Spatial and temporal patterns of territorial mate locating behaviour in *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae)

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Male *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae) defend perch sites as a method of visually locating receptive females. In this study we charted the spatio-temporal activity of perching males in tropical Australia to investigate (a) the extent to which male activity is thermally constrained, and (b) the physical attributes of selected perching sites. Butterflies were surveyed along two 5–15 m wide open corridors through dense vegetation, and this allowed the prediction that males should favour narrower corridor sections in order to maximize their visual search capability. This prediction was supported. Beyond corridor width, the distribution of favoured perches was not explained any further by patterns of shading, larval food plant distribution, or the presence of nectar resources. Males were active from 0800 to 1700 h, but the number of perching individuals varied throughout the day, and this pattern varied between the two transects. Most individuals perched along one transect in the morning (0900–1100 h), whereas activity along the other peaked around midday (1100–1300 h). This between-transect difference in male activity followed changes in shading between the transects, however this variable did not predict male distribution at the territory scale. Although ambient and black body temperatures were significantly related to population-level activity, these variables only predicted 15–55% of the variance in male counts in individual transects. This result, viewed in conjunction with the limited available information on female receptivity, suggests that the timing of mate location in *H. bolina* may be primarily influenced by the daily pattern of female availability.

**KEYWORDS:** Ectotherm, insect, weather, encounter site, flyway, residency.

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**Introduction**

In most animals the reproductive success of males is limited primarily by their ability to locate receptive mates. This task is not trivial, since the overall searching environment is large in relation to male sensory capabilities. Male butterflies rely primarily on vision to detect females (Rutowski, 1991; Vane-Wright and Boppre, 1993), which may be widely distributed both in space and time. As a consequence,
males often focus their efforts on places where receptive females tend to concentrate (Thornhill and Alcock, 1983). These encounter sites include female emergence sites (Rutowski and Gilchrist, 1988; Alcock, 1993), oviposition sites (Baker, 1972), foraging sites (Dennis and Williams, 1987), and landmarks such as hilltops (Alcock, 1983, 1985; Dennis, 1987; Alcock and Gwynne, 1988; Wickman, 1988; Rutowski et al., 1989). As with many invertebrate groups, the type of encounter site used by particular species is likely to be selectively determined by factors influencing the spatio-temporal distribution of receptive females (Thornhill and Alcock, 1983; Rutowski, 1991), such as larval and pupal ecology, and female mating frequencies and refractory periods.

Encounter sites used for mate location are often visited only at certain times of day, and the timing of such activity may differ remarkably, even between closely related insect species (Thornhill and Alcock, 1983). Butterflies, particularly members of the family Nymphalidae, illustrate such differences well (review in Rutowski et al., 1996). At one extreme, males of the neotropical species *Caligo idomeneus* Staudinger are at encounter sites for roughly 15 min prior to sunrise (Freitas et al., 1997); other species such as *Vanessa atalanta* (L.) and *V. kershawi* (McCoy) occupy encounter sites in the late afternoon (Alcock and Gwynne, 1988; Brown and Alcock, 1990; Bitzer and Shaw, 1995). From an adaptionist viewpoint, the timing of male mate locating behaviour should allow individuals to maximize their potential for contact with receptive females. If female receptivity is restricted to predictable periods of the day, then males should concentrate their efforts during these periods (Thornhill and Alcock, 1983; Alcock, 1996). However, because butterflies rely on environmental conditions such as temperature and solar irradiation to elevate their body temperature to that permitting activity (Kingsolver, 1985), the daily pattern of mate-locating activity may be restricted by ambient conditions.

In this study we examined the environmental determinants of the temporal and spatial occurrence of territorial males in a tropical nymphalid butterfly, *Hypolimnas bolina* (L.). This species is widely distributed in South-East Asia (Clarke and Sheppard, 1975). Like the closely related *H. missipus* (L.) (Stride, 1956, 1957) male *H. bolina* perch at and defend encounter sites used in the location of receptive females (Rutowski, 1992). The aim of this study was two-fold. Firstly, we aimed to investigate when male *H. bolina* perch at an encounter site throughout the day, and the extent to which the temporal distribution of butterfly activity (at the population level) is related to ambient thermal and solar conditions. Based on data collected along a single transect, Rutowski (1992) showed that the largest number of males occupy perching sites from 0900 to 1400 h. We expanded on this observation to see if observed day-to-day and transect-to-transect differences in daily activity were correlated with environmental variation in temperature and insolation.

Our second aim was to investigate the spatial distribution of territorial males at an encounter site. In *H. bolina* and other species, males are believed to select perching areas that improve their chances of visually detecting receptive females (Dennis and Williams, 1987; Dennis and Shreeve, 1988; Rutowski et al., 1991; Rutowski, 1992; Lederhouse, 1993; Ravenscroft, 1994). However, few quantitative data are available that describe the spatial distribution of territorial male butterflies with respect to their physical environment (but see Rutowski et al., 1988; Lederhouse et al., 1992). We surveyed butterflies along a vegetative corridor adjacent to a cultivated cane field to see if males are most likely to perch at narrow corridor sections that corral passing receptive females to within their effective visual range.
Methods

Study sites

This study was conducted on 12 days between 21 January to 16 February 1998, in an area adjacent to a section of the Freshwater creek, near Cairns in Queensland, Australia (16°53’S, 145°45’E). Two transects were established, both along existing (mostly 5–15 m wide) mowed corridors located between sugarcane fields and riparian vegetation. The transects were 300 and 470 m long, respectively, and separated by a grassy clearing of approximately 200 m. The local flora included several of the recognized larval food plants of *H. bolina*. *Synedrella nodiflora* (Asteraceae) grew in dense clumps to a maximum height of a metre in shaded areas along the edges of the corridor. *Ipomea triloba* (Convolvulaceae), a climber, grew amongst the sugarcane, reaching heights of approximately 2 m, whilst *Commelina cyanea* (Commelinaceae), a rhizomous creeper, grew extensively along the creek bank and throughout the vegetation lining the transect. The distribution of these food plants was assessed by dividing each transect into 10 m segments, and recording the presence or each species in each transect segment. Although nectar plants along both transects were sparse, the presence of discrete outcrops of flowering *Wedelia trilobata* (Asteraceae) was noted. Male *H. bolina* are routinely seen feeding at this species in this area (Kemp, unpublished). In addition, the minimum width of open vegetative corridor in each of these transect segments was measured to the nearest metre.

Sampling of butterflies and environmental conditions

Transect sampling was limited to days free of rain and strong wind in order to control for the adverse effects of these factors on the diel activity regimes of *H. bolina* (Rutowski, 1992). On sampling days, transects were censused consecutively from 0700 to 1800 h, with the transect order alternated each hour. The sex and location along the transect of all individuals seen during each census was recorded. Transects were censused as quickly as possible, with transect 1 taking approximately 10–15 min to traverse, and transect 2 taking approximately 15–20 min.

In order to quantify environmental conditions, ambient temperature and black globe temperature were measured in the 5 min periods prior to, and following, each hourly census round. Ambient temperature was measured (to the nearest 0.5°C) once at the start and the end of the 5 min period, using a standard mercury thermometer situated 1.5 m off the ground in a shaded understorey region. Black globe temperature was measured (to the nearest 0.5°C) every 60 s using a black globe thermometer (described below). This instrument was placed in a clearing (50 m radius) adjacent to transect 1. In addition, proportional shading was quantified (once only during sunny conditions) along both transects at hourly intervals from 0700 to 1800 h. The proportional area of shaded ground within each 10 m transect segment was visually assessed to the nearest 10%.

The black globe thermometer consisted of a 300 mm length of hollow copper pipe (30 mm radius, 1 mm thick), painted black, with a standard mercury thermometer suspended in the centre by polystyrene mounts. The thermometer was placed on polystyrene blocks in a patch of bare earth at the centre of the clearing, in a position shielded from wind. Similar devices have been used to measure the thermal environment in previous investigations into butterfly activity (Leigh and Smith, 1959; Pivnick and McNeil, 1987).
**General statistical procedures**

Raw data relating to ambient and black globe temperature were averaged for each hourly sampling occasion, with ambient temperature ($T_a$) subtracted from the black globe temperature ($T_{bg}$) to give black globe excess values ($T_e$). Black globe excess temperatures represent the potential for elevation of body temperatures above ambient, and therefore provide an indication of the basking potential of a butterfly (Pivnick and McNeil, 1987). Values of $T_a$ and $T_e$ are used to describe the thermal environment of a mate-locating male *H. bolina* during the sampling period.

Parametric tests were applied in the analysis where possible, with data screened for normality using Kolmogorov–Smirnov goodness of fit tests (Sokal and Rohlf, 1995). Relationships between non-normal bivariate data were analysed using Spearman Rank Order correlation, and Chi-squared analyses were conducted with classes pooled to maintain all expected frequencies above five. Forward stepwise regression was employed to examine the influence of environmental parameters (independent variables, IVs) on the activity of territorial males (dependent variable, DV), with $F$ (to enter) set at 2.0. This $F$ value was chosen to ensure significance of the resultant regression equation. Prior to this analysis, between-days variance was removed from all variables (IVs and DV) by subtracting each variate from its daily mean. This ensured that the analyses focused solely on the daily patterns of rise and fall of each variable. Following calculation of regression solutions (for each transect), residuals were visually inspected to check for violation of regression assumptions. Also, owing to the time-series sampling design, Durban–Watson statistics were calculated to check that the residuals were sufficiently independent. The value of this statistic was close to 2.0 for all analyses ($1.75<d<1.86$), indicating little dependence among residuals. Following stepwise regressions, partial correlation analysis (Sokal and Rohlf, 1995) was used to assess the degree of ‘unique’ variance in male activity described by each of the entered IVs, and the direction of the relationship between each IV and male counts.

**Results**

**Diel environmental conditions**

Weather conditions throughout this study were clear and hot, with daily maximum $T_a$ ranging from 29.5 to 32.5°C. On average, the area was subject to the highest levels of solar irradiation (indicated by $T_e$) throughout the morning, and the highest ambient temperatures (indicated by $T_a$) just after midday (refer to Kemp, submitted). The approximate times of sunrise and sunset for the sampling period were 0612 and 1851 h, respectively, however after approximately 1730 h the sun was obscured by a mountain range. Most of transect 1 was shaded well into the morning, whereas transect 2 was largely unshaded by 0900 h (figure 1). The number of 10 m transect segments covered by greater than 50% shade differed significantly between the transects throughout the day ($\chi^2_5 = 19.1, p<0.01$).

**Patterns of butterfly activity**

More territorial males were counted along the transects than females, and on average, butterfly density was greater along transect 2 (table 1). Generally, females were seen foraging low to the ground (<300 mm) along the edges of the corridor, exhibiting the typical oviposition behaviour of this species (Kemp, 1998). No mated pairs were observed during the course of this study, and all male–female interactions
Mate location in *Hypolimnas bolina*

**Fig. 1.** Diel regimes of mean proportional shading along transect 1 (top) and transect 2 (bottom). Indicated are the average shading along the whole transect (open circles, solid line), and the average shading in male-occupied 10 m transect segments (open squares, dashed line).

**Table 1.** Census details for each transect.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Total counts</th>
<th>Mean count per transect (± SE)</th>
<th>Maximum count</th>
<th>Mean density (counts per 10 m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 1</td>
<td>Males</td>
<td>487</td>
<td>6.16 ± 0.42</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>(300 m)</td>
<td>107</td>
<td>1.35 ± 0.15</td>
<td>6</td>
</tr>
<tr>
<td>Transect 2</td>
<td>Males</td>
<td>944</td>
<td>12.26 ± 0.86</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>(470 m)</td>
<td>194</td>
<td>2.52 ± 0.28</td>
<td>15</td>
</tr>
</tbody>
</table>

took the form of male harassment (described by Rutowski, 1992; Kemp, 1998). In light of these observations, and since females of this species generally mate only once (Kemp, unpublished), the majority of individuals were probably unreceptive to matings. Since it was not clear which females, if any, were receptive, the spatio-temporal distribution of female butterflies is not treated here in further detail.

In general, territorial males were active for an extended daily period, with at least some individuals present along both transects from 0800 to 1700 h (figure 2). Diel patterns of male activity differed significantly between the two transects ($\chi^2 = 66.0, p < 0.01$), with mean activity peaking earlier along transect 2 (figure 2). These activity schedules differed in a manner related to differences in shading between the two transects. Fewer territorial males were seen along transect 1 (relative to transect 2) at times when proportional shading was higher along this transect (Pearson’s correlation between the difference in standardized transect counts and the difference in mean transect shading, $r = -0.72, n = 77, p < 0.001$). This suggested that vegetative shading may have dictated the habitat selection of males in this study. However, investigations at the 10 m segment scale revealed that males routinely occupied heavily shaded segments in both transects at all times of day (figure 1). Mean shading in male-occupied transect sections at each hour did not
Fig. 2. Diel patterns of territorial male residence along transect 1 (open squares, solid line) and transect 2 (solid squares, dotted line). The error bars represent ±1 standard error of sample means, and the fitted lines are weighted least squares approximations calculated by the STATISTICA™ computer program. Sample sizes are given above each hourly point.

differ significantly from the transect mean along either transect 1 (paired \( t_9 = -1.20, p > 0.25 \)) or transect 2 (paired \( t_9 = -1.86, p > 0.05 \)).

Male activity and environmental conditions

Due to between-transect differences in the temporal distribution of males, the relationships between territorial activity and environmental parameters were assessed separately for each transect (table 2). For transect 1, both \( T_a \) and \( T_e \) (but not shading) gained entry into a model which accounted for 55.4% of the variance in male counts. These variables were both positively related to territorial male counts, with \( T_e \) (partial \( r = 0.449, n = 67, p < 0.0001 \)) explaining more unique variance than \( T_a \) (partial \( r = 0.145, n = 67, p < 0.10 \)). Male activity along this transect therefore varied in a manner more closely related to solar irradiation (\( T_e \)) than ambient temperature (\( T_a \)). Along transect 2, however, stepwise regression analysis resulted in a model that incorporated only \( T_e \), and explained only 14.2% of the variance in male counts. This variable was also positively related to the activity of territorial males along this transect (partial \( r = 0.393, n = 67, p < 0.001 \)).

Spatial distribution of territorial males

The spatial distribution of territorial males in relation to the presence of larval and adult food resources is given by figure 3. Because larval food plants grew

<table>
<thead>
<tr>
<th>Transect</th>
<th>Regression equation</th>
<th>ANOVA</th>
<th>Adjusted ( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Males = -2.15 + 0.92T_e + 2.24T_a</td>
<td>( F_{2,66} = 43.3, p &lt; 0.0001 )</td>
<td>0.554</td>
</tr>
<tr>
<td>2</td>
<td>Males = 0.53 + 0.47T_e</td>
<td>( F_{1,67} = 12.3, p &lt; 0.001 )</td>
<td>0.142</td>
</tr>
</tbody>
</table>

Table 2. Results of forward stepwise regression of environmental variables against male counts along each transect. The \( R^2 \) values given are adjusted for the number of variables entered into each model. Between days variance was removed from all variables (IVs and DVs) prior to these analyses (see text).
extensively along both transects, male distribution was not clearly related to the presence/absence of these plants (figure 3). However, counts were low in the section of transect 1 from 100 to 160 m, the only large area with a notable absence of larval food plant. In addition, significantly more males were counted in transect segments containing nectar plant growth (growth of *W. trilobata*) compared to all other segments of both transects (independent $t_{15} = -2.77, p < 0.01$).

The spatial distribution of territorial males supported the prediction drawn from the visual vantage point hypothesis. Along both transects, the number of males counted in 10 m segments tended to decrease as the minimum width of the corridor increased (figure 4). The maximum male count (in transect segments grouped by 5 m corridor width intervals) were inversely correlated with corridor width (the median of each group) along both transects (Spearman $r_s = -0.828, n = 6, p < 0.05$).
for each transect). Although maximum counts were greater in narrower transect segments (those less than 10 m wide), the actual numbers of males counted in these segments varied greatly, ranging from 1 to 38 counts in transect 1 and from 3 to 42 counts along transect 2 (figure 4). This indicates that whilst narrower segments of each transect are potentially very popular perching sites, the realized ‘popularity’ of particular segments may depend on some other intrinsic site factor (or factors). This was not obviously larval food plant distribution, since all narrower transect segments contained growth of at least one food plant species. Also, within the set of narrower segments (all segments <10 m minimum width), average male counts did not differ significantly depending on the presence of flowering *W. trilobata* (independent *t* 36 = −1.85, *p* > 0.05). Finally, male counts within narrow segments were not linearly related to mean diel shading along either transect 1 (Spearman *r* 8 = −0.08, *n* = 22, *p* > 0.70) or transect 2 (*r* 8 = 0.208, *n* = 17, *p* > 0.40), ruling out daily average shading as a predictor of additional variance.

**Discussion**

**Patterns of butterfly residence**

In keeping with previous reports on the activity of *H. bolina* (Rutowski, 1992; Kemp, 1998), butterflies in this study were active for an extended period each day. This indicates that at the population level at least, male *H. bolina* engage in mate location for a longer time each day than many other territorial nymphalid species (refer to introduction, also Rutowski, 1991; Rutowski et al., 1996). From an ultimate viewpoint, the period of male residence at encounter sites is expected to be closely dictated by the availability of receptive females at these sites (Alcock, 1996). If, for reasons such as the timing of pupal eclosion (e.g. Rutowski et al., 1996), female availability is confined to certain periods of the day, then this is expected to establish the limits to the diel activity of mate locating males. This reasoning has been used to explain why males of certain insect species (e.g. *V. atalanta*—Bitzer and Shaw, 1985; *C. idomenaeus*—Freitas et al., 1997) inhabit sites for only a fraction of the daylight period, even though weather conditions are not limiting to activity at other times. In comparison, territorial activity of male *H. bolina* was not strictly confined to an extremely limited part of the daylight period (transects were occupied for 9 out of approximately 13 daylight hours). This result leads to the prediction, based on the ultimate hypothesis, that the arrival of receptive female *H. bolina* to these sites throughout the day should be relatively unpredictable. A comparison of receptive female arrival schedules between *H. bolina* and the other studied territorial nymphalids would provide a meaningful test of this prediction.

Although diel male activity spanned an extended period, the number of individuals active at each hour during this period varied greatly, as shown by the site-specific activity curves (figure 2). Since these curves describe population-level features of the behaviour of *H. bolina*, they represent a product of the variation between individual males in the timing of their daily mate locating behaviour. In particular, the shape of these curves will be determined by individual decisions regarding (a) when to arrive and (b) how long to stay on site (figure 5). Previous work suggests that males remain for most of the day after they arrive (Rutowski, 1992) and in this study, individuals clearly varied when they began perching, especially along transect 1. So, the key question is: why do not all males show up at the encounter sites at the same time each day? There are two primary explanations. First, variation
in territorial behaviour reflects inter-individual variation in male decisions about when to begin, which will be affected by changes in female availability throughout the day. If female availability increases during the morning, the expected returns from site occupation will increase, and then, the number of males electing to begin site occupation in the face of other demands on their time will increase. Alternatively, as environmental conditions change during the day, the number of males that manage to attain the thoracic temperature required for territorial behaviour will rise and fall. This discussion examines the implications of the presented data for the second explanation, that is, the degree to which mate-location in *H. bolina* is constrained by the thermal environment.

The activity of male *H. bolina* is broadly determined by environmental conditions such as temperature, ambient light and wind speed (see Kemp, 1998). However, these factors will only contribute to variance in territorial start (and finish) times if individual males vary in their ability to operate within these broad constraints. This explanation makes the prediction that the number of males perching at an encounter site will relate very closely to environmental conditions, and furthermore, that males should perch in equal numbers at times when thermal conditions are consistently adequate for activity. However, data obtained in this and other investigations do not strongly support these predictions. Firstly, male activity differed significantly between transects, which would not be expected solely on the basis of this hypothesis. Secondly, the relationships between male activity and environmental variables, although significant, were not particularly strong. For instance, less than 15% of the variance in male counts along transect 2 was explained by the environmental factors, with neither shading nor ambient temperature contributing significantly to this linear model. Finally, males did not perch in equal numbers at the times of day when either environmental variable appeared suitable for maximum activity. For instance, counts along transect 2 peaked at 1000 h, at which time neither *Tₐ* nor *Tₑ* were at their maximum level. Butterflies then began to depart the site, even though thermal conditions remained warm, and shading remained low. If environmental conditions passed through a fleeting optimum at 1000 h (that is, conditions thereafter became
too hot for activity) a rise in counts at this site would be expected later in the day when temperatures declined, which did not occur.

A second possibility drawn from the environmental-constraint explanation is that conditions at the site varied such that the number of suitable perching sites varied throughout the day. Shading is one factor known to affect the suitability of available perching sites at butterfly encounter sites (Douwes, 1975; Dennis and Williams, 1987; Rutowski et al., 1994) that may have influenced the spatio-temporal patterns of male behaviour in this study. This possibility is supported by the finding that male activity varied between the transects in a manner related to differences in average shading. Since transect 1 was heavily shaded for much of the early morning (figure 1), males may have chosen to operate in sections of (the mostly unshaded) transect 2 at these times, leading to the discrepancy in morning activity levels between these transects. Similar thermally mediated shifts in habitat use have been previously reported for territorial butterflies (Shreeve, 1984; Wickman, 1988; Rutowski et al., 1994). However, this explanation is negated by the finding that male *H. bolina* did not discriminate significantly in favour of less shaded transect segments, even in early morning censuses. This indicates that differences in shading, although correlated with differences in male activity at the whole transect level, may not be directly acting to determine the thermal suitability of finer-scale sites to territorial male *H. bolina*. This might apply because even heavily shaded areas may contain some sunlit foliage suitable for a perching male butterfly.

It is therefore apparent that the daily pattern of residence of male *H. bolina* is not wholly or easily accounted for by environmental parameters such as temperature, light, and shading. This finding is consistent with the results of other investigations into the diel activity of territorial male butterflies (Bitzer and Shaw, 1995; Rutowski et al., 1996), and suggests that population-level regimes of male activity may be most strongly influenced by the temporal availability of receptive females. At this stage little is known about patterns of female receptivity in *H. bolina* except that females mate only once and refrain from mating for at least 4 days after eclosion (Kemp, unpublished). This implies that the primary source of receptive females will be those individuals flying, either inadvertently or purposely, to male-occupied encounter sites. Unfortunately it was not possible to directly compare the spatial distribution of territorial males with receptive females in this study due to the cryptic nature of female receptivity.

**Spatial distribution of territorial males**

Generally, male *H. bolina* establish territories along paths and stream beds (Rutowski, 1992), vegetative corridors (this study) and in forest clearings (McCubbin, 1971), and selected sites are believed to improve their chances of visually detecting receptive females (Rutowski, 1992). In this study, the result that most territorial males were counted in transect sections of relatively smaller corridor width agrees with this hypothesis. Based on a target of the approximate size and coloration of a conspecific female, perching male *H. bolina* seem to detect females at distances of no more than 4–5 m across varying backgrounds (Kemp, unpublished). With all else being equal, increased search efficiency in a longitudinal vegetative corridor would therefore be afforded by sections of narrower width (i.e. less than 10 m). This prediction was supported, although the relationship was weak and there are probably other factors that determine the overall suitability of perching sites. Although measured qualitatively, larval and adult food resources and diel
shading did not offer any further information regarding the spatial distribution of males. Larger scale factors such as regional vegetative geometry may determine the value of perch sites due to their influence on greater patterns of butterfly travel.

Conclusion
In general, influences on the behaviour of territorial male butterflies at encounter sites are not easily identified due to the often complex covariance between proximate and ultimate influences on mate locating activity (Rutowski et al., 1996). If female activity is strongly dependent on environmental conditions, then male activity will appear to be thermally constrained even if truly a function of female availability. Establishing the causal influence on male activity is therefore a great challenge to field-based studies, because the relevant covariates cannot be easily manipulated. Nevertheless, these investigations provide valuable information on the activity of animals in the environment in which natural selection will operate. The results of this study strengthen the hypothesis that, in butterflies, inter-individual variation in the timing of mate location is strongly determined by the temporal availability of receptive females.

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