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Research

Variable colour patterns indicate multidimensional, intraspecific trait variation and ecological generalization in moths

Anders Forsman, Daniela Polic, Johanna Sunde, Per-Eric Betzholtz and Markus Franzén

A. Forsman (<https://orcid.org/0000-0001-9598-7618>) ✉ (anders.forsman@lnu.se), D. Polic, J. Sunde, P.-E. Betzholtz and M. Franzén (<https://orcid.org/0000-0001-8022-5004>), Center for Ecology and Evolution in Microbial Model Systems, EEMiS, Dept of Biology and Environmental Science, Linnaeus Univ., Kalmar, Sweden.

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Animal colour patterns long have provided information about key processes that drive the ecological and evolutionary dynamics of biological diversity. Theory and empirical evidence indicate that variation in colour patterns and other traits among individuals generally improves the performance of populations and species, for example by reducing predation risk, increasing establishment success, improving resilience to environmental change, and decreasing risk of extinction. However, little is known about whether and how variation in colour pattern among species is associated with variation in other phenotypic dimensions. To address this issue, we analysed associations of colour pattern with morphological, behavioural and life-history traits on the basis of data for nearly 400 species of noctuid moths. We found that moths with more variable colour patterns had longer flight activity periods, more diverse habitats and a greater number of host plant species than species with less variable colour patterns. Variable coloration in adult noctuid moths therefore can be considered as indicative of broader niches and generalist diets. Colour pattern variability was not significantly associated with overwintering stage or body size (wing span), and it was independent of whether the colour pattern of the larvae was non-variable, variable or highly variable. Colour pattern variation during the larval stage tended to increase as the duration of the flight activity period increased, but was independent of the length of the larval period, diet breadth and habitat use. The realization that information on colour pattern variation in adult moths, and possibly other organisms, offers a proxy for niche breadth and dietary generalization can inform management and conservation biology.

Keywords: biodiversity, ecology, evolution, generalization, macroecology, niche

Introduction

Ground colour and the number, size, shape and distribution of pattern elements vary among animal species. There also can be considerable variation in colour patterns among populations that inhabit different environments and among individuals within populations (Poulton 1884, Cott 1940, McLean and Stuart-Fox 2014). Such intraspecific variation may impact many aspects of an individuals' performance, and contribute to individual differences in lifetime reproductive success (Cuthill et al.



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2017). For example, colour patterns can influence susceptibility to predation (Kettlewell 1973, Ruxton et al. 2004), intraspecific social interactions (Andersson 1994, Sinervo and Lively 1996), and the capacity for temperature regulation and heat balance (Watt 1968, Stuart-Fox and Moussalli 2009, Nordahl et al. 2018, Zverev et al. 2018). In many animals, colour patterns are genetically and developmentally associated with other phenotypic dimensions, such as body size, disease resistance, reproductive traits, microhabitat use and diet (Andersson 2001, True 2003, Ducrest et al. 2008, Forsman et al. 2008, McKinnon and Pierotti 2010, Mikkola and Rantala 2010, Karpesta and Forsman 2011, McLean and Stuart-Fox 2014). Therefore, there is ample opportunity for evolutionary modifications and divergence of animal colour patterns among populations and species.

There are considerable differences among animal species in the level of within-population, among-individual variation in colour patterns. Just as such phenotypic differences within populations can affect individual performance and relative fitness, differences in the level of variation among individuals can affect the success of populations and species (reviewed by Forsman and Wennersten 2016). Higher levels of variation among individuals may increase the niche breadth of populations and species (Bolnick et al. 2002, Forsman et al. 2008). Broad niches, in turn, may promote establishment success, stabilize population dynamics, allow for faster range expansions, and reduce extinction risk (Bolnick et al. 2003, Forsman et al. 2008, Hughes et al. 2008, Wennersten and Forsman 2012, Forsman 2014, 2016). Consistent with these predictions, empirical evidence from experiments and comparative analyses largely suggest that variation in colour patterns, and in other traits, among individuals improves the ecological and evolutionary success of populations and species [(Lomnicki 1988, Galeotti et al. 2003, Forsman and Åberg 2008, Hughes et al. 2008, Krüger and Radford 2008, Forsman and Hagman 2009, Pizzatto and Dubey 2012, Delhey et al. 2013, Forsman 2016, Forsman and Wennersten 2016, Betzholtz et al. 2017, Ducatez et al. 2017, Des Roches et al. 2018, Takahashi and Noriyuki 2019), but see Bolton et al. (2015) for a conflicting opinion].

Previous comparisons among moth species indicated that species with relatively high levels of individual variation in adult colour patterns also have an increased capacity for long-distance dispersal (Betzholtz et al. 2019), faster poleward range expansions (Forsman et al. 2016), increased colonization success on islands (Franzén et al. 2019), more stable population dynamics (Forsman et al. 2015), decreased extinction risk (Betzholtz et al. 2017) and larger geographic ranges (Franzén et al. 2019). Species of moths with more-variable colour patterns are also overrepresented in depauperate moth communities that inhabit novel, variable, fragmented and hotter urban environments (Franzén et al. unpubl.), and moth species that are considered to be agricultural pests have more variable colour patterns than other species (Betzholtz et al. 2019). Here, we address whether and how variation in colour pattern is associated with the level of

variation in morphological, behavioural and life-history traits among individuals.

Although existing evidence largely suggests that variation in traits among individual moths can increase the performance of populations and species, little is known about whether and how variation among individuals covaries among different traits across species. Variation in colour pattern might be unrelated to variation in other phenotypic characteristics if the evolution of different traits represents independent responses to different selective processes. Species with highly variable colour patterns also might be hypothesized to have less variation in other traits, if variable colour patterns can compensate for low variation in other traits (Forsman 2015). Alternatively, if overall trait variability is an adaptive and evolutionary response that allows for survival in heterogeneous and changing environments, species with more variable colour patterns also may have variable morphological, behavioural and life-history traits (Pigliucci and Preston 2004, Forsman and Wennersten 2016, Yildirim et al. 2018).

Discriminating among the above competing hypotheses is important for at least two reasons. First, doing so would promote knowledge and mechanistic understanding of how different processes (e.g. gene flow, drift, founder events, adaptations, plasticity, range expansions and local extinctions) shape the spatial and temporal structure of biological diversity in the face of environmental changes caused by human activity. Second, if variable coloration is a reliable proxy for multidimensional trait variation and ecological generalization, coloration can inform management and conservation. For example, previous research suggested that information on colour pattern variation may assist with identifying and prioritizing species for protection (Krüger and Radford 2008, Pizzatto and Dubey 2012, Delhey et al. 2013, Forsman 2016, Betzholtz et al. 2017) and identifying species with a high capacity for population growth and expansion that are more likely to become agricultural pests (Forsman 2016, Betzholtz et al. 2019).

In the present study, we first used data on almost 400 species of moths in the family Noctuidae to evaluate intraspecific associations of colour pattern variation with morphological and ecological characteristics. We investigated whether differences in adult colour patterns among individuals are associated with body size, adult flight period, habitat use, number of larval host plants and overwintering life stage. Second, we compared colour pattern variation between adults and larvae. In holometabolous insects such as moths, the larval and adult stages have different demands, use different environments and face different challenges; they are shaped by different selective pressures. The contributions of canalization and environmentally induced developmental plasticity to trait variance, including coloration, also may differ between adults and larvae. However, there is potential for genetic correlations, shared developmental pathways, correlated responses to selection and integration of plasticity between life-stages (Olson and Miller 1958, Arnold and Wade 1984, Pigliucci and Preston 2004). Third, we examined whether variable

colour patterns during the larval stage were associated with duration of the flight or larval activity period and number of host plants.

Methods

We studied all noctuid species known to occur in Sweden (Aarvik et al. 2017). The taxonomy, distribution, life history and ecology of noctuid moths in the Nordic countries is well known (Svensson 1993, Huldén et al. 2000, Aarvik et al. 2017), variation in the colour patterns of adults have been quantified (Betzholtz et al. 2019), and larvae have been illustrated and described (Ahola and Silvonen 2005, 2008, 2011).

Variation in colour pattern among adult moths previously was assessed by 12 independent Swedish lepidopterologists as non-variable (0), variable (1) or highly variable (2) (for details see Supporting information I–II in Betzholtz et al. 2019). The 12 lepidopterologists, all with extensive experience and expertise of the moth fauna in Sweden and adjacent countries, were provided with a list of 489 moth species in the families Noctuidae and Erebidae, and asked to classify variability in forewing colour pattern among individuals of each species on the basis of their personal experience with individuals observed or captured in Sweden. Therefore, it is unlikely that differences in range sizes among species influenced their assessments of colour-pattern variability. The coloration of species that were sexually dichromatic was classified as variable only if variation was apparent within one or both sexes.

Despite variation among the independent scorers in assessment of the average level of variation in forewing colour pattern (fixed effect of scorer: $F_{11,4704} = 195.76$, $p < 0.001$), there were statistically significant, consistent differences in average colour pattern variation among moth species (fixed effect of species: $F_{488,4681} = 10.86$, $p < 0.001$, covariance parameter estimate associated with the random effect of scorer = 0.095 ± 0.041 SE, $Z = 2.31$, $p = 0.01$) (for details see Supporting information I in Betzholtz et al. 2019). To obtain a continuous measure of colour pattern variability for each species, the mean of the 12 values of colour pattern variation was calculated for each species, and then divided by 2 (the highest possible value) to generate a variable that ranges from 0 to 1. The continuous measures of colour pattern variation were approximately normally distributed (see Supporting information Fig. S1b in Betzholtz et al. 2019), and closely related to the three discrete categories (non-variable, variable and highly variable) used in previous studies ($F_{1,487} = 984.31$, $p < 0.001$, $R^2 = 0.67$) (see Supporting information Fig. S2 in Betzholtz et al. 2019). The list of the 489 species, and the anonymized 12 assessments, are available in the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.k6djh9w3h>> (Forsman et al. 2019).

Here, we use data for 396 species of moths in the family Noctuidae present in Sweden. Data on other traits and descriptions of colour pattern variation of larvae were available for most of these species (see below). For the statistical analyses of multidimensional, intraspecific trait variation

reported below, we used natural log-transformed values of the adult colour pattern variation score +0.1, which generated an approximately normal distribution (Kolmogorov–Smirnov test, $D = 0.06$, $p = 0.01$, skewness = -0.004).

Colour pattern variation of larvae was classified (by JS) on the basis of species descriptions in Ahola and Silvonen (2005, 2008, 2011) as 0 (non-variable), 1 (variable) or 2 (highly variable). A species was classified as variable if the description stated that the entire larva, or a significant part of the larva (e.g. head; pro-, meso- or metathorax; abdomen; or anal shield) had two colour variants. A species was classified as highly variable if the description stated either that the one of the body parts of the larva had more than two colour variants or two or more body parts had two or more colour variants, and that the colour variants were not restricted to certain combinations.

We collected information on adult body size (male wing span in mm) from the literature (Emmet 1991, Skou 1991). Comparative analyses of moths indicate that adult wing span and larval body length are correlated, and that evolutionary changes in wing span and larval body length are correlated positively (Nilsson and Forsman 2003). We estimated the average duration of each species' adult flight activity period in southern Sweden, in weeks from 1 April to 31 October, as a continuous variable (Skou 1991, Svensson 1993). For species with two or more generations per year, we used the summed flight period (excluding the intervening larval period with no adults), which captures reproductive capacity (Iwasa et al. 1994). We obtained information on the length of the larval period, in weeks, from (Svensson 1993). We obtained information on the habitat of each species (open, deciduous forest, coniferous forest or generalist) from the literature (Emmet 1991, Skou 1991, Huldén et al. 2000). We extracted information on larval dietary breadth from the literature (Emmet 1991, Svensson 1993, Huldén et al. 2000) and classified species as specialists (feed mainly on a single plant species), oligophagous (feed on two to five plant species or mainly on a particular genus) or generalists (feed on six or more plant species or on genera in at least two families). Examples of how dietary breadth classification was derived are available in Table S1 in Appendix S2 in Pöyry et al. (2017). We classified overwintering stage as egg, larva, pupa or adult (Emmet 1991, Skou 1991, Svensson 1993).

Statistical analysis

Our analysis indicated that the colour pattern variation of adult moths varied among taxa (see Results). We therefore tested whether traits were associated with adult colour-pattern diversity while statistically adjusting for taxonomic variation (subfamily, tribe, subtribe and genus or subsets thereof).

Depending on the nature and distribution of the response variable, we analyzed data with general linear mixed models implemented with procedure MIXED (wing span, duration of activity period, both variables after log-transformation) or with generalized linear mixed models implemented with procedure GLIMMIX (variation in larval colour pattern

variation, habitat use, dietary breadth and overwintering stage) (Littell et al. 2006, Bolker et al. 2009). We implemented these models in SAS ver. 9.4. We modeled variation in larval colour pattern and diet as multinomial ordered

response variables with cumulative logit link functions, and modeled habitat use and overwintering stage as multinomial response variables with general logits link function and random intercepts. In the analyses of associations

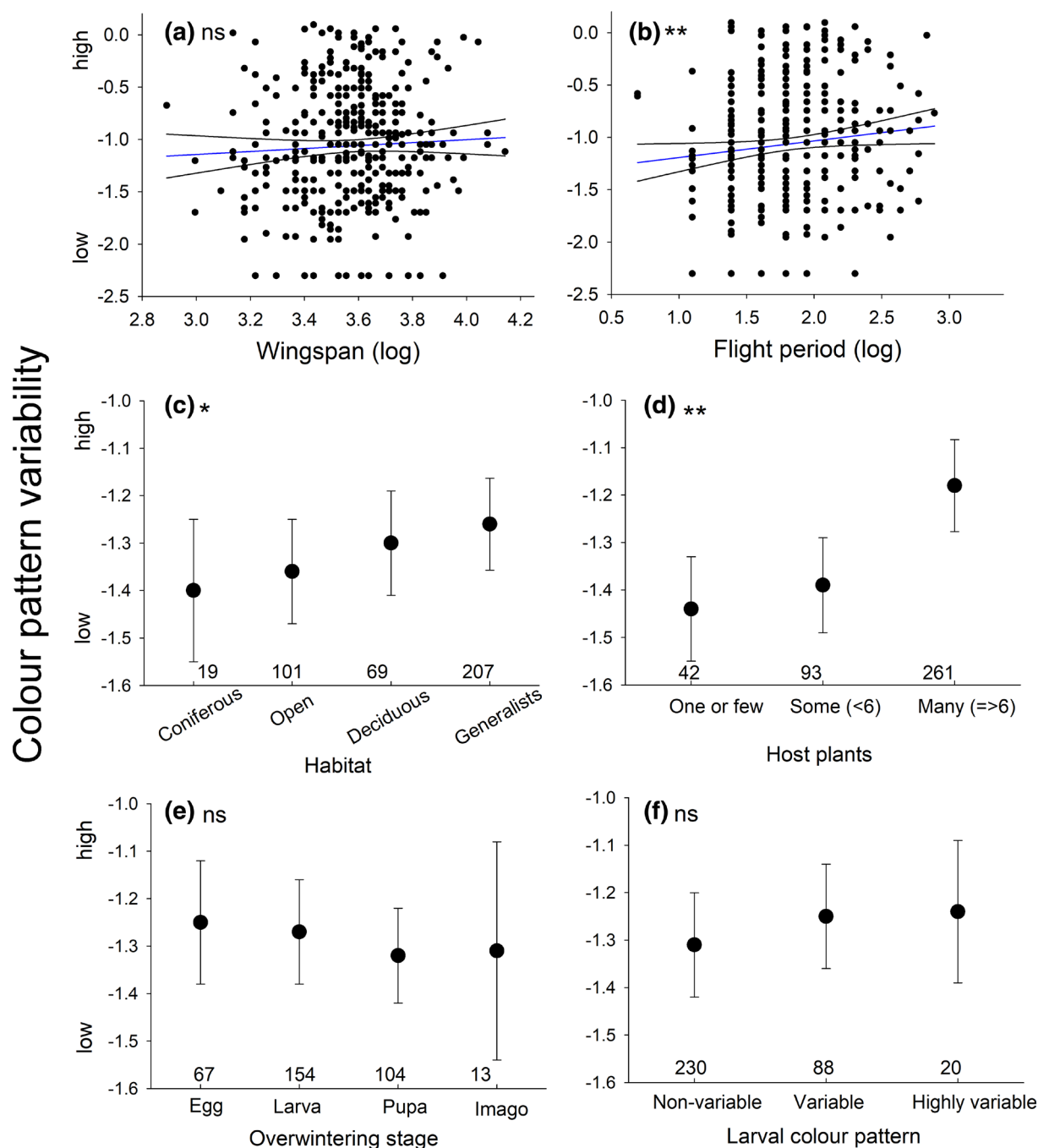


Figure 1. Associations of morphological and ecological characteristics with variation in adult colour pattern in noctuid moths. Associations in panels (a–b) are based on raw data. Lines indicate least-squares linear regressions (not accounting for higher taxon) and 95% confidence intervals (wingspan: $F_{1,393} = 0.87$, $p = 0.35$, $R^2 = 0.002$; flight period: $F_{1,393} = 4.39$, $p = 0.0369$, $R^2 = 0.011$). (c–d) Least-squares means \pm SE as estimated from general linear mixed model analysis of variance (Supplementary material Appendix 2 Table A2A) for effects on habitat use, diet breadth, overwintering stage and variation in larval colour pattern, respectively, of variation in adult colour pattern among individuals. Subfamily, tribe, subtribe and genus (or subset thereof, see Methods) were included as random factors in the models. Numbers above horizontal axes in (c–f) indicate sample sizes. *, $p < 0.05$; **, $p < 0.01$; ns, $p > 0.25$. Random effects of taxon were included in the models (Table 1).

with body size, activity period, diet and larval coloration, we included subfamily, tribe, subtribe and genus as random factors to account for greater similarity among more closely related species (cf. Forsman and Åberg 2008, Koehler et al. 2012, Forsman et al. 2015, 2016, Betzholtz et al. 2017). We used the systematics of Aarvik et al. (2017), Fibiger and Lafontaine (2005), and the Swedish taxonomic database Dyntaxa (2017). When information on subfamily, tribe or subtribe was not available, we used the information at the next higher taxonomic level.

We included subtribe as a random factor in the analysis of association between adult colour pattern and habitat use, and tribe in the analysis of association with overwintering stage. We decided which random factor to include in the final models on the basis of the Akaike information criterion (AIC) of models that included either subfamily, tribe or subtribe as random factors. However, the results and inferences related to habitat use and overwintering stage were not qualitatively affected by which taxonomic level was included as a random factor.

We evaluated the association of larval variation in colour pattern with the durations of the adult flight activity period and the larval stage with general linear mixed models implemented with procedure MIXED. We included subfamily, tribe, subtribe and genus as random factors in the models. We used the Cochran–Mantel–Haenszel stratified test statistic (Mantel and Haenszel 1959, Mantel 1963, SAS Inst. 2010) to test whether variable coloration in larvae was associated with dietary breadth while controlling for tribe. We used the Mantel–Haenszel Chi-square statistic to evaluate the association of larval colour variation with habitat use.

Adjusting critical significance levels for multiple tests has problems (Moran 2003, Nakagawa 2004). Nevertheless, we indicate in the results sections whether the reported test results remained statistically significant after sequential Bonferroni corrections, thereby enabling readers to judge for themselves.

Results

Colour pattern variation of adult moths varied among higher taxa (with tribe nested within subfamily as the explanatory

variable; $F_{35,359} = 3.95$, $p < 0.001$). We therefore tested whether traits were associated with colour-pattern diversity while statistically adjusting for variation according to higher taxon (see Methods).

Associations with variable colour patterns in adults

Overall, species of moths in which variation in colour pattern among individuals was high had longer flight activity periods, were more likely to be habitat generalists, and used a greater number of host plant species than species with less variable colour patterns (Fig. 1, Table 1). Variability of adult colour pattern was not significantly associated with overwintering stage (Fig. 1, Table 1) or body size (wing span). Diet breadth was weakly associated with flight activity period ($r = 0.20$, $n = 396$, $p < 0.001$).

The relative proportions of moth species with colour patterns classified as non-variable (ca 70%), variable (ca 25%) and highly variable (ca 5%) were similar between adults and larvae (Table 2). However, variability of adult colour pattern was independent of whether the colour pattern of the larvae was non-variable, variable or highly variable (Fig. 1, Table 1).

Multivariate ecological divergence varied among moths with non-variable, variable or highly variable colour patterns (Fig. 2).

Variability of larval colour patterns in relation to activity period, diet and habitat use

Variation in larval colour pattern tended to increase as the duration of the adult flight activity period increased ($F_{1,330} = 3.57$, $p = 0.06$, Fig. 3a), but was independent of the length of the larval stage ($F_{2,305} = 0.76$, $p = 0.47$). The length of the flight period was negatively associated with the duration of the larval period ($r_s = -0.13$, $n = 396$, $p = 0.01$, but the association fell short of statistical significance after sequential Bonferroni correction). The incidence of species with non-variable, variable or highly variable larval colour patterns was independent of whether the species used few, some or many different host plants (Cochran–Mantel–Haenszel stratified test statistic, $\chi^2 = 4.24$, $df = 4$, $p = 0.37$, Fig. 3b). Variation in larval colour pattern variation also was independent of habitat use (Mantel–Haenszel Chi-square test, $\chi^2 = 2.11$, $df = 1$, $p = 0.15$).

Table 1. Associations of adult colour-pattern variation with morphological and ecological traits in noctuid moths. Subfamily, tribe, subtribe and genus (or subset thereof; see Methods) were included as random factors. * indicates that the association remained significant after sequential Bonferroni correction.

Trait (explanatory variable)	Associations with variable adult coloration		
	Test	Test statistic	p-value
Body size (log wingspan)	MIXED	$F_{1,356} = 0.95$	0.330
Activity period (log number of weeks of flight)	MIXED	$F_{1,390} = 9.22$	0.003*
Habitat (coniferous, open, deciduous, generalist)	GLIMMIX, multinomial, glogit, (order=freq ref=first, random intercept, subtribe)	$F_{3,206} = 3.39$	0.019
Diet (few, some or many host plants)	GLIMMIX, multinomial, ordered	$F_{1,393} = 10.76$	0.001*
Overwintering stage (egg, larva, pupa or imago)	GLIMMIX, multinomial, glogit, (order=freq ref=first, random intercept, tribe)	$F_{3,227} = 0.64$	0.590
Larval coloration (0, 1, 2)	GLIMMIX, multinomial, ordered	$F_{1,327.4} = 0.23$	0.630

Table 2. Absolute and relative percentages of species of noctuid moths with colour patterns that were classified as non-variable, variable or highly variable. Total sample sizes differ between larvae and adults because data on larval coloration was not available for all species.

Life stage	Non-variable	Variable	Highly variable
Larva	230 (68)	88 (26)	20 (6)
Adult	277 (70)	91 (23)	28 (7)

Discussion

Animal colour patterns long have provided information about key processes that drive the evolutionary dynamics of biological diversity, and the causes and the consequences of colour-pattern variation have attracted much attention (Cuthill et al. 2017). However, relatively little is known about whether coloration covaries with other traits, or between life stages. Our results indicated that the average level of colour-pattern variation of adult moths varied among higher taxa, is associated with morphological and ecological generalization, and is independent of variability in larval coloration; and that variable coloration of larvae is weakly (but not significantly, $p = 0.07$) associated with longer flight activity periods but independent of the length of the larval period, dietary breadth and habitat use.

Variation in adults

We propose that broader niches and ecological generality are both a cause and a consequence of variable colour patterns in adult moths, reflecting a feedback loop. Variable colour patterns might allow for the use of a broader range of resources and enable populations and species to cope with heterogeneous conditions (Forsman et al. 2008). This in turn may relax the variance-reducing effect of stabilizing selection and replaced it by divergent or fluctuating selection that promotes diversity (Endler 1986, Roff 1997). Evidence from various organisms indicates that genetic and phenotypic variation can increase establishment success and enable range expansions (Delhey et al. 2013, Forsman 2014, 2016). There is also evidence that populations that occupy disturbed and changing environments may be genetically and phenotypically more diverse than populations in more stable environments (Yildirim et al. 2018).

Our finding that variable colour pattern is associated with ecological generalization is consistent with the proposed mechanism underlying the hypothesis (Forsman et al. 2008) that populations and species with polymorphic or variable colour patterns have greater ecological and evolutionary success, and are better able to adapt to environmental variability and change (but see 'Variation in colour-pattern variation' below). Ample evidence from observational, comparative and experimental studies supports the hypothesis that variable colour pattern improves ecological performance (reviewed by Forsman 2016, Forsman and Wennersten 2016, Takahashi and Noriyuki 2019). Previous investigations indicated that

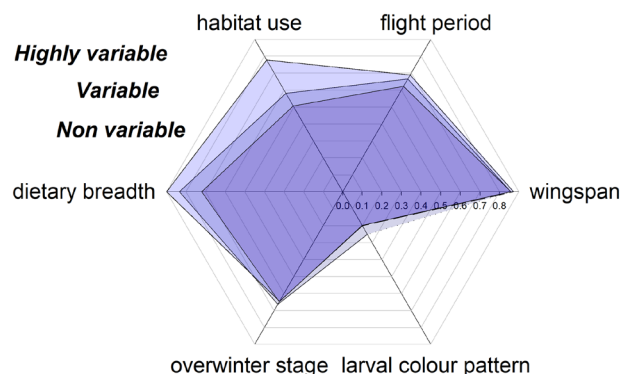


Figure 2. Relations between multivariate ecological divergence and variability of colour pattern in adult noctuid moths. The three polygons represent how species of moths with non-variable, variable and highly variable colour patterns compare along six morphological and ecological dimensions (habitat use, length of adult flight period, wing span, colour-pattern variation in larvae, overwintering life stage and dietary breadth). Original values were transformed to a continuous scale from 0 to 1. Results of statistical tests are reported in Table 1 and Fig. 1.

variable coloration in moths is associated with long-distance dispersal, improved colonization success, range expansions, lower abundance fluctuations and extinction risk, larger range sizes and representation in urban environments and among agricultural pests (Forsman et al. 2015, 2016, Betzholtz et al. 2017, 2019, Franzén et al. 2019, Franzén et al. unpubl.). The association between variable colour pattern and improved population performance reported did not change after controlling for the potential effects of ecological and life-history traits that covary with variable colour pattern.

There are at least two explanations why the beneficial effects of variable colour may extend beyond the morphological, behavioural and life-history dimensions of ecological generalization. First, our results may underestimate the increase in ecological generalization that accompanies variable colour patterns in moths. For example, colour pattern may affect functional aspects of the phenotype that were not included in our data. Perhaps the most obvious such candidate trait is thermal biology. It is well established that animal coloration influences and is associated with heating rates, equilibrium body temperatures, preferred temperatures, activity periods, microhabitat utilization, climate niche breadth and overall organismal performance, particularly in ectotherms (Watt 1968, Kingsolver and Wiernasz 1991, Huey and Kingsolver 1993, Forsman 1999, 2000, Forsman et al. 2002, Ahnesjö and Forsman 2006, Takahashi and Noriyuki 2019). There are also recent reports of spatial and temporal shifts in overall darkness or heat tolerance of lepidopteran communities associated with environmental variation and change (Zeuss et al. 2014, Heidrich et al. 2018, Merckx and Van Dyck 2019, Munro et al. 2019, Stelbrink et al. 2019). Given that individuals that differ in coloration also differ in thermal biology and physiology (Forsman et al. 2002, Ahnesjö and Forsman 2006), it is not surprising that species and populations with

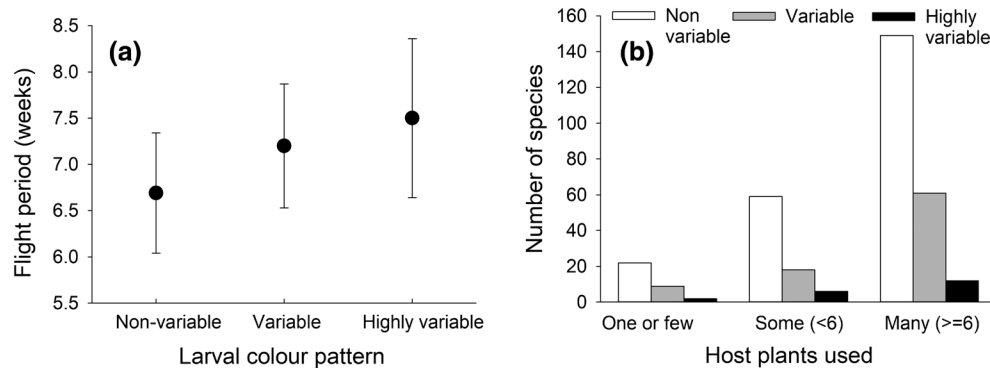


Figure 3. Relation between variable larval colour pattern in noctuid moths and activity period and dietary breadth. (a) Least-squares means \pm SE as estimated from general linear mixed model analysis of variance of effects on duration of activity period of variation in larval colour pattern among individuals. (b) Absolute percentages of species with non-variable, variable or highly variable larval colour patterns as a function of dietary breadth.

variable colour patterns also have broader thermal niches (Takahashi and Noriyuki 2019), and high ability to cope with heterogeneity and change (Forsman 2016).

Animal colour patterns also can influence susceptibility to predation, either by reducing probability of detection and recognition or by eliciting avoidance behaviours. Variable and polymorphic coloration can offer camouflage and protection from predators (Ruxton et al. 2004, Karpestam et al. 2013, Merilaita et al. 2017), and thereby increase niche breadth. Colour pattern variation can also impair searching by predators and increase the survival of prey (Glanville and Allen 1997, Bond and Kamil 2002, Karpestam et al. 2016, Cuthill et al. 2017). Facultative aposematism (Ruxton et al. 2004, Speed and Ruxton 2005) may be more beneficial in species that have broader diets, in which adults may have more or less sequestered defensive compounds.

Variation in larvae

Our results suggest that variable colour pattern in moths is equally common in the adult and larval stages (Table 2). However, the distribution among species of variable colour pattern during the larval stage was independent of that during the adult stage. A plausible explanation is that the larvae and adults of holometabolous insects such as moths differ in morphology, physiology and behaviours, and are exposed to dissimilar environmental conditions and selective regimes. The relative importance of colour patterns for thermoregulation and predator avoidance therefore are likely different for larvae and adults. It is also possible that the contribution of individual differences in colour pattern to variation in relative fitness depends on whether the colouration differences manifest in the larvae or the adults. For example, the protective role of colour pattern may shift between the larval and the adult life stage from camouflage to aposematism, or vice versa. In addition, the importance of different protective modes (e.g. camouflage as opposed to aposematism, combinations of cryptic and signalling colour patterns used by underwing moths, or solitary versus gregarious behaviour

of larvae) vary across lineages (Cott 1940, Edmunds 1990, Forsman and Merilaita 2003, Nilsson and Forsman 2003, Ruxton et al. 2004). Developmental constraints also differ between larvae, in which colour is expressed directly through integument and influenced by moulting restriction, and adults, in which colour is expressed through scales (Nijhout 1991).

We found that species of moths with longer flight activity periods tended to have more variable colour patterns during the larval stage, although the association was not statistically significant. This relation may be partly explained by changes in environmental conditions and selection on larval coloration imposed by visual predators throughout the season (Mappes et al. 2014). An association of more-variable larval coloration in species with longer flight activity periods might also reflect environmentally induced phenotypic variation. The potential for developmental plasticity to generate variation in colour pattern is probably higher if individuals develop during different time periods, such that they are exposed to a broader range of conditions and environmental cues (Brakefield 1996, Saulich et al. 2017). However, the finding that variable coloration during the larval stage was independent of the length of the larval stage is not consistent with this interpretation.

Contrary to our expectation, variable colour pattern in Noctuidae moth larvae was not significantly associated with the length of the larval stage, diet breadth or habitat use. The lack of association with diet breadth is particularly surprising, because one would expect selection for camouflage to result in the evolution of canalization of both phenotype and behaviours in diet specialists. The lack of association might reflect that colour patterns of larvae are subject to ontogenetic change as the larvae pass through different instars, and that the larvae of several noctuid moth species live their lives inside the stems and roots of plants where they are not exposed to visually oriented predators or direct sunlight (Emmet 1991). Furthermore, larvae of some species feed above ground only during the night and hide at plant bases, or in the soil or leaf litter, during the day (Svensson 1993).

Variation in colour-pattern variation

Most of the noctuids in our study have non-variable colour patterns (Table 2). This raises two questions: what are the underlying causes of colour-pattern variation, and why do some species have more-variable colour patterns than others? The feedback loop hypothesized earlier may be part of the explanation. Species that occupy broader niches and heterogeneous environments are more influenced by oscillating and divergent selection that may promote the evolution and maintenance of diversity. Moths with variable colour patterns tend to have larger ranges (Franzén et al. 2019) and larger and more stable population sizes (Forsman et al. 2015), which likely weakens the effects of genetic drift on variation (Frankham 1996, O'Hara 2005). Conversely, variable colour pattern in moths seems to be associated with a higher capacity for long-distance dispersal (Betzholtz et al. 2019), and the resulting immigration and gene flow can increase variation (Yildirim et al. 2018). It is also possible that some species of moths are influenced by negative frequency-dependent (apostatic) selection that can help preserve population genetic variation (Whiteley et al. 1997, Bond and Kamil 2002).

Given the many hypothesized and empirically established advantages conferred by genetic and phenotypic diversity, it might seem puzzling that more or all species are not highly variable. However, natural selection reduces variance and can lead to the evolution of local adaptations, regardless whether the adaptations are beneficial for long-term population persistence. Not all elements of lepidopteran wings are equally variable, and many developmental constraints, some of which likely are more flexible than others, influence colour pattern (Nijhout 1991). The potential contributions of canalization, developmental perturbations and environmentally induced plasticity to colour-pattern variation may also vary among species (Forsman and Merilaita 2003), perhaps reflecting phylogenetic constraints.

There are potential costs to genetic and phenotypic diversity, and potential benefits to populations and species that are non-variable (Bolton et al. 2015, Forsman 2016, Forsman and Wennersten 2016). In temporally stable environments, the average fitness of locally adapted populations at evolutionary equilibrium may be reduced due to the addition of less-fit genotypes by mutation, segregation and substitution by selection (i.e. genetic load) (Haldane 1957, Maynard Smith 1976, Crow 1993). In spatially heterogeneous environments, local fitness may be depressed by genetic swamping that is mediated by recurrent immigration and negative effects associated with admixture (McClelland and Naish 2007, Rius and Darling 2014).

Environmental conditions, ecological processes and selective pressures in Sweden, at high latitude and with a young post-glacial age, are different from those in other parts of the world. Latitudinal gradients and positive species richness-specialization relations are apparent in large-scale analysis of other taxa (e.g. Mimet et al. 2019 and references therein). The incidence of generalist species may be higher at higher latitudes, where abiotic stressors are dominant, than in tropical

and other species-rich regions, where the relative importance of biotic interactions is stronger. The majority (ca 85%) of all insects are tropical or from the southern hemisphere (Stork 2018), and the majority (ca 90%) of Lepidoptera are dietary specialists (Forister et al. 2015). Recent evidence suggests that latitudinal patterns of bird and arthropod predation on Lepidopteran larvae are opposites, and that selection for prey colouration may vary geographically and according to predator identity (Zvereva et al. 2019). To our knowledge, however, it has not yet been systematically investigated whether tropical species of moths have less variable colour patterns.

Future directions

To our knowledge, this was the first study that examined whether variable coloration covaries with variability in other traits. It remains to be investigated whether our results are generalizable across geographical regions and animal groups, to communities of moths with greater species richness and temporally variable environments, and to other moth taxa.

Most phenotypic variation reflects genetic variation and environmentally induced developmental plasticity or phenotypic flexibility (West-Eberhard 2003, Forsman 2015), and not all phenotypic variability measured here may indicate genetic variability. Trait associations quantified at the phenotypic level might reflect genetics (Lande 1984, True 2003, McKinnon and Pierotti 2010) or plasticity integration (Pigliucci and Preston 2004). The ecological and evolutionary consequences for populations and species can vary depending on the causes of trait variation and on the strength and direction of trait covariance (Schluter 1996, Arnold et al. 2001, Wennersten and Forsman 2012). Recent developments of novel techniques for sequencing and analysing genetic variation (e.g. restriction site associated DNA-sequencing, whole genome sequencing, genome wide association studies, and single nucleotide polymorphism-genotyping (Andrews et al. 2016)) can help identify genes and underlying genomic regions involved, clarifying the diversity in animal coloration and how it covaries with other traits.

We relied on expert classifications of variation in adult colour pattern and published descriptions of variation in larval colour pattern. Although the expert classifications are valid and repeatable (Betzholtz et al. 2019), more-objective recent methods, such as the use of image data, allow one to quantify variation in the colours and patterns of diverse organisms (Cuthill et al. 2017, Van Belleghem et al. 2018). Colour-pattern variation may help identify and prioritize species for conservation efforts and identify potentially invasive species with a high capacity for range expansions and population growth.

Intraspecific trait variation can influence community structure and ecosystems (Hughes et al. 2008, Des Roches et al. 2018). Moths serve as pollinators; as food for birds, bats and other animals (Both et al. 2006, Robison et al. 2006, Macgregor et al. 2015, Brosi et al. 2017); and as major pests in forests and agricultural areas (Morris 1985, Betzholtz et al. 2019). Therefore, intraspecific trait variation in moths can

change species composition, species interactions and ecosystem function.

Data availability statement

Data available in Supplementary material Appendix 1–2.

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Author contributions – AF, MF and PEB conceived the study. AF, MF and PEB collected information on colour pattern variation of adult moths, JS extracted information on colour pattern variation of larvae, and MF and PEB extracted information on the other morphological and ecological traits. AF and DP analysed the data. AF, DP and JS wrote the first draft. All authors contributed to the final version and approved the submitted manuscript.

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Supplementary material (available online as Appendix ecog-04923 at <www.ecography.org/appendix/ecog-04923>). Appendix 1–2.