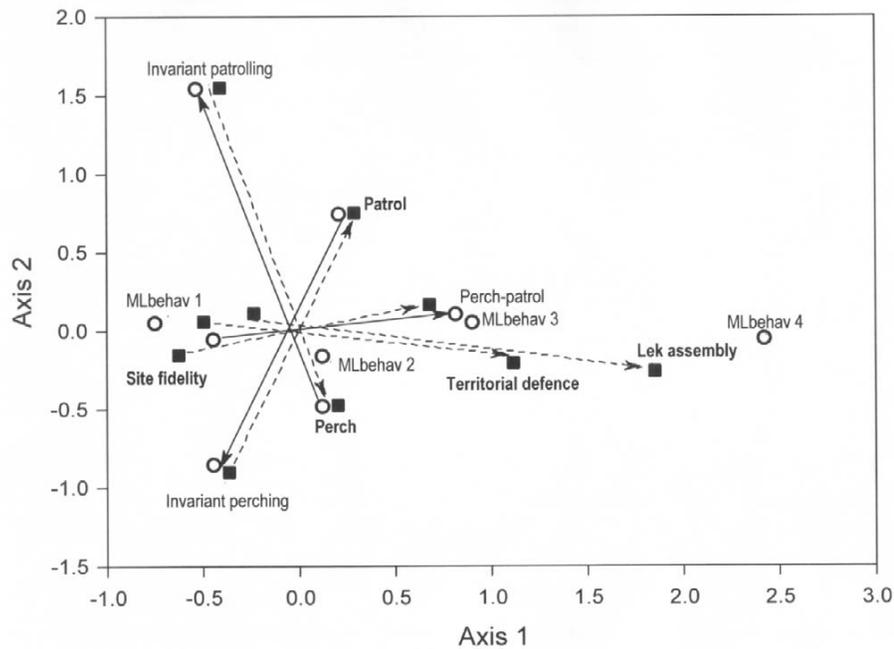
Multiple correspondence analysis based on the five basic male mate location behaviours (perch, patrol, site fidelity, territorial defence and lek assembly) for the 72 butterfly species discloses a distinctive pattern of associations (figure 2). There is clear separation of invariant patrolling, invariant perching and perch-patrol entered as supplementary to analysis. There is also a clear gradient in number (complexity) of mate location behaviours with increased



**Figure 1.** Frequency distribution of percentage perching among butterfly species at Nagpur, India. Only species with observations on  $n \geq 10$  individuals are included in the histogram.

perch-patrol (figure 2); the links between variables are supported by high negative and positive correlations (table 2). All but four correlations among the eight variables of mate location behaviour (perch, patrol, invariant perching, invariant patrolling, perch-patrol, site fidelity, territoriality and lek assembly) are significant; there was no significant correlation between perch and invariant patrolling with site fidelity, nor between the two variables patrol and invariant perching with territoriality.

Cluster analysis and non metric scaling have been used to search for groupings of species with distinctive behaviours. UPGMA cluster analysis based on Euclidean distances for the five basic male mate location behaviours (perch, patrol, site fidelity, territorial defence and lek assembly) identified 15 of the 24 possible discrete groups (Supplementary table 1) distinguished by unique combinations of variable states. Not all combinations are possible; for instance, territorial defence and lek assembly cannot occur without perching and/or patrolling. Three prime clusters are distinguished, prior to complete amalgamation (Supplementary table 1), with Euclidean distance  $> 2$  (figure 3). When individual distances between species are subject to non-metric scaling the three clusters are non-overlapping but do not obviously cluster in the plot of the first 2 dimensions (figure 3) and relationships among the 15 base groups are determined primarily by gradients in different mate location behaviours and for number of mate location behaviours. Even so, species in the three main clusters differ significantly with respect to invariant patrolling ( $\chi^2_{(2)} = 29.0$ ,  $P < 0.0001$ ), invariant perching ( $\chi^2_{(2)} = 72.0$ ,  $P < 0.0001$ ), perch-patrol ( $\chi^2_{(2)} = 37.1$ ,  $P < 0.0001$ ) and territorial defence ( $\chi^2_{(2)} = 42.0$ ,  $P < 0.0001$ ) (table 3). Two pairs of groups also differ significantly for



**Figure 2.** Multiple correspondence analysis of five basic mate location behaviour variables (perch, patrol, site fidelity, territorial defence, lek assembly) for 72 butterfly species. Dimension 1, 33.6% inertia; dimension 2, 30.1% inertia. Squares, active variables; circles, supplementary variables. Arrows indicate direction of increased activity with labels (bold, active; not bold, supplementary) for variables placed at the termini for activities. Invariant perching, invariant patrolling, perch-patrol (solid arrows) and numbers of mate location behaviours (MLBehav1 to 4, sums of perch, patrol, territorial defence and lek assembly) are entered as supplementary to analysis. Butterfly taxa (families) occur around the origin except Papilionidae (near patrol) but are omitted for clarity.

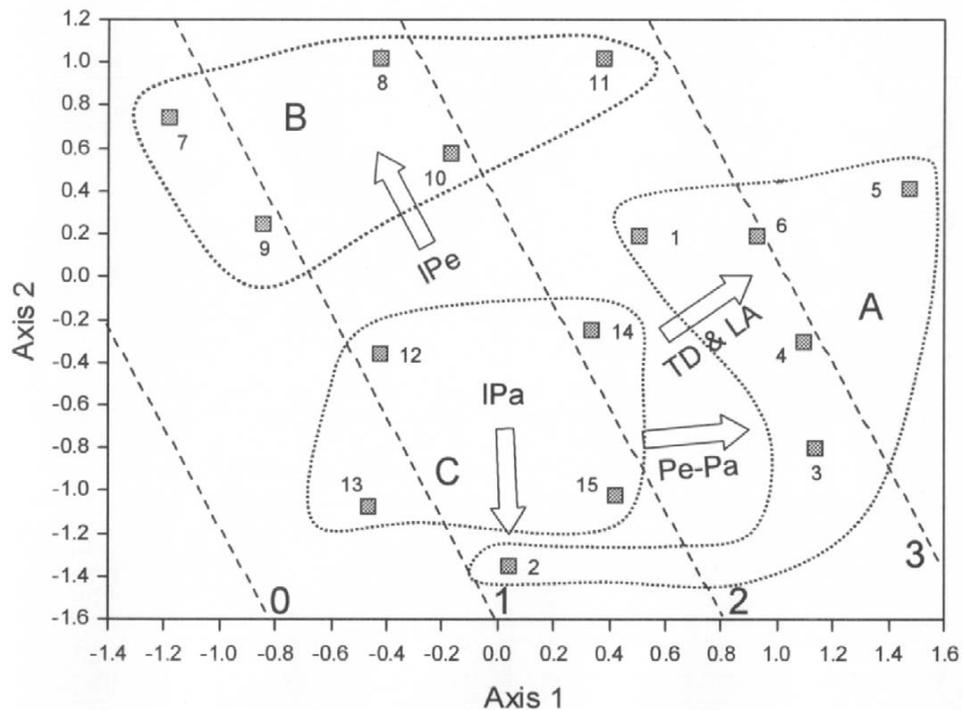
**Table 2.** Kendall tau associations among eight mate location behaviours in 72 butterfly species

	Perch	Patrol	Invariant perch	Invariant patrol	Perch-patrol	Fidelity	Territorial defence	Lek assembly
Perch								
Patrol	0.48 **							
Invariant perch	0.48 **	-1.00 **						
Invariant patrol	-1.00 **	0.48 **	-0.48 **					
Perch-patrol	0.39 **	0.61 **	-0.61 **	-0.39 **				
Fidelity	0.03 NS	0.19 †	-0.19 †	-0.03 NS	0.23 *			
Territorial defence	0.22 **	0.15 NS	-0.15 NS	-0.22 **	0.36 **	0.30 **		
Lek assembly	0.21 **	0.15 *	-0.15 *	-0.21 **	0.35 **	0.21 **	0.29 **	

Significance levels. NS, not significant, †  $P < 0.05$ , \*  $P < 0.01$ , \*\*  $P < 0.001$  ( $\tau > 0.21$ ,  $P < 0.05$  Bonferroni correction).

lek assembly (Fisher exact test: A versus B,  $P = 0.004$ ; A versus C,  $P = 0.005$ ) and one pair for site fidelity (Fisher exact test: A versus B,  $P = 0.03$ ). The three groups also differ

significantly for the number of mate location behaviours recorded (sum of four mate location behaviours; Kruskal-Wallis ANOVA by ranks,  $H(2, N = 72) = 40.7$ ,  $P < 0.0001$ );



**Figure 3.** Non-metric scaling plot (2 dimensions) of Euclidean distances among 72 species based on five mate location behaviours (patrol, perch, site fidelity, territorial defence and lek assembly) (Kruskal stress 16.4%, alienation 19.5%). Isolines are number of mate location behaviours fitted by trend surface analysis and envelopes are the three penultimate sequential agglomerative hierarchical non-overlapping clusters (unweighted pair group average method, Euclidean distance  $d > 2$ ); Capital letters indicate cluster groups (see Supplementary table 1): A, mainly perch-patrollers, with high site fidelity engaged in territorial defence and lek assembly, B, Invariant perchers, C, mainly invariant patrollers. Numbers refer to discrete basal units in dendrogram ( $d = 0$ ) (Supplementary table 1). Arrows indicate increasing trends for invariant perching (Ipe), invariant patrolling (IPa), perch-patrol (Pe-pa), territorial defence (TD) and lek assembly (LA).

in a multiple comparisons test, group A is significantly distinct from B and C ( $P < 0.0001$ ), whereas the latter two groups do not differ for number of mate location behaviours ( $P \approx 1.00$ ). One of the three clusters is distinguished by an exclusive behaviour (B with invariant perching) (table 3).

### 3.2 Taxonomic distribution of mate location behaviour

Apart from absence of lek assembly in the Hesperidae and invariant perching in the Papilionidae, all mate location behaviours, as well as the three main behavioural classes, were recorded in each butterfly family (Supplementary table 1). Patrolling occurs more frequently than perching among Papilionidae, a pattern that is reversed in Pieridae, Nymphalidae and Hesperidae; among Lycaenidae the two behaviours occur equally (table 4). A Fisher exact test for pairs of taxa for different behaviours produced 5 significant differences out of 80 tests. Papilionidae were found to differ from Nymphalidae for patrolling and invariant perching (both  $P = 0.018$ ) and Lycaenidae differed from Papilionidae

( $P < 0.0001$ ), Pieridae ( $P = 0.002$ ) and Nymphalidae ( $P = 0.014$ ) for site fidelity. A number of congeneric taxa are noted to adopt identical behaviour; thus, for example, *Mycalesis* and *Melanitis* species are invariant perchers, both *Pachliopta* species are invariant patrollers and *Junonia* species tend to be territorial. A non-parametric Mann-Whitney test of 44 congeneric distances versus 2511 non-congeneric distances, applying a Monte Carlo  $P$  value, indicated significantly lower Euclidean distances for congeneric species ( $P < 0.001$ ). A Mantel test between genetic distances and behavioural distances on the 29 selected species produced a significant result ( $r = 0.10$   $P = 0.048$ ).

### 3.3 Associations between mate location behaviour and butterfly morphology

No significant across-species correlations occur between butterfly morphology and perching and patrolling (perch, patrol, invariant perching, invariant patrolling, perch-patrol) or lek assembly. Body length, wing span, weight and wing

**Table 3.** Comparisons of mate location groups from UPGMA cluster analysis based on Euclidean distances for five basic mate location variables<sup>1</sup>

Group (suggested label)	Invariant patrolling	Invariant perching	Perch-patrol	High Site fidelity	Territorial defence	Lek assembly	<i>N</i>
A (perch-patrol)	2 (12.5)	0 (0.0)	14 (87.5)	12 (75.0)	15 (93.8)	7 (43.8)	16
B (invariant perchers)	0 (0.0)	31 (100.0)	0 (0.0)	12 (38.7)	7 (22.6)	2 (6.5)	31
C (invariant patrollers)	15 (60.0)	0 (0.0)	10 (40.0)	12 (48.0)	0 (0.0)	0 (0.0)	25
Total	17	31	24	36	22	9	72 species

<sup>1</sup>see figure 2. Upper numbers, number of species engaged in behaviour; lower numbers in brackets, percentage of total numbers (*N*) in UPGMA group.

**Table 4.** Summary of mate location behaviour among butterfly taxa (families)

Family	Patrol	Perch	Perch-patrol	Site fidelity (high)	Territorial	Lek assembly	Total
Papilionidae	6 (100.0)	3 (50.0)	3 (50.0)	6 (100.0)	2 (33.3)	1 (16.7)	6
Pieridae	7 (58.3)	9 (75.0)	4 (33.3)	9 (75.0)	3 (25.0)	2 (16.7)	12
Lycaenidae	13 (68.4)	13 (68.4)	7 (36.8)	3 (15.8)	3 (15.8)	2 (10.5)	19
Nymphalidae	11 (39.2)	24 (85.7)	7 (25.0)	15 (53.6)	11 (39.3)	4 (14.3)	28
Hesperiidae	4 (57.1)	6 (85.7)	3 (42.9)	3 (42.9)	3 (42.9)	0 (0.0)	7
Total	41 (56.9)	55 (76.4)	24 (33.3)	36 (50.0)	22 (30.6)	9 (12.5)	72

Numbers for invariant patrolling and invariant perching are obtained by subtracting numbers for perch-patrol from patrol and perch respectively. Table records actual number of species, with percent of total in butterfly family in brackets.

load index increase across species with increased site fidelity ( $P < 0.002$ ; table 5) and body length and wing load index increase significantly with territorial defence ( $P = 0.015$ ; table 5). Proboscis length also increases significantly with site fidelity ( $P = 0.026$ ; table 5). An intra-species comparison of patrolling and perching butterflies for species that both perch and patrol disclosed that body length is significantly greater in patrolling butterflies, whereas wing span and weight are significantly greater in perching butterflies, there being no significant difference for wing loading (table 6). The morphological variables (but for proboscis index) cluster tightly in a PCA plot and the axes account for some 92% of the variance; the two variables significantly associated with butterfly morphology, site fidelity and territorial defence are linked most closely with body length and wing load index respectively (figure 4A). Although clusters of species from the same family form distinct morphological clusters and clusters also occur for the same basic mate location behaviour within families, there is also a considerable mix of mate location behaviour within butterfly families (figure 4B).

A Mantel test between overall morphological distances and behavioural distances on 69 species produced a low but significant correlation ( $r = 0.06$ ,  $P = 0.03$ ). Morphological distances are more strongly correlated with genetic distances in the subset of 29 species (Mantel test  $r = 0.23$ ,  $P = 0.003$ ) (see Supplementary table 3 for species). However, in the subsample of 29 species the correlation between behavioural and morphological matrices is not significant ( $r = 0.014$ ,  $P = 0.37$ ) suggesting a subsidiary effect of morphology compared to taxonomy in predicting butterfly behaviour.

### 3.4 Distribution of mate location behaviours over biotopes

Butterfly individuals have been scored for six biotopes (seres) in which observations have been made. An MCA plot identifies a systematic trend in seres on the basis of distinctive male mate location behaviours in butterfly species (figure 5). An index (Sere Index [SI] = number of closed seres – number of open seres, converted into a simple

**Table 5.** Logit regression parameters for mate location behaviour against morphology variables<sup>1</sup>

Mate location variable	Estimate Const. BO±SE	Estimate Morphology Variable±SE	Wald $\chi^2$	Final loss	<i>P</i>
Site fidelity	1.20±0.639	PL 0.11±0.053	4.16	45.36	0.026
	2.52±0.833	BL 0.16±0.049	10.25	41.55	0.0004
	1.71±0.646	WS 0.03±0.012	8.33	43.02	0.002
	0.86±0.382	WT 0.01±0.003	7.80	42.27	0.0009
	1.20±0.484	WL 0.75±0.263	8.20	42.78	0.002
Territorial defence	-2.49±0.854	BL 0.10±0.047	4.86	40.56	0.02
	-1.76±0.518	WL 0.56±0.237	5.57	40.23	0.015

<sup>1</sup>Only parameters for significant models reported. Butterfly family in forwards stepwise models was not entered. PL, proboscis length; BL, body length; WS, wing span; WT, weight; WL, wing load index. No relationships for behaviours not mentioned. *N*= 69 species.

**Table 6.** Paired within-species morphology comparisons (sign test) for patrolling and perching activity

Variable	<i>Z</i>	<i>P</i>	Difference
Body length	3.06	0.002	patrollers > perchers
Wing span	3.62	0.0003	perchers > patrollers
Weight	4.17	0.00003	perchers > patrollers
Wing loading	0.42	0.68	no difference

*N* = 24 species.

scale of 1, 0, -1), entered as supplementary to analysis with behaviours and taxa (families) describes the trend. Lek assembly and territorial defence are most closely associated with later seres (shrub to high forest) as is higher fidelity to sites, whereas patrolling activity is linked more closely with early seres. This pattern is largely supported by significant associations between seres and mate location behaviour (Kendall  $\tau$ ,  $P < 0.05$  for 21 of a possible 48 associations; Supplementary table 2a). Territorial defence and lek assembly are strongly associated with all late seres 4 to 6 ( $P < 0.02$ ,  $< 0.0001$ ). There are no significant associations with sere 1, but sere 2 is most strongly associated with patrolling (Kendall  $\tau$ ,  $P < 0.0001$ ) and inversely associated with invariant perching (Kendall  $\tau$ ,  $P = 0.0001$ ). Sere 3 is only significantly associated with site fidelity and territorial defence (Kendall  $\tau$ ,  $P < 0.0001$ ). The radiation of butterfly families in the plot is supported by significant associations with seres (Supplementary table 2b). Eight of 30 possible associations are significant at  $P < 0.05$ .

### 3.5 Associations between mate location behaviours and landscape structures (landmarks and edges)

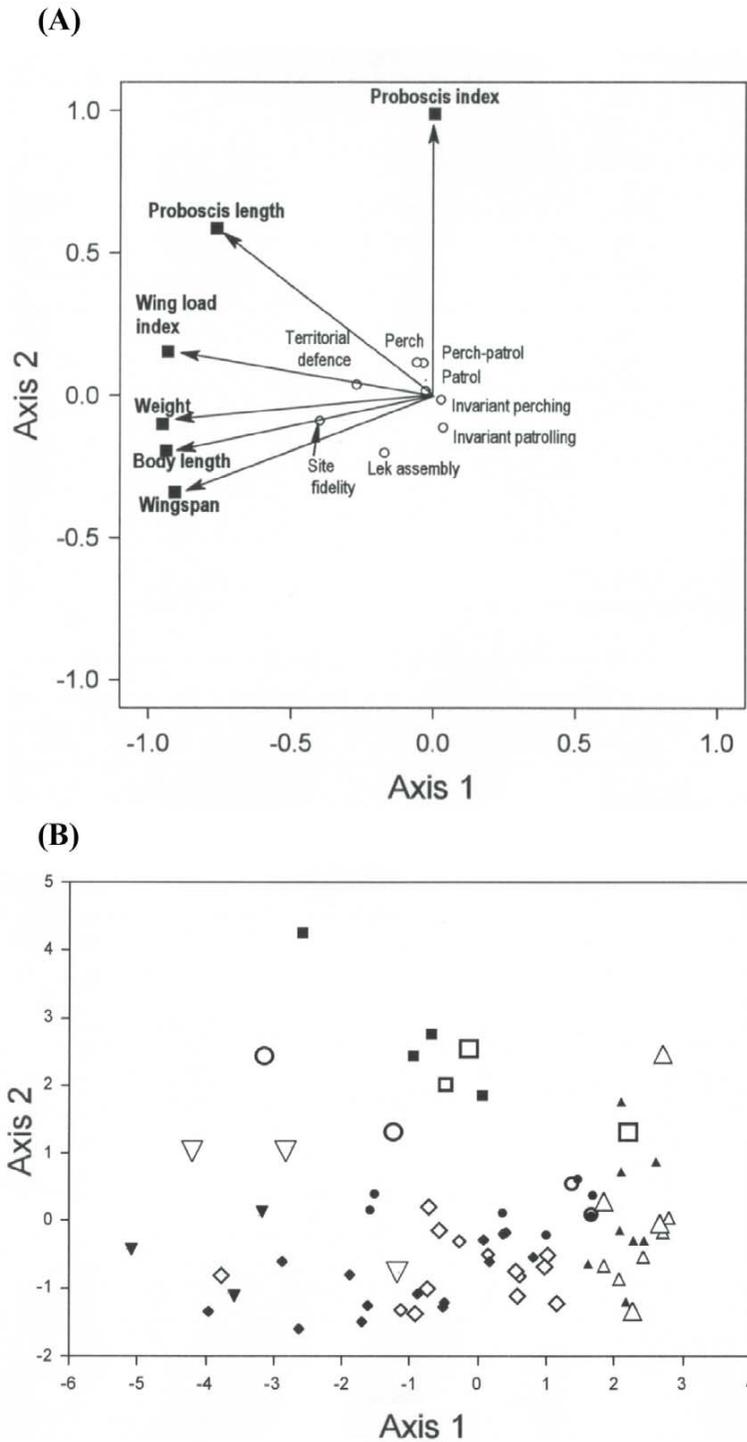
There are strong associations between landscape structure and mate location behaviours. In a MCA plot (figure 6), more complex behaviour (perch-patrol, territorial defence and lek assembly) is closely linked to edge features and hilltops (Kendall  $\tau$ ,  $P < 0.04$ ,  $< 0.0001$ ) whereas patrolling,

especially invariant patrolling, is associated with tracks through vegetation of different heights (Kendall  $\tau$ ,  $P < 0.0001$ ) and is negatively associated with all other edge structures. Thirty nine of a possible 64 associations are significant at  $P < 0.05$  (Supplementary table 2c). The set of relationships are summed for comparisons with the three clusters from the UPGMA clustering (figure 3). The three groups differ significantly for use of numbers of edge features (Kruskal-Wallis ANOVA by ranks  $H(2, N = 72) = 18.79$ ,  $P < 0.0001$ ); a multiple comparisons test indicates that the differences lie between group A (mainly perch-patrollers) and groups B (invariant perchers) and C (mainly invariant patrollers), the latter being homogeneous. However, two of the UPGMA groups are not exclusive categories for the identified behaviours (*see above*); when invariant patrollers and invariant perchers are compared directly, they are found to differ (number of edge sites used: invariant patrollers mean 1.59, median 1, invariant perchers 2.29, median 2 Mann-Whitney *U*,  $Z = -2.56$ ,  $P = 0.009$ ; number of landmarks used: invariant patrollers mean 2.35, median 2, invariant perchers mean 3.19, median 3, Mann-Whitney *U*,  $Z = -2.67$ ,  $P = 0.007$ ). A number of mate location behaviours are closely associated with edge features (Supplementary table 2d).

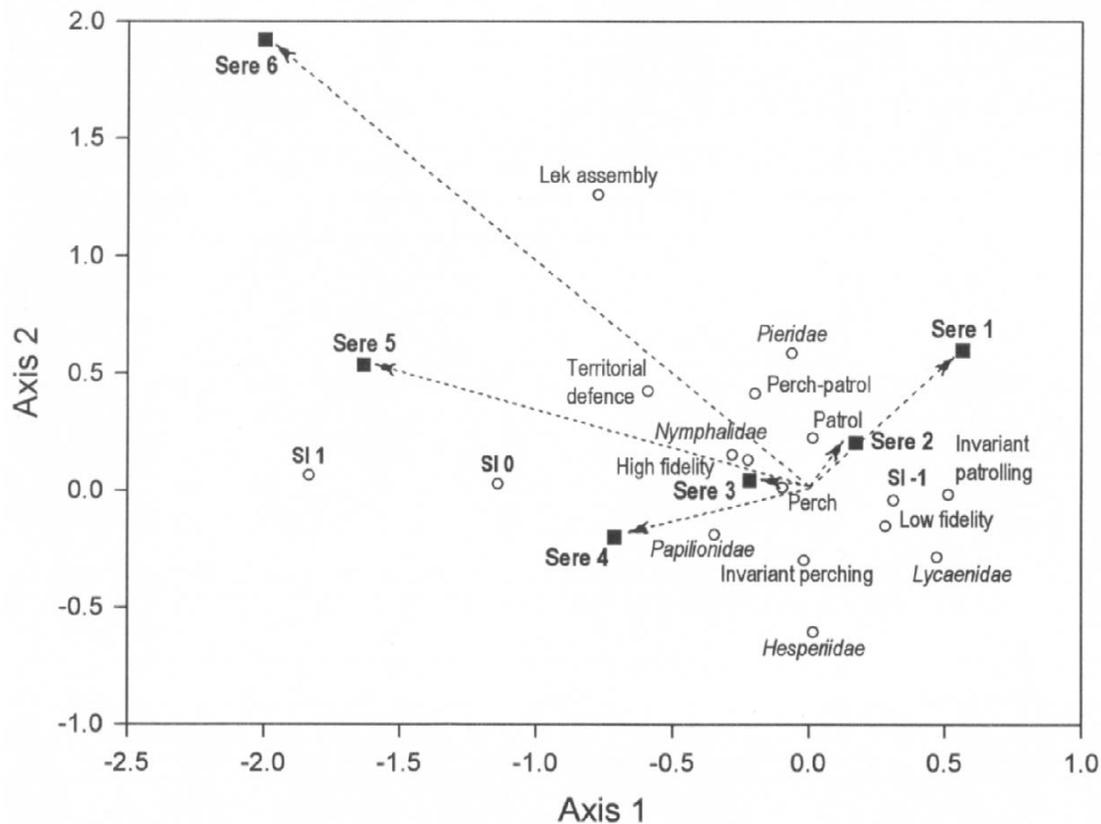
There are also distinctions among broad taxa (families) for affiliation with landform structures (Supplementary table 2e). Eighteen of a possible 40 associations are significant at  $P < 0.05$ ; Nymphalidae show a greater propensity to using distinct abiotic structures (i.e. rock face, stream banks and hilltops) compared to Papilionidae, Pieridae and Hesperidae, which are more closely associated with vegetation edges.

### 3.6 Associations between mate location behaviours, butterfly resources and population variables

Significant associations occur between mate location behaviours and all resource variables but not with egg laying behaviour, despite the fact that egg laying mode is



**Figure 4.** Principal components analysis plots of butterfly species for 6 morphology variables (body length, wing span, weight, wing loading, proboscis length, proboscis index). **(A)** the placement of male mate location behaviours in the first two axes as supplementary variables (axis 1 67.6% and axis 2 25.0% of variance, squares, active variables; circles, supplementary variables); **(B)** placement of butterfly species coded for mate location behaviour and taxon (family) in the first two axes of the PCA. Loadings of PI increase with axis 2 and the remaining variables increase to the left of axis 1. Butterfly families: inverted triangle, Papilionidae; circle, Pieridae; triangle, Lycaenidae; diamond, Nymphalidae; square, Hesperiidae. Mate location behaviour: large open symbol, invariant perching; black symbol, perch-patrol, territorial defence and lek assembly; small open symbol, invariant patrolling.  $N = 69$  species.



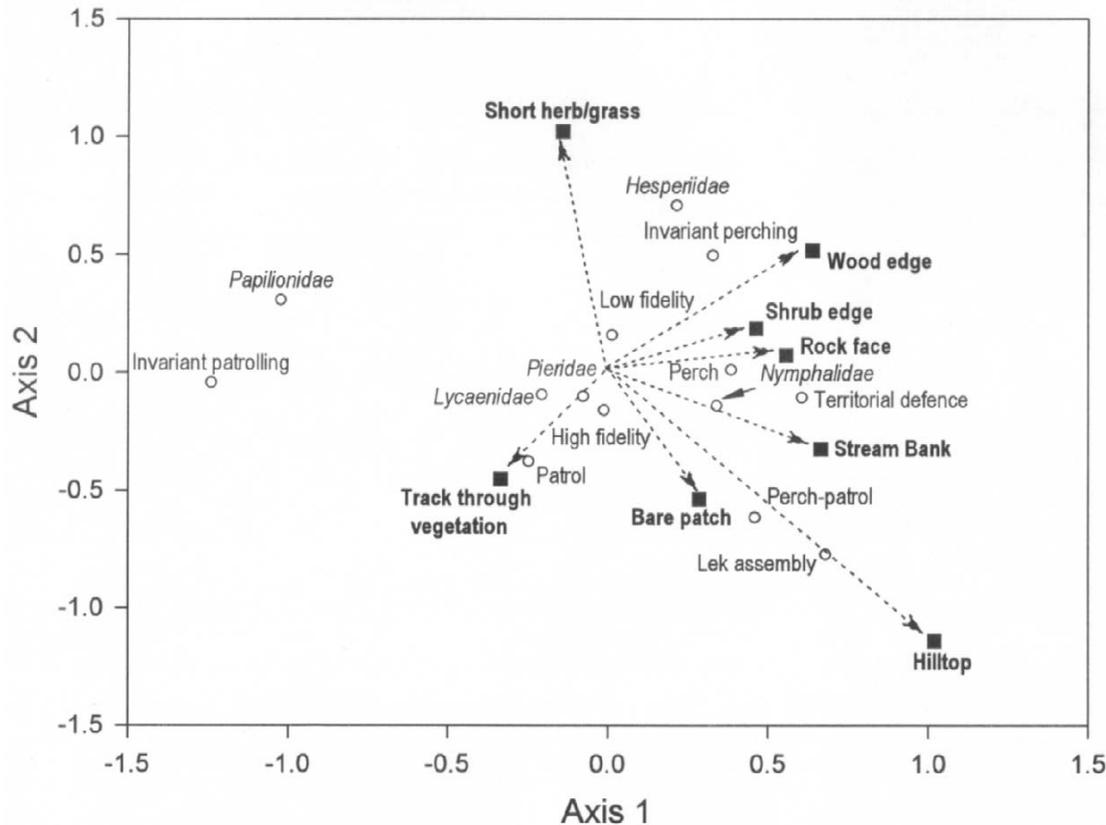
**Figure 5.** Multiple correspondence analysis of six biotopes (seral stages) in which mate location has been observed in 72 butterfly species. Squares, active variables; circles, supplementary variables; mate location behaviours and butterfly families have been entered as supplementary to analysis. Axis 1 38.5% of inertia, axis 2 18.0% of inertia. A sere index (SI = number of closed seres – number of open seres, converted into a simple scale of 1, 0, -1) indicates the shift from open (-1) to closed (1) biotopes.

significantly associated with higher taxa, positively with Pieridae and Lycaenidae and negatively with Papilionidae, Nymphalidae and Hesperidae (Kendall  $\tau$ ,  $P < 0.007$ ,  $N = 71$  species).

Significant associations of mate location behaviours with resource variables occur for 44 of 64 possible pairs tested (Supplementary table 2f). More complex behaviours (perch-patrol, territorial defence, lek assembly) are associated more with increased larval host plant dispersion (clumping) and host plant abundance (Kendall  $\tau$ ,  $P < 0.04$ ,  $< 0.0001$ ) whereas site fidelity is associated more with increased nectar plant use (Kendall  $\tau$ ,  $P < 0.0001$ ) than host plant variables (Kendall  $\tau$ ,  $P < 0.03$ ,  $< 0.01$ ) (figure 7). All mate location behaviours but invariant patrolling and invariant perching are significantly associated with the broadcast summed measure of host plant edge and landform affiliations (HPela). In detail, associations between different mate location behaviours and different edge and landform distributions reflect this general pattern (Supplementary table 2g). Patrolling is positively associated with tracks through such biotopes. Perch-patrol is positively associated with all seven edge and landform distributions of

host plants, territorial defence with five (not tracks through biotopes), lek assembly with four (wood edges, rock faces, hilltops and stream banks) and site fidelity with two (tracks through shrubs and shrub edges). The subjective measure of host plant predictability correlates primarily with host plant dispersion (Kendall  $\tau$ ,  $P < 0.0001$ ) but also with host plant abundance (Kendall  $\tau$ ,  $P < 0.0001$ ) and the summed measure for host plant landform and edge affiliation (Kendall  $\tau$ ,  $P < 0.001$ ). Invariant patrolling is negatively associated with host plant predictability (Kendall  $\tau$ ,  $P = 0.0003$ ), whereas perching and more complex behavioural suites increase with host plant predictability (Kendall  $\tau$ ,  $P < 0.003$ ). There is a positive and significant association between use of edge sites and landmarks by male adults for mate location and the characteristic distribution of host plants at edge sites and landforms (Kendall  $\tau$ ,  $P < 0.0001$ ).

Eight of the 16 pairs of associations between the mate location behaviours and two population measures are significant. Invariant patrolling is most associated with high female to male numbers on transects (Kendall  $\tau$ ,  $P = 0.0003$ ), whereas perching decreases with an increase of female to



**Figure 6.** Multiple correspondence analysis of eight landscape structures (landmarks and edges) in which mate location has been observed in 72 butterfly species. Squares, active variables; circles, supplementary variables; mate location behaviours and butterfly families have been entered as supplementary to analysis. Axis 1 25.2% of inertia, axis 2 18.2% of inertia.

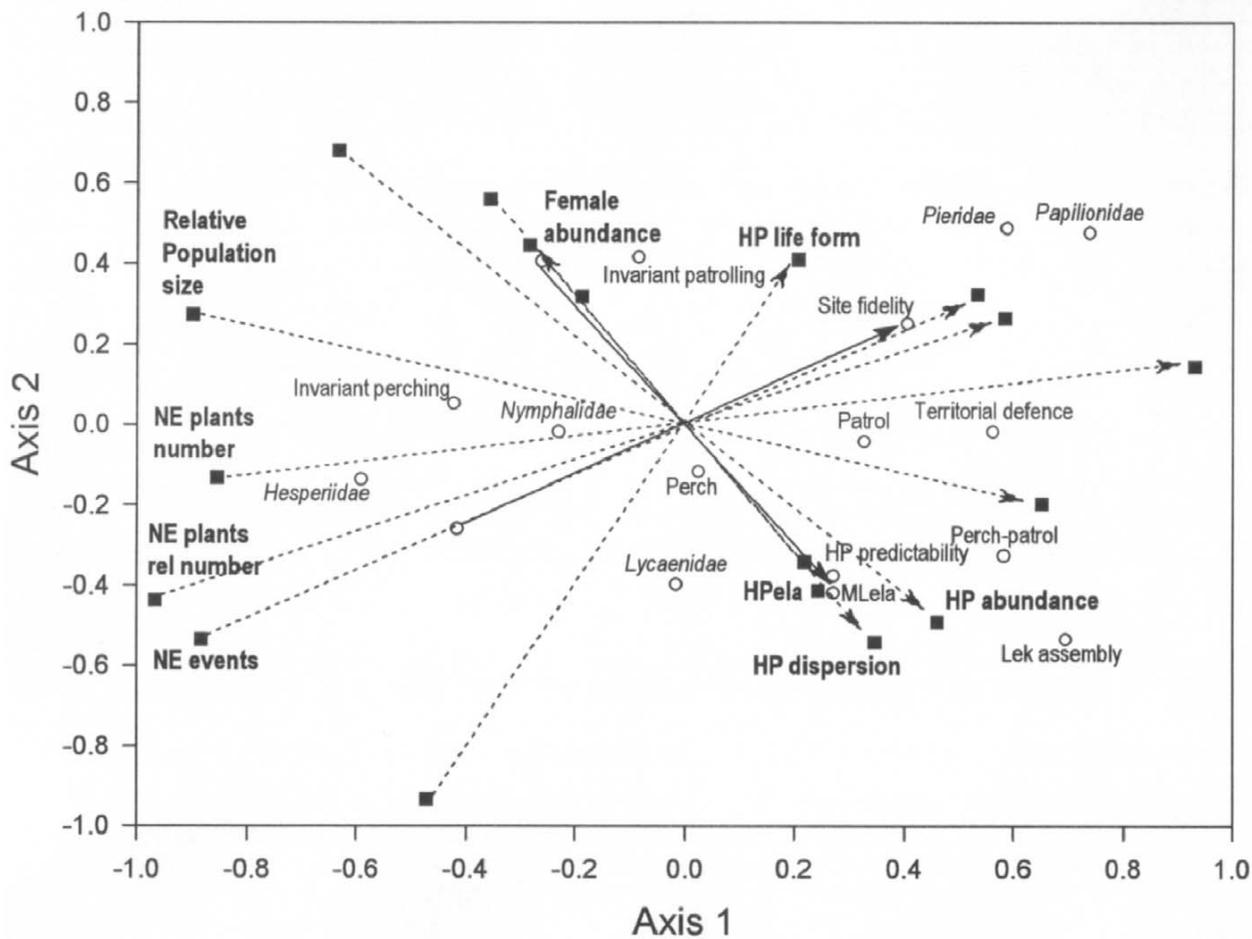
male numbers (Kendall  $\tau$ ,  $P < 0.03$ ). Invariant perching is associated with lower transect population counts for species whereas patrol behaviour is associated with increases in transect population counts (Kendall  $\tau$ ,  $P = 0.007$ ) as are other more complex mate location behaviours (Kendall  $\tau$ ,  $P < 0.0004$ ) (Supplementary table 2h).

Eight of a potential 35 associations between taxa (families) and resources variables are significant (Kendall  $\tau$ ,  $P < 0.05$ ) (Supplementary table 2i). Incidence of Papilionidae is associated with higher host plant life forms (Kendall  $\tau$ ,  $P = 0.0005$ ) and nectar plants used (Kendall  $\tau$ ,  $P = 0.017$ ) and Pieridae with all three nectar variables (Kendall  $\tau$ ,  $P = 0.01$ ,  $< 0.001$ ). Fifteen of 35 pairs of associations between taxa and host plant edge and landform feature affiliations are significant (Supplementary table 2j).

#### 4. Discussion

The current study of male mate location behaviour in 72 tropical butterfly species at Nagpur in India confirms a number of findings previously established for temperate

butterflies. In doing so, seven initial broad hypotheses are substantiated. First, discrete types of male mate location behaviour are shown to occur; in particular, invariant patrolling, invariant perching and a group of more complex behaviours linked to high site fidelity of limited areas are distinguished. Second, there are taxonomic distinctions for male mate location behaviour. Third, there are morphological distinctions for two male mate location behaviours, site fidelity and territorial defence, including significant differences between patrolling and perching individuals in paired within-species comparisons. Fourth, significant associations occur linking different male mate location behaviours with biotopes, different stages (seres) in vegetation succession. Fifth, different male mate location behaviours are associated with distinctive physical structures in the landscape, both vegetation (edges) and abiotic features. Sixth, different male mate location behaviours are linked to different consumer resources (larval host plants, nectar sources) and measures of status for these resources. Finally, there are significant associations between distinct male mate location behaviours and measures of relative population size. These findings are examined in detail below; they all



**Figure 7.** Multiple correspondence analysis of resource variables (larval host plants, adult nectar sources) and population variables for 72 butterfly species engaged in different mate location behaviours. Resources and population variables active (black squares); mate location behaviours and butterfly families, host plant predictability, mate location edge and landform association (MLela) supplementary to analysis (open circles). Axis 1 34% of inertia, axis 2 19% of inertia. Arrows indicate direction of increase for variables, those for active resource and population variables shown by pecked lines, and for site fidelity and MLela as solid lines. Variables - HP (host plant) life form: 0 herbs, 1 shrubs/trees; HP dispersion: 0 scattered, 1 clumped/scattered; HP predictability: 0 unpredictable, 1 predictable; HP abundance: mean of number of plants used on 3 point scale for each transect, 1 sparse, 2 abundant; HP edge and landform affiliation (number of seven variables including tracks, edges, banks, walls, hilltops; HPela): 1 <3.5, 2 > 3.5 affiliated edges and landforms; NE (nectar) plants number: number of nectar plants used, 1 few, 2 many; NE events: number of nectar records, 1 few, 2 many; NE plants rel number: number of nectar plants standardized by number of nectar events, 1 few, 2 many; MLela: 1  $\leq 3$  and 2  $\geq 4$  features used; female abundance: females/males+females, 1 < 50%, 2 > 50%. Continuous variables divided at the mean of the normalized distribution.

convey important implications for butterfly habitats within tropical environments.

#### 4.1 Distinctions and associations among male mate location behaviours

There is good evidence in the data for distinctions among male mate location behaviours. The generally high correlations among mate location attributes initially suggests a tightly bound, integrated behavioural complex, especially

the gradient in the number of mate location behaviours along axis 1 of the MCA plot and the regular (evenly spaced) pattern of some 15 discrete behaviours in the NMMS plot with the accompanying high Kruskal stress. However, there are shifts in behavioural repertoire. The trimodal distribution of percentage perching suggests clear divisions in the perch-patrol continuum proposed by Dennis and Shreeve (1988). Invariant perching and invariant patrolling (axis 2) separate out from perch-patrol, territorial defence, lek assembly and an increase in site fidelity (axis 1) in the MCA plot; species fall into mutually exclusive clusters in the UPGMA

clustering. In these groupings, invariant patrolling and invariant perching are disassociated from high site fidelity and territorial defence respectively. The implication is that butterfly species tend to engage one of three kinds of behaviour, invariant patrolling, invariant perching or perch-patrolling, and if the latter especially may vary substantially in site fidelity, territorial defence and lek assembly.

Nevertheless, it is evident from the existence of intermediate values in percentage perching and from the absence of strict familial patterning in behaviour (*see below*) that species may switch behavioural repertoire over evolutionary time. Potential for shifts in behaviour has its basis in flight (movement between resource units) and settled behaviour (thermoregulation, resting, nectar feeding) (Shreeve 1984). Thus, despite the home ranges of many patrolling species being up to a hundred times larger than those of perching species (Wickman 2009), some invariant patrolling species at Nagpur (e.g. *Junonia hierta*) are territorial in the sense of generating aggressive encounters, confirming this observation in other locations (e.g. *Battus philenor* L., Rutowski *et al.* 1989) and despite inspections from settled positions providing the foundation for heightened intra-specific interactions and lek assembly. It is unlikely that invariant perchers do not engage in occasional inspection of their perch surrounds in flight (e.g. as in *Papilio glaucus* L., Papilionidae; Krebs and West 1988), even though this may be limited in extent and time. *Inachis io* L. (Nymphalidae) was thought to be entirely a territorial perch (Rutowski 1991), but has recently been observed to patrol territories as well (Dennis and Sparks 2005).

#### 4.2 Taxonomic differences in male mate location behaviours

Taxonomic bias is known to occur in mate location behaviours (Scott 1974; Ehrlich 1984; Dennis and Shreeve 1988) and it is confirmed here in the overall correlation between genetic and behavioural distances. Among Nagpur butterflies some large differences occur in the frequency of male mate location behaviours among families. Even so, most behaviours are found in each butterfly family and where absent, this is likely owing to small numbers of species investigated. For instance, lek assembly has not been found in Nagpur Hesperidae, but does occur elsewhere (e.g. *Ochlodes sylvanus* Esper, Dennis and Williams 1987).

There are more powerful links between congeneric species and male mate location behaviours. This is entirely to be expected as congeneric taxa are more likely to share related host plants, thus habitat structures, and to be similar in morphology, potential drivers and feedbacks of mate locations behaviours. The importance of taxonomic distinctions is evident in the divergence of butterfly families in the MCA plots for predictors of mate location behaviour

for biotopes, landscape elements, resources and population variables.

#### 4.3 Morphological distinctions in male mate location behaviours

It has long been suggested that different strategies of mate location are related to morphological design for flight (Scott 1983). Wickman (1992) predicted and found that perching males have larger thorax/body mass ratios, higher wing loadings and higher aspect ratios (longer and more elongated wings). Perching male *Pararge aegeria* (L., Satyrinae) have also been found to have heavier thoraxes than patrolling males (Van Dyck *et al.* 1997; Van Dyck 2003). As would be expected this has been found to be linked to higher acceleration capacity in species that perch, required for intercepting intruders (Berwaerts *et al.* 2002). Inter-species relationships between male mate location behaviour and butterfly morphology are few in the Nagpur dataset but an increase in site fidelity accompanies increases in butterfly dimensions (body length, weight, wing span, wing load index and proboscis length). Body length and wing load index also increase with territorial defence; no interactions emerged in these relationships involving higher taxa. The findings for territorial defence, particularly for wing load index, tally with the tendency of butterflies that perch to be able to intercept intruders rapidly.

The findings across species are matched by two within-species observations on butterflies that both patrol and perch; perching individuals were heavier and had larger wing spans in line with greater capacity to retain perches from intruders. However, butterflies patrolling had longer bodies than conspecifics perching. If, as seems to be the case that among butterflies there is a proportional increase (positive allometry) in abdomen mass and abdomen nutrients with an increase in body size (Wickman and Karlsson 1989), and polyandrous species – which may also tend to patrol rather than perch – have larger abdomens (Karlsson 1995), body mass (here measured as body length) may well be a distinguishing feature in mate location behaviour.

#### 4.4 Biotopes, landscape elements and mate location behaviours

From knowledge of mate location behaviours in temperate regions, close links of male mate location are expected to occur with landscape elements: biotopes, vegetation structures (ecotones, edges), landforms and consumer resource distributions. The greater number of significant associations occurs for structural and resource components rather than biotopes (vegetation types). The main finding for biotopes is that more complex behaviours (high site fidelity,

territorial defence, lek assembly and to a lesser extent perch-patrol) are commonly found in later seres, more advanced vegetation units. Areas of short herbs and grassland are characterized mainly by patrolling males and invariant perchers.

In temperate latitudes, many of the close associations linking male mate location behaviour and landscape structures would be thought to be driven by a key utility resource in cooler climates, local climate contrasts, especially sunny aspects with high ambient temperatures (Dennis 1982, 1982-83; Dennis and Shreeve 1988; Wickman 1988). However, among Nagpur butterflies, a large number of prominent associations exist though it is unlikely that these are driven by thermoregulatory constraints to the same extent as in temperate locations; there are indications that consumer resource distributions may be more prominent in driving edge and landform mating encounter sites. Regardless of consumer resource distributions, edges and landforms are more likely to be chosen because they have the effect of increasing contacts between males and receptive females despite differences in local climate. To find one another, either butterflies themselves need to be apparent or some component of the landscape they use that can substitute as a predictable cue (Dennis 1982-83). There are three findings that point to more complex behaviours being most closely associated with edge structures. First, the highest individual positive associations occur between these behaviours (i.e. perch-patrol, territorial defence and lek assembly) and distinctive edge features and landmarks, whereas patrolling is recorded less often than expected at such structures. Second, group A species (mainly perch-patrollers) from the UPGMA cluster analysis use significantly more edge features than do group B species (invariant perchers) and group C species (mainly invariant patrollers). Third, behaviours linked to group A species (higher fidelity, territorial defence and lek assembly) also use significantly more edge features, whereas invariant perchers and invariant patrollers use significantly fewer edge features. Nevertheless, invariant patrollers are most closely linked to the use of tracks through vegetation. As throughout their length such landforms tend to be uniform, the implication is that this may be the most efficient mode of mate location behaviour to exploit such biotopes.

#### 4.5 *Butterfly resources, populations and mate location behaviour*

Relationships between consumer resource variables and mate location behaviours are intuitively predictable (Rutowski 1991); in this assessment population attributes are interpreted as being consumer resources. Males and females form resources for one another (Wickman 2009),

not only in the transfer of sperm but of nutrients (Boggs and Gilbert 1979; Arnqvist and Nilsson 2000; Wiklund 2003). As expected, characteristically higher female to male numbers and greater population density are linked to patrolling behaviour, whereas small population size or lower densities are associated with perching. There is an assumption here that transect numbers provide a suitable surrogate for differences in population numbers among species and that differences in sex ratios observed on transects reflect real differences among species or at least biased ratios experienced by the butterfly species. A further observation matching expectations is that unpredictable and scattered host plant resources accompany patrolling whereas predictable, abundant, clumped, vegetation-edge and landform affiliated host plant resources are associated with perching and more complex behaviours such as perch-patrol, territorial defence and lek assembly. One notable exception is the tie between patrolling and host plant resources distributed along tracks through herbs, shrubs and forest. A fundamental observation is the cross species high correlation between the concentration of mate location behaviours at edge sites and the distribution of their host plant resources at these sites. This feature is predicted by mate location theory but is not usually encountered in autecological studies of mate location encounter sites (Rutowski 1991; Wickman 2009). It is an important finding but a degree of caution is required in interpreting this as a causal basis for use of edge sites in the current study. Use of host plant sites for mate acquisition by males may lead to an increased number of failed encounters with unreceptive females, thus wasted time and energy for both males and females. Moreover, the study has not made a quantitative assessment of the link between the use of all butterfly host plants and their distribution in biotopes, ecotones and on landforms throughout the sites.

#### 4.6 *Implications for conservation*

Conservation of species from a resource-based view of habitats stipulates that all resources and conditions required by species during their life cycles are available and of suitable quality and quantity (Dennis 2010). The current study has disclosed a number of important findings on male location behaviour in butterflies at Nagpur, India, reflecting on this specific non-consumer resource component in butterflies; mate location encounter sites form a key utility resource for butterfly species. The message from this study is that mate location behaviour and encounter sites are far from uniform, reflecting on the importance of green spaces and resource heterogeneity to maintain biodiversity in city environments. The present study supports the notion of the importance and availability of distinctive landscape structures underlying mate location behaviour for butterfly species within Nagpur,

a fast developing city environment. Providing space and resources for wildlife in city environments presents one of the most testing challenges for conservation (Forman 2008). The findings in this survey valuably enhance the resource data base for Indian butterflies, an essential preliminary for understanding species' habitats, their abundance and spacing in tropical biomes (Dennis *et al.* 2008). The data also lay the foundation for advancing theory on butterfly mate location behaviour. Even so, the study has focussed on short time slice observations for species; more detailed observations on each species over longer periods will inevitably and valuably disclose greater complexity and variety of behaviour. Also, the relationships will become clearer once complete and accurate phylogenies are established so that the influence of phylogenetic relationships among species can be factored into associations and contrasts (Purvis and Rambaut 1995).

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