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Early or late: Associations between adult emergence timing and fitness-related traits in the grapevine moth *Lobesia botrana*

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Abstract

The timing of adult emergence is often closely associated with individual condition and reproductive success across a wide range of taxa. In insects, emergence timing can reflect both intrinsic developmental differences and environmental conditions experienced during earlier life stages and is often correlated with key fitness traits. Individuals also have to synchronise their emergence with fluctuating resource availability, and the population benefits when individuals emerge at different times, by reducing the chance that a single adverse event will affect all offspring in one season. This balance is particularly evident in insects, where synchronising life stages with optimal environmental conditions, such as the phenological stages of host plants, is essential. In this study, we described associations between adult emergence timing and multiple components of individual quality in a wild population of the grapevine moth *Lobesia botrana* (a major pest of grapevines) according to their host plant. Our findings revealed a reduction in pupal mass and adult longevity with later emergence. Later emergence also impacted mating (decreased mating success, increased mating latency and mating duration) and reproductive-related traits (reduction in spermatophore volume, fecundity and fertility). Additionally, the impact of emergence timing is more pronounced in individuals originating from Mourvedre compared to Syrah, two distinct grape varieties. This suggested that the quality of larval host is closely tied to the timing of emergence, indicating a complex interplay between emergence timing and host plant quality.

KEYWORDS

emergence wave, fitness, grape variety, host plant quality, *Lobesia botrana*, mating success

INTRODUCTION

The timing of life history events plays a pivotal role in shaping the fitness of many organisms (Flatt & Heyland, 2011; Nylin & Gotthard, 1998; Zera & Harshman, 2001). Among these events, the timing of adult emergence (hereafter simply termed 'emergence') can be strongly associated with individual condition and subsequent reproductive output. In many taxa, individuals that emerge later in a season often exhibit lower fitness than early-emerging conspecifics (Einum & Fleming, 2000; Forister & Shapiro, 2003; Veiga & Salvador, 2001). These patterns may arise because individuals in poorer condition develop more slowly and perform worse reproductively, or because environmental conditions deteriorate as the season progresses (Blanckenhorn, 1998; Rowe et al., 1994). Importantly, individuals also have to synchronise with fluctuating resource availability, and they have to adopt strategies to spread the risk of adverse conditions over time (Sun et al., 2020; Varpe, 2017). Indeed, the population benefits when individuals emerge at different times. By spreading emergence over time, the population reduces the chance that a single adverse event will affect all offspring in one season, thereby increasing the likelihood that at least some individuals will reproduce successfully.

This is particularly important in insects, exhibiting a wide range of emergence strategies, that reflect adaptations to their specific ecological niches (Hill et al., 2021). The timing of emergence is crucial for synchronising life stages with favourable environmental conditions, which can vary with seasonality and temperature (Forrest, 2016; Forrest & Thomson, 2011; Nash et al., 2023; Newbold et al., 1994). Particularly, the nutritional value, chemical defences and phenological stage of the host plant can significantly impact larval development, survival rates and subsequent adult performance (Bede et al., 2007; Lin et al., 2018; Moreau et al., 2017; Muller, Vogelweith, et al., 2015). Timing of emergence plays a crucial role in synchronising the life cycle of insects with the optimal phenology of their host plants. Thus, the timing of emergence, aligned with host plant phenology, might be a crucial adaptive strategy for maximising their fitness. Indeed, the timing of emergence can influence a wide array of phenotypic traits that are crucial for individual fitness (Brommer et al., 2002; Reed et al., 2009). As such, capital breeder species, in which the cost of reproduction is set up using stored energy, may face a trade-off in the allocation of their energy reserves (Williams et al., 2017). Indeed, early-emerging individuals can capitalise on the initial availability of resources with minimal competition (Gidoin et al., 2015), while late-emerging individuals can exploit resources that become available later, reducing the risk of resource depletion, thus avoiding competition (Schlyter & Anderbrant, 1993), but with the risk of limited resources and less favourable conditions (Verhulst & Nilsson, 2007), depending on the resource phenology. Still, phenological diversity enhances the overall resilience of the population (Encinas-Viso et al., 2012; Miller-Rushing et al., 2010), makes the population less vulnerable to environmental change (Ovaskainen et al., 2013; Singer & Parmesan, 2010), and may increase geographic range distribution (Dunn et al., 2023; Macgregor et al., 2019). Phenological diversity may also be due to between-family or genotypic variation, where different families exhibit distinct, genetically determined phenologies, reflecting individual-level adaptive strategies or population genetic structure (Lehmann & Wheat, 2022; Yurk & Powell, 2010). Ultimately, the timing of emergence may shape the life history strategies and evolutionary dynamics of the population, making it a critical factor in understanding ecological interactions and species adaptation.

In this study, we analysed the temporal pattern of individual quality (determined by morphological, phenological and reproductive patterns in males and females) throughout the emergence waves of one wild population of phytophagous insects, *Lobesia botrana* (Order: Lepidoptera, family: Tortricidae [Denis & Schiffermüller, 1775]), collected from different host plants. We measured the emergence phenology (emergence rank throughout an emergence wave) of adult males and females originating from larvae that we collected in a vineyard on two different grape varieties (Mourverdre and Syrah). We use the term 'emergence' throughout to refer specifically to the timing of adult eclosion from pupae. This timing can reflect both intrinsic factors (such as genetic or physiological differences) and extrinsic factors (such as variation in egg-laying date or larval development speed), and may therefore integrate multiple stages of the life cycle, and is notably dependent on larval quality. Under controlled conditions, we tested for the link emergence rank and grape variety have on different parameters related to freshly emerged females (probability of successful mating, latency to mate, mating duration, fecundity, fertility and longevity) and males (probability of successful mating, latency to mate, mating duration, size of the spermatophore transferred to females and longevity). By pairing wild-caught individuals with standardised laboratory mates, we aimed to isolate variation due to the wild individuals themselves. Our goal is to document how emergence timing is correlated with multiple components of individual quality in this system.

METHODS

Ethical note

All experiments adhered to French regulations governing animal experimentation. The subjects were reared in controlled laboratory conditions and regularly fed to ensure a healthy population (details on rearing methods are provided below). Moths were handled with care, and the abiotic conditions, including temperature, humidity and photoperiod (24 ± 1°C, 60 ± 10% RH at natural photoperiod, see below), were matched to those in their natural habitat. Prior to dissection, females were placed in a freezer at −25°C for 10 min.

Study model and field sampling

L. botrana is one of the major pests of grapes (*Vitis vinifera*) (Gilligan et al., 2011). It is widely distributed, occurring in almost all European vineyards, and is expanding geographically, with various favourable areas for its establishment around the globe (Rank et al., 2020). *L. botrana*, undergoes several generations per year, with each generation potentially experiencing different environmental conditions. In this species, reproduction and many life history traits are a nutrient-limited process for both sexes, largely related to the individuals' energy reserves accumulated during the larval stages, and particularly to the nature of the host plants on which the larvae fed (Moreau et al., 2017; Muller, Thiéry, et al., 2015; Torres-Vila et al., 2005). The larvae are polyphagous and can develop on almost any grape cultivar, but important differences in male and female reproductive output occur as a result of the plant quality (Moreau et al., 2017; Thiéry & Moreau, 2005).

L. botrana larvae (2047 individuals) were collected in the field during two consecutive days in early June 2016 which correspond to the first generation in the year. Larvae were sampled from two grape (*V. vinifera*) cultivars ('Syrah' and 'Mourvedre', $n = 852$ and $n = 1195$ respectively) in a single vineyard (Perpignan, France; N 42°44′7.063″, E 2°52′56.441″), ensuring the same abiotic conditions (temperature, light exposure, humidity) for larval development (Moreau et al., 2007; Muller, Thiéry, et al., 2015). The two chosen grape varieties are biochemically very different, especially in their phenolic contents (Jensen et al., 2008; Teissedre & Chervin, 2011), and they are known to influence moth life-history traits (Moreau et al., 2007; Thiéry & Moreau, 2005). While it is difficult to assess compositional factor with certainty, some evidence suggests lower concentrations of gallic acid, catechins, anthocyanins and sugars in Mourvedre relative to Syrah (Jensen et al., 2008). The collected larvae were late instars (L5), which are the most visible and recognizable in the field. L5 larvae were identified based on their size, following the head-capsule width criteria described by (Delbac et al., 2010). All individuals were at the L5 stage at collection, ensuring comparable larval developmental status despite potential variation in oviposition dates. L5 of *L. botrana* were collected in young flower buds called 'nests', following (Moreau et al., 2006). Each nest contains only a single larva. Characteristically in this pest species, most larvae complete their development in a single grape bunch, and generally a single nest (Delbac & Thiéry, 2016; Torres-Vila & Rodríguez-Molina, 2002). Only one larva was collected from a single grape bunch, reducing effects of genetic relatedness, and brought back to the laboratory.

Larvae were maintained in small polyethylene boxes (18 × 12 cm, height 6 cm) and fed ad libitum on bunches from their own cultivar, collected in the same locality, at 24 ± 1°C, 60 ± 10% RH at natural photoperiod until the end of their development. Larvae were checked daily until pupation, upon which pupae were carefully removed from the flower buds, weighed to the nearest 0.01 mg using a Precisa 262 SMA-FR microbalance and placed individually in glass tubes (70 × 9 mm diameter) stoppered with cotton plugs, labelled and stored at 23°C under natural photoperiod. Adults were sexed immediately after emergence by examination of the ventral tip of the abdomen. We recorded: (i) pupal mass, (ii) the date of emergence (used to assess the position of individuals in the emergence wave, hereafter termed as emergence rank) and (iii) the emergence rate (emergence success) from all pupae collected. Emerged adults resulting from the two grape varieties were used to evaluate the reproductive output of females and males. Emergence rank is a numeric variable representing the chronological sequence of emergence based on calendar day. Rank 1 corresponds to individuals emerging on the first observed emergence day. The rank number then increased with each subsequent day of the experiment, regardless of whether emergence occurred or not. For example, if emergence occurred on day 1 (rank 1), none on day 2 (rank 2) and individuals emerged on day 3, these individuals were assigned rank 3. Individuals emerging on the same day were assigned the same rank. This variable was used instead of raw emergence day to standardise emergence timing across experimental cohorts and to capture the position of individuals within the emergence wave.

Origin of laboratory male and female L. botrana

To assess the reproductive success of insects collected from the field as larvae, we paired them with standardised laboratory-reared partners from an INRAe Bordeaux strain. This approach, based on established procedures (Lorrain-Soligon et al., 2024; Thiéry & Moreau, 2005), allowed us to isolate the effects of the grape cultivar on the reproductive traits of the field-collected individuals by providing a standardised mating partner. This rearing line is maintained with a substantial number of caged adults (several thousand a week) to avoid genetic drift. The stock colony is maintained without diapause on an artificial diet, with the following composition: 150 mL water, 3 g agar, 9 g maize flour, 11 g wheatgerm, 9 g yeast, 0.9 g ascorbic acid, 0.3 g benzoic acid, 0.3 mL maize oil, 0.3 g Nipagine and 0.2 g Iprodione, at 24 ± 1°C, 60 ± 10% RH with a photoperiod of light/dark (LD) 15: 8 h + 1 of dusk. The first 15 photophase hours were at 1000 lux luminosity and the last one (dusk) at 25 lux. Males and females were placed in a large cage and bands of waxed paper (15*2 cm) were hung for oviposition support. Once the paper had received a sufficient number of eggs, it was placed in a plastic box containing the artificial larval diet. The larvae were maintained at a density of 100 individuals per 300 mL of diet.

We collected final instar larvae from our colony stocks daily and placed them in small piece of cardboard. Larvae were checked daily until pupation, upon which pupae were gently extracted from cardboard. To minimise potential effects of emergence timing on reproductive performance, only individuals from the laboratory strain emerging within the central emergence peak were retained as standardised mating partners, while early and late emerging individuals were discarded. Pupae were weighed to the nearest 0.01 mg on a Precisa 262 SMA-FR microbalance and placed individually in glass tubes (70 × 9 mm diameter) stoppered with cotton plugs, and then stored at 22°C under natural photoperiod, in the same laboratory and under the same conditions as field originating larvae. Pupae were checked every morning, and newly emerged adults were sexed. Only newly emerging virgin adults were used for subsequent experiments under the same conditions as rearing.

Mating success and reproductive output of field collected females

Three hundred seventy-five females reared from larvae collected in the field (187 from Syrah and 190 from Mourvedre, on average 13 per day) were used for this experiment and tested across 13 days from 16/06/2016 to 29/06/2016, just 1 day after their emergence. At dusk, one 1-day-old virgin female from one cultivar was placed into a mating tube (100 × 15 mm diameter) with one 1-day-old virgin standardised male originating from the stock population. We observed the pair for up to 4 h and recorded whether they copulated (Iltis et al., 2020; Muller, Arenas, et al., 2016), because individuals did not mate after this duration. Immediately after copulation, the male was removed from the mating tube (opening the cotton plug and carefully transferring the targeted individual into a new tube using a smaller glass tube to avoid physical contact and minimise handling stress) and the female was free to lay its eggs into the tube until its death (females do not feed or drink while laying eggs). We recorded: (i) the percentage of mated females, as determined by the production of at least one fertile egg during the female's lifetime, (ii) the latency period before mating (the time from the formation of the pair to copulation),

(iii) the duration of mating (the time spent copulating) was recorded only for fertile mating, (iv) total achieved fecundity (total number of eggs produced per female), (v) female fertility (percentage of hatched eggs) and (vi) female longevity, as determined by the number of days till death. All life-history traits were recorded blind (origin of the female cultivar unknown by the experimenter).

Mating success of field males and spermatophore size

Two hundred forty-nine males reared from larvae collected in the field (114 from Syrah and 135 from Mourvedre, in average 9 per day, range = [0–37]) were used for these analysis and tested across 9 days from 17/06/2016 to 26/06/2016, just 1 day after their emergence. At dusk, one 1-day-old virgin male from one cultivar was placed into a mating tube (100 * 15 mm diameter) with one 1-day-old virgin standardised female originating from the stock population. We observed the pair for up to 4 h and recorded whether they copulated. Immediately after copulation, females were frozen at −25°C for 10 min and then were dissected on a glass slide. The bursa copulatrix containing the male spermatophore was removed in order to estimate its size. The spermatophore produced by males *L. botrana* is very small (less than 1 mg) and consequently difficult to accurately weigh. Estimating spermatophore size by extrapolating its volume is a classical method used in previous works on *L. botrana* (Lorrain-Soligon et al., 2024; Muller, Thiéry, et al., 2015; Torres-Vila et al., 1999). To assess this size, dimensions (length l, width w and thickness t) were measured under a stereomicroscope (NIKON SMZ1500) with a magnification of 20X. The volume of the spermatophore was estimated as an ellipsoid balloon as in (Torres-Vila et al., 1999) ($V = \pi/6\ (l \times w \times t)$). We recorded: (i) the percentage of mated males, as determined by the presence of spermatophore in the genital duct of females, (ii) the latency period before mating (the time from the formation of the pair to copulation), (iii) the duration of mating (the time spent copulating) for fertile mating, (iv) the size of the spermatophore and (v) male longevity, as determined by the number of days till death.

Statistical analysis

All statistical analyses were performed using R 3.6.3 (R Core Team, 2020) and Rstudio v1.1.419. We computed Linear Models (LMs, lm function) and Generalised Linear Models (GLMs, glm function) using the *lme4* package (Bates et al., 2015). Models were chosen according to the distribution of residuals and the adequacy of model assumptions (including error distribution, link function, collinearity between predictors and dispersion), tested using the check_model function from the *performance* package (Lüdecke et al., 2020). The normal distribution of residuals from linear models was checked using a Shapiro test (shapiro.test function, implemented in the R environment (R Core Team, 2020)). Binomial and Poisson GLMs were checked for overdispersion. For all tests, the significance level was set at 0.05, and marginally significant results were considered at 0.10. We used a top-down selection process (function drop1) with p-value as a criterion, to define the best model, retaining only variables that were kept during the selection process. When the interaction between two categorical co-variates was significant, we used an emmeans post-hoc test within the *emmeans* package (Lenth, 2023). When the interaction between one categorical and one continuous variable was significant, we performed the regression independently for each category as a post-hoc test. As described above, for all analyses, we used the emergence date to assess the position of individuals in the emergence wave, termed as emergence rank.

Pattern of emergence

Difference in emergence rate (binomial glm), as well as differences in day at emergence (Poisson glm) were tested according to grape variety, sex (determined in emerging adults) and their interaction (which were set as predictor variables). Difference in pupal mass (gamma glm) was tested according to grape variety, sex, emergence rank and their triple interaction as predictor variables.

Females' mating success

Females' probability of successful mating and fertility (as a proportion of fertile eggs compared to the total number of eggs laid, both tested using binomial GLMs), latency to mate, mating duration, fecundity and longevity (quasipoisson GLMs) were tested using grape variety, emergence rank and their interaction as predictor variables. As latency to mate (glm quasipoisson; Estimate = −0.274, SE = 0.120, t-value = −2.275, p-value = 0.025), duration of mating (glm quasipoisson; Estimate = 0.064, SE = 0.036, t-value = 1.774, p-value = 0.079) and longevity (glm quasipoisson; Estimate = 0.104, SE = 0.031, t-value = 3.347, p-value = 0.001) were influenced by female pupal mass; female pupal mass was added as a covariate in the models regarding these parameters.

Males' mating success

Males' probability of successful mating (binomial glm), latency to mate, mating duration (both using quasipoisson glms), spermatophore volume (gamma glm) and longevity (lm) were tested using grape variety, emergence rank and their interaction as predictor variables. As latency to mate (glm quasipoisson; Estimate = 0.358, SE = 0.176, t-value = 2.039, p-value = 0.043), spermatophore size (glm gamma; Estimate = −0.008, SE = 0.002, t-value = −5.033, p-value <0.001) and longevity (lm; Estimate = 0.892, SE = 0.178, t-value = 5.006, p-value <0.001) were influenced by male pupal mass, male pupal mass was added as a covariate in the models regarding these parameters.

RESULTS

Pattern of emergence

From the 2047 collected larvae, we obtained 1526 emerged adults (Syrah: $n = 638$, 74.88% of the collected larvae; and Mourvedre: $n = 888$, 74.31% of the collected larvae). Emergence rate was identical between larvae originating from the two varieties and independent of sex (estimated at the adult stage, Table 1). Emergence rank was significantly earlier for larvae originating from Syrah as compared to larvae originating from Mourvedre, and significantly earlier for males as compared to females (Figure 1a, Table 1). However, emergence rank was not influenced by the interaction between grape variety and sex. Emergence wave spanned from day 3 to 14 in Mourvedre (median = 7) and from day 1 to 14 in Syrah (median = 6).

Pupal mass significantly varied according to sex, emergence rank, grape variety and the interaction between sex and grape variety. Specifically, pupal mass decreased with later emergence, was higher for

TABLE 1 Statistical models used and results on the different variables studied.

Dependant variable	Model	Explanatory variable	Estimate	SE	t/z value	*p*-value	Significance
Emergence rate	Binomial glm	Grape variety	<0.001	9098.000	0	1	
		Sex	−18.550	6062.000	−0.003	0.998	
		Grape variety*Sex	18.550	12170.000	0.002	0.999	
Emergence Rank	Poisson glm	Grape variety	−0.173	0.021	−8.353	<0.001	***
		Sex	−0.052	0.020	−2.562	0.0104	*
Pupal mass	Gamma glm	Sex	0.040	0.002	25.949	<0.001	***
		Emergence Rank	0.002	0.000	8.545	<0.001	***
		Grape variety	−0.004	0.001	−2.829	0.005	**
		Grape variety*Sex	−0.006	0.002	−2.681	0.007	**
Females' probability to mate	Binomial glm	Grape variety	−1.324	0.673	−1.967	0.049	*
		Emergence Rank	−0.127	0.066	−1.932	0.053	.
		Grape variety*Emergence Rank	0.197	0.087	2.276	0.023	*
Females' latency to mate	Quasipoisson glm	Grape variety	0.563	0.241	2.334	0.022	*
Females' mating duration	Quasipoisson glm	Grape variety	−0.283	0.270	−1.05	0.296	
		Emergence Rank	−0.056	0.036	−1.568	0.120	
		Grape variety*Emergence Rank	0.051	0.041	1.253	0.213	
Females' fecundity	Quasipoisson glm	Grape variety	−1.414	0.539	−2.623	0.010	*
		Emergence Rank	−0.184	0.059	−3.107	0.002	**
		Grape variety*Emergence Rank	0.158	0.079	1.987	0.050	*
Females' fertility	Binomial glm	Grape variety	−0.735	0.444	−1.654	0.098	.
		Emergence Rank	−0.263	0.098	−2.692	0.007	**
Females' longevity	Quasipoisson glm	Grape variety	−0.404	0.302	−1.338	0.181	
		Emergence Rank	−0.058	0.039	−1.465	0.143	
		Grape variety*Emergence Rank	0.056	0.046	1.223	0.221	
Males' probability to mate	Binomial glm	Grape variety	−0.963	0.351	−2.742	0.006	**
		Emergence Rank	−0.183	0.074	−2.485	0.013	*
Males' latency to mate	Quasipoisson glm	Grape variety	0.748	0.254	2.944	0.004	**
		Emergence Rank	0.193	0.059	3.299	0.001	**
Males' mating duration	Quasipoisson glm	Grape variety	0.235	0.055	4.27	<0.001	***
Spermatophore size	Gamma glm	Grape variety	0.018	0.008	2.331	0.021	*
		Emergence Rank	0.003	0.001	3.043	0.003	**
		Grape variety*Emergence Rank	−0.002	0.001	−1.856	0.065	.
Males' longevity	Lm	Emergence Rank	−0.312	0.061	−5.151	<0.001	***

Note: Emergence rank is a numeric variable indicating the chronological order of emergence based on calendar day. Rank 1 corresponds to individuals emerging on the first observed day, with rank numbers increasing on each subsequent day. The reference level for grape variety is Syrah, and the reference level for sex is female. Note that for the models explaining variations in pupal mass and spermatophore size, Gamma GLMs with an inverse link function were used, meaning that the direction of the response is inverted.

females compared to males, higher for larvae originating from Syrah, and the difference between grape varieties was bigger in males compared to females (Figure 1b, Table 2).

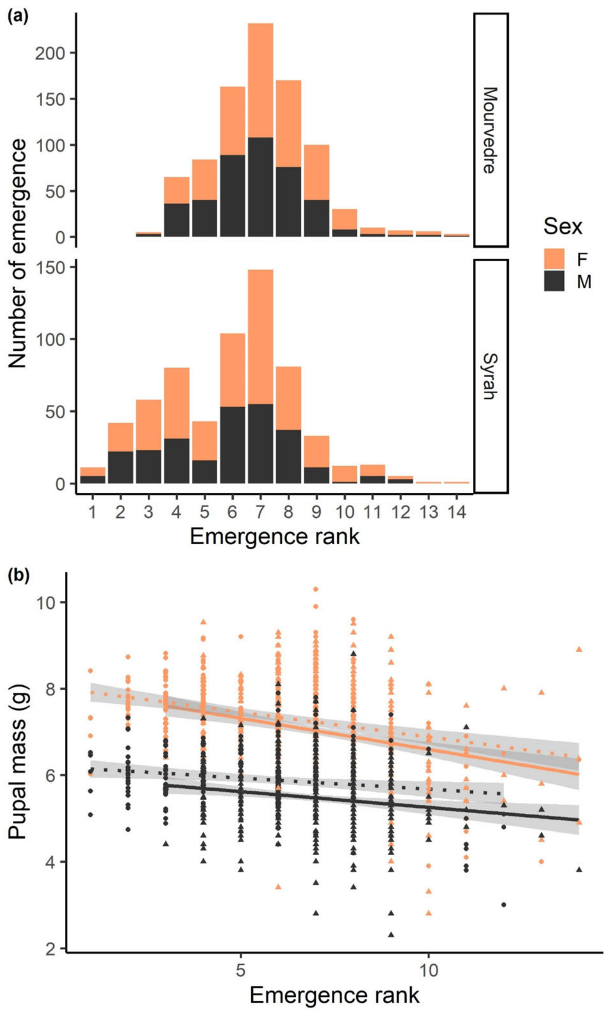

FIGURE 1 (a) Emergence wave of females and males and (b) pupal mass of *Lobesia botrana* emerging from larvae collected on two grape varieties (Mourvedre or Syrah) as a function of emergence rank. Emergence rank 1 correspond to the first observed emergence. In panel (b), triangles and circles represent Mourvedre and Syrah, respectively. Orange and black indicate females and males, respectively. Solid and dotted lines, along with their 95% confidence intervals, depict regression trends for Mourvedre and Syrah, respectively.

Females' mating success

Females' probability of successful mating was marginally influenced by emergence rank, and significantly influenced by grape variety and their interaction (Figure 2a, Table 1). Specifically, females' probability of successful mating marginally decreased for late emerging individuals in females originating from Mourvedre (Estimate = −0.127, SE = 0.066, z-value = −1.932, p-value = 0.053, Figure 2a), but it was not influenced by emergence rank in females originating from Syrah (Estimate = 0.070, SE = 0.056, z-value = 1.243, p-value = 0.214, Figure 2a). Females' latency to mate was significantly influenced only by grape variety, latency to mate being longer for females originating from Syrah (Figure 2b, Table 1), while mating duration was neither influenced by grape variety, emergence rank nor their interaction (Figure 2c, Table 1). Females' fecundity was significantly influenced by grape variety, emergence rank and their interaction. Specifically, females' fecundity overall decreased for late emerging individuals and was higher for larvae originating from Mourvedre (Figure 2d, Table 1). Females' fecundity significantly decreased for late emerging individuals in females originating from Mourvedre (Estimate = −0.184, SE = 0.062, t-value = −2.980, p-value = 0.005, Figure 2d), but it remained constant across emergence wave for larvae originating from Syrah (Estimate = −0.026, SE = 0.051, t-value = −0.518, p-value = 0.606, Figure 2d). Fertility however was only influenced by emergence rank and marginally by grape variety, but not by their interaction (Figure 2e, Table 1), significantly decreasing for late emerging individuals for both cultivars, and being marginally higher for larvae originating from Mourvedre (Figure 2e, Table 1). Females' longevity was neither influenced by grape variety, emergence rank nor their interaction (Figure 2f, Table 1).

Males' mating success

Males' probability of successful mating and latency to mate were significantly influenced by grape variety and emergence rank but not their interaction (Figure 3a, Table 1). Specifically, males' probability of successful mating significantly decreased for late-emerging individuals for both cultivars and was significantly higher for larvae originating from Mourvedre. Males' latency to mate significantly increased for late-emerging individuals and was significantly lower for larvae originating from Mourvedre (Figure 3b, Table 1). Mating duration was only significantly influenced by grape variety, being shorter for males

TABLE 2 Post-hoc analyses for the differences between males and females and between the two grape varieties (Mourvedre and Syrah), for the mass of emerging pupae found on the field.

Contrast	Comparison	Estimate	SE	Df	t/z	*p*
F	Mourvedre-Syrah	−0.004	0.001	1502	−2.829	0.005
M	Mourvedre-Syrah	−0.01	0.002	1502	−5.259	<0.001
Mourvedre	F-M	0.04	0.002	1502	25.949	<0.001
Syrah	F-M	0.034	0.002	1502	19.418	<0.001

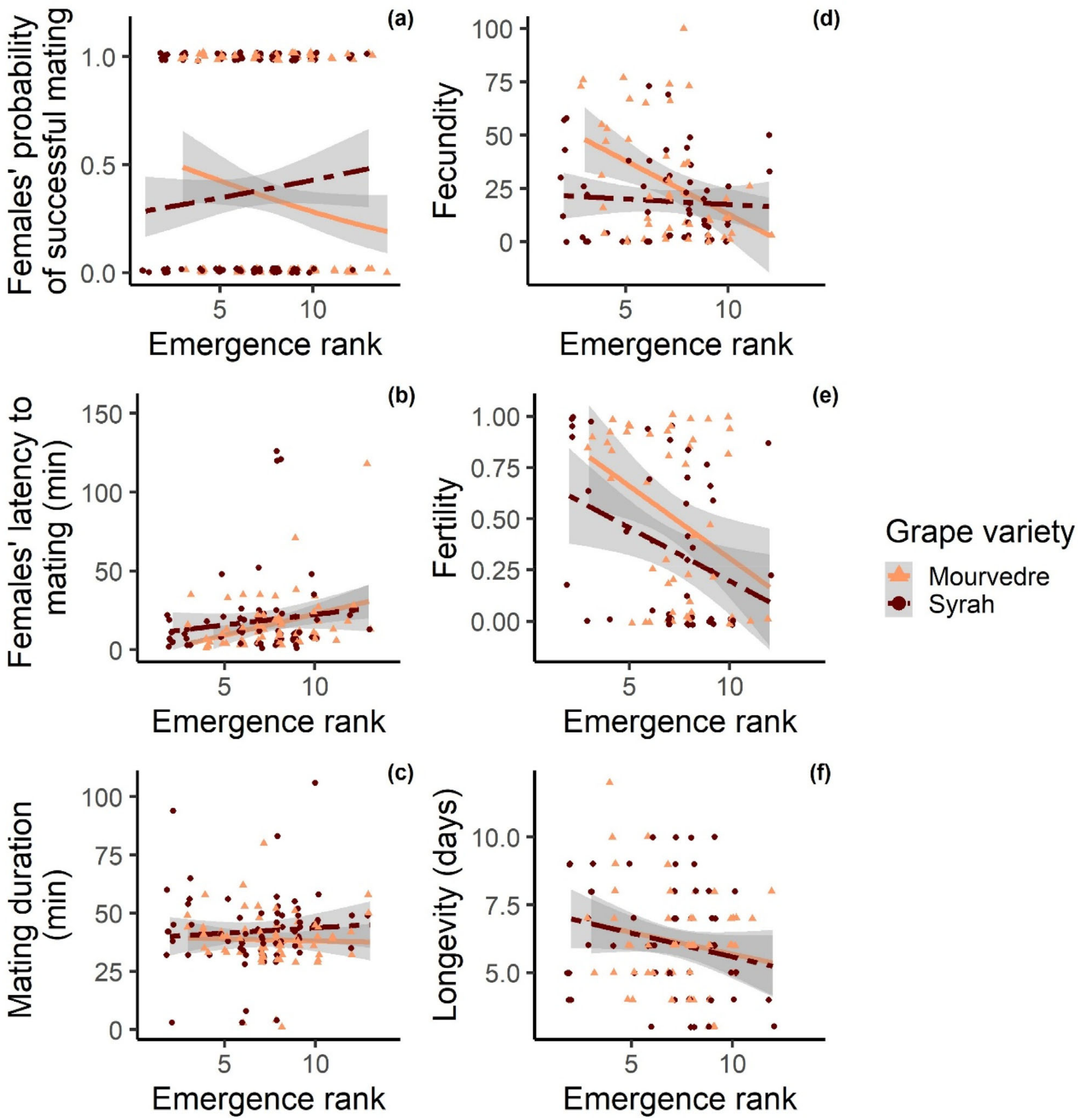

FIGURE 2 (a) Probability of successful mating, (b) latency to mating, (c), mating duration, (d) fecundity, (e) fertility and (f) longevity for field-originating females *Lobesia botrana* emerging from larvae collected on two grape varieties (Mourvedre or Syrah) as a function of emergence rank. Emergence rank 1 corresponds to the first observed emergence. Lines represent the regression line with the 95% confidence interval.

originating from Mourvedre (Figure 3c, Table 1). The size of the spermatophore transferred to females was influenced by grape variety, emergence rank and marginally by their interaction (Figure 3d, Table 1). Spermatophore size overall significantly decreased for late-emerging individuals and was significantly bigger for individuals originating from Mourvedre (Figure 3d, Table 1). Specifically, spermatophore size significantly decreased for late-emerging individuals originating from Mourvedre (Estimate $= -0.004$, SE $= 0.001$, t-value $= -4.125$, p-value<0.001), but spermatophore size of males originating from Syrah was not influenced by emergence rank (Estimate $= -0.001$, SE $= 0.001$, t-value $= -1.375$, p-value $= 0.175$). Lastly, males' longevity was only significantly influenced by emergence rank, decreasing for late-emerging individuals (Figure 3e, Table 1).

DISCUSSION

This study documents clear associations between adult emergence timing and multiple fitness-related traits in *L. botrana*. Specifically,

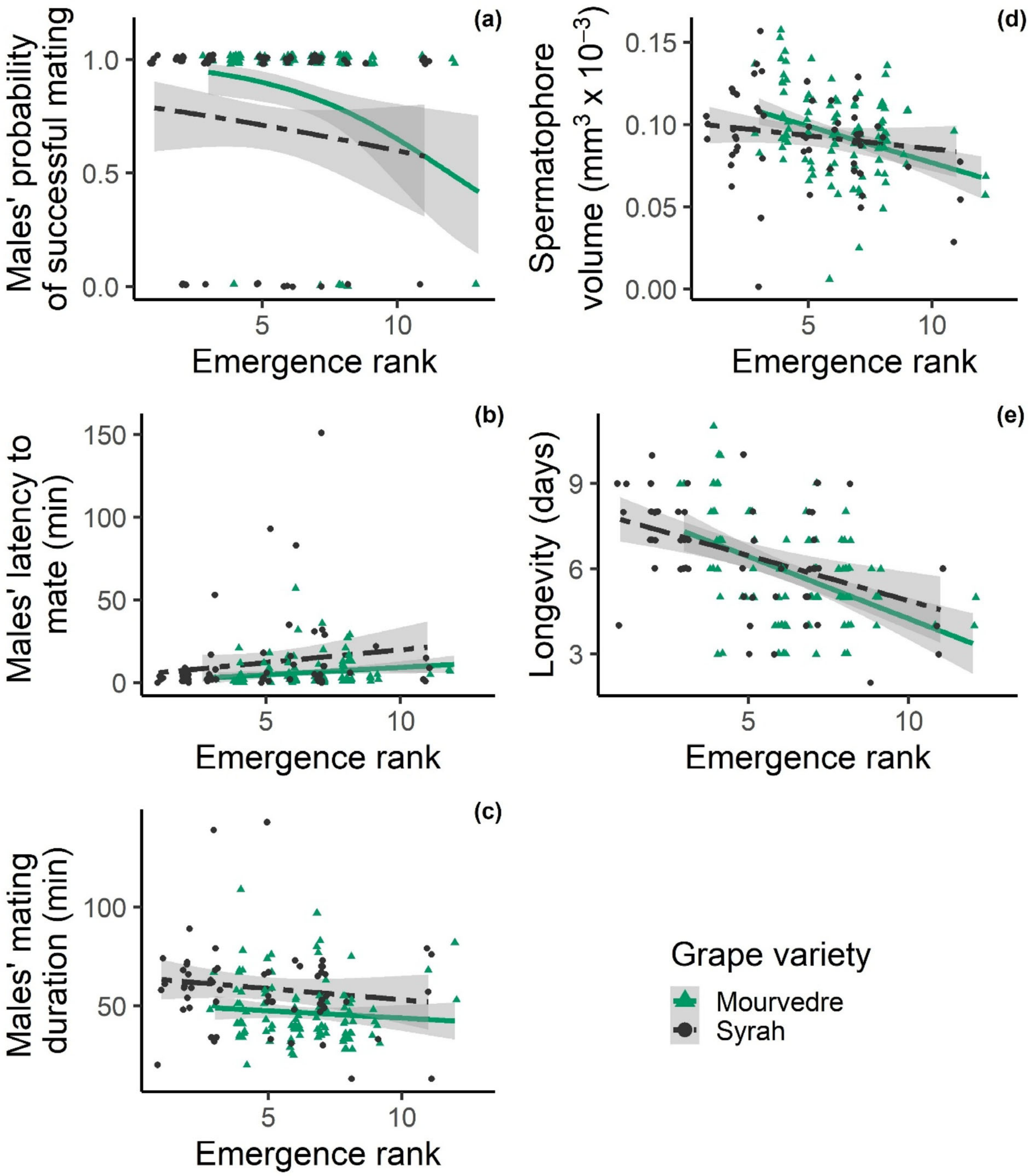

FIGURE 3 (a) Probability of successful mating, (b) latency to mating, (c), mating duration, (d) spermatophore volume and (e) longevity for field-originating males *Lobesia botrana* emerging from larvae collected on two grape varieties (Mourvedre or Syrah) as a function of emergence rank. Emergence rank 1 corresponds to the first observed emergence. Lines represent the regression line with the 95% confidence interval.

our findings reveal several critical patterns: (i) later emergence reduces pupae mass and mating success in all individuals, (ii) in females, later emergence was additionally linked to reduced fecundity and fertility and (iii) in males later emergence was also associated with increased mating latency, reduced longevity and, in those fed on Mourvedre, spermatophore volume. These effects were further modulated by the grape variety the larvae fed on, being more pronounced in individuals originating from Mourvedre, indicating a complex interplay between emergence timing and host plant quality. Importantly, because we did not experimentally manipulate emergence timing, we cannot determine whether late emergence causes low fitness, or whether individuals in poorer condition develop more slowly and consequently emerge later.

Host plant effects on the developmental dynamics

Larval host plant quality is considered to be a key determinant of the adult phenotype, and the performance of both males and females (Bede et al., 2007; Lin et al., 2018; Moreau et al., 2017; Muller, Vogelweith, et al., 2015). As such, our study emphasises that the emergence phenology of *L. botrana* was different between the two grape varieties we studied ('Syrah' and 'Mourvedre'), a classical result in the species (Thiéry et al., 2014). Despite a comparable emergence rate for both cultivars, larvae from Syrah emerged earlier on average. Grape varieties have different concentrations of specific molecules, such as sugars, amino acids and phenolic compounds (Jensen et al., 2008; Orlandi et al., 2015; Zapata et al., 2017), that are crucial for larval growth and energy storage (Moreau et al., 2006). The earlier adult emergence in Syrah could thus be due to energy available from the larval development stage, and derived from the host plant (Awmack & Leather, 2002; Oberhauser, 1997). The lower concentrations of gallic acid, catechins, anthocyanins and sugars in Mourvedre relative to Syrah found in some studies (Jensen et al., 2008) suggest that this cultivar may provide larvae with lower nutritional quality. If this happens to be true, lower sugar content may limit energy accumulation during larval development, while lower phenolic content may reduce both antioxidant availability and plant defences. This chemical profile is consistent with our observation that individuals from Mourvedre emerged later and at lower pupal mass than those from Syrah, suggesting slower larval development on this host. If we suppose that eggs were laid in the same time, then differences in emergence timing between individuals and cultivars may indicate a plastic larval development time within the same cohort (Blanckenhorn, 1998) or reflect between-family or genotypic variation (Lehmann & Wheat, 2022; Yurk & Powell, 2010). This strategy may compensate for the risk of exposure to extreme climatic events or predation/parasitism risk (Denver et al., 1998; Relyea, 2007), whose demographic consequences need to be investigated. Additionally, for the two cultivars, our observations revealed that males typically emerge earlier than females, a general pattern in insects known as protandry (Wiklund & Fagerström, 1977). Our results align with the classical results observed in the species *L. botrana* regarding sexual dimorphism in emergence timing and size (Torres-Vila et al., 2005).

Reduction in pupal mass and adult longevity with later emergence

For the two cultivars, later-emerging *L. botrana* individuals emerged with a decreased mass, and later emerging males also expressed shorter adult longevity. This difference between early- and late-emerging individuals may primarily originate from lower larval resource assimilation efficiency over time (Barbehenn et al., 2014), or from intrinsic differences in metabolic efficiency and immune investment. Individuals emerging at a smaller size might have had smaller nutrients or energy during development (Briegel, 1990; Calvo & Molina, 2005; Honěk, 1993), finally impacting longevity (Moreau et al., 2006). It is important to note that in the first annual generation, the emergence rank of individuals is not purely stochastic but may be strongly influenced by the emergence pattern of parental moths following diapause in the field. This post-diapause timing may reflect inherited physiological traits or responses to environmental cues during overwintering, which could influence both emergence phenology and subsequent fitness (Posledovich et al., 2015; Powell et al., 2020). The timing of adult emergence in our study likely reflects a combination of factors occurring earlier in development. All larvae were collected in early June, but they may have originated from eggs laid on different dates, or developed at different rates depending on microclimatic conditions or genetic background. We therefore emphasise that emergence timing here is a useful integrative measure of phenological variation, but does not identify the developmental stage at which differences first arise.

Pre-mating: motivation to mate with late-emerging individuals

Mating success of male and female *L. botrana*, when paired with standardised, lab-reared individuals, decreased throughout the emergence wave. This decline can be attributed to the fact that later-emerging males and females are smaller in our study, and therefore less attractive to potential mates (Beeler et al., 2002; Bonduriansky, 2001). Consequently, the standardised laboratory partner may also be less inclined to mate with these smaller individuals. Additionally, these later-emerging individuals may be less active due to having fewer energy reserves. Under natural conditions, this would limit their ability to search for and compete for mates effectively (Boggs, 2009; Wiley & Poston, 1996). This underscores the importance of early emergence, where larger body size and greater energy reserves enhance mating success and overall fitness. For lab standardised males, the latency period before mating was longer when they were confronted with late emerging females. This seems to be adaptive as mating with late emerging females might imply lower fecundity and fertility as exemplified in this study. But these results also suggest that both males and females are able to detect the quality (through mass for example, which is related to their emergence wave) of their mate, which might be achieved by differences in pheromone or individuals' cuticular pheromones (Lorrain-Soligon et al., 2024). Late emerging individuals may have fewer energy reserves available to produce such chemical compounds, which might need to be investigated.

Post-mating: consequences to mate with late-emerging individuals

When individuals manage to mate despite emerging late, they incur significant costs due to having fewer resources available, which affects both males and females. These later-emerging individuals generally have smaller pupal sizes, which correlates with reduced fecundity in females and smaller spermatophore sizes in males. A high-quality food ingested by larvae and a bigger size may promote higher reproductive output for both sexes (Dmitriew & Rowe, 2011; Moreau et al., 2006). As such, for lab-standardised females, to mate with late emerging males is costly since we showed that these males had smaller spermatophores, which might be linked to energy limitations, and which might impact female fecundity (McNamara et al., 2014; Muller, Thiéry, et al., 2016; Wedell & Karlsson, 2003). For lab-standardised males, to mate with late emerging females might imply lower fecundity and fertility as exemplified in this study.

Influence of host plant on emergence rank and related mating properties

Interestingly, we found that the larval cultivar might influence mating properties (Colasurdo et al., 2009; Moreau et al., 2006, 2016). Indeed, larvae originating from Mourvedre produced adults with a higher probability of successful mating (male and female), higher female fecundity, lower latency to mate in males, shorter mating duration and larger spermatophores transferred to females, despite a later emergence date, lower pupal mass and longer latency to mate for females. Since all adult reproductive traits were measured under standardised laboratory conditions, where moths had unrestricted access to food. Such favourable conditions may allow individuals to partially compensate for developmental deficits, for example by increasing reproductive investment or mating activity once resources become abundant. Traits that are fixed before emergence, such as pupal mass, are less likely to be compensated, whereas behavioural and physiological traits expressed during adult life may be more plastic. Therefore, the apparent superior mating performance of adults originating from Mourvedre in the laboratory may reflect physiological compensation or selective survival of higher-quality individuals.

Interestingly, the impact of emergence timing on mating success and fitness is more pronounced in individuals originating from Mourvedre compared to Syrah. Indeed, as the emergence wave progresses, these advantages diminish significantly, with the fecundity of the female and spermatophore size of males originating from Mourvedre decreasing more with the timing of emergence than those coming from Syrah. This suggests that the quality of Mourvedre as a larval host is closely tied to the timing of emergence, with early-emerging individuals benefiting more from the resources available (Gidoin et al., 2015). In contrast, by the end of the emergence wave, the quality difference between Mourvedre and Syrah is no longer evident, indicating that the qualities of the host plant are not sustained throughout the entire emergence period. Consequently, the Mourvedre cultivar exhibits a greater penalty for late emergence, emphasising the importance of early emergence for maximising fitness benefits (Gidoin et al., 2015; Zonneveld, 1996). There might also be underlying genetic variation in the ability to develop on these varieties (LazareviĆ et al., 1998). These temporal effects may also be modulated by grapevine phenology, as the timing of plant developmental stages can influence the availability and composition of nutritional and defensive compounds in the berries (Caffarra et al., 2012). Thus, synchrony between larval development and optimal phenological stages of the host plant may be critical to fully exploiting host quality. Future research should focus on the underlying mechanisms driving these temporal changes in resource quality and their implications for population dynamics and management strategies.

CONCLUSION

This study, on large samples of wild individuals but conducted under controlled conditions, unequivocally demonstrates that the fitness of early- and late-emerging *L. botrana* adults is significantly different, highlighting the need to account for this parameter in behavioural studies. Overall, our results highlight that variation in adult emergence timing is strongly linked to variation in individual quality in this population of *L. botrana*. Future work should aim to disentangle the causal mechanisms underlying these associations, for example by manipulating host plant quality or rearing individuals at different times. Such studies would clarify whether emergence timing itself drives fitness differences, or whether both timing and fitness are consequences of underlying individual condition. Understanding these dynamics is crucial for developing more effective population dynamics mathematical models and management strategies for *L. botrana*, particularly in the context of changing environmental conditions and agricultural practices.

AUTHOR CONTRIBUTIONS

Léa Lorrain-Soligon: Writing – original draft; validation; visualization; writing – review and editing; formal analysis; data curation. **Mathilde Lebbar:** Investigation; methodology; writing – review and editing. **Denis Thiéry:** Investigation; methodology; validation; writing – review and editing. **Jérôme Moreau:** Conceptualization; investigation; funding acquisition; methodology; validation; writing – review and editing; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting the finding of this study are deposited in Zenodo under the doi: 10.5281/zenodo.17367188, https://zenodo.org/records/17367188 (Lorrain-Soligon et al., 2025).

ETHICS STATEMENT

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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