

Supplementary

Butterfly Biology Systems: Connections and Interactions in Life History and Behaviour

Supplementary Figure legends

The following figures are supplementary to those in the text. Most of the figures represent neat versions

of working diagrams produced by the author during the process of writing the text. Each is accompanied by its key for the symbols used, but there is also a key to all symbols used. They have been provided for researchers to examine, correct and extend.

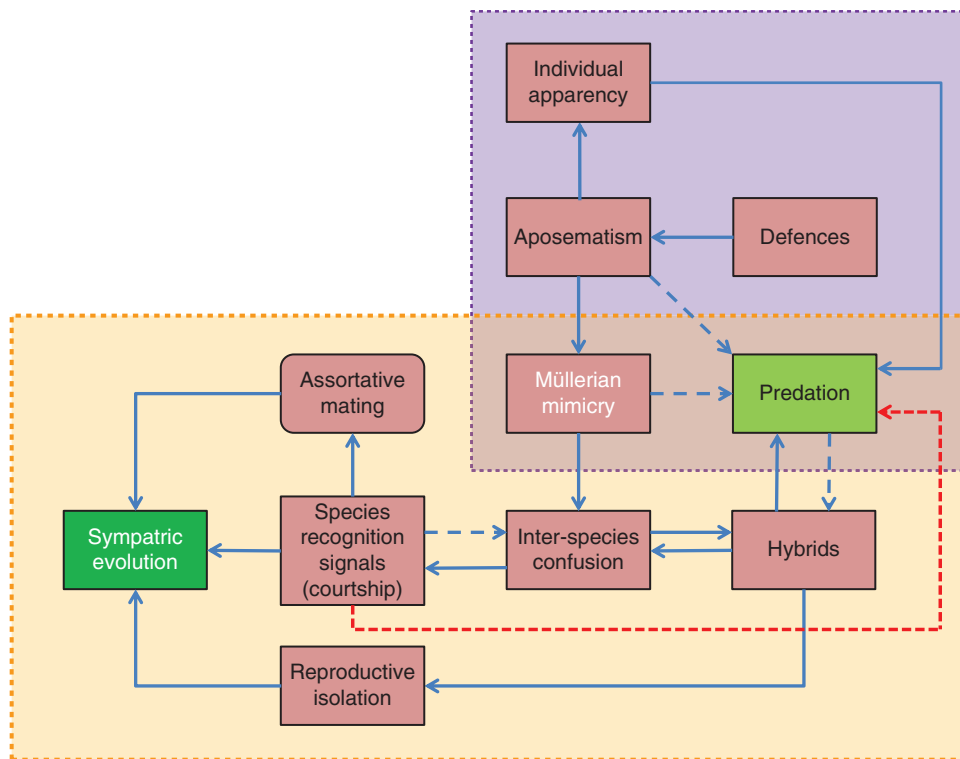


Fig. S1. A simple model for advancement of sympatric evolution in Müllerian mimics. The process of speciation through Müllerian mimicry is more likely to be one of enhancement of sympatric evolution (pre- and post-zygotic isolation mechanisms) than causation of sympatric speciation *ab initio*, but which may occur through hybridisation. The development of Müllerian mimics leads to a confusion between species that is considered to produce inter-racial hybrids with non-mimetic wing patterns (e.g. *Heliconius erato* × *H. melpomene*), thereby triggering additional species recognition signals (i.e. mating cues; sex pheromones; specialised visual signals) and assortative mating that further distinguishes closely matching Müllerian mimic forms as in *Heliconius*. Hybridisation between closely related species may create novel wing patterns, generating reproductive isolation from the two parental species, effecting sympatric speciation (e.g. *Heliconius heurippa*). The purple zone identifies factors leading to aposematism and Müllerian mimics (see Chapters C.7 and C.8), the orange zone factors enhancing sympatric evolution; these zones overlap. Links: continuous, positive associations; pecked, negative associations; red pecked link (after Finkbeiner *et al.*, 2014) indicates that ineffectiveness in inducing mating behaviour may reduce the ability of butterflies to escape from predation (and vice versa). (See Jiggins *et al.*, 2001a; Naisbit *et al.*, 2003; Mavárez *et al.*, 2006; Merrill *et al.*, 2011, 2012, 2015; Elias and Joron, 2015.)

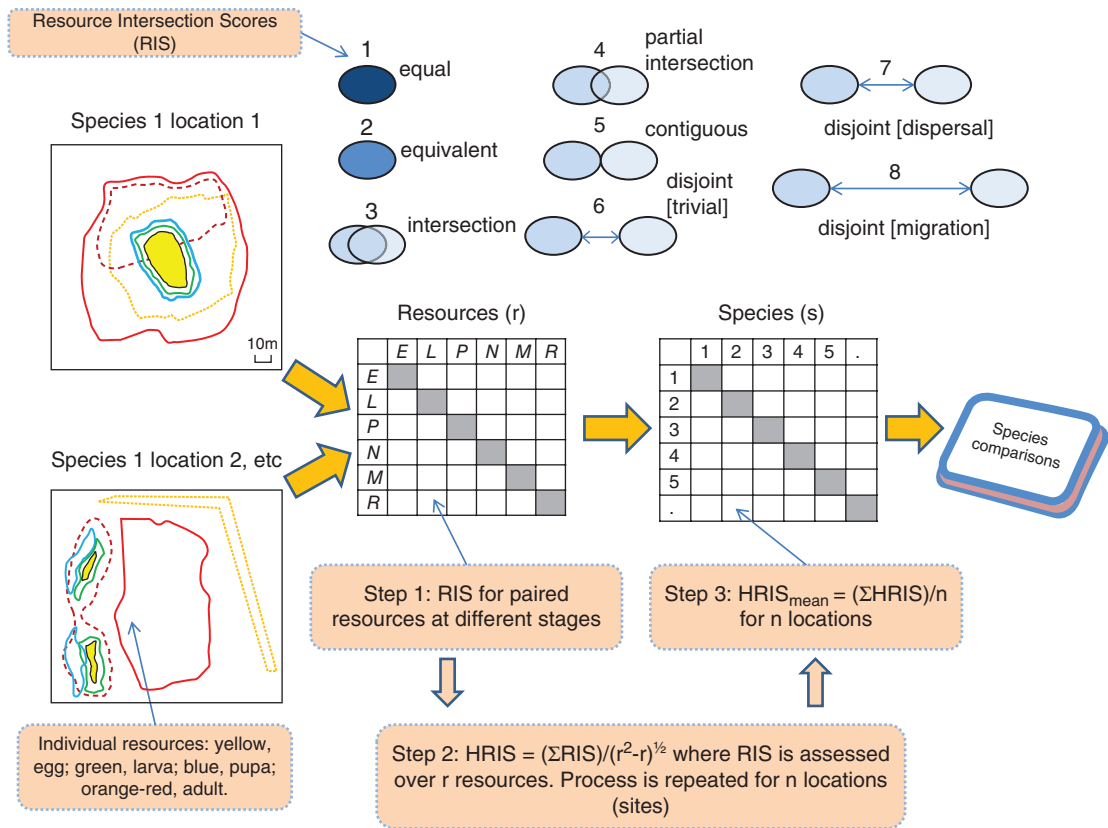


Fig. S2. Assessment of resource intersection making up a species' habitat based on the mean sum of resource intersection scores (RISs) over samples of sites. RISs obtained for pairs of consecutively used resources (8-point scale) can be summed over sites and the average taken across pairs of resources providing a matrix of mean habitat resource intersection scores (HRIS) for species. For RIS 8, there is little likelihood of an individual (or its progeny) visiting the same site in a following year. Letter codes for resource use in this simplified example: E, egg; L, larva; P, pupa; N, adult nectar. M, adult mate location; R, adult roosting. (See Dennis *et al.*, 2014a.)

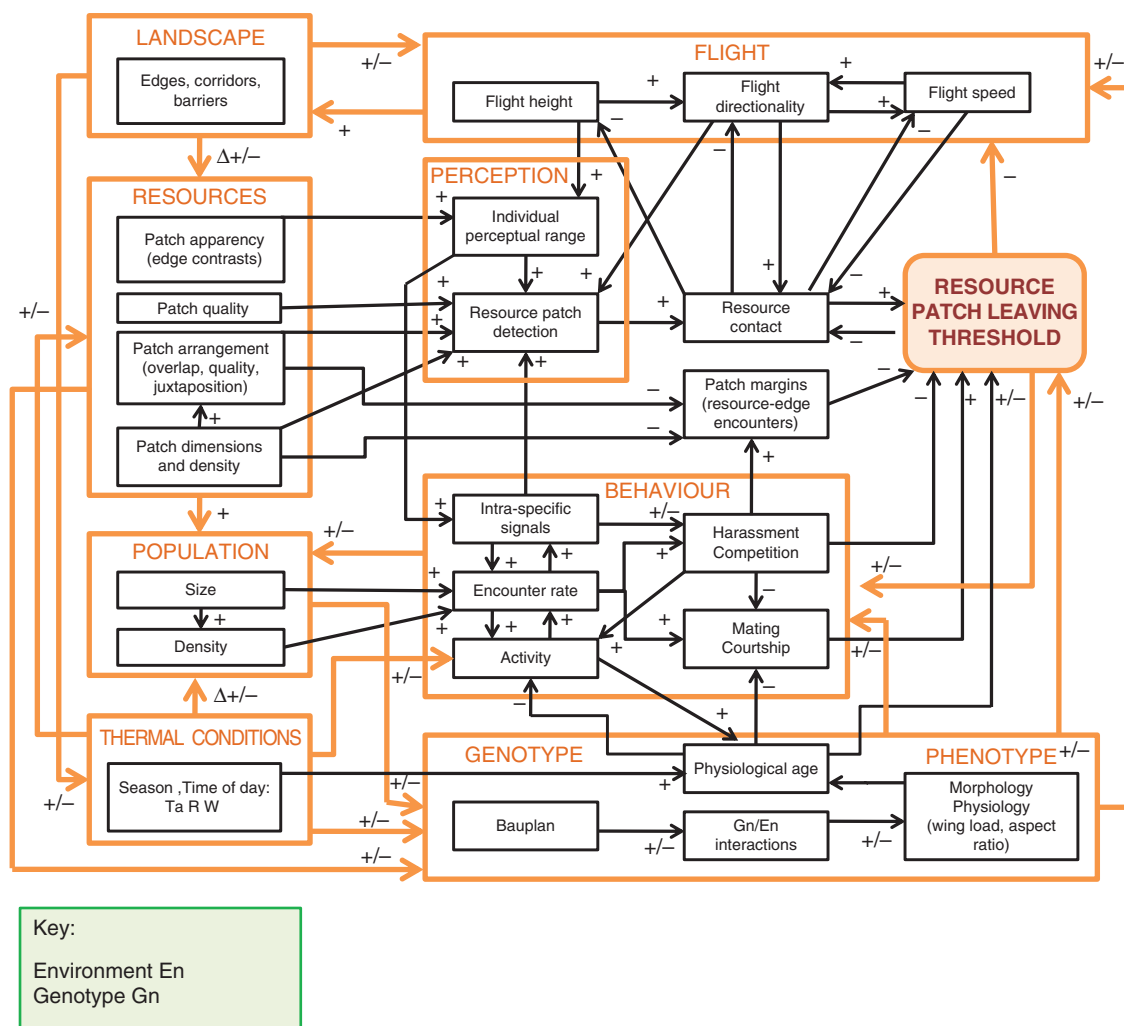


Fig. S3. A process-response model of the behavioural components of adult butterfly responses to landscape resources and matrix. Major variable subsystems and behavioural responses are indicated by thick orange box margins and the component parts of each by thin black box margins. Arrows indicate connections between processes and responses and a plus (+) or minus (-) symbol indicates, respectively, a positive or a negative relationship between factors. The symbol \pm indicates that the relationship could be either. Central to the model is the decision butterflies make to stay or move from a resource (**resource patch leaving threshold**), which can lead to increased or reduced residence times at a resource and a cascade of consequences for use of patches, and how individuals interact with landscape features and other individuals within population units or elsewhere. (From Shreeve and Dennis, 2011.)

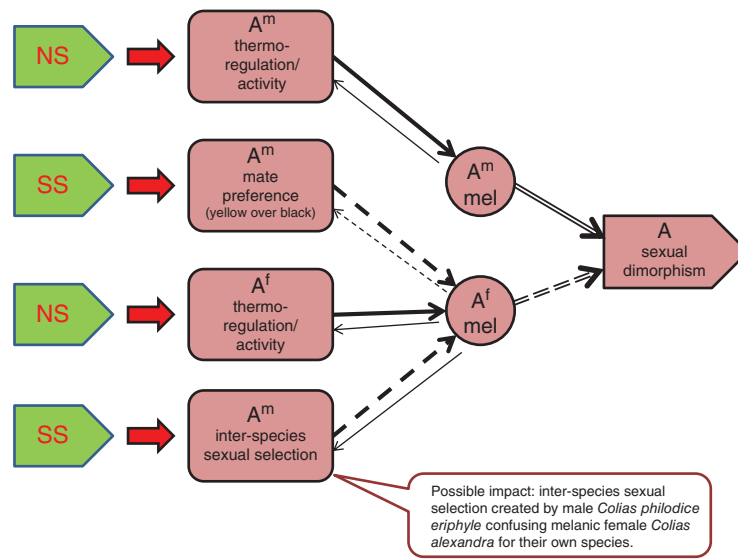
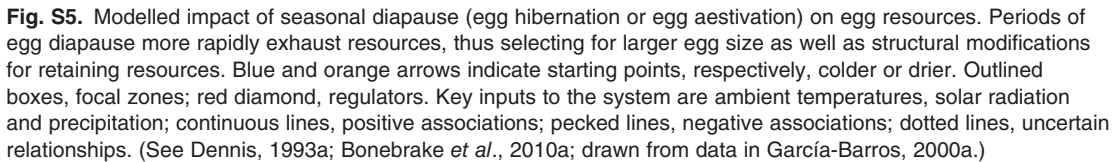
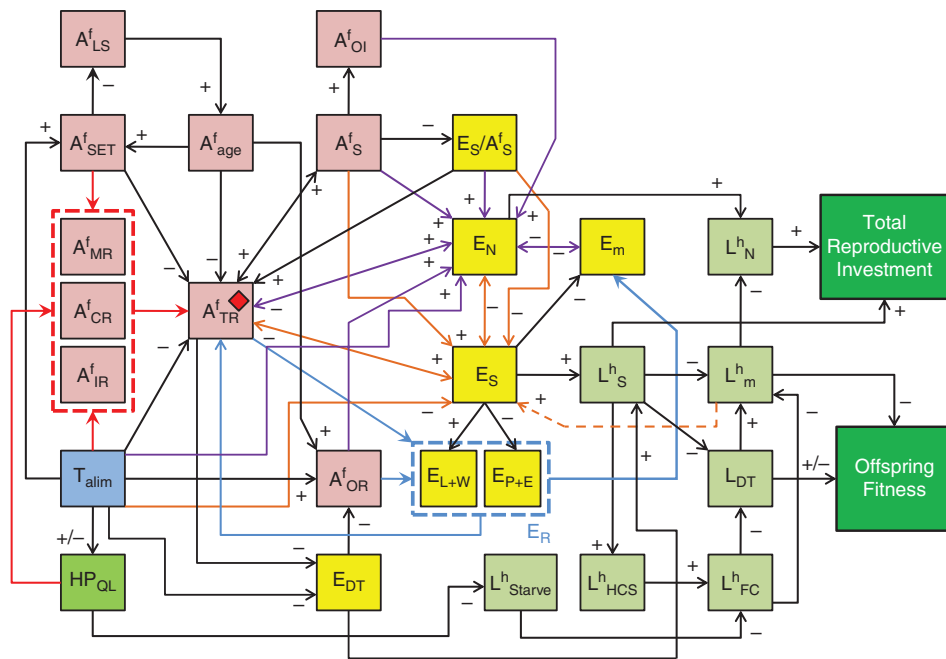


Fig. S4. A basic model driving sexual dimorphism in wing colour. Trade-offs in sexual dimorphism for ventral wing colour (yellow and degree of melanism in a lateral basking species). The figure illustrates antagonism in female ventral wing colour/pattern between mate (male) preference (yellow colour) and thermoregulation efficiency (melanism) compared with the main driver for efficient thermoregulation and enhanced activity in males (melanism) (taken from details on lateral basking *Colias philodice eriphyle* in Ellers and Boggs, 2003). SS, sexual selection; NS, natural selection; A_{mel} , adult melanism; superscript m, male; superscript f, female.

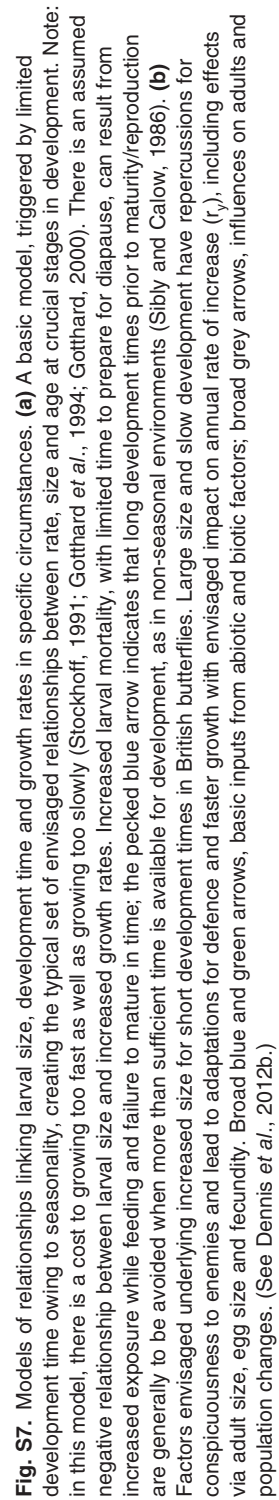




Key:

- Adult (female) age A^f_{age}
- Adult (female) life span A^f_{LS}
- Adult (female) capital resources A^f_{CR}
- Adult (female) income resources A^f_{IR}
- Adult (female) mating resources A^f_{MR}
- Adult ovigyny index A^f_{OI}
- Adult (female) oviposition rate A^f_{OR}
- Adult (female) size A^f_S
- Adult (female) stress experience total A^f_{SET}
- Adult (female) total resources A^f_{TR}
- Ambient air temperature (within finite limits) T_{alim}
- Egg development time E_{DT}
- Egg lipid and water E_{L+W}
- Egg mortality E_m
- Egg number E_N
- Egg protein and energy E_{P+E}
- Egg resources E_R
- Egg size E_S
- Host plant quality HP_{QL}
- Larval development time L_{DT}
- Larval (hatchling) feeding capacity L^h_{FC}
- Larval (hatchling) head capsule size L^h_{HCS}
- Larval (hatchling) mortality L^h_m
- Larval (hatchling) number L^h_N
- Larval (hatchling) size L^h_S
- Larval (hatchling) starvation L^h_{Starve}
- Negative allometry of egg size on adult size $(\beta < 1)E_S/A^f_S$

Fig. S6. A hypothetical model of factors influencing, and influenced by, the within-species trade-off between egg size and egg number (fecundity). Red diamond, adult female total resources from maternal plastic behaviour acting as the key regulator of resource allocation to offspring. Ambient temperature (T_a) assumed to be within limits of development. Coloured links, links to egg size and egg number, and subsystems of variables, respectively; pecked orange link, feedback to egg size from hatchling mortality.



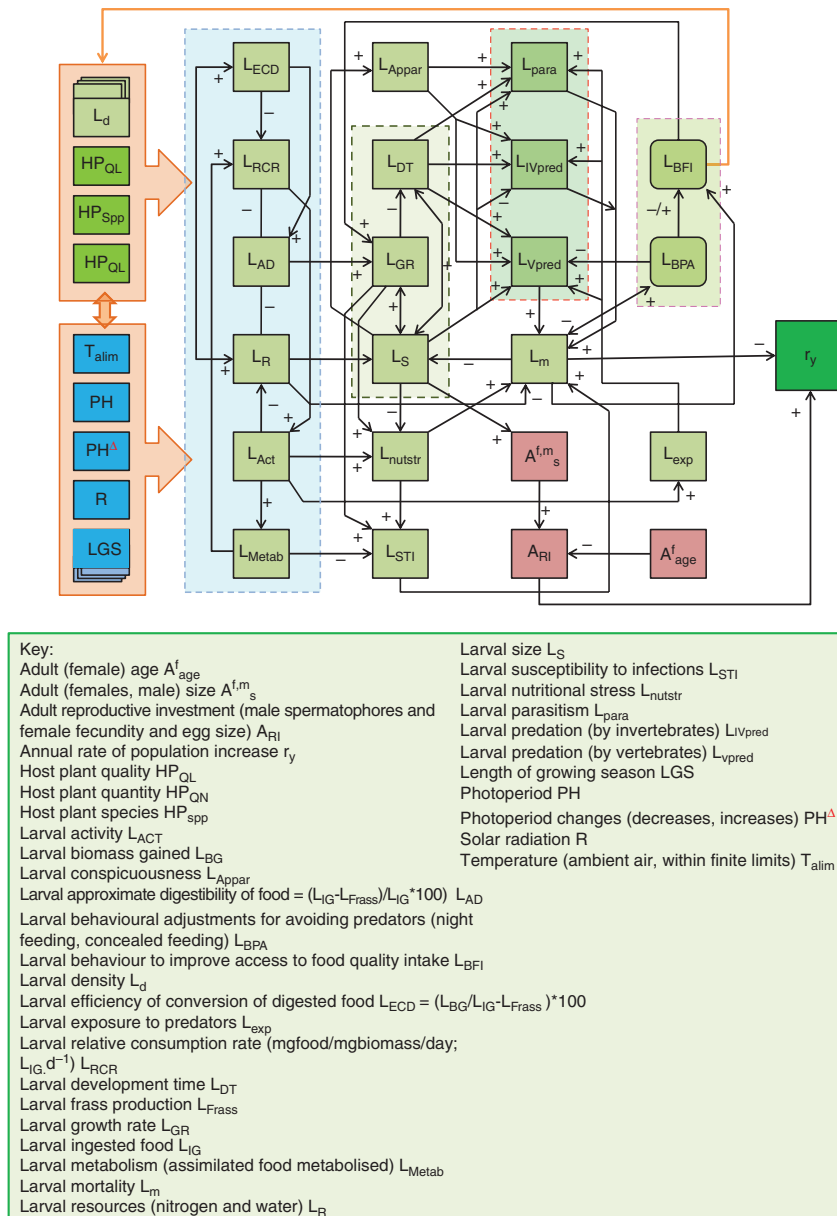


Fig. S8. A composite model of effects on larval development time, mean larval growth rate and mature larval size (mass) from immediate food and community factors. The model involves parameters of food conversion to biomass and the direct consequences of being small or large, growing fast or slow, of short and long periods of development. Assumptions made are that broods and moults are constant, there is no larval diapause and larvae feed singly; also, no differences in development between sexes are considered (see Fig. S9). A number of factors are taken from observations outside the laboratory (e.g. predation). Even with the restrictions imposed on the model, the message is that, from so many inputs and variables, species' development systems can vary widely. Four subsystems are outlined in colour. Arrowless links, correlations only indicated. Orange arrow, behavioural shifts may lead to environment and larval density changes. (After text details in Pullin, 1986, 1987; Arendt, 1997; Nylin and Gotthard, 1998; Lavoie and Oberhauser, 2004; Berger *et al.*, 2006; Berger and Gotthard, 2008; Gotthard, 2008.)

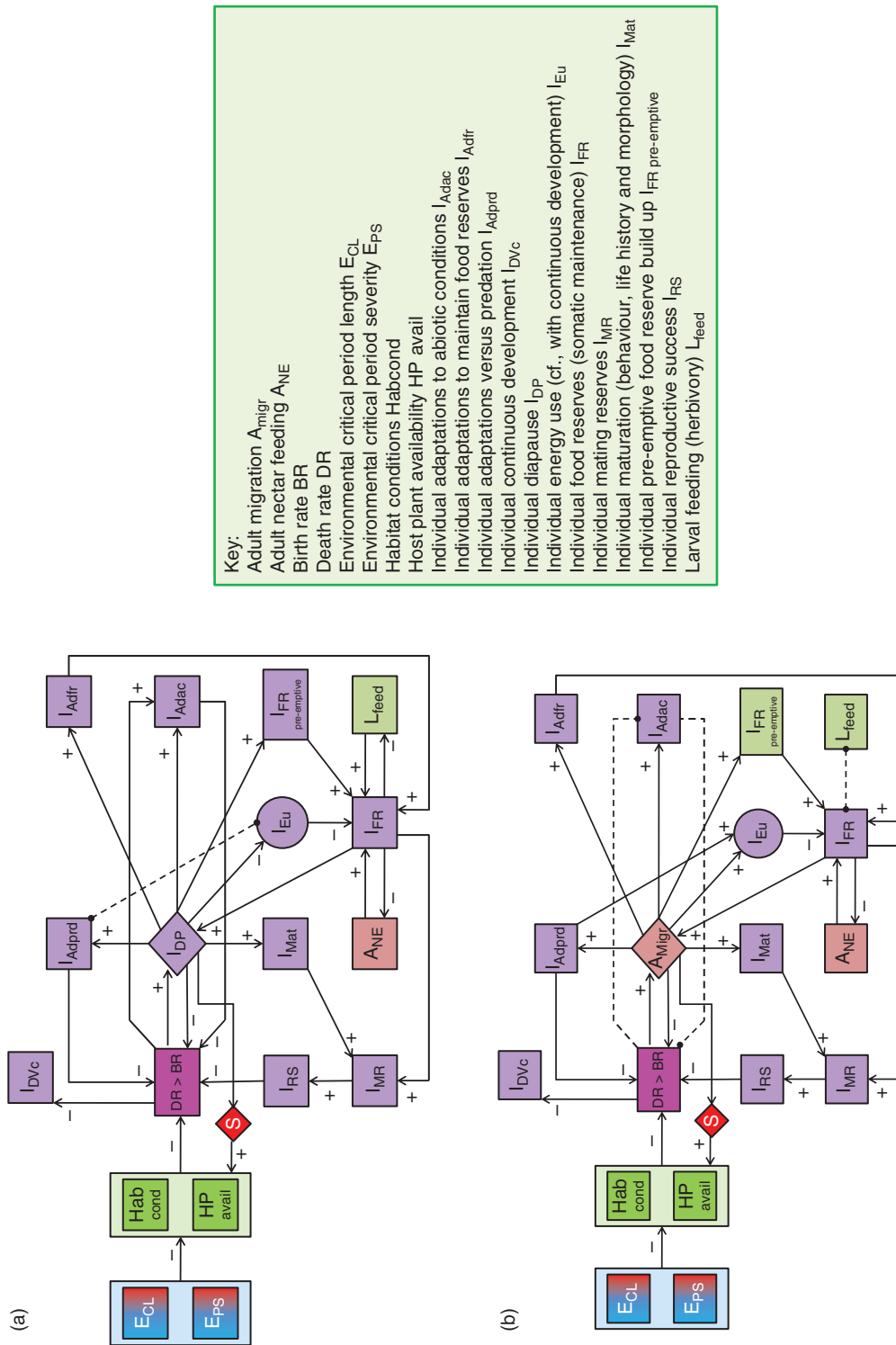


Fig. S10. Comparison of energetics and adaptations for responses to critical periods of heat, drought and/or cold. **(a)** diapause and **(b)** migration. Effectively, they apply different switches (red diamond) to synchronise with the availability of food and living conditions in either waiting for change or moving. Pecked lines ending in dots indicate dead link in a specific system.

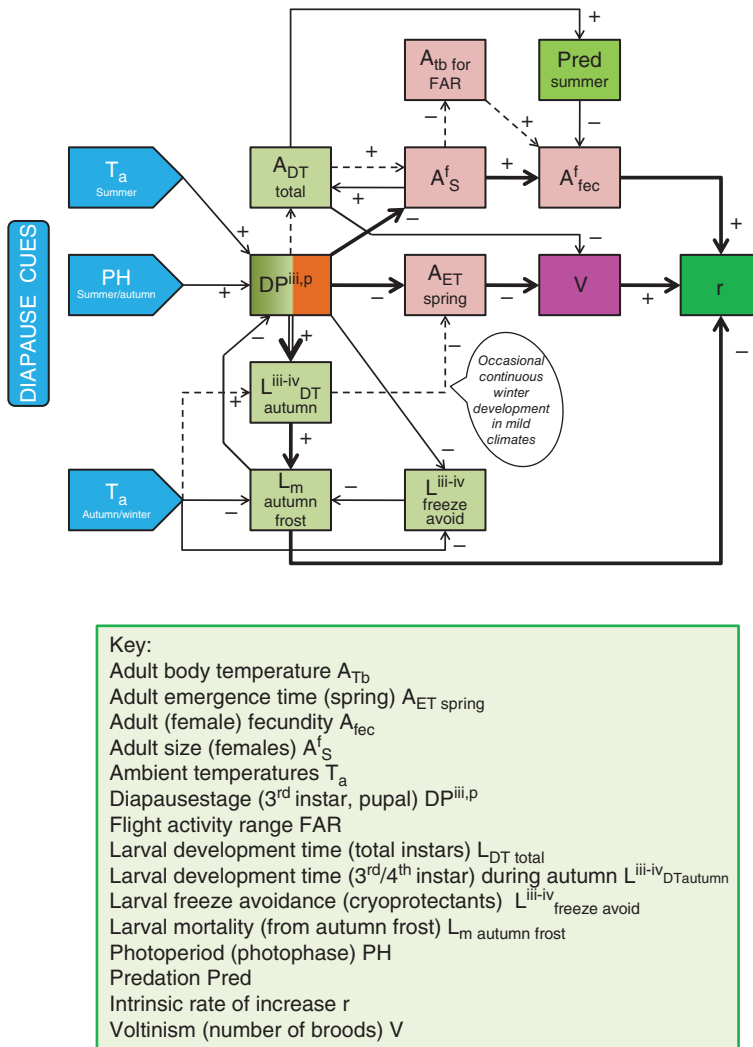


Fig. S11. Factors influencing the balance in the frequency of two diapause stages in *Pararge aegeria*. Bold arrows, main path of effects; pecked lines, ancillary paths. Diapause in pupal stage (benefits: early emergence and more broods; costs: mortality in larval 4th instar from autumn frosts) and larval 3rd instar stage (benefits: autumn frost preparation (cryoprotectants) and increased size and fecundity; costs: fewer broods and higher summer predation). Increased development time of pupal path and increased size of third instar are ‘strategic decisions’ and not environmentally induced (compound arrow). (Details from Wiklund and Friberg, 2011.)

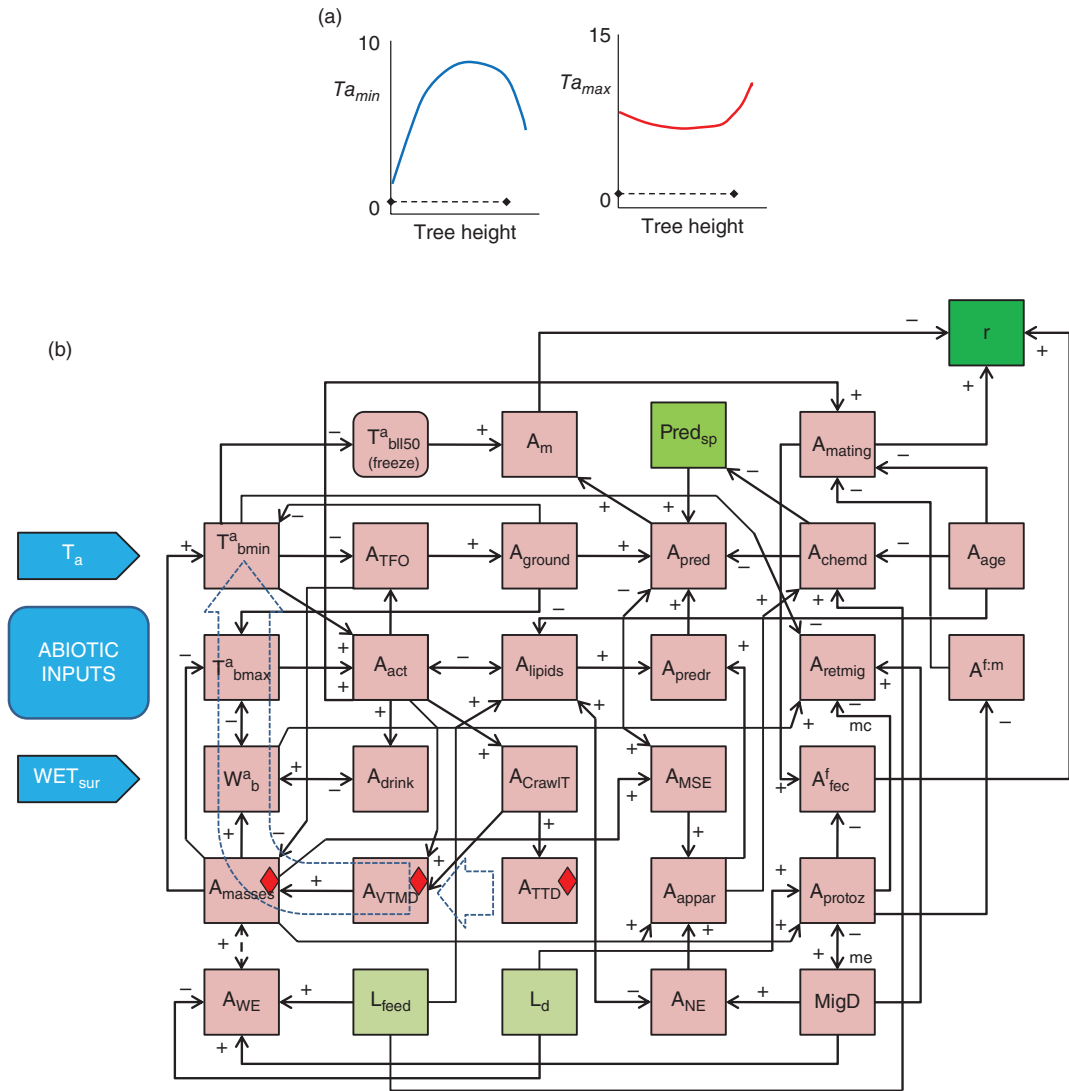


Fig. S12. Overwintering in monarch butterflies *Danaus plexippus* in the Mexican oyamel fir forest. **(a)** Relationship of: (i) minimum ambient temperatures ($T_{a_{min}}$) and (ii) maximum ambient temperatures ($T_{a_{max}}$) with tree height. **(b)** Process and feedback of factors within the Mexican oyamel fir forest on *Danaus plexippus* diapause status, mortality and re-migration success in March/April. Large ghost arrows indicate basic feedbacks to adult body conditions by clumping and positioning on trees; pecked arrow, correlation in absence of known causal link; me, migratory escape from infections; mc, migratory culling of infected individuals. (Basic links and relationships from Brower *et al.*, 1977, 1985, 2006, 2008, 2009, 2011; Tuskes and Brower, 1978; Calvert *et al.*, 1979; Fink and Brower, 1981; Alonso-Mejía and Brower, 1994; Calvert, 1994; Anderson and Brower, 1996; Alonso-Mejía *et al.*, 1997, 1998; Burger and Gochfeld, 2001; de Roode *et al.*, 2009; Lindsey *et al.*, 2009; Altizer and Davis, 2010; Davis and Rendon-Salinas, 2010; Bartel *et al.*, 2011; Guerra and Reppert, 2013.) **(c)** Reproductive advantages and disadvantages of overwintering male *Danaus plexippus* differing in weight, condition and size, and the impact on individual fitness. Red arrows indicate focal pathways; blue arrow, effect on female fitness; yellow boxes, intervening attributes. (Links obtained from relationships determined and discussed in Van Hook, 1993, 1996; including Beall, 1946; Gibo and Pallett, 1979; Boggs and Gilbert, 1979; Boggs, 1981b; Waltz and Wolf, 1984; Brower *et al.*, 1989; Oberhauser, 1988, 1989; Herman, 1993; Zalucki, 1993.) For recent modelling of conditions for overwintering monarchs in California see Fisher *et al.* (2018).

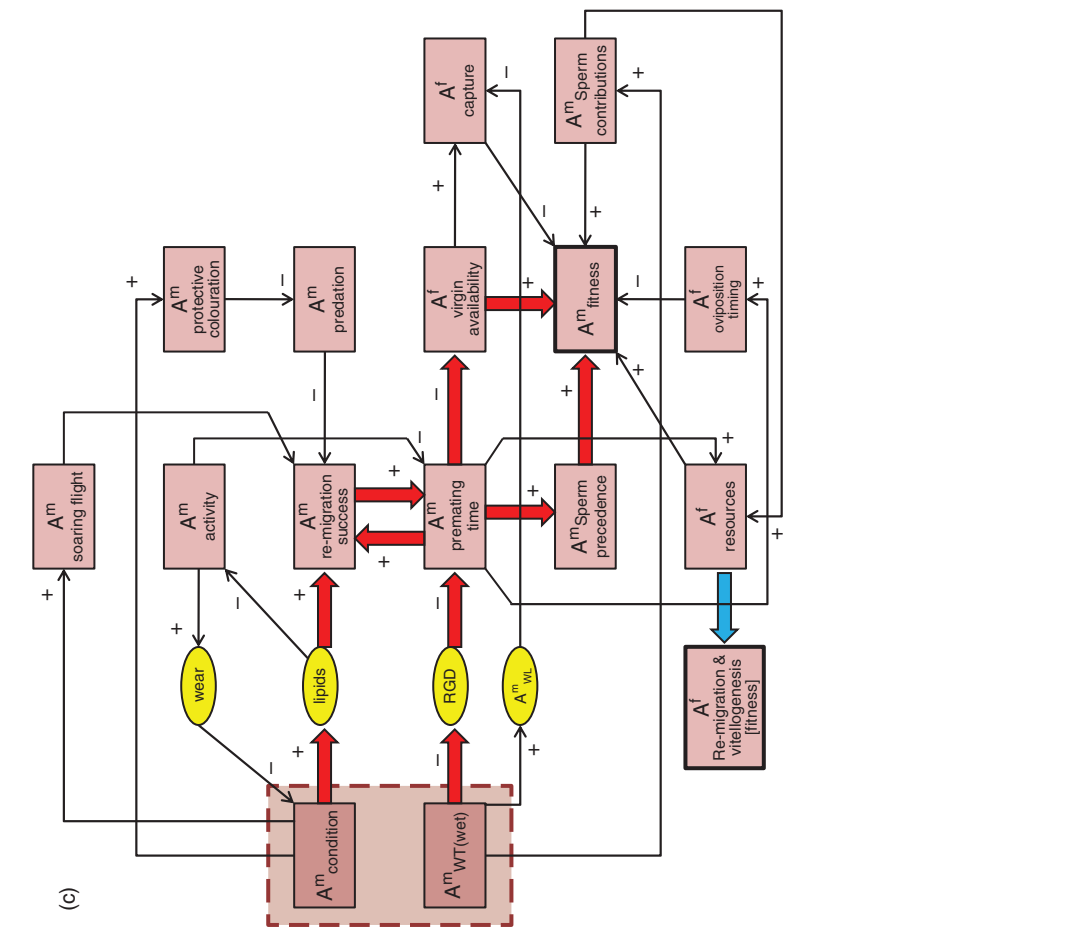


Fig. S12b Continued.

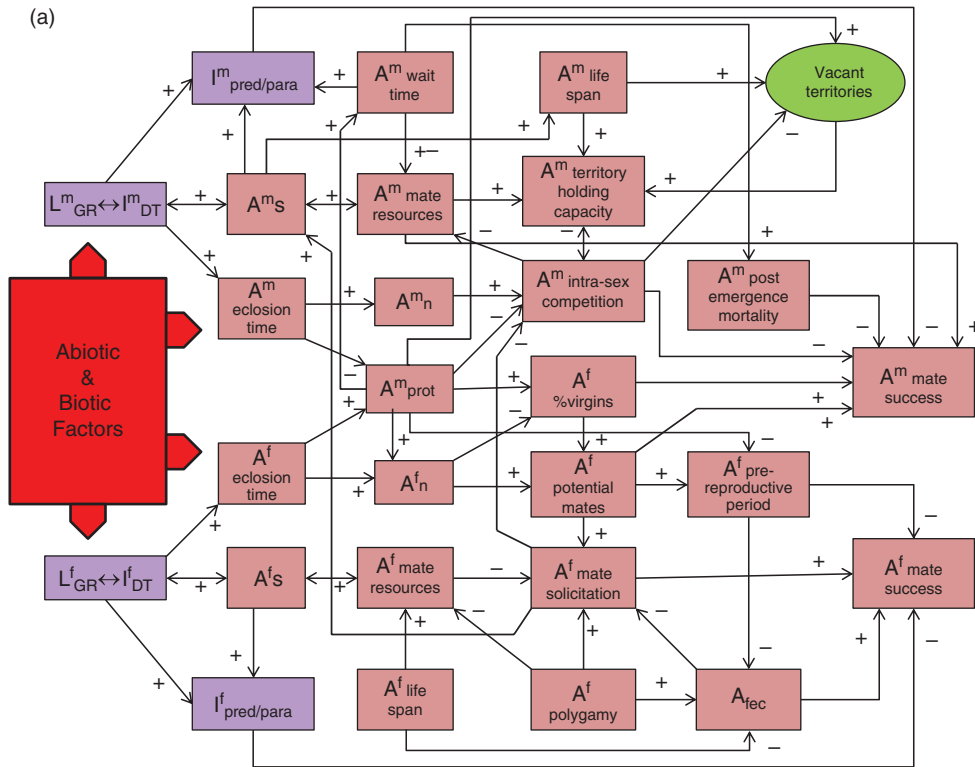


Fig. S14. Variables influencing and influenced by protandry in butterflies. **(a)** Protandry has effects on females and males and the diagram divides into two halves, upper males and lower females, to illustrate these impacts. Early-stage growth rates and development times have both benefits and costs for each sex; primarily, fast male (slower female) development times ensure male protandry and reduce premature losses to enemies, but may also (directly or indirectly) affect size and reproductive resources and mate holding capacity in its widest sense. There is also a potential male energy loss and male maturity gain in the lag between male and female emergence, indicated by the non-linear relationship (+−). The model is greatly affected by female monogamy/polygamy and therefore the number of accessible females in a population throughout the flight season. Altogether, the impression is of a complex of effects and experimentation has great difficulty in sifting out the precise nature of effective links, direct and indirect, from this simplified version of artefacts. (After Singer, 1982; Thornhill and Alcock, 1983; Iwasa *et al.*, 1983; Lederhouse *et al.*, 1989; Wiklund *et al.*, 1991; Stearns, 1992; Wiklund *et al.*, 1996; Carvalho *et al.*, 1998; Zonneveld, 1996a, b; Morbey and Ydenberg, 2001; Fischer and Fieldler, 2001c; Nève and Singer, 2008; Zwaan *et al.*, 2008; Takeuchi and Honda, 2009; Allen *et al.*, 2011.) **(b)** Details of mating advantages and disadvantages of protandry and male size for mate acquisition and holding capacity in a population of polygamous females where more advanced forms of mate holding exist (mate guarding, spergias deposition). Protandry presents a number of potential advantages for incumbents (first arrivals), but this is balanced against costs of competing with larger later-emerging males, and female solicitation for further matings. This diagram exposes just some of the trade-offs that may exist in more complex mating systems (see text for examples). (After Thornhill and Alcock, 1983; Morbey and Ydenberg, 2001; Vlasanek and Konvicka, 2009; Estrada *et al.*, 2010; Bennett *et al.*, 2012.)

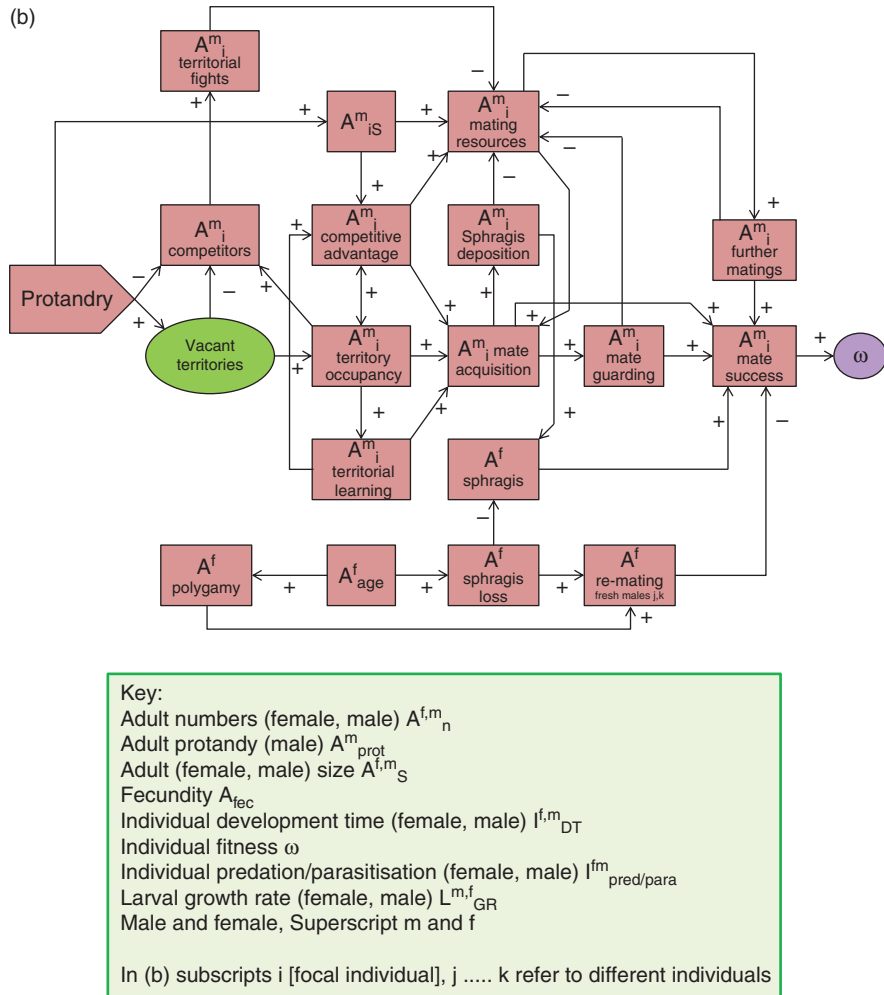


Fig. S14 Continued

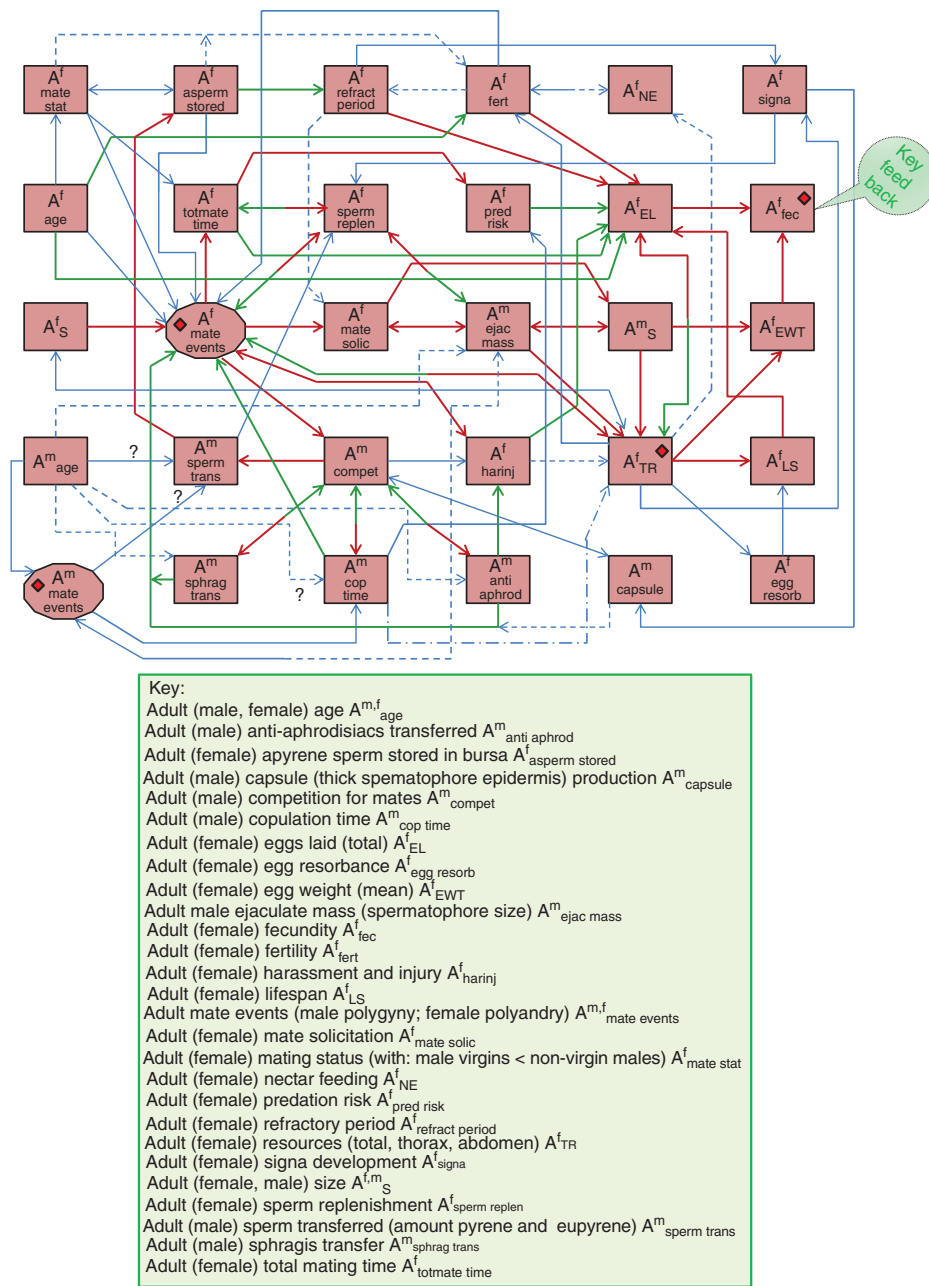


Fig. S15. Basic connections and interactions associated with polyandry. Frequency of female matings: dodecagon. Most factors affecting number of male matings (polygyny) not shown. To avoid overloading the diagram, more obvious paths (bold lines, dark red positive, green negative) have been separated from finer lines (blue, unbroken positive, pecked negative); diamonds indicate key regulators. The basic theme is that multiple female matings increase mate (male) competition which results in a number of consequences to ensure sperm precedence; the end product, female fecundity, produces feedbacks (green bubble) to female mating frequency. See text for references.

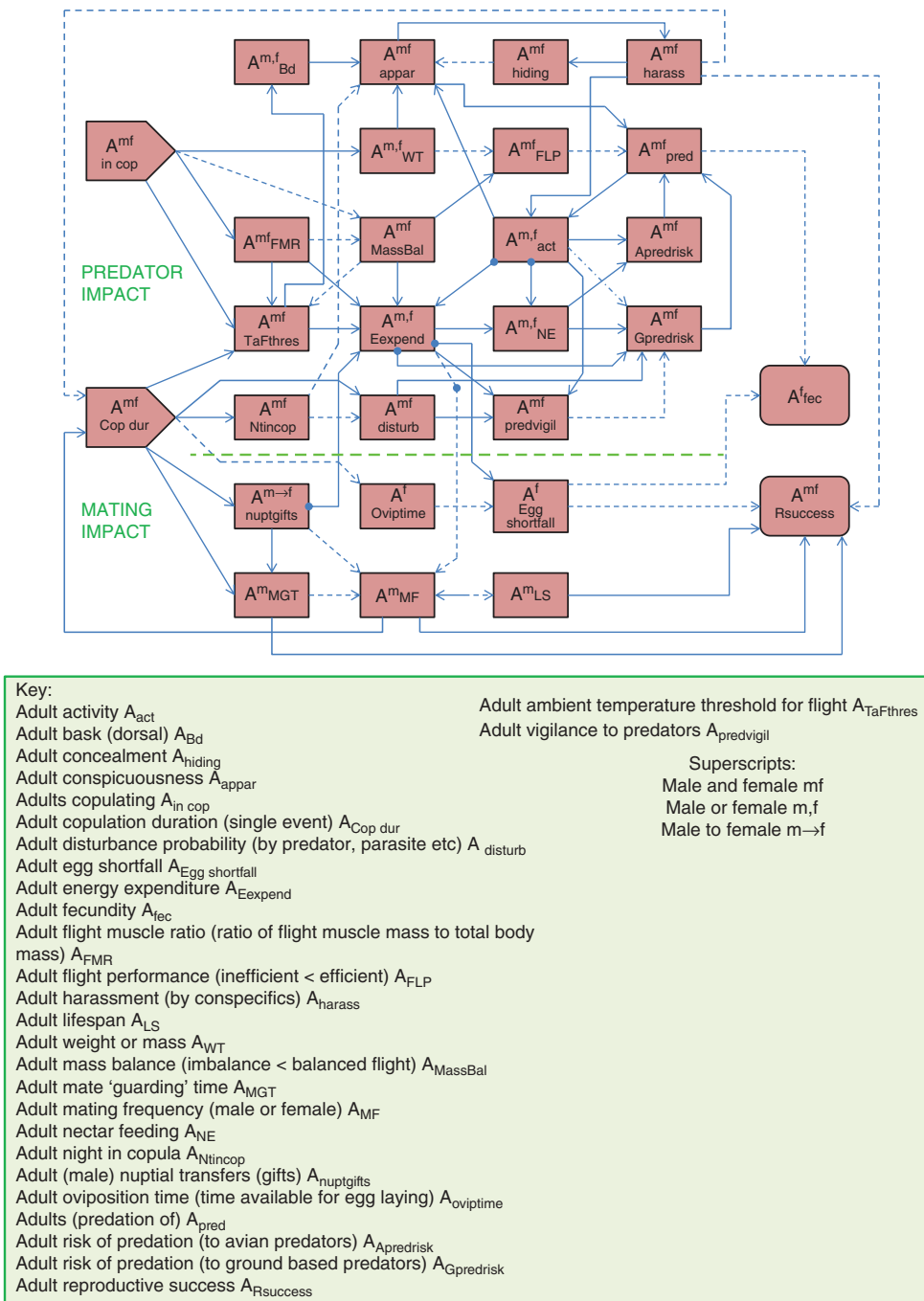


Fig. S16. Some potential consequences of copulation times in butterflies. For clarity, just two feedbacks to in copula duration are illustrated; the reader is encouraged to seek out others. The diagram is divided into predator effects (upper) and effects on reproduction (lower). Links: continuous, positive; pecked, negative; pecked/dotted, negative and/or positive; link initiated with large dot distinguishes sex responsible for in copula flights; mf, male and female; m, f, male or female; m→f, male to female.

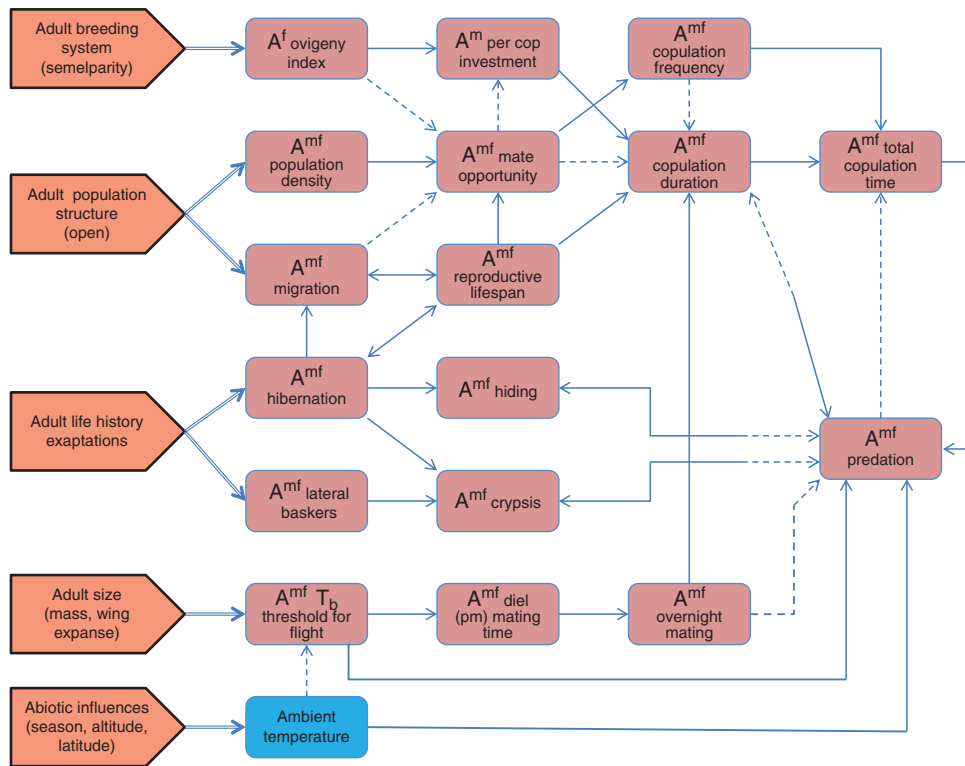


Fig. S17. Schematic illustration of the potential integration of some factors likely to be involved in interspecies extended copulation times. Five groups of basic factors are considered to be involved. Continuous lines, positive links; pecked lines, negative links; double lines, complex influences. A, adult; m, male; f, female; mf, male and female; T_b, body temperature; pm, post meridian (afternoon).

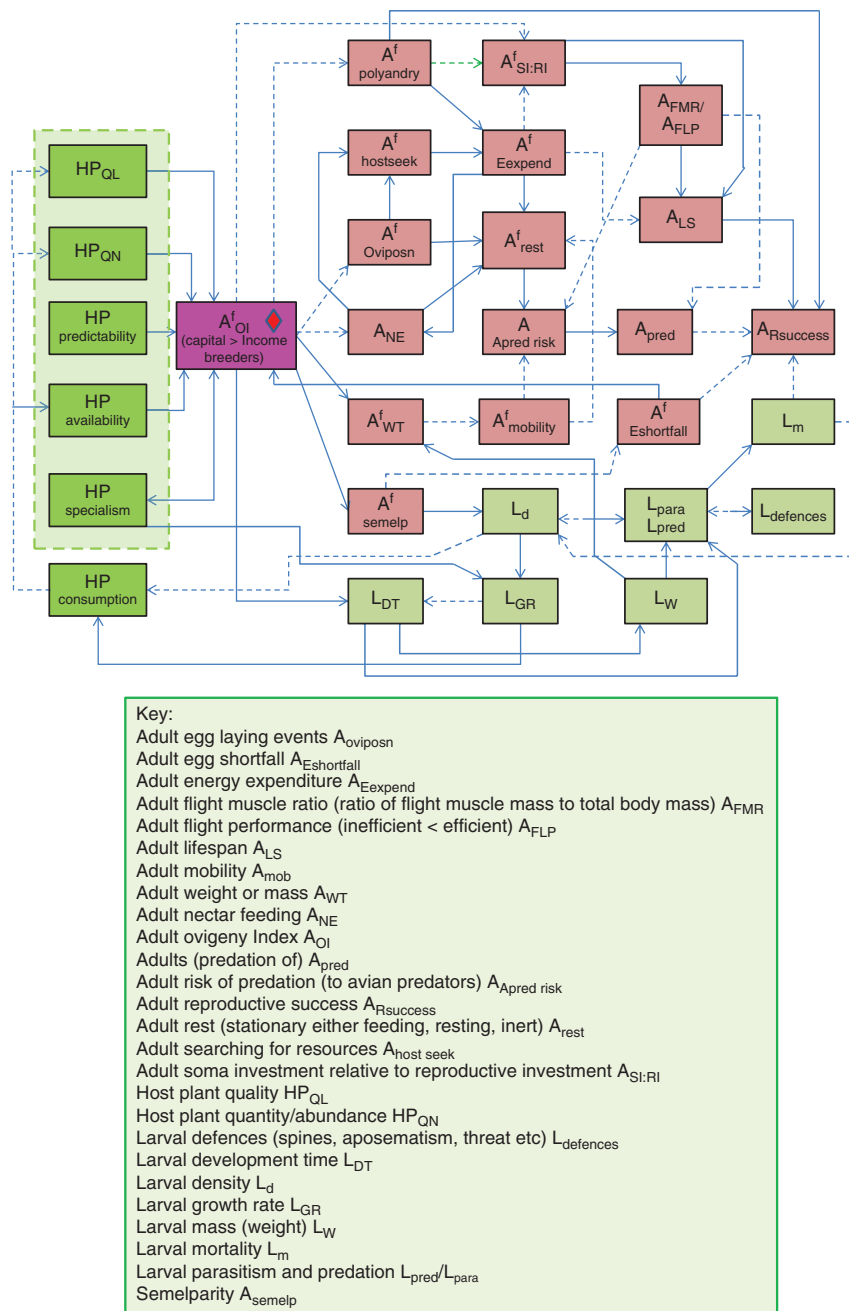


Fig. S18. Scheme to illustrate some of the consequences of capital/income breeding among butterflies capable of feeding as adults. Links: continuous, positive; pecked, negative. Trade-offs occur within the adult and larval stages as well as between them. Basic factors generating changes in capital resource investment are likely to be largely resource-induced (i.e. host plant, nectar, nuptial gifts); the balance in investment strategy (degree of capital:income investment) subjects individuals to varying reproduction and mortality pressures as larvae and adults. (From an amalgam of concepts in Fritz *et al.*, 1982; Tammaru and Haukioja, 1996; Jönsson, 1997; Bonnet *et al.*, 1998; Jervis *et al.*, 2005; Javoiš *et al.*, 2011.)

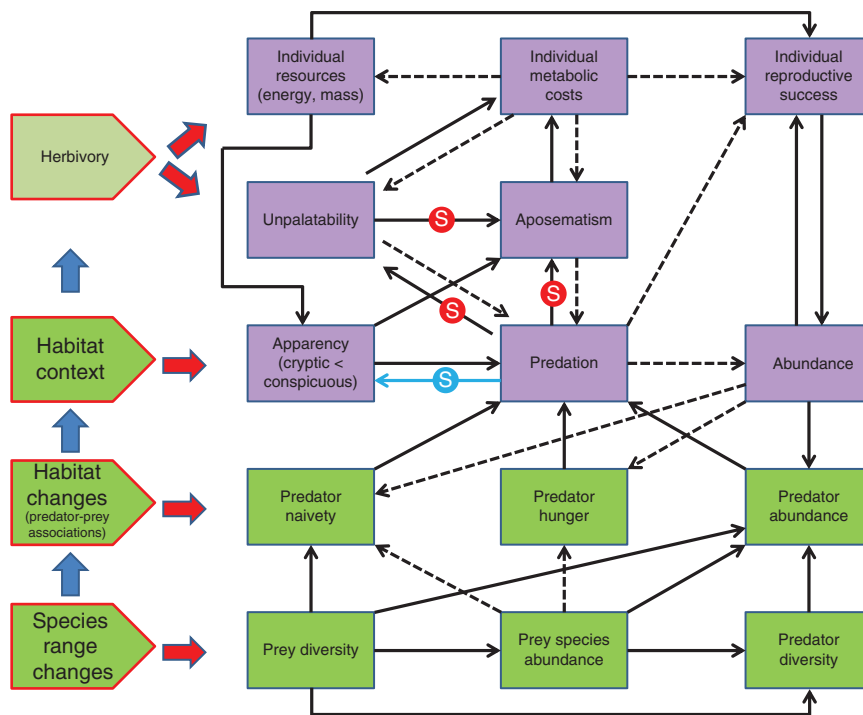


Fig. S19. A simple model of some basic links affecting degree of aposematism and unpalatability in butterflies. Any explanation of variation in warning colours and unpalatability of butterflies to predators must necessarily separate warning coloration and distastefulness. The basic problem facing biologists is to determine the relative timing of their evolution and how these two components of defence evolved (S in red circle) and were integrated in organisms. Any explanation must consider a multivariate context of predator and prey species in an ever-changing context of habitat components (resources, structures) and species. The alternative route towards greater crypsis (blue arrow; S in blue circle) is not followed in this model. S, selection; broad red arrows, basic inputs; broad blue arrows, link between input factors; black links: continuous, positive associations; pecked, negative associations.

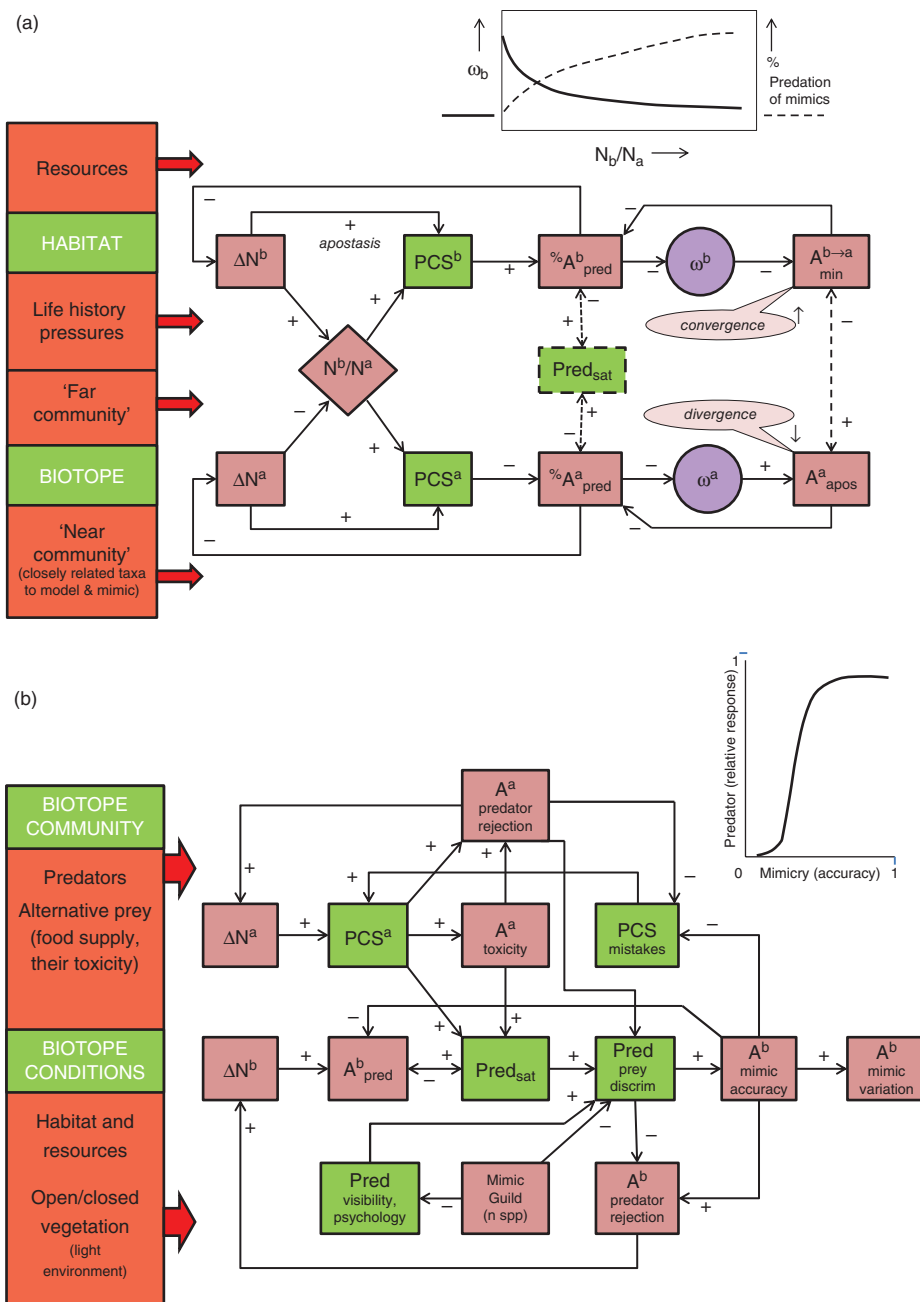


Fig. S20. Further influences of Batesian and Müllerian mimicry. **(a)** Basic absolute and relative population influences on development and maintenance of Batesian mimicry, leading to convergence of mimic on model and divergence of model away from mimic phenotype. A large number of biotope/habitat factors influence the numbers and behaviour of model, mimic and key predator(s). Inset: graph relating fitness of mimic and predation rate to number of mimics (fixed number of model and predator) modified from Turner (1978). **(b)** Some immediate controls of degree of mimicry (accuracy, variability) triggered by changing numbers of model and mimic influenced by site environmental influences and community. The motivation of predators to distinguish mimics from models depends on predator hunger, which will depend on prey abundance, alternative prey, degree of unpalatability (Carpenter and Ford, 1933). Inset graph shows

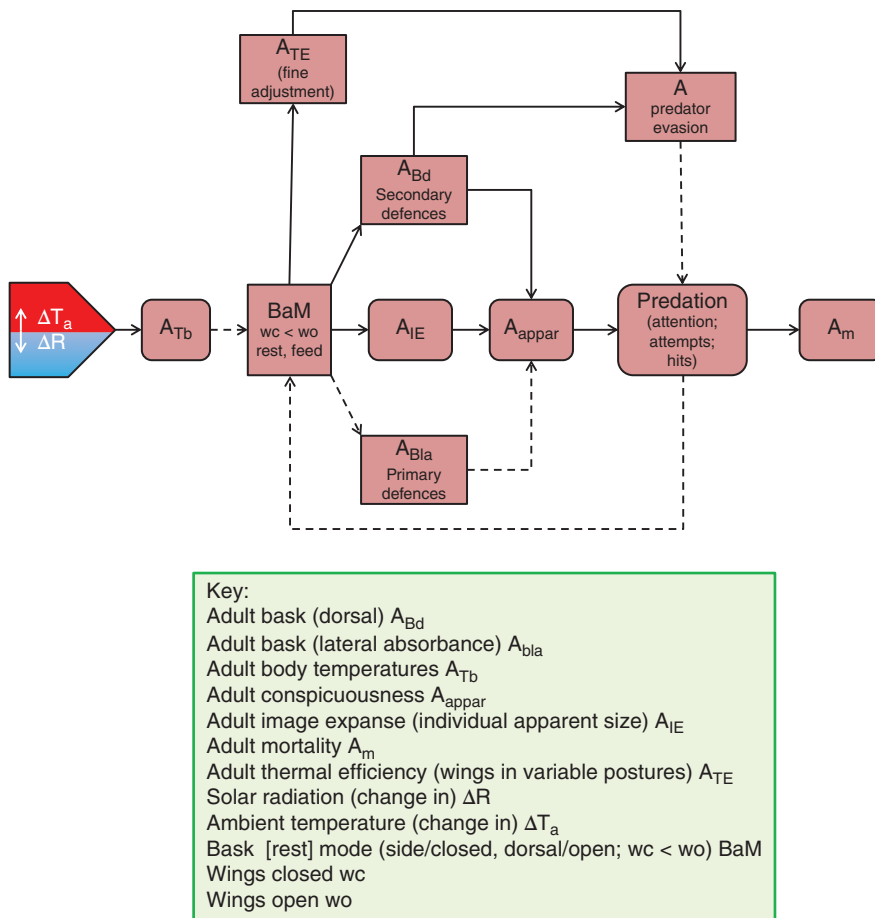


Fig. S21. Some of the prime factors in behavioural shifts affecting single individuals between dorsal and lateral basking postures in relation to changing abiotic conditions, particularly ambient temperature (ΔT_a) and radiation (ΔR). Dorsal basking, on reduced T_a or R , increases conspicuousness to predators as well as mates, increasing the likelihood of predator strikes and encouraging adoption of lateral postures which conceal dorsal displays and reduce the image exposed to predators. However, dorsal displays engage secondary defences, and also provide finer tuning of postures to regulate optimum thoracic temperatures, ensuring better responses to predator attacks. When ambient radiation/temperature is too high, or even too low, then a closed-wing posture may provide better means for static resource exploitation (resting; roosting) than an open-winged posture.

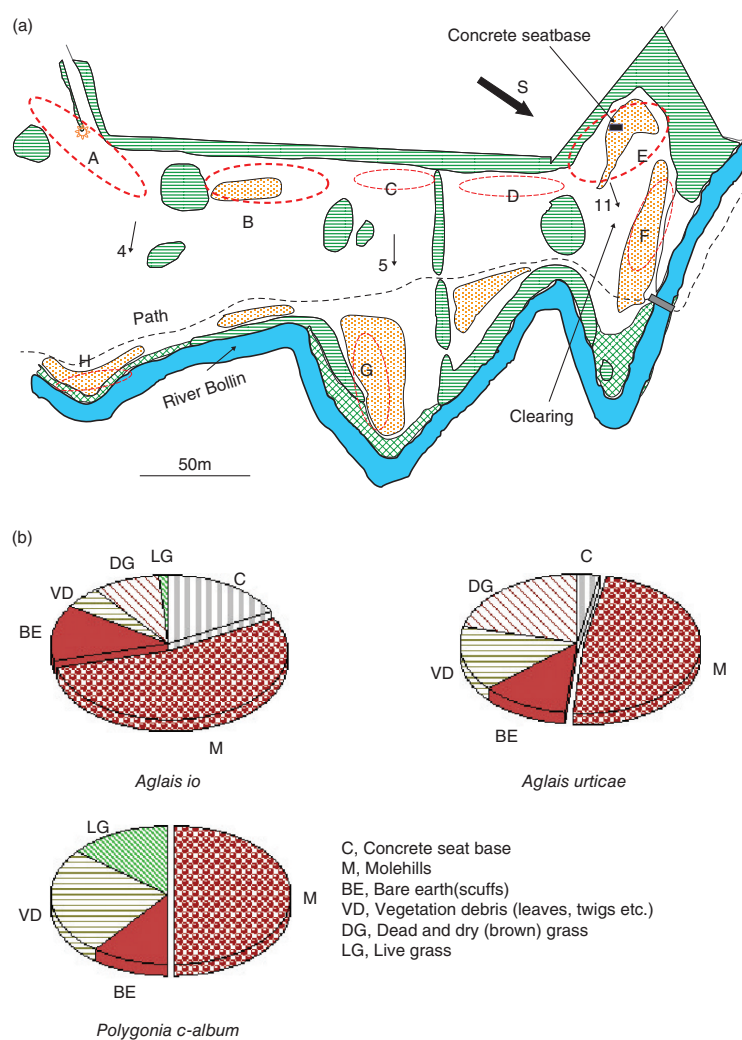


Fig. S22. Thermal adjustments to hierarchical exploitation of mate-location resources at different spatial scales by nettle-feeding nymphalids on the Carrs, Wilmslow, Cheshire, UK. **(a)** The Carrs, Wilmslow, Cheshire study site (340 m x 110 m) comprises a south-west-facing slope above the river Bollin, bounded by the river's north bank at the foot of the slope and by a narrow woodland separating the Carrs from housing at the top of the slope. In 2004/2005, molehills were concentrated in seven zones: two at the top of the slope (2004: 127 molehills) and five at the base of it (835 molehills); molehill zone E includes a concrete rectangle (116 x 167 cm), which is a disused seat base, 5 m from the top of the slope and cut horizontally into it. The mean diameter of molehills in 2004 was 50.1 ± 1.3 cm with total area 193.7 m², occupying 1.54% of the study area. The main nymphalid territories were concentrated at the two zones of molehills (B, E) and on a hollow (> 50 cm deep) located on the apex of a bank, the previous site of a tree trunk, at an abrupt reflex angle in the wood edge. Molehill field attributes studied included size, shape, surrounding shelter, location across and up slope, and isolation from other molehills weighted by their size. **(b)** Pie graphs of surfaces used by the three nymphalid butterflies on the Carrs; bare sites dominate despite covering a small area of the parkland (grassland) biotope. **(c)** A plot of the molehills in territory E illustrating the shift in territories with winds from the north and south. Bold pecked line is the break of slope with the arrows indicating direction of slope. The finer pecked lines give the median number of territories (standardised) for different wind directions. The symbols illustrate molehills in three size categories (white, smaller than lower quartile; grey, between lower and upper quartile; black, larger than upper quartile). CSB and triangular object to right are the concrete seat base and remains. Scale in metres. **(d)** A multiple correspondence analysis plot describing simultaneous associations between behaviour,

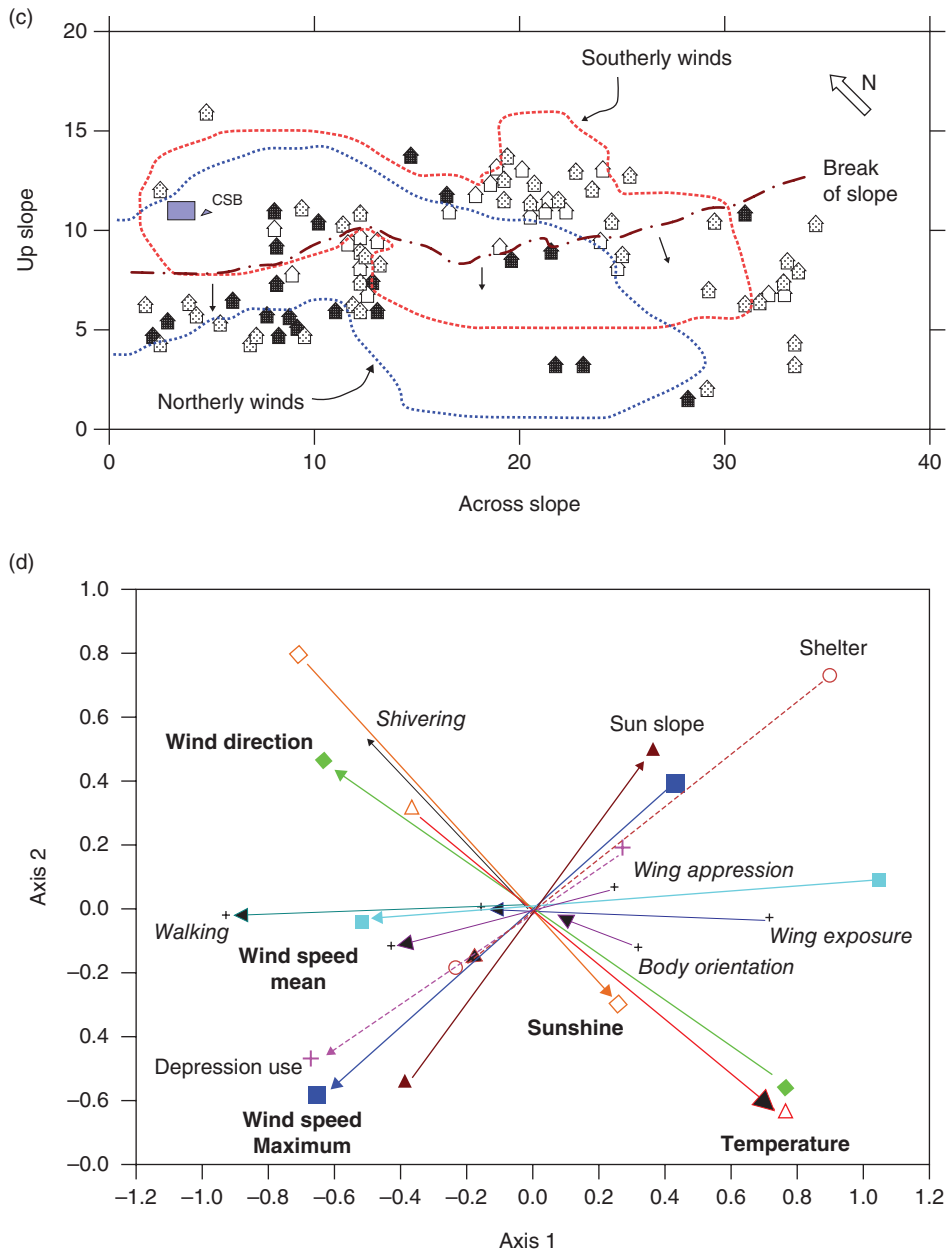


Fig. S22. Continued.

micro-feature use and weather conditions for individual observations on the molehills at territory E. Variables are simplified into binary states (insolation: 0 cloudy, 1 sunny; temperatures: 1 < 16.0°C, 2 > 16.0°C; mean wind speed: 1 < 3 m sec⁻¹, 2 > 3 m sec⁻¹; maximum wind speed: 1 < 6 m sec⁻¹, 2 > 6 m sec⁻¹; wind direction: 1 < 270°, 2 > 270°). Behavioural variables (open-wing exposure, body orientation to sun, appression of wings to substrates, shivering, walking; binary coded as present or absent) were entered as supplementary to analysis. Variance of axes = 46%. Of 20 possible associations, 13 are significant ($P < 0.05$). With lower temperatures, cloud, stronger winds and more northerly winds, there is an increase in the use of sheltered fringes of molehills, depressions on the surface, as well as shivering, wing appression and walking to sheltered micro-sites. With increasing sunshine there is greater use of exposed sun-facing slopes on the molehills. (Figures from Dennis and Sparks, 2005.)

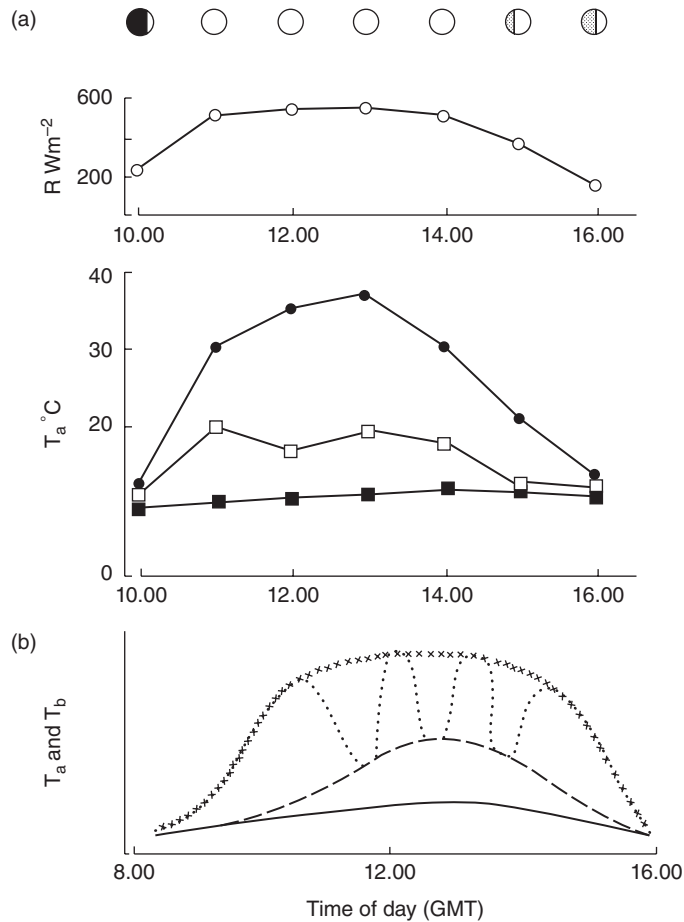


Fig. S23. Further features of thermoregulation in gregarious *Euphydryas aurinia* (Nymphalidae) larvae. **(a)** The relationship between 4th instar larval cluster temperature and the environmental temperatures during the course of a sunny day. Black square, air temperature at 15°C; white square, surface temperature of host plant; small black circle, larval cluster temperature; small white circle, solar radiation intensity. The cloud cover is indicated as absent (large white circle), hazy (large grey circle) or overcast (large black circle). **(b)** A diagrammatic representation of the feeding strategy of 4th instar larvae through a clear day in which solar radiation reaches a peak at midday. (. . . individual larval T_b , x x x basking cluster T_b , — T_a at 15cm, - - - T_a at vegetation level) (From Dennis, 1993a; from original research by Porter, 1982 and courtesy of Dr Keith Porter; see Konvicka *et al.*, 2003 for conditions linked to optimal web (nest) siting.)

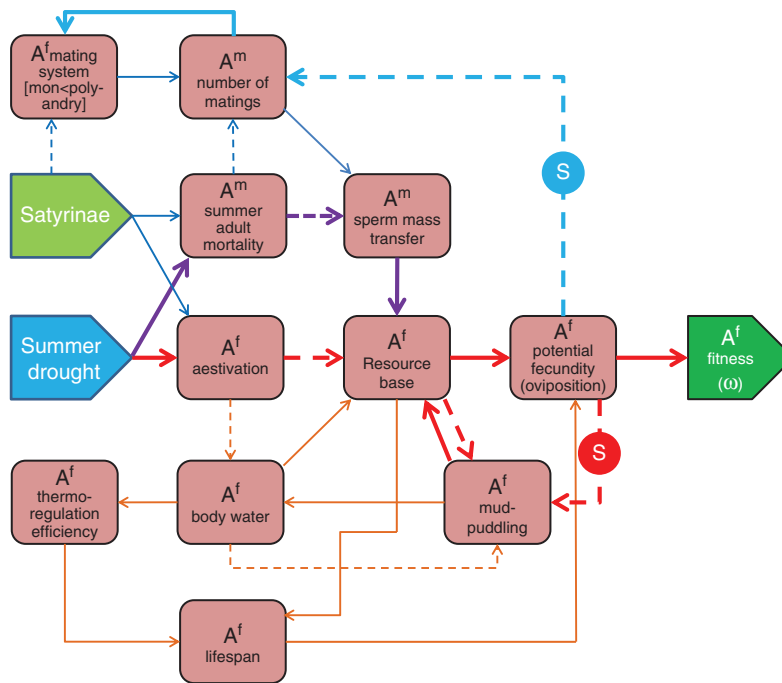
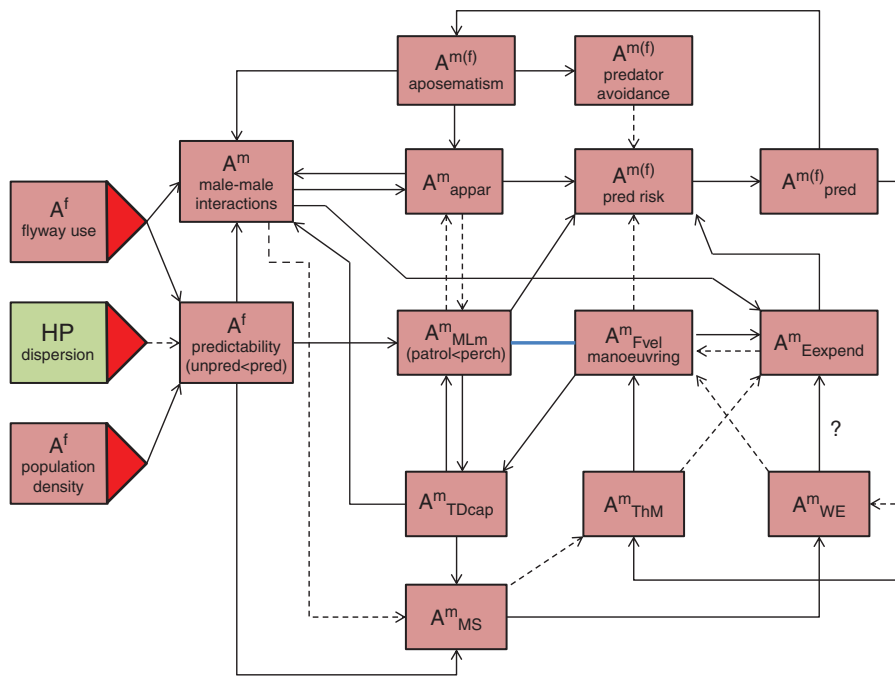


Fig. S24. A model of potential factors leading to female mud-puddling in Cyprus Satyrinae. The key feature is female aestivation and high levels of pre-summer drought mortality in males. Both female aestivation and male losses should lead to depletion in both water and nutrients in females during a time of drought and limited nectar sources. The males pass nutrients over to females in spermatophores, but this source of nutrients may be limited by monandry and smaller spermatophores in males that have already mated. Nutrient and water resources (hydration) are maintained by mud-puddling. The additional nutrients then add to female maintenance (i.e. water by controlling thermoregulation) and egg-laying, which ensures high levels of fecundity and female fitness. Red arrows: mud-puddling links related to aestivation; orange arrows: links with hydration; purple arrows: links associated with male contributions; thin blue arrows are associated with the mating system; thick pale blue arrows indicate a possible evolutionary pathway to polyandry, triggered by the need for additional contributions from males; A, adult; S, potential selection pathway; continuous arrows, positive associations; pecked arrows, negative associations. (From John and Dennis, 2019.)



Key:
 Adult conspicuousness A_{appar}
 Adult energy expenditure $A_{Eexpend}$
 Adult flight velocity (manoeuvring capacity) A_{Fvel}
 Adult mate location mode (male; seek or wait; patrol < perch) A_{MLm}
 Adult mating success A_{MS}
 Adult territorial defence of sites (holding capacity) A_{TDcap}
 Adult predation A_{pred}
 Adult risk of predation $A_{pred\ risk}$
 Adult thorax musculature A_{ThM}
 Adult wing expanse A_{WE}
 Larval host plant distribution (concentration < dispersion) HP dispersion
 m male, f female

Fig. S25. Behaviour–morphology links between mate location behaviour (perch versus patrol) and defence (crypsis and aposematism). Wiklund (2003) has suggested a link between perching and crypsis, and patrolling and aposematism, with butterfly morphology; perching species tend to have short broad bodies with larger thoracic muscles, shorter wings with smaller wing areas; patrolling species tend to have longer thinner bodies with less muscle development and longer, more expansive wings. Aposematic species do not need fast flight and their individual conspicuousness to conspecific and enemy alike ensures longer-distance mate recognition. Cryptic palatable species are compromised by flight in alerting predator attention and thus require wings for faster flight and better manoeuvrability. But this distinction is likely to be incomplete, as shown by this model; the relationship is likely to be imperfect inasmuch as – owing to population density, resource disposition and habitat structure – many male aposematic species will still be inclined to wait for females at suitable vantage points and there compete with conspecifics for female attention. Therefore, aposematic perching species must be expected to develop larger thoracic muscles for competition with conspecifics. Cryptic perching species should still show further morphological distinction, as they are under two pressures for flight: competition for mates and predation. Energy expenditure leads on to related morphological links in relation to nectar feeding. Continuous lines, positive relationship; pecked lines, negative relationship; blue line, correlation without causal direction.

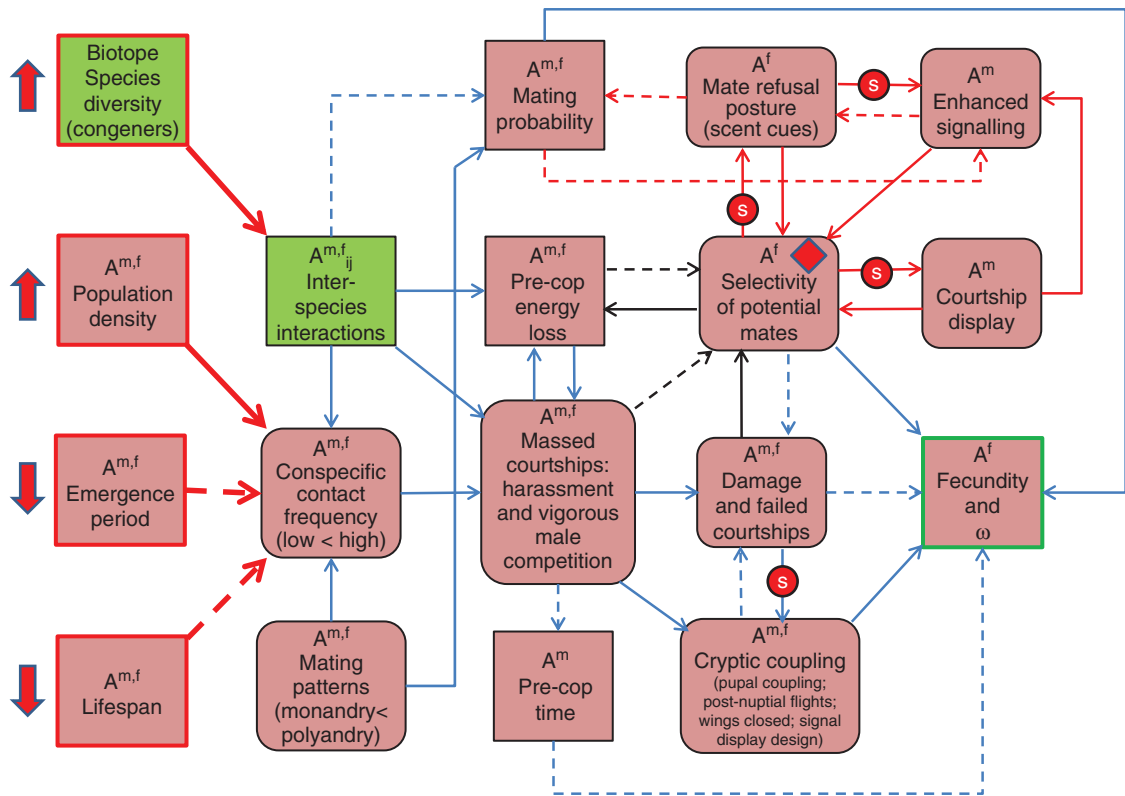


Fig. S26. Some potentially conflicting factors underlying the degree of elaboration of courtships. At the intra-species level, factors that impinge on fecundity and survival (especially high population density, short emergence periods and lifespans) are likely to encourage rapid 'pre-nuptial' courtships; this may lead to cryptic signalling or evolution of signal display design in which signals are maximised to mates but simultaneously minimised to competitors and predators (see White *et al.*, 2015). When selectivity by females and male–male competition increases, so too will elaboration of courtship routines. In rich biotopes with high species diversity, the occurrence of closely related sympatric and synchronous species will tend to induce greater elaboration of routines. Thin red arrows indicate zone of positive feedback leading to increased elaboration of signalling by both sexes, centred on female selectivity (red diamond). S in red circle, selection for trait which may allow escape for paired victims of courtship harassment; links: continuous, positive associations; pecked, negative associations; black lines, uncertain outcome and need of investigation. Broad blue-outlined red arrows indicate forcing trends (increase (up) and decrease (down) of) for scramble polygyny; A, adult; m, male; f, female; ω , fitness of both sexes of a courting pair.

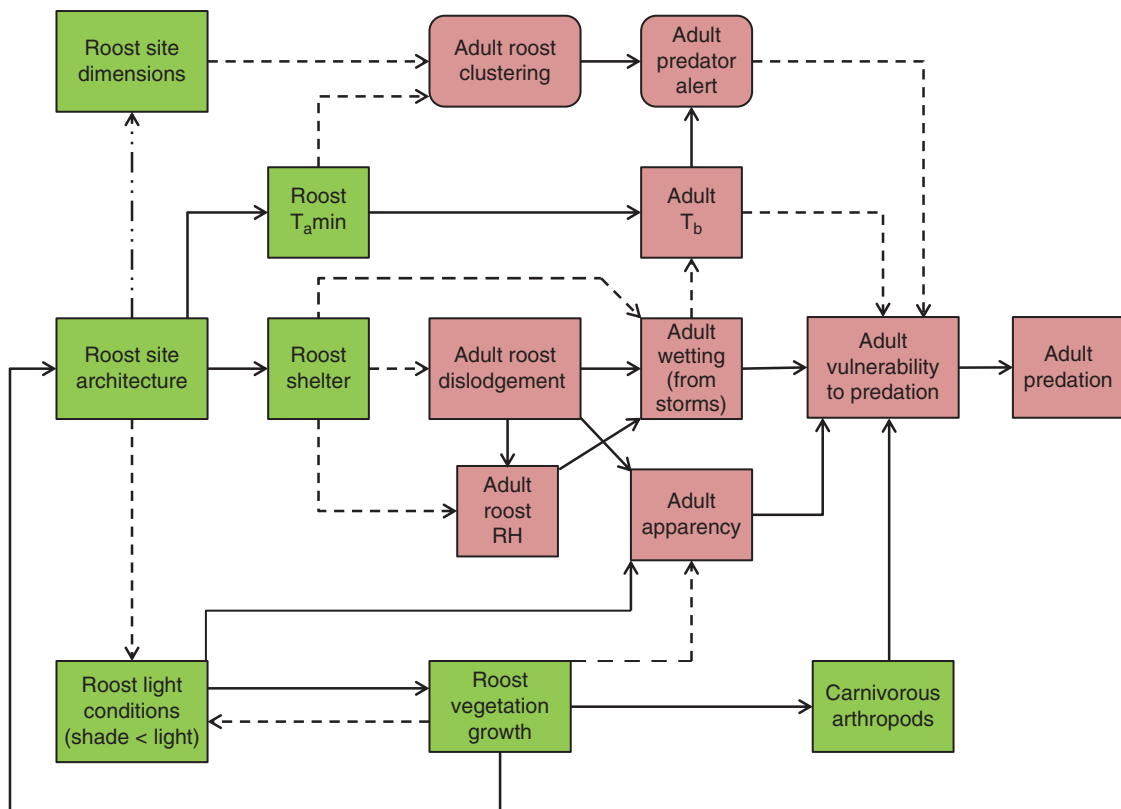


Fig. S27. Some environmental consequences of *Heliconius* roost site architecture (Mallet, 1986; Salcedo, 2010a). Sites selected for roosting are dry, shaded and sheltered affecting local climate, predators and conspicuousness to predators; see book text for description of roost architecture. Links: continuous, positive associations; pecked, negative associations; dash/two dots, negative or positive. RH, relative humidity; $T_{a\min}$, minimum ambient temperature, T_b , body temperature.

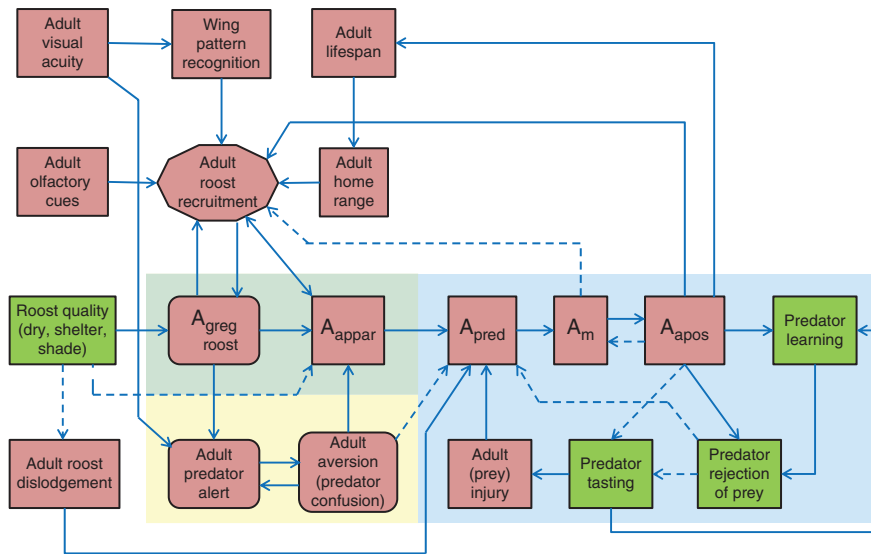
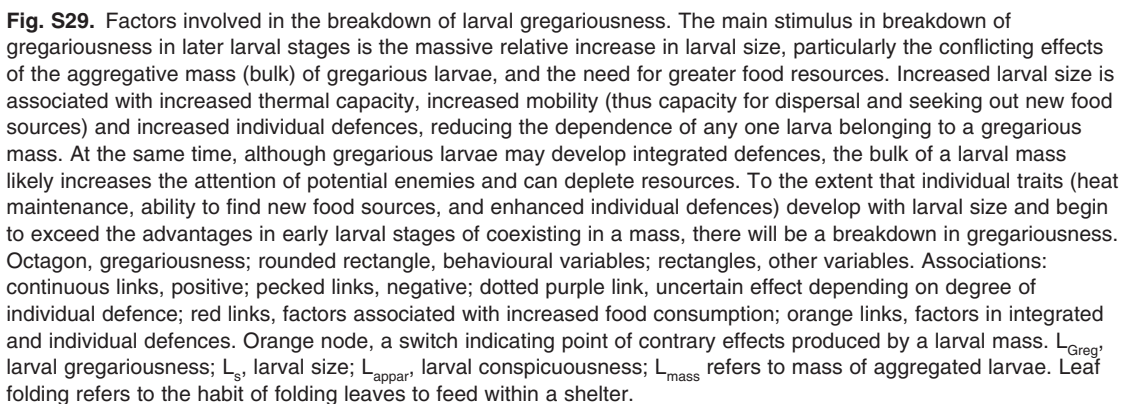


Fig. S28. Factors leading to integration of the prey dilution effect and collective aposematism as anti-predator defences in communal roosting (see Finkbeiner *et al.*, 2012, Finkbeiner, 2014). Yellow zone, prey dilution effect; blue, collective aposematism; green overlap zone, both mechanisms operating. For detailed effects of roost quality, see Fig. S27. Links: continuous, positive associations; pecked, negative associations. A_{apos} , adult aposematism; A_{appar} , adult conspicuousness; $A_{\text{greg roost}}$, adult gregarious (communal) roosting; A_{m} , adult mortality; A_{pred} , adults (predation of).



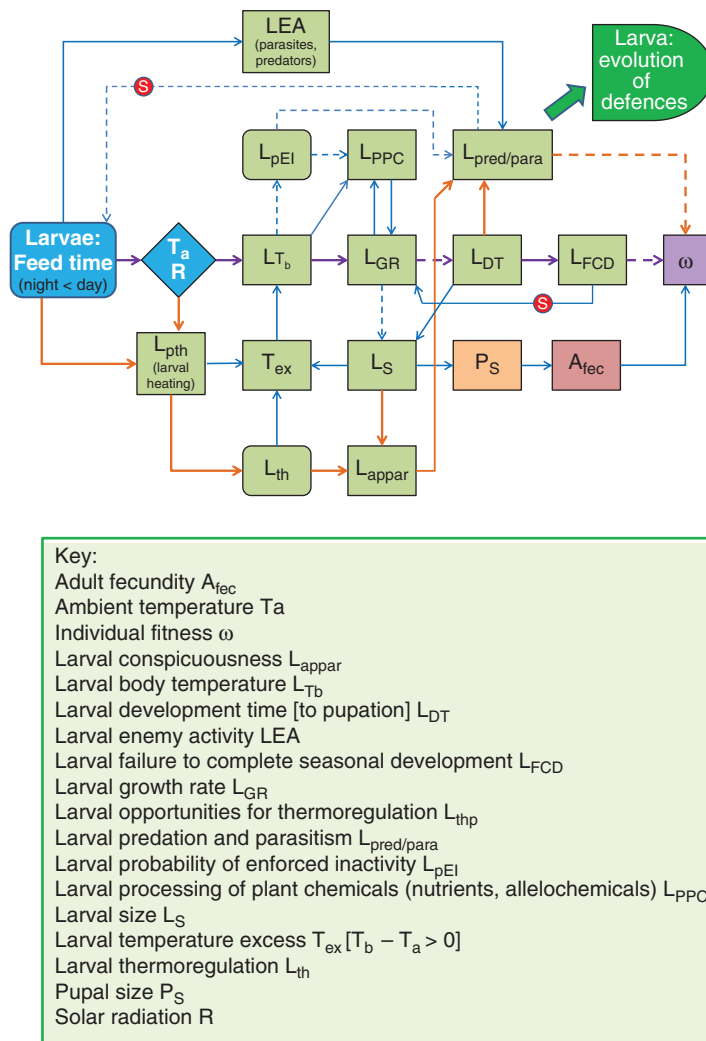
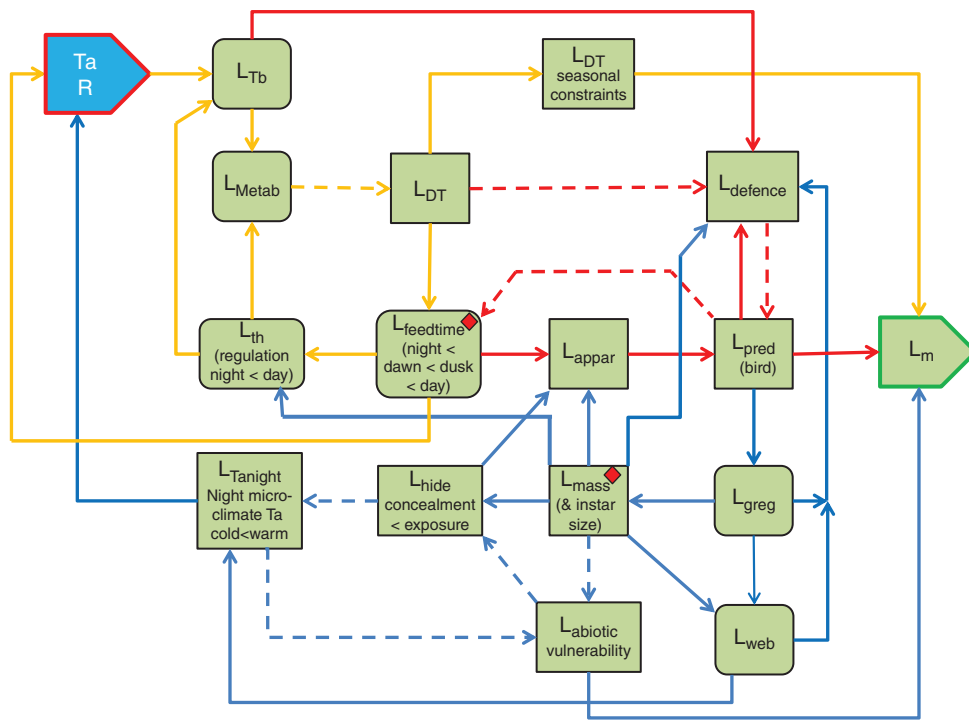


Fig. S30. Key impacts of night-time and daytime larval feeding on aspects of individual fitness in high-latitude or high-altitude butterflies. The main impact is via body temperatures which, with night feeding, can only mirror ambient temperatures; but ambient conditions are more likely to be marginal for any kind of activity, feeding included, especially in cooler biomes. With daytime feeding, not only will feeding (feeding rate, ingestion, assimilation, etc.) be enhanced by high ambient temperatures but also with solar radiation there is the opportunity for the evolution of thermoregulatory behaviour, further enhancing body temperatures (T_{ex}). Body temperatures then influence growth rates, development time, completed development size, fecundity (purple links) and predation/parasitisation rates (orange arrows). The crucial feature here is that although daytime feeding ensures higher body temperatures, it also occurs at a time when enemies are most active. Daytime feeders faced with high predation levels have a number of options while feeding: concealment (under-leaf feeding), crypsis, aposematism or switching to a less injurious time of day (night feeding) (see Berger and Gotthard, 2008; Seifert *et al.*, 2016). Associations: continuous links, positive; pecked links, negative; S in red circle, selection for trait.



Key:

Ambient temperature T_a
 Larval vulnerability to abiotic conditions $L_{abiotic\ vulnerability}$
 Larval basking (behavioural thermoregulation) L_{th}
 Larval conspicuousness L_{appar}
 Larval body temperature (regulation; day superior to night) L_{Tb}
 Larval defences (spines, wriggling, chemical emissions, etc.) $L_{defence}$
 Larval development time [to pupation] L_{DT}
 Larval development time [seasonal time constraints] $L_{DT\ seasonal\ constraints}$
 Larval feeding time during daily cycle (day superior to night) $L_{feedtime}$
 Larval gregarious L_{greg}
 Larval hiding (concealment in vegetation) L_{hiding}
 Larval mass (when gregarious or size if single) L_{mass}
 Larval metabolism L_{Metab}
 Larval mortality L_m
 Larval night time microclimate temperatures (night colder than day) $L_{Tanight}$
 Larval predation L_{pred}
 Larval web formation L_{web}
 Radiation R

Fig. S31. Basic factors influencing larval diurnal foraging rhythms in temperate Lepidoptera. Seasonal and ecological issues not entered. Red connections, links with predation; orange connections, links with development constraints; blue connections, other links mainly size and mass of larvae. Associations: continuous links, positive; pecked links, negative. Red diamonds, key starting variables.

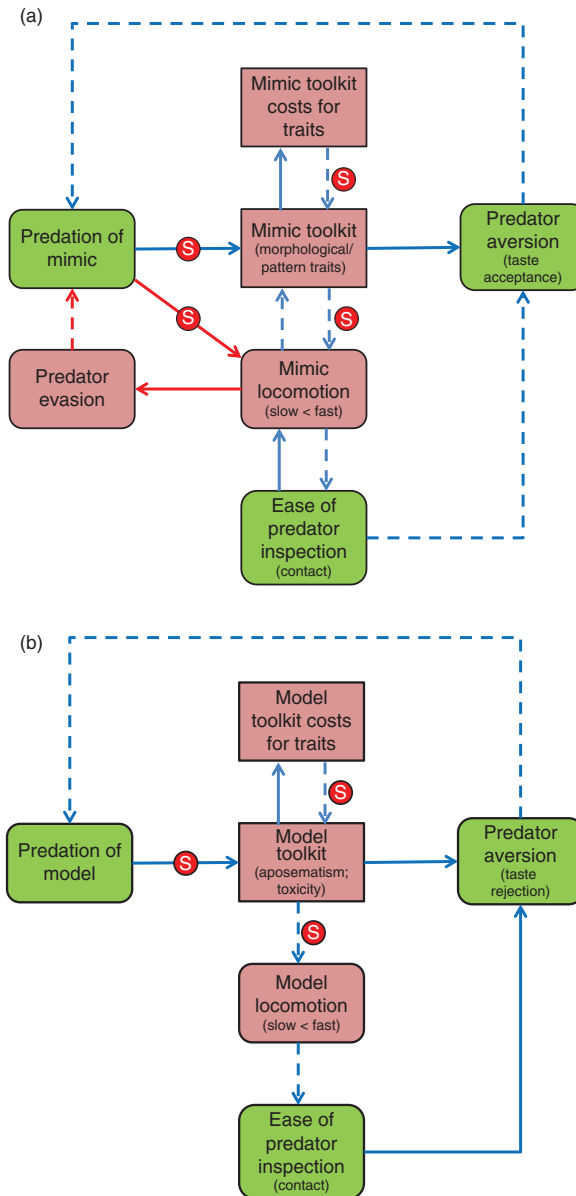


Fig. S32. Contrasts between mimic and model in feedbacks between predation and trait evolution in Batesian mimicry systems. **(a)** Mimic. **(b)** Model. Underlying the basic observation of the mimic converging on the model, in which the model is selected for divergence from the mimic (Sherratt and Beatty, 2003), there is a potential limit to locomotion mimicry in Batesian mimics. Both models and mimics are subject to costs, models for toxicity and mimics for pattern traits. But mimics, by adopting the slow linear flight patterns of models, become increasingly vulnerable to closer inspection by predators and taste 'acceptance'. Thus, although both model and mimic are subject to a negative feedback for pattern and costs of production, the mimic is also subject to negative feedback for speed and manoeuvrability (locomotion) (red links). There is a question of the extent to which the development of wing patterns and locomotion traits in mimics are decoupled. On the other hand, although the model also becomes easier to capture while flying, the slower flight provides a clearer honest signal of toxicity to a predator to reject the model without consequences for limiting slow flight advertisement (Sherratt *et al.*, 2004; Srygley, 2004); continuous links, positive associations; pecked links, negative associations; S in red circle, selection for traits.

Symbols used in supplementary online figures

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
% A_{pred}	Adult predation (percent of prey)	S20
A	Adult	S04, S05, S06, S07, S08, S09, S10, S11, S12, S13, S14, S15, S16, S17, S18, S20, S21, S24, S25, S26, S28
a (superscript)	Model (butterfly species)	S20
$A_{disturb}$	Adult disturbance probability (by predator, parasite etc)	S16
$A_{sperm\ trans}$	Adult sperm transferred (amount pyrene and eupyrene)	S15
A^a_{apos}	Adult aposematism (enhanced warning colouration)	S20
A_{act}	Adult activity	S12, S16
$A_{activity}$	Adult activity	S20
A_{age}	Adult age	S06, S08, S12, S15
$A_{anti\ aphrod}$	Adult anti-aphrodisiacs transferred	S15
A_{apos}	Adult aposematism	S28
A_{appar}	Adult apparency/conspicuousness	S12, S16, S21, S25, S28
$A_{Apredrisk}$	Adult risk of predation (to avian predators)	S16, S18
$A_{asperm\ stored}$	Adult apyrene sperm stored in bursa	S15
A_{Bd}	Adult bask (dorsal)	S16, S21
A_{bla}	Adult bask (lateral absorbance)	S21
$A^b_{mimic\ accuracy}$	Adult accuracy (degree) of mimicry	S20
$A^b_{mimic\ variation}$	Adult variation in mimicry	S20
$A^b_{predator\ rejection}$	Predator rejection of adult mimics	S20
$A_{capsule}$	Adult capsule (thick spermatophore epidermis) production	S15
A_{chemd}	Adults, chemical defence/aposematism	S12
A_{compet}	Adult competition for mates	S15
$A_{conspic\ advr}$	Adult conspicuous advertisement	S20
$A_{Cop\ dur}$	Adult copulation duration (single event)	S16
$A_{cop\ time}$	Adult copulation time	S15
A_{CR}	Adult capital resources	S06
A_{CrawlT}	Adults crawling up trees	S12
A_{dgens}	Adult discrete generations	S09
A_{drink}	Adult drinking (water intake)	S12
AE^E_t	Egg aestivation time	S05
$A_{Eexpend}$	Adult energy expenditure	S16, S18, S25
$A_{egg\ resorb}$	Adult egg resorbance	S15
$A_{ejac\ mass}$	Adult male ejaculate mass (spermatophore size)	S15
A_{EL}	Adult eggs laid (total)	S15
$A_{Egg\ shortfall}$	Adult egg shortfall	S16
$A_{ET\ spring}$	Adult emergence time (spring)	S11
A_{EWT}	Adult egg weight (mean)	S15

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
$A_{n}^{f,m}$	Adult numbers (female, male)	S14
$A_{S}^{f,m}$	Adult (female, male) size	S08, S14, S15
$A_{f:m}^{f,m}$	Adults female to male ratio (1:x)	S12
A_{fec}	Adult fecundity (potential)	S11, S12, S14, S16, S30
A_{fecr}	Adult fecundity (realised)	S13
A_{fert}	Adult fertility	S15
A_{FLP}	Adult flight performance (inefficient < efficient)	S16, S18
A_{FMR}	Adult flight muscle ratio (ratio of flight muscle mass to total body mass)	S16, S18
A_{Fvel}	Adult flight velocity (manoeuvring capacity)	S25
$A_{G\ predrisk}$	Adult risk of predation (to ground based predators)	S16
$A_{greg\ roost}$	Adult gregarious (communal) roosting	S28
A_{ground}	Adults grounded	S12
$A_{habitat\ light\ environ}$	Adult habitat light environment	S20
A_{harass}	Adult harassment (by conspecifics)	S16
A_{harinj}	Adult harassment and injury	S15
A_{hiding}	Adult concealment	S16
$A_{host\ seek}$	Adult searching for resources	S18
A_{IE}	Adult image expanse (individual apparent size)	S21
$A_{in\ cop}$	Adults copulating	S16
A_{IR}	Adult income resources	S06
A_{lipids}	Adult lipid levels	S12
A_{LS}	Adult lifespan	S06, S15, S16, S18
A_m	Adult mortality	S12, S21, S28
$A_{MassBal}$	Adult mass balance (imbalance < balanced flight)	S16
A_{masses}	Adult masses or clusters	S12
$A_{mate\ events}$	Adult mate events (male polygyny; female polyandry)	S15
$A_{mate\ solic}$	Adult mate solicitation	S15
$A_{mate\ stat}$	Adult mating status (with: male virgins < non-virgin males)	S15
$A_{mate\ success}$	Adult mating success	S20
A_{mating}	Adult mating	S12
A_{mel}	Adult melanism	S04
A_{MF}	Adult mating frequency	S09, S16
A_{MGT}	Adult mate 'guarding' time	S16
A_{migr}	Adult migration	S10
A_{mim}	Adult mimicry	S20
A_{MLm}	Adult mate location mode (male; seek or wait; patrol < perch)	S25
$A_{mobility}$	Adult mobility	S18
A_{MR}	Adult mating resources	S06
A_{MS}	Adult mating success	S09, S25
A_{MSE}	Adults, mass confusion & startle effect	S12
A_{NE}	Adult nectar feeding	S10, S12, S15, S16, S18
$A_{Ntincop}$	Adult night in copula	S16
$A_{nuptgifts}$	Adult nuptial transfers (gifts)	S16
A_{OI}	Adult ovigeny index	S06, S18
$A_{oproduct}$	Adult oöcyte production/fertilisation	S09
A_{OR}	Adult oviposition rate	S06
$A_{ovipos\ n}$	Adult egg laying events	S18
$A_{oviptime}$	Adult oviposition time (time available for egg laying)	S16
$A_{phys\ lifespan}$	Adult physiological lifespan	S20

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
A_{pmt}	Adult pre-mating time	S09
A_{pred}	Adults, predation of	S12, S16, S18, S25, S28
$A_{pred\ risk}$	Adult predation risk	S15, S25
A_{predr}	Adults, as predation resources	S12
$A_{predvigil}$	Adult vigilance to predators	S16
A_{prot}	Adult protandry	S09, S14
A_{protoz}	Adults, protozoan infections	S12
$A_{refract\ period}$	Adult refractory period	S15
$A_{reproductive\ success}$	Adult reproductive success	S20
A_{rest}	Adult rest (stationary either feeding, resting, inert)	S18
A_{retmig}	Adults, return migration	S12
A_{RI}	Adult reproductive investment (male spermatophores and female fecundity and egg size)	S08
$A_{Rsuccess}$	Adult reproductive success	S16, S18
A_S	Adult size	S05, S06, S07, S09, S11
$A_S\ (WE)$	Adult size (wing expanse)	S20
A_{semelp}	(Adult) semelparity	S18
A_{SET}	Adult stress experience total	S06
$A_{SI:RI}$	Adult soma investment relative to reproductive investment	S18
A_{signa}	Adult signa development	S15
$A_{sperm\ replen}$	Adult sperm replenishment	S15
$A_{sphrag\ trans}$	Adult sphragis transfer	S15
A_{Ss}	Adult size variation	S09
$A_{TaFthres}$	Adult ambient temperature threshold for flight	S16
A_{Tb}	Adult body temperature	S11, S21
A_{TDcap}	Adult territorial defence of sites (holding capacity)	S25
A_{TE}	Adult thermal efficiency (wings in variable postures)	S21
A_{TFO}	Adult tree fall out (drop from masses)	S12
A_{ThM}	Adult thorax musculature	S25
$A_{totmate\ time}$	Adult total mating time	S15
A_{TR}	Adult resources (total, thorax, abdomen)	S06, S15
A_{TTD}	Adults tree trunk disposition	S12
A_{VTMD}	Adult vertical tree mass disposition	S12
A_{WE}	Adult wing expanse	S12, S25
A_{WL}	Adult wing loading	S12
A_{WT}	Adult weight or mass	S13, S16, S18
$A_{WT(wet)}$	Adult weight (wet weight)	S12
$b\ (superscript)$	Mimic (butterfly species)	S20
BaM	Bask [rest] mode (side/closed, dorsal/open; $wc < wo$)	S21
BE	Bare earth (scuffs)	S22
BR	Birth rate	S10
C	Concrete seat base	S22
CSB	Concrete seat base and remains	S22
DG	Dead and dry (brown) grass	S22
$DP^{iii,p}$	Diapause stage (3rd instar, pupal)	S11
Dp_{stage}	Diapause stage/phase attainment	S07
DR	Death rate	S10
$E\ and\ E$	Egg	S02, S05, S06, S07, S09
E_{CL}	Environmental critical period length	S10
E_{PS}	Environmental period of critical severity	S10
E_{DT}	Egg development time	S05, S06
E_{L+W}	Egg lipid and water	S06

Continued

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
E_m	Egg mortality	S05, S06
E_N	Egg number	S05, S06, S07, S09
E_{P+E}	Egg protein and energy	S06
E_R	Egg resources	S05, S06
E_S	Egg size	S05, S06, S07, S09
E_S/A_S	Negative allometry of egg size on adult size ($b < 1$)	S06
E_{Smod}	Egg structural modifications (for resource retention and resistance to ambient conditions)	S05
f (superscript)	Female	S04, S06, S08, S09, S11, S13, S14, S15, S16, S17, S19, S20, S24, S26
FAR	Flight activity range	S11
G/E interaction	Genotype/environmental interactions	S03
Hab cond	Habitat conditions	S10
H_t^E	Egg hibernation time	S05
HP	Host plant	S06, S07, S08, S10, S13, S18, S25, S29
HP _{avail}	Host plant availability	S10
HP _{dispersion}	Larval host plant distribution (concentration < dispersion)	S25
HP _{pal}	Host plant palatability	S13
HP _{QL}	Host plant quality	S06, S07, S08, S18
HP _{QN}	Host plant quantity	S07, S08, S18
HP _{spp}	Host plant species	S07, S08
HS ^I	Hibernation stage (larva)	S07
i [focal individual], j k	In subscripts refer to different individuals	S14
I_{Adac}	Individual adaptations to abiotic conditions	S10
I_{Adfr}	Individual adaptations to maintain food reserves	S10
I_{Adprd}	Individual adaptations versus predation	S10
I_{autox}	Individual autotoxicity costs	S13
I_{DP}	Individual diapause	S10
I_{DT}	Individual development time	S14
I_{Dvc}	Individual continuous development	S10
I_{Eu}	Individual energy use (cf., with continuous development)	S10
I_{FR}	Individual food reserves (somatic maintenance)	S10
$I_{FR \text{ pre-emptive}}$	Individual pre-emptive food reserve build up	S10
I_m	Individual mortality	S13
I_{Mat}	Individual maturation (behaviour, life history and morphology)	S10
I_{MR}	Individual mating reserves	S10
$I_{pred/para}$	Individual predation/parasitisation (female, male)	S14
I_{RS}	Individual reproductive success	S10
I_S	Individual size	S13
L and L	Larva (larvae, larval)	S02, S06, S07, S08, S09, S10, S11, S12, S13, S14, S18, S29, S30, S31
$L_{abiotic \text{ vulnerability}}$	Larval vulnerability to abiotic conditions	S31
L_{ACT}	Larval activity	S08
L_{AD}	Larval approximate digestibility of food = $(LIG - LFrass) / (LIG * 100)$	S08
L_{apos}	Larval aposematism (linked to chemical defence)	S07, S13

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
L_{appar}	Larval conspicuousness/apparency	S07, S08, S13, S29, S30, S31
L_{BFI}	Larval behaviour to improve access to food quality intake	S08
L_{BG}	Larval biomass gained	S07, S08
L_{BPA}	Larval behavioural adjustments for avoiding predators (night feeding, concealed feeding)	S08
L_{chdef}	Larval chemical defence	S13
L_{compet}	Larval competition (intra group)	S13
L_{cryp}	Larval crypsis (matching of environmental object)	S07
L_{d}	Larval density	S08, S12, S13, S18
L_{defence}	Larval defences (spines, wriggling, chemical emissions, aposematism, threat, etc.)	S18, S31
L_{desic}	Larval desiccation	S13
L_{DT}	Larval development time [to pupation]	S06, S07, S08, S09, S13, S18, S30, S31
$L_{\text{DT seasonal constraints}}$	Larval development time [seasonal time constraints]	S31
$L_{\text{DT total}}$	Larval development time (total instars)	S11
$L_{\text{DT,DP}}$	Larval development time to diapause	S07
LEA	Larval enemy activity	S30
$L_{\text{ECD}} = (L_{\text{BG}}/L_{\text{IG}} - L_{\text{Frass}}) * 100$	Larval efficiency of conversion of digested food	S08
L_{exp}	Larval exposure to predators	S08, S13
L_{FCD}	Larval failure to complete seasonal development	S30
L_{feed}	Larval feeding (herbivory)	S10, S12
L_{feedef}	Larval feeding efficiency	S13
$L_{\text{feedt}}/L_{\text{feedtime}}$	Larval feeding time during daily cycle (day superior to night)	S07, S31
L_{fortrl}	Larval foraging trails (distances travelled)	S13
L_{Frass}	Larval frass production	S08
LG	Live grass	S22
L_{GR}	Larval growth rate	S07, S08, S09, S13, S14, S18, S30,
L_{Grg}	Larval aggregation and gregariousness	S07, S13, S29, S31
LGS	Length of growing season	S07, S08
L_{FC}^h	Larval (hatchling) feeding capacity	S06
L_{HCS}^h	Larval (hatchling) head capsule size	S06
L_{hide}^h	Larval hiding/concealment	S07, S31
L_{m}^h	Larval (hatchling) mortality	S06
L_{N}^h	Larval (hatchling) number	S06
L_{S}^h	Larval (hatchling) size	S06
L_{starve}^h	Larval (hatchling) starvation	S06
L_{IG}	Larval ingested food	S08
$L_{\text{iii,iv}}^{\text{DT autumn}}$	Larval development time (3rd/4th instar) during autumn	S11
$L_{\text{iii-v}}^{\text{freeze avoid}}$	Larval freeze avoidance (cryoprotectants)	S11
L_{imdef}	Larval immune defences	S13
L_{infect}	Larval infections (diseases)	S13
L_{IVpred}	Larval predation (by invertebrates)	S08
L_{m}	Larval mortality	S07, S08, S13, S18, S31
$L_{\text{m autumn frost}}$	Larval mortality (from autumn frost)	S11
L_{mass}	Larval mass (when gregarious or size if single)	S29, S31
L_{Metab}	Larval metabolism (assimilated food metabolised)	S08, S31
L_{mltdef}	Larval multiple defence arsenal	S13
L_{nHPs}	Larval novel food supply (new host plant source)	S13

Continued

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
L_{nutstr}	Larval nutritional stress	S08
L_{obsc}	Larval concealment (hidden from view)	S13
L_{palat}	Larval palatability	S13
L_{para}	Larval parasitism	S08, S13
L_{pbdef}	Larval physical and behavioural defences	S13
L_{PDE}	Larval predator dilution effect	S13
L_{pEI}	Larval probability of enforced inactivity	S30
L_{PPC}	Larval processing of plant chemicals (nutrients, allelochemicals)	S30
L_{pred}	Larval predation	S13, S31
L_{pred}/L_{para}	Larval parasitism and predation	S18
$L_{pred/para}$	Larval predation and parasitism	S30
L_R	Larval resources (nitrogen and water)	S08, S13
L_{Ravail}	Larval resource availability	S07
L_{RCR}	Larval relative consumption rate (mgfood/mgbiomass/day; LIG.d-1)	S08
L_S	Larval size	S07, S08, S09, S13, S29, S30
L_{spines}	Larval spines/dense hairs	S07
L_{starve}	Larval starvation	S07
L_{STI}	Larval susceptibility to infections	S08
L_{Tnight}	Larval night time microclimate temperatures (night colder than day)	S31
L_{Tb}	Larval body temperature (regulation; day superior to night)	S30, S31
L_{th}	Larval basking (behavioural thermoregulation)	S30, S31
L_{thp}	Larval opportunities for thermoregulation	S30
L_{TRBeh}	Larval thermoregulation behaviour	S13
L_{vpred}	Larval predation (by vertebrates)	S08
L_W	Larval mass (weight)	S18
L_{web}	Larval web formation	S07, S13, S31
M	Adult mate location	S02
M	Molehills	S22
m (superscript)	Male	S04, S09, S12, S14, S15, S16, S17, S20, S24, S25, S26
mc	Migratory culling of infected individuals	S12
me	Migratory escape from infections	S12
$MigD$	Migration distance (adults)	S12
$mim\ phen$	Mimic phenotype	S20
$Mimic\ Guild\ ({}_n\ spp)$	Guild of mimicking species	S20
N	Adult nectar	S02
N	Numbers (changes in population size DN; + positive; - negative)	S20
NS	Natural selection	S04
P and P	Pupa (pupal)	S02, S09, S30
PAL	Predator avoidance learning	S13
PCS	Predator contact sampling	S20
P_{DT}	Pupal development time	S09
PH	Photoperiod (photophase)	S08, S11
PH^D	Photoperiod changes (decreases, increases)	S08
pm	Post meridian (afternoon)	S17
Ppt	Precipitation	S05
$Pred$	Predation	S11
$Pred_{visibility, psychology}$	Predator visibility and psychology	S20

SYMBOL	DEFINITION	SUPPLEMENTARY FIGURES IN WHICH THEY APPEAR
Pred _{prey discrim}	Predator discrimination of prey	S20
Pred _{sat}	Predator satiation	S20
Pred _{sp}	Predatory species (number of)	S12
P _s	Pupal size	S30
PSI	Predator search image	S20
R	Adult roosting	S02
r	Intrinsic rate of population increase	S11, S12, S13
R	Radiation	S31
R	Solar radiation	S07, S08, S30
RGD	Rate (fast>slow) of gonadal development	S12
RH	Relative humidity	S27
RIS	Resource intersection scores	S02
r _y	Annual rate of population increase	S07, S08, S09
S	Synchronisation (switches) with conditions and resources	S10
S in red circle (and sometimes blue circle)	Selection for traits	S19, S24, S26, S30, S32
SS	Sexual selection	S04
T _a	Ambient temperature	S05, S07, S11, S30, S31
T _{bl50}	Temperature (adult, body min critical limit at which 50% die)	S12
T _{bmax}	Temperature (adult, body, max)	S12
T _{bmin}	Temperature (adult, body, min)	S12
T _{alim}	Ambient air temperature (within finite limits)	S06, S08
T _a _{max}	Temperature (ambient, max)	S12
T _a _{min}	Temperature (ambient, min)	S12, S27
T _b	Body temperature	S17, S27
T _b ^l	Temperature (body, larval)	S07
TC _{nsp}	Trophic community (additional predator species)	S13
T _b ^E	Egg body temperature	S05
T _{bl50} ^E	Critical body temperature (eggs) (causing 50% loss)	S05
T _{ex} [T _b - T _a > 0]	Larval temperature excess	S30
T _b ^l	Body temperature (larvae)	S13
V	Voltinism (number of broods a year)	S07, S11
VD	Vegetation debris (leaves, twigs, etc.)	S22
W _b ^a	Water (adult, body)	S12
wc	Wings closed	S21
WET _{sur}	Wetness (surfaces)	S12
W _b ^l	Body water (larvae)	S13
wo	Wings open	S21
WS	Wind speed	S03, S12
ΔR	Solar radiation (change in)	S21
ΔT _a	Ambient temperature (change in)	S21
ω	Individual fitness	S14, S20, S26, S30

