

## Research



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## Animal behaviour

# Dispersal and migration have contrasting effects on butterfly flight morphology and reproduction

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Movement may fundamentally alter morphology and reproductive states in insects. In long-distance migrants, reproductive diapause is associated with trade-offs between diverse life-history traits such as flight morphology and lifespan. However, many non-diapausing insects engage in shorter resource-driven dispersals. How diapause and other reproductive states alter flight morphology in migrating versus dispersing insects is poorly understood. To find out, we compared flight morphology in different reproductive states of multiple butterfly species. We found that dispersers consisted of ovulating females with higher egg loads compared with non-dispersing females. This trend was in stark contrast with that of migrating female butterflies in reproductive diapause, which made substantially higher investment in flight tissue compared with reproductively active, non-migrating females. Thus, long-distance migration and shorter resource-driven dispersals had contrasting effects on flight morphology and egg loads. By contrast, male flight morphology was not affected by dispersal, migration or associated reproductive states. Thus, dispersal and migration affected resource allocation in flight and reproductive tissue in a sex-specific manner across relatively mobile versus non-dispersing individuals of different species. These findings suggest that dispersals between fragmented habitats may put extra stress on egg-carrying females by increasing their flight burdens.

## 1. Introduction

Animal movement involves a spectrum of strategies, including long-distance migration [1], facultative dispersal [2], exploratory behaviour by boundary individuals in metapopulations [3] and sporadic movements by localized individuals. Mass movements such as migration and dispersal are usually accompanied by dramatic morphological [4], physiological [5] and behavioural changes, including modifications of flight behaviour [6], feeding strategy [7] and reproduction (e.g. reproductive diapause) [8].

Migrants and dispersers do not always enter reproductive diapause [9,10], and the inability to delay reproduction may make them more sensitive to changes in habitat conditions [11,12]. Insects typically have innate sex- [13] and population-specific [14] differences in resource investment, and adaptive phenotypic plasticity allows some insects to modulate their investments [7,8,15]. In the absence of such plasticity, dispersing animals may either suffer fitness disadvantages [16] or evolve compensatory mechanisms that allow dispersals without a loss in fecundity (i.e. species that lack the oogenesis–dispersal syndrome) [10].

Dispersal and migration are defined in various ways [17]. Based on common usage, we define migration as the seasonally cyclical, long-range (hundreds of kilometres) and unidirectional movement of populations over the span of weeks or months, with little feeding, as seen in milkweed butterflies and *Vanessa atalanta* [18–20]. By contrast, we define dispersal as the resource-driven, relatively short-range, non-cyclical and multidirectional movement of individuals or small groups over hours or days during which individuals may feed frequently, as seen in *Catopsilia* [21] and *Euphydryas editha* [22]. Thus, migration and dispersal may produce contrasting movement-related life-history outcomes involving physiology and behaviours, which are affected by seasonal climatic factors and resource availability. This has implications for population persistence and species survival among increasingly fragmented habitat patches, especially in tropical areas [23,24].

We here investigate the impact of continued reproductive investment on insect dispersal phenotypes and elucidate the contrasting resource allocation strategies of dispersing and migrating butterflies. To do this, we compare the flight morphology and egg loads of dispersing and non-dispersing populations of two non-diapausing *Catopsilia* butterflies (*Catopsilia pomona* and *Catopsilia pyranthe*; Pieridae), five non-dispersing close relatives (*Colias*, *Eurema*, *Leptosia*, *Ixias* and *Hebomoia*; Pieridae), and two milkweed butterflies (*Euploea sylvester* and *Tirumala septentrionis*; Nymphalidae: Danainae) that migrate in a state of reproductive diapause and reproduce only after migration. We tested the following hypotheses:

- (i) Reproductively active dispersers have greater abdominal investments compared with non-dispersing reproductive populations. This is because non-dispersers with access to adequate host plants would periodically oviposit and thus retain relatively fewer mature ova and eggs compared with dispersers.
- (ii) Greater reproductive investment in dispersing females adversely affects their flight morphology compared with non-dispersing reproductive females as well as migrating females in reproductive diapause.

We tested these hypotheses by conducting intra- and intergroup comparisons among dispersing, migrating and non-dispersing individuals, populations and species. Our results show that flight morphology and reproductive investments are affected in a sex- and movement-specific manner.

## 2. Material and methods

### (a) Annual leaf flushes and *Catopsilia* dispersals

Peninsular India experiences an annual dual monsoon system that regulates the life cycles of numerous plants and insect herbivores. The chief host plants of *C. pomona* and *C. pyranthe*—*Cassia* spp. and *Senna* spp. (Fabaceae)—experience a major leaf flush before the monsoon (May and June), with minor continued leaf flushes from July to September [25]. Fresh leaves that emerge during these leaf flushes are a prime exploitable resource for *Catopsilia* larvae, and the cyclical nature of leaf flushing causes intermittent, multidirectional and resource-driven dispersals of *Catopsilia* adults after local host plants are stripped of fresh leaves (figure 1a and electronic supplementary material, table S1).

*Catopsilia* engage in single-species dispersals at different times of the year—*C. pomona* disperses prior to the summer monsoon (Mar–Jun), while *C. pyranthe* dispersals occur post monsoon (Oct–Nov). Dispersing swarms may be loose or more cohesive and contain from tens of thousands to hundreds of thousands of butterflies, which may fly up to 200 km away from their natal patch (unpublished observations, KK). As a result, dispersing *Catopsilia* individuals populate new, previously unoccupied or sparsely populated habitat patches [26].

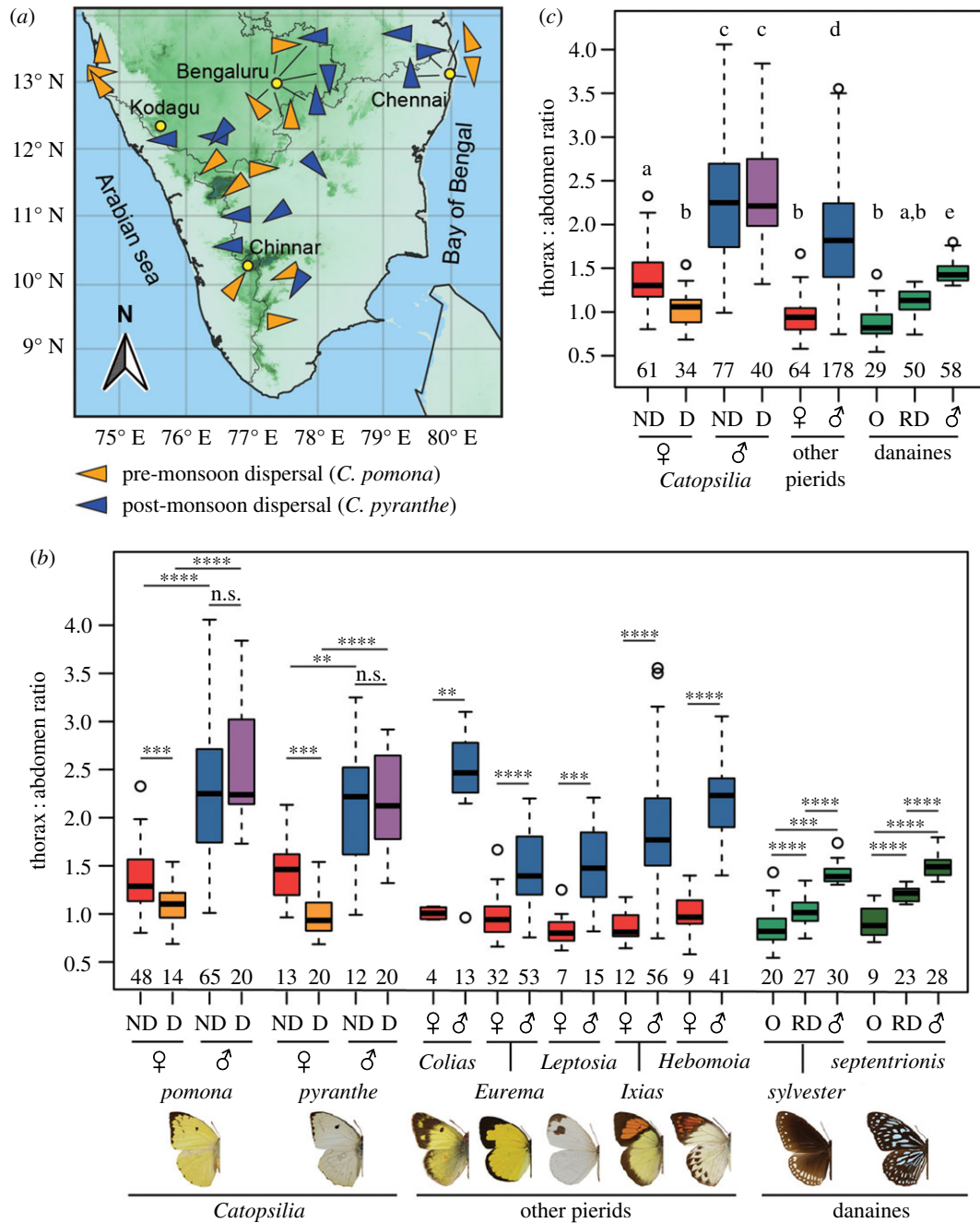
### (b) Specimen and data collection

We identified dispersing *Catopsilia* groups by the characteristic directional flight of large, dispersing swarms [2,27]. Dispersing individuals were briefly distracted by nectar-flowers and mud-puddling sites, but typically soon resumed directional flight. We collected dispersing *C. pomona* individuals between March and June 2013–2019, and dispersing *C. pyranthe* individuals in October 2017 from various localities in Bengaluru. We collected non-dispersing individuals of both species from Peninsular India throughout the year, outside the months when dispersals were observed. For comparison with other pierids, we used the data from five genera of non-migrating and non-dispersing pierids (*Colias fieldii*, *Colias nilagiriensis*, *Eurema hecabe*, *Leptosia nina*, *Ixias marianne*, *Ixias pyrene* and *Hebomoia glaucippe*). For comparison with species that enter reproductive diapause during migration, we used two species of danaines from our previously published dataset [18]. This dataset consisted of individuals in reproductive diapause collected from migrating swarms, and reproductively active females collected from non-migrating populations. Our combined dataset consisted of 591 individuals in 24 categories [28], accounting for taxon, sex, movement type (dispersal versus migration) and the presence or absence of reproductive diapause (electronic supplementary material, table S2).

Dispersal-related trait variation and trade-offs can be quantified through different morphological features ranging from body size to thorax:abdomen ratio [12,18,29]. We measured body mass, thorax mass and abdomen mass of freshly collected individuals. We also dissected and examined the abdomens of females under up to 40× magnification (Leica S6E, Leica Microsystems) to count the number of chorionated, mature ova. We used the ratio of thorax mass to abdomen mass as a proxy for relative investment in flight muscles (thorax mass) versus reproductive tissue (abdomen mass) [18,30], and the relative egg load (number of ova per unit abdomen mass) as an indicator of relative reproductive investment. We also performed linear regressions of number of mature ova against thorax:abdomen ratio for all females to investigate how investment in flight morphology affected egg loads in different butterfly groups.

### (c) Statistical analyses

We performed all statistical analyses in R [31]. We used the Shapiro–Francia normality test [32] to check for normality, and Student's *t*-tests or Wilcoxon rank sum tests for pairwise comparisons. We pooled data by sex and dispersal or migration among various taxonomic groupings to find generality in patterns of flight morphology, and used a Kruskal–Wallis test followed by Dunn's test with Bonferroni correction [33] for multi-group comparisons. To compare regression slopes, we used the 'emmeans' (estimated marginal means) package in R [34]. Finally, we performed sex-specific ANCOVAs with thorax:abdomen ratio as the dependent variable, species (*pomona*, *pyranthe*, *Colias* spp., *hecabe*, *nina*, *Ixias* spp., *glaucippe*, *sylvester* and *septentrionis*) and dispersal behaviour (non-dispersing/ovulating, dispersing/reproductive diapause) as independent variables, body mass as a covariate and number of ova as an additional predictor for females.



**Figure 1.** Dispersal records and morphometric features of *Catopsilia*. (a) *Catopsilia* dispersal records from southern India from 2013 to 2019 (additional details in electronic supplementary material, table S1), with arrows indicating direction of flight. Dispersals during Mar–Jun generally consist of *C. pomona*, while dispersals during Sep–Nov consist mainly of *C. pyranthe*. (b) Thorax:abdomen ratios of males and females of all species (wings not to scale). (c) Pooled thorax:abdomen ratios of each sex in *Catopsilia*, other pierids and danaines. Statistically different groups are indicated with different lower case letters, and inset numbers indicate sample sizes. ND = non-dispersing, D = dispersing, O = ovulating, RD = reproductive diapause (females). Horizontal bars indicate p-values: n.s. (non-significant), \*\* < 0.01, \*\*\* < 0.001, \*\*\*\* < 0.0001.

### 3. Results

#### (a) Females invest relatively more in reproductive tissue compared with males

Females had significantly higher relative investment in abdominal tissue compared with males in each species (thorax:abdomen ratio, all  $p < 0.05$ ; figure 1b and electronic supplementary material, table S3). When individuals across species were pooled into groups (figure 1c), sexual dimorphism was still apparent in each group, showing this to be a global pattern irrespective of species identity (table 1).

#### (b) Dispersing females invest more in reproductive tissue compared with non-dispersing females

Dispersing *Catopsilia* females had significantly lower thorax:abdomen ratios compared with non-dispersing females (*pomona*:  $t_{29} = -3.625$ ,  $p = 0.0005$ ; *pyranthe*:  $t_{18,318} = -4.3978$ ,  $p = 0.0002$ ; figure 1b and electronic supplementary material, table S3). This trend was in contrast with that of migratory danaines, where migratory females in reproductive diapause had higher thorax:abdomen ratio than non-migrating, ovulating females (*sylvester*:  $W = 42$ ,  $p < 0.0001$ ; *septentrionis*:  $W = 28$ ,  $p = 0.0004$ ). However, there were no such differences between dispersing and non-dispersing males in either

**Table 1.** *Z* statistics and adjusted *p*-values for Dunn's test with Bonferroni correction. Comparisons of thorax : abdomen ratio (Kruskal–Wallis test;  $\chi^2_8 = 351.7129$ ,  $p < 0.0001$ ; figure 1c) and relative egg loads ( $\chi^2_4 = 123.9837$ ,  $p < 0.0001$ ; figure 2b) among different groups. ND = non-dispersing, D = dispersing, O = ovulating, RD = reproductive diapause (females). Comparisons with  $p < 0.05$  are italicized.

contrast	<i>Z</i>	<i>p</i> -value
thorax : abdomen ratio		
<i>Catopsilia</i> (♀ND)– <i>Catopsilia</i> (♂ND)	–6.8629	<0.0001
<i>Catopsilia</i> (♀D)– <i>Catopsilia</i> (♂D)	–8.9836	<0.0001
other pierids (♀)–other pierids (♂)	–11.1479	<0.0001
danaines (O)–danaines (♂)	–5.843	<0.0001
danaines (RD)–danaines (♂)	–3.2675	0.0195
<i>Catopsilia</i> (♀D)–other pierids (♀ND)	0.7874	1
danaines (O)– <i>Catopsilia</i> (♀D)	–1.3223	1
<i>Catopsilia</i> (♀ND)– <i>Catopsilia</i> (♀D)	3.6474	0.0048
<i>Catopsilia</i> (♀ND)–other pierids (♀)	5.2964	<0.0001
danaines (O)– <i>Catopsilia</i> (♀S)	–4.9427	<0.0001
<i>Catopsilia</i> (♂ND)–other pierids (♂)	3.6604	0.0045
<i>Catopsilia</i> (♂D)–other pierids (♂)	3.6451	0.0048
<i>Catopsilia</i> (♂ND)–danaines (♂)	5.5352	<0.0001
<i>Catopsilia</i> (♂D)–danaines (♂)	5.3565	<0.0001
number of ova : abdomen mass		
<i>Catopsilia</i> (♀ND)– <i>Catopsilia</i> (♀D)	–7.4797	<0.0001
<i>Catopsilia</i> (♀ND)–other pierids (♀)	–6.306	<0.0001
danaines (O)– <i>Catopsilia</i> (♀ND)	3.7212	0.001
danaines (O)–danaines (RD)	5.2655	<0.0001

*Catopsilia* species (both  $p > 0.1$ ; figure 1b and electronic supplementary material, table S3).

When combined across groups, dispersing *Catopsilia* females had similar resource investment to other pierid females ( $Z = 0.7874$ ,  $p = 1$ ; table 1 and figure 1c), whereas non-dispersing *Catopsilia* females had significantly higher thoracic investment compared with dispersing *Catopsilia* females ( $Z = 3.6474$ ,  $p = 0.0048$ ) and other pierid females ( $Z = 5.2964$ ,  $p < 0.0001$ ). Among males, both non-dispersing and dispersing *Catopsilia* had higher thorax : abdomen ratios than other pierids ( $Z = 3.6604$ ,  $p = 0.0045$  and  $Z = 3.6451$ ,  $p = 0.0048$ , respectively) and danaines ( $Z = 5.5352$ ,  $p < 0.0001$  and  $Z = 3.3565$ ,  $p < 0.0001$ , respectively; table 1 and figure 1c). Considered together, these results indicated that while most *Catopsilia* had higher thoracic investment compared with other pierids and danaines, dispersing *Catopsilia* females were closer to other pierid females in terms of flight morphology and reproductive investment.

### (c) Dispersing females have higher egg loads compared with non-dispersing females

The aforementioned differences in thorax : abdomen ratio between non-dispersing and dispersing *Catopsilia* females were likely due to a higher number of mature ova in dispersers (*pomona*:  $W = 37$ ,  $p < 0.0001$ ; *pyranthe*:  $W = 45$ ,  $p = 0.0009$ ), even when controlled for abdominal mass (no. of ova per

abdomen mass; *pomona*:  $W = 29$ ,  $p < 0.0001$ ; *pyranthe*:  $W = 56$ ,  $p = 0.0033$ ; figure 2a). When pooled across groups, non-dispersing *Catopsilia* females had lower egg loads than dispersing *Catopsilia* females and non-dispersing females of other pierid species ( $Z = -7.4797$ ,  $p < 0.0001$  and  $Z = -6.306$ ,  $p < 0.0001$ , respectively; table 1). This trend was also in contrast with danaine migratory species, where non-migrating females had higher egg loads—and therefore, higher reproductive investment—compared with migrating females in reproductive diapause, which had no mature ova at all (electronic supplementary material, table S2) [18].

### (d) *Catopsilia* dispersers show an inverse relationship between number of eggs and relative thorax mass

Dispersing *Catopsilia* females had a significantly steeper slope compared with non-dispersing females (pairwise slope comparisons, *t* ratio<sub>dat</sub>:  $-5.355_{166}$ ,  $p < 0.0001$ ) and ovulating danaines ( $-3.61_{166}$ ,  $p = 0.0027$ ; figure 2c and electronic supplementary material, table S4), indicating that with increasing relative investment in flight muscles (high thorax : abdomen ratio), dispersers experienced a swift decline in the number of mature ova.

### (e) Species, dispersal behaviour, and egg loads predict resource investment and flight morphology in females

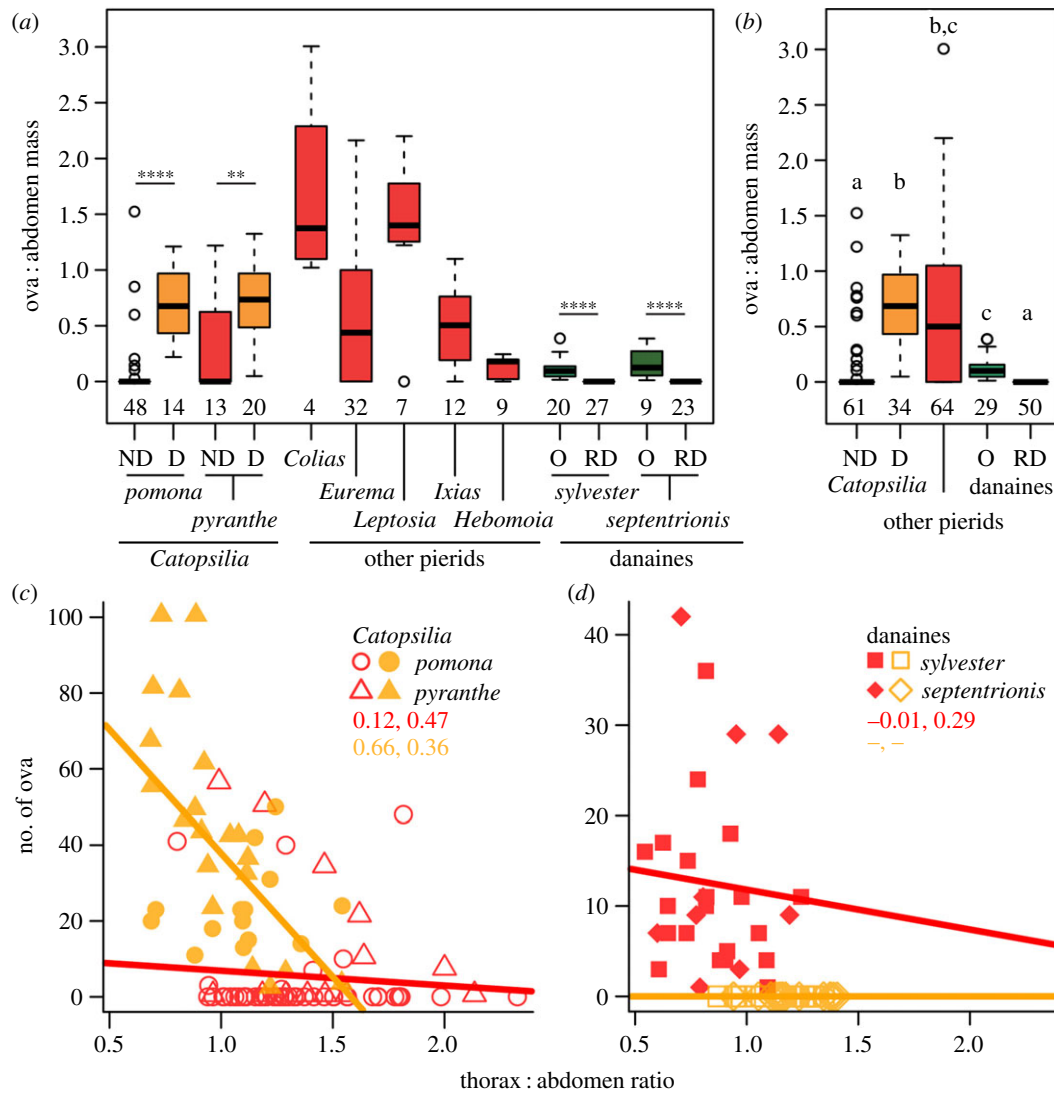
Male body proportions varied considerably with species and body mass, but not with dispersal behaviour (table 2). By contrast, female resource investment was influenced significantly by species, dispersal behaviour, number of ova and body mass as independent predictors (table 2). These results indicated that female flight morphology was more susceptible to modulation by multiple factors related to reproductive load, especially in the context of migration and dispersal.

## 4. Discussion

Although sexual dimorphism in body proportions is common in butterflies [35], reproductive diapause reduces the disparity in long-distance migrants and allows females to migrate with a relatively lighter, ova-free abdomen [36]. In accordance with previous findings in migrating danaines [18], sexual dimorphism remains conspicuous in *Catopsilia*, with females modulating investment in contrasting functional morphology (e.g. thorax versus abdomen) in response to movement.

*Catopsilia* are strong fliers and disperse by active flight [37]. We showed that despite having higher egg loads compared with non-dispersing females, dispersers experience a steeper decline in number of ova with increasing relative investment in thoracic tissue. This might indicate an adaptive response to larval food limitation or flight stress via plasticity in adult resource allocation [38,39]. However, low egg loads among non-dispersing females may indicate that mating soon after eclosion and frequent oviposition is of selective advantage to females in habitats with cyclical resource availability. Egg loads and relative investment in abdominal tissue are also influenced by host plant characteristics, abdominal fat and reproductive diapause. For instance, *Catopsilia* attain sexual maturity soon after eclosion, oviposit frequently on





**Figure 2.** Reproductive dynamics in females. (a) Egg loads of females in each species. (b) Pooled egg loads of *Catopsilia*, other pierids and danaines. Statistically different groups are indicated with different lower case letters, and inset numbers indicate sample sizes (*a,b*). ND = non-dispersing, D = dispersing, O = ovulating, RD = reproductive diapause. Horizontal bars indicate *p*-values: \*\* < 0.01, \*\*\*\* < 0.0001. (c,d) Regressions between number of ova and thorax : abdomen ratio. Yellow symbols indicate dispersing (*Catopsilia*) or diapausing (danaine) populations, and red symbols indicate non-dispersing (*Catopsilia*) or ovulating (danaine) populations. Dispersing *Catopsilia* had a significantly steeper regression slope compared with non-dispersing *Catopsilia* and ovulating danaines (electronic supplementary material, table S4). Inset numbers indicate adjusted  $R^2$  and *p*-values ( $R^2$ , *p*) for respective groups with ova as the dependent variable and thorax : abdomen ratio, species, and body mass as predictors.

**Table 2.** Summary of ANCOVA results. Main effects of species, dispersal behaviour and body mass on the thorax : abdomen ratio of each sex, with number of ova as an additional predictor for females. There were no significant interaction effects. Comparisons with  $p < 0.05$  are italicized.

sex	covariate	df	SS	MS	<i>F</i>	<i>p</i> -value
male	species	8	51.783	6.473	25.07	0.0000
	dispersal behaviour	1	0.65	0.654	2.532	0.1124
	body mass	1	2.907	2.907	11.26	0.0009
	residuals	331	85.45	0.258		
female	species	8	4.757	0.595	37.502	0.0000
	dispersal behaviour	2	4.462	2.231	50.335	0.0000
	number of ova	1	0.740	0.740	4.991	0.0076
	body mass	1	0.742	0.742	6.23	0.0133
	residuals	190	9.566	0.05		

commonly occurring Fabaceae plants and remain reproductively active even as they disperse. On the other hand, aposematic danaines enter reproductive diapause under

adverse environmental conditions and oviposit on milkweed bushes (e.g. *Gymnema sylvestre* and *Wattakaka volubilis*, Apocynaceae), which occur in forest patches in low densities

[40–42]. It remains to be seen how traits such as dispersal propensity, aposematism and host plant specificity might modulate diversification of reproductive capacity across taxa.

Dispersal-related trait variation is often more prominent in females [43], and ova production and maturation are intrinsically linked to dispersal and migration [8,18,36]. Taken together, these findings suggest that flight- and reproduction-related morphological plasticity in females is modulated by multiple factors related to dispersal and migration, and that butterfly life-history traits are subject to sex- and movement-specific selective pressures. Our results also suggest that in increasingly fragmented habitats, heavier egg loads could adversely affect females that disperse between suitable habitat patches through a resource-poor matrix.

**Ethics.** No ethical clearance was needed for this study on insects. Wild-caught samples were obtained largely from the NCBS campus/field stations and private lands, and from wildlife sanctuaries and national parks in India under the following research and collection permits issued by the state forest departments in Karnataka (permit no. 227/2014-2015, dated 2015/04/16), Kerala (permit no. WL 10-3781/2012, dated 18/12/2012, and GO (RT) no. 376/2012/F and WLD dated 26/07/2012), Goa (permit no. 2/21/GEN/WL and ET(S)/2013-14/387, dated 2013/06/20), Meghalaya (permit no.

FWC/G/173/Pt-II/474-83, dated 27/05/2014), Arunachal Pradesh (permit no. CWL/G/13(95)/2011-12/Pt-III/2466-70, dated 16/02/2015) and West Bengal (permit no. 2115(9)/WL/4 K-1/13/BL41, dated 2013/11/06; and permit no. 1107/42/2 W-705/18, dated 2018/05/07), for which we thank the Principal Chief Conservator of Forest, Deputy Conservators of Forest, Wildlife Wardens and field officers of those states.

**Data accessibility.** The datasets used in this study are deposited in the Dryad repository (<https://doi.org/10.5061/dryad.nvx0k6dnh>) [28].

**Authors' contributions.** V.B. collected and analysed the data, and wrote the manuscript with K.K. K.K. designed and coordinated the research, and collected specimens with V.B.. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

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