

Seasonal variability in yellow abdominal colour of *Episyrphus balteatus* (Syrphidae, Diptera)

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Abstract

This study analyses seasonal variation in yellow abdominal colouration in *Episyrphus balteatus* (de Geer, 1776) (Syrphidae, Diptera). A total of 643 field-collected specimens were examined. The proportion of yellow on abdominal tergites (T2–T5) was quantified from dorsal photographs using image analysis. Yellow colouration was highly variable in both sexes. Females were generally darker and showed greater variability than males. In both sexes, the highest proportion of yellow was consistently recorded on tergite 5, while yellow decreased anteriorly, with tergite 2 dominated by black pigmentation. Linear mixed-effects modelling revealed a significant sex $\times$ tergite interaction: the male advantage in yellow pigmentation amplified posteriorly, from 4.0 pp on T2 to 14.7 pp on T5. Day-of-year showed a marginally negative trend on yellow proportion ($\beta = -0.027$, $p = 0.053$), consistent with seasonal darkening.

Keywords: marmalade hoverfly, abdominal tergites, yellow colour

Introduction

Seasonal phenotypic plasticity in Diptera frequently affects body colour, body size, pilosity, and wing morphology. In Syrphidae, darker adults typically emerge during cooler periods, while lighter individuals occur during warmer seasons. These changes are largely influenced by temperature during pupal development (e.g. Dušek & Láska 1974; Heal 1981, 1989; Holloway 1993; Ottenheim et al. 1996).

Episyrphus balteatus (de Geer, 1776), commonly known as the marmalade hoverfly, is a widespread and abundant species in Europe (Speight 2011; Mazánek et al. 2025). It plays an important role in biological control of aphids (Hondelmann et al. 2005). In Central Europe, up to four generations per year have been reported (Nawrocka 1988). Both migration and overwintering contribute to population dynamics, but their relative importance remains unclear (Hondelmann & Poehling 2007). Previous studies suggested that seasonal variation in abdominal colour pattern may be linked to thermoregulation (Holloway et al. 1997). The duration of pupal development appears to be a key factor determining adult colour pattern (Ottenheim et al. 1995; Marriott & Holloway 1998). However, the proximate and ultimate causes of abdominal colour plasticity remain incompletely understood.

Unlike previous work that described seasonal trends qualitatively or at the species level, the present study provides quantitative, sex-resolved estimates of yellow pigmentation across four tergites simultaneously, accounting for the non-independence of within-individual measurements using linear mixed-effects modelling. The aim of this study was to quantify seasonal changes in yellow pigmentation on abdominal tergites (T2–T5) in males and females of *E. balteatus* and to describe sex-related differences.

Material and methods

Specimens were obtained from Malaise traps operated in 2008 in Šúr (Slovakia) at five habitats. Sampling was conducted at two-week intervals from April to early November. Specimens were preserved in ethanol, dried, and photographed dorsally under standardized laboratory conditions using a trinocular microscope (10 $\times$ magnification).

The proportion of yellow pigmentation on tergites T2–T5 was measured from photographs using ImageJ software. Total tergite area and yellow area were measured manually using the Polygon Selection tool, and the percentage of yellow was calculated. Because sample sizes varied throughout the season, analyses were restricted to June, July, and August and evaluated by decades (10-day periods). Measurement error was assessed by repeated measurements of [N] selected specimens. Proportional error was highest on T2 and lowest on T3, consistent with the greater structural complexity and colour variability of the anterior tergite. Yellow pigmentation (%) on tergites T2–T5 was analysed using linear mixed-effects models (LMM) fitted by maximum likelihood. Analyses were performed in R 4.3.3 (R Core Team 2024) using the packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), and nlme (Pinheiro et al. 2024). Because each specimen contributed four repeated measurements (one per tergite), individual identity was included as a grouping factor with a random intercept to account for within-individual correlation. Tergite position (coded 1–4) was included as a continuous random slope per specimen to model spatial autocorrelation between adjacent tergites. Temporal autocorrelation was addressed by including day-of-year (DOY), centred at its grand mean, as a continuous fixed-effect covariate. Six candidate models were compared using the Akaike Information Criterion

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(AIC; Table 1). Model M5 (nlme, with AR1 residual correlation structure) had the lowest AIC (1685.83); the next best model, M4 (lme4, without AR1 structure), had $\Delta\text{AIC} = 1.24$. Although a ΔAIC below 2 represents weak support for one model over another, M5 was selected for inference because it directly and explicitly addresses the spatial autocorrelation between adjacent tergites, whereas M4 only approximates this through a random slope. The estimated AR1 autocorrelation parameter was $\phi = 0.305$, confirming that residuals for adjacent tergites were moderately correlated within individuals. Fixed-effect coefficients with standard errors, p-values, and 95% Wald confidence intervals of the best model (M5, refitted with REML) are reported in Table 2. The complete dataset and R analysis script are available from the corresponding author upon reasonable request.

Results

A total of 643 specimens (328 females, 315 males) were examined. Most individuals (84%) were collected in July. Per-decade sample sizes were unequal: the largest subgroups were June decade 2 (females $n=9$, males $n=14$) and June decade 3 (females $n=7$, males $n=3$), while several periods – particularly late July and August – were represented by only one or two individuals per sex (Figures 3 and 4). Boxplot elements for decades with $n=1$ represent single observations and should be interpreted with caution; model-based estimates (Table 2, Figure 1) are more reliable for inference as they pool information across the full seasonal range. Yellow pigmentation was highly variable in both sexes. Females

were generally darker and showed greater variability than males. Across all decades and both sexes: the highest proportion of yellow was consistently recorded on T5; yellow pigmentation decreased anteriorly (T5 $\rightarrow$ T2); T2 showed the lowest proportion of yellow and was predominantly black.

Model selection based on AIC strongly supported model M5 (LME with AR1 residual correlation structure; $\Delta\text{AIC} \geq 27$ relative to all simpler models; Table 1). At the grand-mean day-of-year (DOY = 206, approximately 25 July), predicted yellow was 37.5% (females) vs. 41.5% (males) on T2, increasing to 80.7% vs. 95.4% on T5 (Table 2, Figure 1). The sex $\times$ tergite interaction was significant (Table 2), confirming that the male advantage grew progressively from T2 (difference: 4.0 pp, 95% CI: 1.0–7.1) to T5 (difference: 14.7 pp, 95% CI: 11.6–17.8). Day-of-year showed a marginally negative association with yellow pigmentation ($\beta = -0.027 \pm 0.014$ SE; 95% CI: -0.055 to 0.001 ; $p = 0.053$). Although this effect did not reach conventional significance, the direction is consistent with the known seasonal darkening trend.

The stepwise increase in yellow colouration from T2 to T5 was not uniform: the transitions between T2 and T3 (females: +21.6 pp; males: +24.4 pp) and between T4 and T5 (females: +16.8 pp; males: +22.5 pp) were substantially larger than the transition between T3 and T4 (females: +4.9 pp; males: +6.9 pp), indicating that T3 and T4 form a plateau of intermediate colouration (Table 2, Figure 1).

Greater individual variability in yellow proportion was observed in females than in males across all tergites, as visible in the seasonal variation plots (Figures 3 and 4).

Table 1. AIC comparison of candidate linear mixed-effects models for yellow abdominal colouration in *Episyrphus balteatus*. df = number of estimated parameters; logLik = log-likelihood; AIC = Akaike Information Criterion; ΔAIC = difference from best model. M0 included as reference only (violates independence assumption).

Model	Description	df	logLik	AIC	ΔAIC
M5	LME (nlme) – as M4 + AR1 residual correlation within individuals	14	-828.92	1685.83	0
M4	LMM (lme4) – random intercept + random tergite slope + sex $\times$ tergite	13	-830.54	1687.07	1.24
M2	LMM (lme4) – random intercept + random tergite slope per specimen	10	-846.75	1713.5	27.67
M1	LMM (lme4) – random intercept per specimen	8	-855.85	1727.7	41.87
M3	LMM (lme4) – random intercept + random DOY slope per specimen	10	-854.56	1729.11	43.28
M0	OLS – no random effects (violates independence; reference only)	7	-882.13	1778.26	92.43

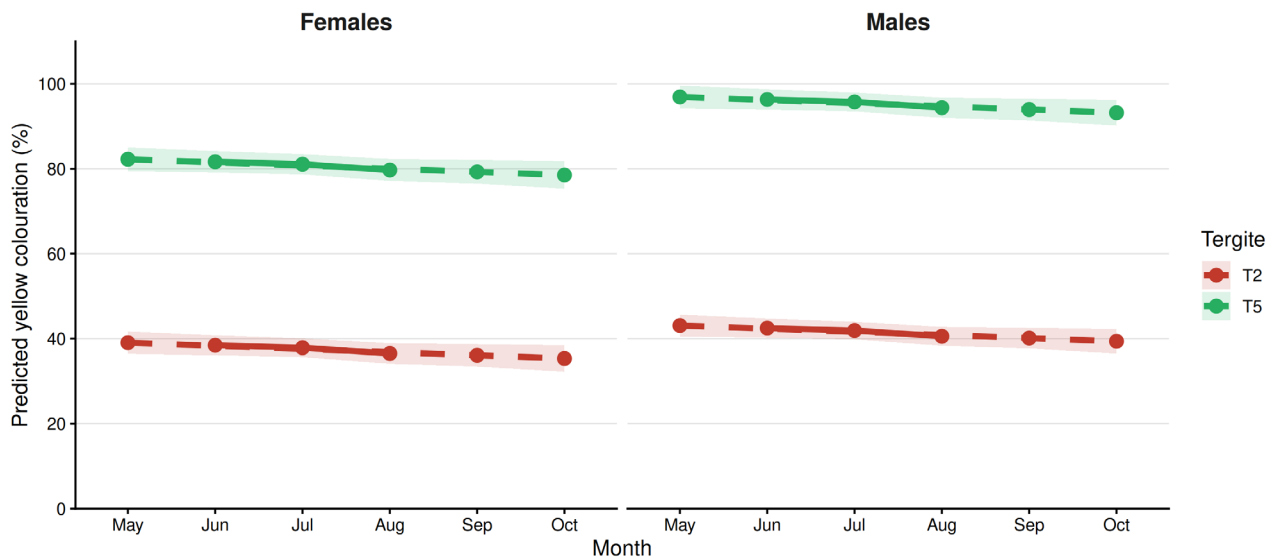


Figure 1. Seasonal trend in model-predicted yellow abdominal colouration (%) for tergites T2 and T5 in females and males of *Episyrphus balteatus* (de Geer, 1776). Lines = fixed-effect predictions of the best-fit model (M5) at the mean day-of-year of each calendar month (June – October); shaded ribbons = 95% Wald confidence intervals. The slight decline from summer to autumn is consistent with the marginally negative DOY effect ($\beta = -0.027$, $p = 0.053$; Table 2).

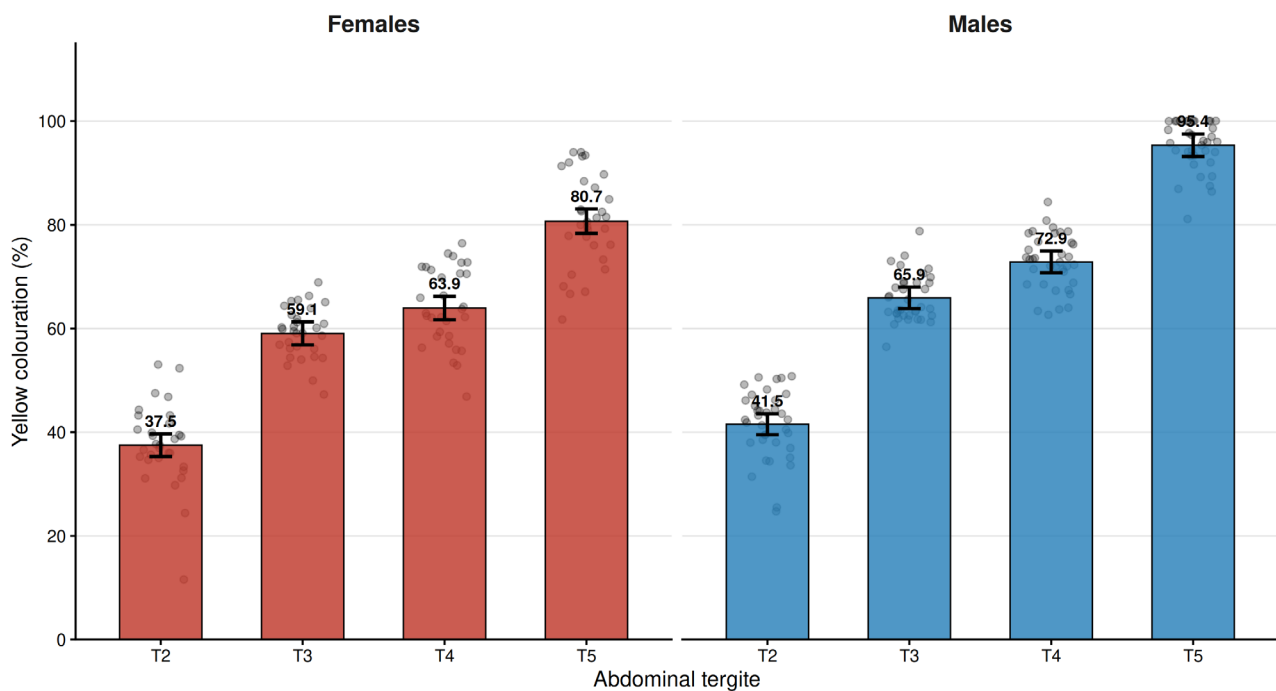


Figure 2. Model-predicted yellow abdominal colouration (%) by tergite and sex in *Episyrphus balteatus* (de Geer, 1776). Bars = population-level fixed-effect predictions of the best-fit model (M5, LME with AR1 residual correlation structure) evaluated at the grand-mean day-of-year (DOY = 206, approximately 25 July); error bars = 95% Wald confidence intervals; dots = individual observed values (jittered for clarity). Dashed lines indicate months outside the analytical range (June – August) and represent model extrapolation. Parameter estimates are given in Table 2.

Table 2. Fixed-effect coefficients of the best model (M5: LME with random intercept + random tergite slope per individual + AR1 residual correlation; refitted with REML). Reference category: tergite T2, sex Female, grand-mean DOY. SE = standard error; df = Satterthwaite degrees of freedom; CI = 95% Wald confidence interval.

Parameter	Estimate	SE	t value	df	p value	CI 95 lower	CI 95 upper
Intercept (T2, Female, mean DOY)	37.49	1.113	33.695	195	< 0.001	35.295	39.684
Tergite T3 vs T2	21.568	1.047	20.594	195	< 0.001	19.502	23.633
Tergite T4 vs T2	26.448	1.211	21.837	195	< 0.001	24.06	28.837
Tergite T5 vs T2	43.203	1.278	33.804	195	< 0.001	40.682	45.723
Sex: Male vs Female (at T2)	4.044	1.519	2.663	64	0.010	1.01	7.078
Day-of-year (centred)	-0.027	0.014	-1.974	64	0.053	-0.055	0.001
Tergite T3 x Male (interaction)	2.804	1.429	1.963	195	0.051	-0.013	5.622
Tergite T4 x Male (interaction)	4.868	1.652	2.946	195	0.004	1.61	8.127
Tergite T5 x Male (interaction)	10.614	1.744	6.088	195	< 0.001	7.175	14.053

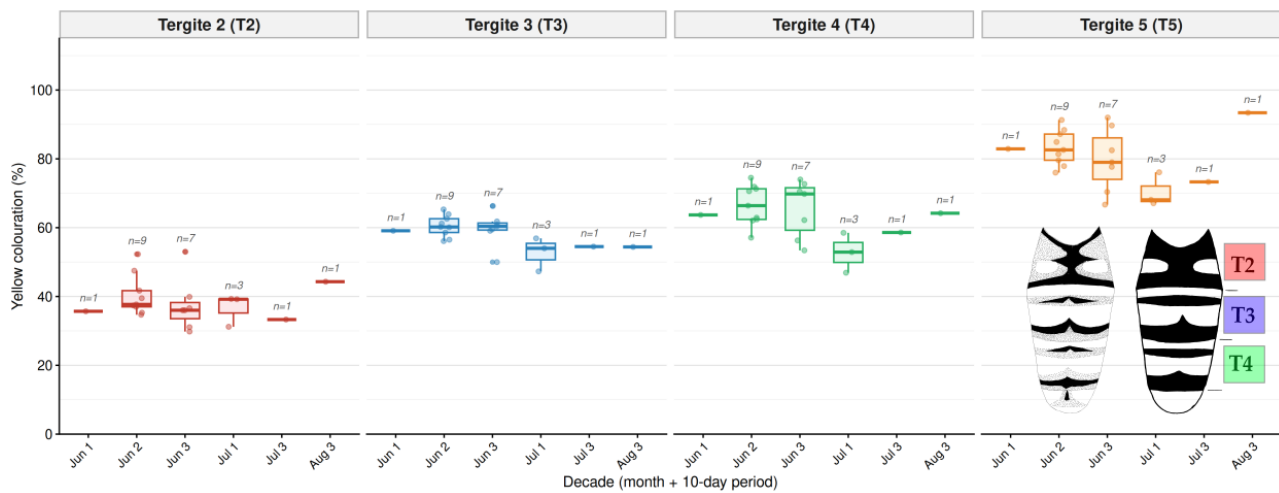


Figure 3. Seasonal variation in yellow abdominal colouration in females of *Episyrphus balteatus* (de Geer, 1776). (A) Schematic representation of the range of phenotypic variation: pale (summer) form (left) and dark (autumn/spring) form (right); labels indicate abdominal tergites T2–T4. (B) Observed values shown as boxplots by 10-day sampling decade (June – August) for each abdominal tergite (T2–T5). Box = interquartile range (IQR); centre line = median; whiskers = $1.5 \times \text{IQR}$ beyond box edges; dots = individual specimens. Numbers above each box (n) indicate the count of individuals in that decade. Decades with zero observations are omitted. For model-predicted values see Figure 1. In the bottom right corner, extremely colored individuals are visualized, with the tergites displayed.

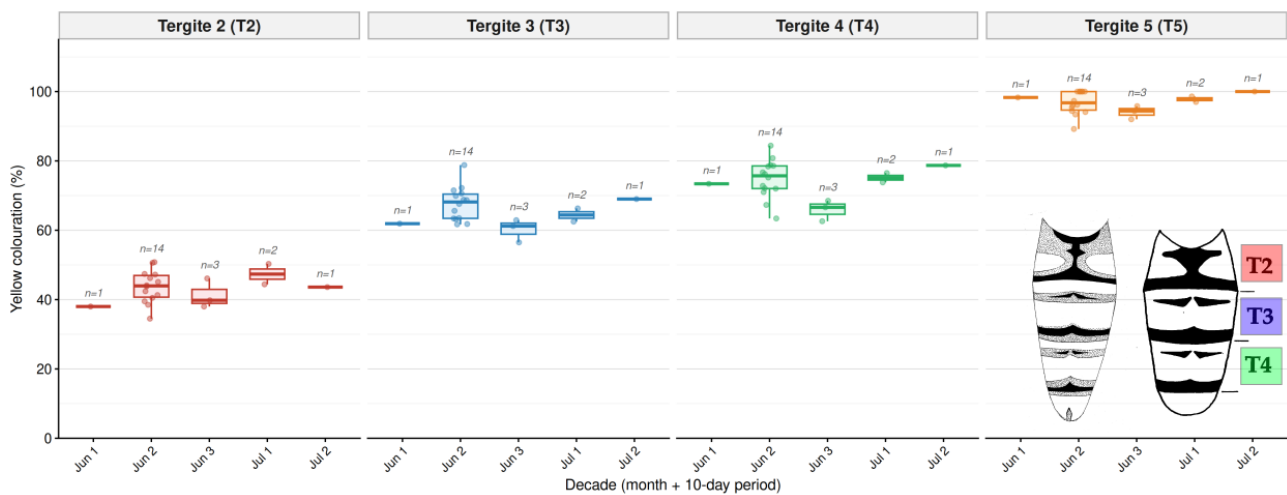


Figure 4. Seasonal variation in yellow abdominal colouration in males of *Episyrphus balteatus* (de Geer, 1776). (A) Schematic representation of the range of phenotypic variation: pale (summer) form (left) and dark (autumn/spring) form (right); labels indicate abdominal tergites T2–T4. (B) Observed values shown as boxplots by 10-day sampling decade (June – August) for each abdominal tergite (T2–T5). Box = interquartile range (IQR); centre line = median; whiskers = $1.5 \times \text{IQR}$ beyond box edges; dots = individual specimens. Numbers above each box (n) indicate the count of individuals in that decade. Decades with zero observations are omitted. For model-predicted values see Figure 1. In the bottom right corner, extremely colored individuals are visualized, with the tergites displayed.

Discussion

The use of linear mixed-effects models, which accounted for within-individual non-independence of tergite measurements and spatial autocorrelation between adjacent tergites, extended the previous qualitative and univariate findings with statistically robust, tergite-resolved estimates. The significant sex $\times$ tergite interaction indicates that sex differences in pigmentation are not uniform across the abdomen but amplify posteriorly, a pattern that warrants further investigation in the context of thermoregulatory or signalling hypotheses. The present study therefore confirms that abdominal yellow pigmentation in *E. balteatus* is highly variable across the season. Females were generally darker and exhibited greater variability than males. This pattern is consistent with findings of Marriott & Holloway (1998), who reported sex-specific differences in colour plasticity in this species. In both sexes, the highest proportion of yellow pigmentation was consistently recorded on T5, with a gradual decrease towards T2. T2 showed the lowest proportion of yellow and the greatest variability. A similar pattern of differential plasticity among tergites was reported by Marriott & Holloway (1998), who identified T2 as the most plastic segment and T3 as the least plastic. In our dataset, measurement error was highest on T2 and lowest on T3, which corresponds with the observed biological variability. Although measurement error does not explain the pattern, it reflects the higher structural variability of T2.

Seasonal variation in colour pattern in Syrphidae has repeatedly been linked to temperature-dependent phenotypic plasticity during the pupal stage (Dušek & Láská 1974; Heal 1981, 1989; Holloway 1993; Ottenheim

et al. 1995, 1996). Holloway et al. (1997) demonstrated that darker individuals of *E. balteatus* are more frequent during cooler parts of the season, supporting a thermoregulatory hypothesis. Our results show clear seasonal variation in yellow proportion; however, because temperature data were not directly analysed in this study, we cannot test the thermoregulation hypothesis explicitly. The observed pattern is nevertheless consistent with previously described seasonal plasticity.

Periods of relatively lower yellow pigmentation visible in the third decade of June and the second decade of August in the seasonal plots (Figures 3 and 4) may reflect overlapping generations. In Central Europe, *E. balteatus* can produce up to four generations per year (Nawrocka 1988), and both migration and local overwintering contribute to seasonal population structure (Hondelmann & Poehling 2007; Speight 2011). Overlapping generations may therefore obscure clear temporal differentiation in colour pattern. Given that generations overlap substantially, precise assignment of individuals to particular generations is not possible based on sampling date alone. The proximate and ultimate bases of abdominal colour plasticity in hoverflies remain unresolved. Although thermoregulation has been proposed as a primary mechanism (Holloway et al. 1997), the developmental duration of the pupal stage appears to be a key proximate factor influencing adult colour pattern (Ottenheim et al. 1995; Marriott & Holloway 1998). Our results support the existence of strong phenotypic plasticity but do not allow discrimination between adaptive thermoregulatory function and developmental constraint. The finding that T3 and T4 form a plateau of intermediate colouration – with much smaller inter-

tergite differences than the T2→T3 and T4→T5 transitions – is consistent with Marriott & Holloway (1998), who identified T2 as the most plastic and T3 as the least plastic segment. Whether this plateau reflects a developmental compartmentalisation of pigment deposition, or is partly an artefact of the increasing proportion of yellow area relative to tergite size in more posterior segments, warrants targeted experimental study.

Long-term sampling covering winter months, combined with direct environmental data (e.g. temperature during development), would allow stronger inference about the mechanisms underlying seasonal colour variation. Integration of multiple sampling methods may also improve temporal coverage. Image-based quantitative analysis, as applied here, provides a reliable and non-destructive approach for future studies of colour plasticity. The study is based on material from a single locality and season, and environmental variables were not directly measured. Overlapping generations and migration may also have influenced the observed seasonal patterns.

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