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ORIGINAL ARTICLE

Effects of population density on adult morphology and life-history traits of female Mediterranean flour moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae)

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Abstract. Intraspecific competition and food shortage due to high population density during early life can have a profound effect on adult fitness. Organisms often mitigate negative effects of high population density by adjusting resource allocation to adult morphological and life-history traits. In Lepidoptera with short-lived adults that do not feed, it is predicted that females developed from dense larval aggregations invest more in reproduction and traits linked to offspring survival. Here, we investigated the effects of larval population density on adult morphology and life-history traits in the female Mediterranean flour moth, *Ephestia kuehniella* by raising larvae at a range of population densities. Adults from high population density (16 larvae per g of food) had smaller head, thorax, and forewing compared to other densities. The allometric slope of forewing length with body mass did not differ among population densities, indicating no changes in adult wing morphology at high population density. However, we found that females emerged from larvae at high population density had bigger abdomens relative to body mass, indicating resource investment in reproduction, probably to mitigate the negative effects of crowding on egg production. Ovipositor length did not differ among population densities, indicating conservation of resources to structures with egg-laying function that affect offspring survival. Taken together, these results suggest that female *E. kuehniella* responding to high larval population density invest relatively more in reproduction, a life-history strategy that could alleviate negative effects of population density on fitness. This study also highlights the importance of a species' reproductive strategy in its adaptive response to environmental conditions, which is relevant to many capital breeders dependent on larval resources for reproduction.

INTRODUCTION

During development there is potential for organisms to allocate resources that can ultimately affect their fitness in response to environmental conditions, and particular growth phases can be influential watersheds (Campero et al., 2008; English et al., 2016; Pilakouta et al., 2016; De Gasperin et al., 2019). Holometabolous insects including moths and butterflies present exceptional examples because resources obtained during the larval stage are substantially reallocated during a transitional pupal stage (Rolff et al., 2019). Adults emerging from metamorphosis have forms and functions that are radically different from the larval stage (Yang, 2001); a phenomenon that is considered to have been a key driver of insect diversification (Rainford et al., 2014). As a result, juvenile resourcing has a strong influence on the developmental direction of adults, including phenotypic optimisation (Monaghan, 2008).

In Lepidoptera, intraspecific competition during early life-stages has a negative effect on the adult behaviour and life-history traits (Yang et al., 2015; Sanghvi et al., 2021). Moreover, crowding during development may also result in changes in the size and proportion of different morphological traits leading to allometric shifts (Dmitriew et al., 2009; Shi et al., 2015; Boggs & Niitepold, 2016). Among others, dispersal is a behaviour that could mitigate adverse larval crowding effects on reproductive output and offspring survival (Rankin & Burchsted, 1992). Flight, however, is an energy demanding process that draws resources away from reproduction and other life-history traits (Johnson, 1969; Tigreros & Davidowitz, 2019). In Lepidoptera, adult dispersal as a response to resource limitation and high population density differs among species (Tigreros & Davidowitz, 2019). In some butterflies and moths, adults that emerge from crowded and food-stressed larvae have reduced wing loading and relatively long forewings or high thoracic mass compared to adults emerged from non-stressed larvae (Saastamoinen et al., 2010; Shi et al., 2015; Jaumann and Snell-Rood, 2019; Rhainds, 2020). Such changes can enhance flight performance (Dudley, 1999; Tigreros & Davidowitz, 2019) and facilitate dispersal from deteriorating habitats, but are not observed in all Lepidoptera.

Lepidopterans that are income breeders with adults that forage and survive for long periods (Tammaru & Haukioja, 1996) use both larval- and adult- acquired resources for reproduction and survival. In capital breeders, however, adults are short-lived and do not feed (Tammaru & Haukioja, 1996) so dispersal can impose constraints on reproduction in many ways including delayed gonad development and oviposition (Kong et al., 2010). In those Lepidoptera in which reproduction and dispersal occur simultaneously (Jiang et al., 2010; Cheng et al., 2016), flight and reproduction draw from the same resource pool (Wheeler, 1996), so resources invested in flight cannot be utilized for egg production. In capital breeders, egg number is determined at the pupal stage (Boggs, 2009; Davis et al., 2016) and resource limitation during larval crowding can reduce fecundity. The egg load with which capital breeders emerge from the pupa (Davis et al., 2016) effects wing loading and relative forewing size and so lowers flight performance and increases its energetic cost (Tigreros & Davidowitz, 2019). Hence, any benefits of dispersal are likely to depend on reproductive strategy (capital or income breeders), adult lifespan, mating system and external factors such as predictability of future environment, distance to potential habitat and mate availability (Evenden et al., 2015; Boggs & Niitepold, 2016; Le Roy et al., 2019; Sanghvi et al., 2021). It is predicted that in species with a short adult life span and little or no adult feeding, crowded and food stressed females should respond by investing more in reproduction.

The resources obtained by butterfly and moth larvae determine the body mass and energy reserves of adults, and are allocated during metamorphosis to soma (head, thorax and wings) and non-soma (abdomen- reproductive tissue and gametes) in a hierarchical manner (Jervis et al., 2007; Boggs, 2009). The availability and allocation of resources determines the size of the body part and its body mass allometry (Nijhout & Grunert, 2010). In adult Lepidoptera, resources allocated to the abdomen are used for egg production (Boggs, 1981; Wickman & Karlsson, 1989) so that in capital breeders, female fecundity is positively correlated with adult abdomen mass/size (Wickman & Karlsson, 1989; Boggs, 2009; Kivela et al., 2012) and pupal/body mass (Berdegue et al., 1998; Tammaru et al., 2002; Heisswolf et al., 2009; Garrad et al., 2016; Walczak et al., 2017).

Females emerged from high larval population density may enhance reproductive success by investing directly in egg production (Boggs & Niitepold, 2016) or indirectly investing in offspring. Investment in offspring could include allocation to ovipositor and oviposition behaviour. The ovipositor is an egg laying structure and its morphology has evolved in response to substrate type and abiotic conditions (Sivinski et al., 2001; Sota et al., 2007; Hou et al., 2019) and is also developmentally- and morphologically-constrained by egg morphology (Yanagi & Tuda, 2012). Thus, changes in ovipositor size may interfere with the egg laying process and subsequent offspring development and survival. When and where eggs are placed determines the post-hatching environment of offspring including the level of intraspecific competition and resource quality. By spatially and temporally dispersing eggs, females may reduce the competition offspring experience (Anderson & Lofqvist, 1996; Jaumann & Snell-Rood, 2017). However, there is limited empirical evidence that females mitigate the negative effects of high population density on reproduction through changes in resource allocation patterns (Jannot et al., 2007; Boggs & Niitepold, 2016).

To our knowledge, no studies have reported the effects of population density on female adult morphology and life-history traits in the Mediterranean flour moth, *Ephestia kuehniella* (Lepidoptera: Pyralidae). This economically-important stored-product pest is particularly associated with flour mills and grain stores (Rees & Rangsi, 2004) where larvae are the most destructive stage feeding on flour and whole grains, and producing webbing attached to flour particles that can clog machinery and cause significant wastage (Jacob & Cox, 1977). Adults typically emerge in 4 weeks, do not feed and have a short life-span (Norris, 1934). Adult females lay about 300 eggs (Moghadamfar et al., 2020) deposited in clusters containing up to 200 (pers. observ.). It is not uncommon for females to lay their eggs in close proximity to each other. Newly emerged larvae feed at the site of hatching and have limited mobility, so that intraspecific competition for food increases as they develop. Therefore, it can be predicted that larval crowding conditions are correlated with adult female *E. kuehniella* fitness and any change in the environment experienced by juveniles will affect the adult phenotype.

Resource limited conditions force trade-offs between reproduction and other life-history traits. As short-lived capital breeders, *E. kuehniella* transfer larval resources directly to egg production so that adult females emerge with a full egg load. Increased relative resource allocation to reproduction may be the optimal strategy to alleviate the impacts of high population density. In this study, *E. kuehniella* were reared at four different population densities to examine the effects of larval crowding on morphological and life-history traits of adult females. We predicted that larval crowding that resulted in reduced per capita resources would cause females to increase investment in abdominal depth and ovipositor rather than thorax and forewing, which are related to dispersal. We expected that the pattern of daily oviposition would differ between females from high and low population densities and so examined total oviposition period, oviposition pattern, mating frequency, and adult longevity.

MATERIALS AND METHODS

Insects

Insects for this study were obtained from a laboratory colony of *E. kuehniella* initially established with more than 100 adults collected from feed mills at Turks Poultry Farm, Foxton, New Zealand and maintained at 25 ± 1°C and 60 ± 10% relative humidity with a photoperiod of 14L : 10D cycle. Adults were sexed based on genitalia (Bhavanam & Trewick, 2017) and seven males and seven females were introduced into 8 cm diameter × 10 cm height clear containers with a ventilated lid. After mating, females laid eggs in the same containers on a porous plastic sheet provided as oviposition substrate. Eggs were collected and incubated in

12 cm Petri dishes. Larvae were reared in 500 mL transparent plastic containers containing 50 g of prepared dietary medium comprising wholemeal wheat flour (43.5%), maize meal (43.5%), brewer's yeast (3%) and glycerine (10%) until pupation (Lima Filho et al., 2001). Two hundred larvae were reared per container, which is the optimal rearing density for this species (Bhavanam et al., 2012). A paper towel (25 × 25 cm) was placed in each container for pupation, and mature pupae were transferred to individual glass vials (2 cm in diameter × 7.5 cm in height). Upon emergence, adults were sexed and transferred to containers for mating and oviposition for further rearing. Moths were reared for three generations in the laboratory prior to this study and in each generation several thousand larvae were reared to maintain heterogeneity.

Population densities

Ephestia kuehniella were reared at four population densities: 100, 200, 400 or 800 larvae on a constant amount of diet (50 g), which is equivalent to densities of 2, 4, 8 and 16 larvae per g of food, respectively. These densities simulate the conditions often experienced by *E. kuehniella*, when feeding on stored food products (Moghadamfar et al., 2020) in closed environments such as storage facilities. Females have high fecundity (Moghadamfar et al., 2020) and during peak oviposition, female lays eggs in clusters of 150–200 inside flour and often in the vicinity of other clusters, that can lead to larval crowding. Previous studies have shown that a negative influence of population density on larval and adult life-history traits occurred at a density of 800 larvae/50 g of diet (16 larvae per g of diet) (Bhavanam et al., 2012; Bhavanam & Trewick, 2017).

Establishment of population densities

To establish twenty replicates of each for the four population densities, 20 sets of containers with stock culture adults were developed. Each set was prepared on a different day and consisted of 5 mating containers. In each mating container, ten 1-d-old virgin adults (equal sex-ratio) were housed. On the 3rd day after pairing, eggs from all five containers of each set were collected into a 12 cm Petri dish and used to set-up a single replicate of each of the four experimental population densities. Thus, twenty replicates of each population density were developed using eggs taken from twenty different sets of adults. This procedure minimized pseudo-replication. Out of the 20 replicates prepared for each density, ten replicates were used to determine the effects of population density on adult morphology and the remaining replicates were used to study the impact of population density on adult life-history traits.

A preliminary study conducted in the same environmental conditions as this study showed that the egg hatching success of this species was 96 ± 0.3%. Therefore, to obtain population densities of 2, 4, 8 and 16 larvae per g of food, 104, 208, 416 and 832 eggs, respectively were carefully inoculated in separate 500 mL clear plastic containers with a fine paint brush and the containers were closed with a lid. Each container had 50 g of the food medium and a crumpled paper towel (25 × 25 cm) for pupation. Larvae of *E. kuehniella* live and feed in the upper layer of food (Hill, 2002), and move deeper as it is consumed but remain inside the food medium until pupation. In the present study, the diet occupied about 1/4th of the container space and at population densities of 2, 4 and 8 larvae per g of food, the dietary medium was not entirely consumed by larvae. However, at a population density of 16 larvae per g of food, food was exhausted towards the end of the larval stage. Hence, last instars experienced both food shortage and crowding but were never space-limited as larvae tended to move to the top of the container and paper towel. Mature pupae were collected daily from each container of each population density and placed in individual labelled glass vials (2 cm in diameter × 7.5 cm in height). Pupae were checked daily for adult emergence and used for the data collection.

Adult morphology

To determine effects of population density on adult morphological traits and their allometric relationship with body mass, within 12 h of adult emergence, 30 adult females from each population density (three or four females per container) were selected at random and anesthetized with CO_2. For each female adult body mass was measured using an electronic dual range balance (Mettler AE100, Mettler-Toledo Inc., Switzerland) with a precision of 0.01 mg. The abdominal depth of each adult was measured as the distance between dorsal and ventral surfaces of the 4th abdominal segment. Abdomen mass or size are good estimates of female fecundity in newly emerged capital breeders that do not feed as adults (Wickman & Karlsson, 1989; Boggs, 2009; Kivela et al., 2012; Yanagi & Tuda, 2012), and abdominal thickness correlates positively with female fecundity in *E. kuehniella* (Xu & Wang, 2010). Adults were then killed by freezing at –20°C for 24 h before further measurements were taken. The length of the forewing between the point of articulation and the distal end, and the width of the head and thorax at their widest points were measured. Subsequently, females were dissected to determine the length of the ovipositor between the top of ovipositor lobes and the bottom of posterior apophyses (Corbet & Tams, 1943). All morphological traits were measured using digital images captured by a USB 2.0 Video/Audio Grabber (Lindy Electronics Ltd, UK) with Universal Desktop Ruler software (AVPSoft, USA).

Adult life-history traits

Egg load

To examine the effects of population density on the number of mature eggs at adult emergence, a sub-set of pupae collected from each population density were checked every 15 min for adult emergence. Within 15 min of their emergence, females were killed by chilling at –20°C and their abdomen dissected under a stereomicroscope so that the number of mature eggs could be determined using the procedure of Edwards (1954). Ovaries were separated, immersed in 1% acetocarmine for 10 s and then washed in insect saline solution. Eggs that retained stain were considered immature, and unsaturated eggs were recorded as mature (Edwards, 1954). A total of 20 unmated females (2 adults per container) were examined from each population density.

Oviposition experiment

Using a separate set of females, we examined the effects of population density on daily oviposition, total oviposition period, mating frequency and adult longevity. Forty 1-d-old adults (20 males and 20 females) were randomly selected from each population density (2 males and 2 females per container). Each female was paired with a mate from the same population density for her life in separate 8 cm diameter × 10 cm height plastic containers. Female oviposition started on second scotophase after adult pairing, but the first day of egg laying is hereafter referred to as the first oviposition scotophase, second day as the second oviposition scotophase and so on. Every day eggs from each female were collected and counted until the female died. The number of eggs laid in each oviposition scotophase represents the daily fecundity of each female. *Ephestia kuehniella* females do not use male spermatophore and accessory gland contents transferred at mating for egg production and hence female mating frequency has no effect on its fecundity (Xu & Wang, 2009). However, reproduction is costly and trades off adult lifespan and mating

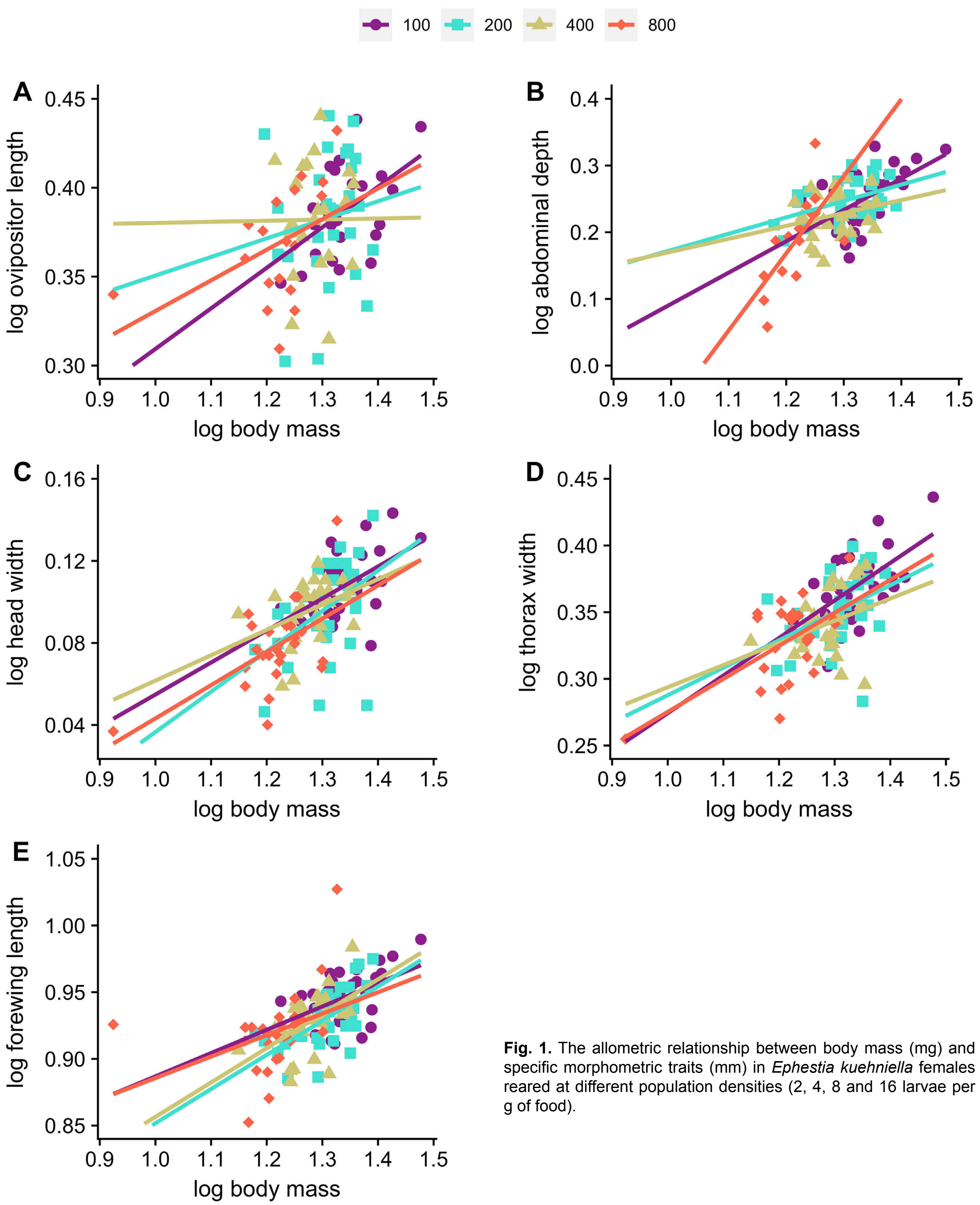

Fig. 1. The allometric relationship between body mass (mg) and specific morphometric traits (mm) in *Ephestia kuehniella* females reared at different population densities (2, 4, 8 and 16 larvae per g of food).

frequency under crowded conditions (Gibbs & Van Dyck, 2010; Haeler et al., 2014). Hence, the length of the oviposition period and adult longevity of each female were recorded. In *E. kuehniella,* males transfer a spermatophore to females during mating, and the spermatophore persists in female bursa copulatrix. Therefore, the number of spermatophores within the female represents the number of times she had mated in her life (Xu et al., 2008) and this was determined post mortem for each female.

Statistical analysis

Statistical analyses were conducted using R v 4.1.2 (R Core Team, 2021) installing packages 'car' (Fox & Weisberg, 2019), 'emmeans' (Lenth, 2016) and 'multcomp' (Torsten et al., 2008). Packages 'cowplot' (Wilke, 2020), 'ggplot2' (Wickham, 2016) were used to prepare graphs. Residual normality and homogeneity of variances were assessed using Shapiro-Wilk test and Levene's test, respectively. The effects of population density on adult

Table 1. Mean (± SE) adult body mass (mg) and sizes (mm) of various morphological traits of female *Ephestia kuehniella* selected at random after culture at a range of densities (2, 4, 8 and 16 larvae per g of food).

Morphological trait	2	4	8	16
Adult body mass	22.10 ± 0.50a	20.42 ± 0.46b	19.09 ± 0.37b	16.52 ± 0.44c
Abdominal depth	1.80 ± 0.04a	1.78 ± 0.02a	1.69 ± 0.02ab	1.56 ± 0.06b
Fore wing length	8.85 ± 0.07a	8.53 ± 0.08ab	8.50 ± 0.08b	8.34 ± 0.12b
Head width	1.28 ± 0.01a	1.25 ± 0.01a	1.25 ± 0.01a	1.20 ± 0.01b
Thorax width	2.35 ± 0.03a	2.25 ± 0.03b	2.19 ± 0.02bc	2.12 ± 0.03c
Ovipositor length	2.45 ± 0.03a	2.43 ± 0.04a	2.40 ± 0.04a	2.31 ± 0.05a

Mean values followed by the same letters in each row are not significantly different (P > 0.05).

body mass, abdominal depth, forewing length, head width, thorax width, ovipositor length, number of mature eggs, mating frequency, daily oviposition and total oviposition period were analysed using one-way ANOVA followed by Tukey's HSD to determine differences among population densities. Survival analysis was performed on adult longevity. Allometric relationships between morphometric traits and body mass were assessed by regressing log-transformed linear measurements of each morphological trait against log-transformed adult body mass. ANCOVA with population density as the main effect and log adult body mass as the covariate was performed to compare the slopes of all regressions.

RESULTS

Adults that emerged from low population density (2 larvae per g of food) were significantly heavier than those that emerged from other population densities (F = 27.44; df = 3,114; P < 0.0001, Table 1). Population density had no significant effect on ovipositor length (F = 2.10; df = 3,96; P = 0.060), however, forewing length (F = 5.90; df = 3,111; P = 0.001), head width (F = 11.87; df = 3,111; P < 0.0001), thorax width (F = 13.02; df = 3,111; P < 0.0001) and abdominal depth (F = 9.47; df = 3,97; P < 0.0001) were significantly greater at population densities of 2 and 4 larvae per g of food than 16 larvae per g of food (Table 1).

ANCOVA results showed that the allometric slopes of ovipositor with body mass did not differ among population densities (F = 0.67; df = 3,92; P = 0.575; Fig. 1A) and there was no significant effect of population density on ovipositor length (F = 0.38; df = 3,95; P = 0.771). There was a significant positive relationship between body mass and abdominal depth (F = 12.91; df = 1,93; P = 0.001; Table 2). ANCOVA indicated that the slope of the abdominal depth at high population density (16 larvae per g of food) was steeper than at other population densities (F = 4.25; df = 3,93; P = 0.007; Fig. 1B). For other morphometric traits, ANCOVA indicated no differences in the slopes of the allometric relationship between head width (F = 0.23; df = 3,107; P = 0.873; Fig. 1C), thorax width (F = 0.35; df = 3,107; P = 0.786; Fig. 1D) and forewing length (F = 0.53; df = 3,107; P = 0.665; Fig. 1E) with body mass among population densities. After removal of the interaction between body mass and population density, ANCOVA showed that forewing length (F = 1.18; df = 3,110; P = 0.321), head width (F = 1.25; df = 3,110; P = 0.294) and thorax width (F = 1.91; df = 3,110; P = 0.133) did not differ significantly between adults at different population densities and only increased significantly with body mass (Forewing length:

Table 2. The relationship between body mass (mg) and morphological traits (mm) of *Ephestia kuehniella* females reared at different larval population densities (2, 4, 8 and 16 larvae per g of food). Regression equations are given as y = a + bx, where y is the morphological trait, x is body mass, a is intercept and b is slope. All trait and body mass values were log-transformed before the regression. Significant P values are indicated in bold.

Morphological trait	Population density	Linear regression	R^2	df	F	P
Fore wing length	2	y = 0.71 + 0.17 x	0.215	1,28	7.69	**0.010**
	4	y = 0.60 + 0.26 x	0.390	1,28	17.93	**0.000**
	8	y = 0.60 + 0.26 x	0.277	1,27	10.35	**0.003**
	16	y = 0.72 + 0.16 x	0.139	1,24	3.87	0.061
Head width	2	y = – 0.10 + 0.16 x	0.268	1,28	10.24	**0.003**
	4	y = – 0.16 + 0.19 x	0.206	1,28	7.24	**0.011**
	8	y = – 0.06 + 0.12 x	0.165	1,27	5.32	**0.030**
	16	y = – 0.11 + 0.16 x	0.334	1,24	12.05	**0.002**
Thorax width	2	y = – 0.00 + 0.29 x	0.324	1,28	13.43	**0.001**
	4	y = 0.08 + 0.21 x	0.172	1,28	5.80	**0.023**
	8	y = 0.12 + 0.17 x	0.109	1,27	3.30	0.081
	16	y = 0.00 + 0.27 x	0.311	1,24	10.87	**0.003**
Abdominal depth	2	y = – 0.38 + 0.47 x	0.313	1,27	12.31	**0.002**
	4	y = – 0.07 + 0.25 x	0.185	1,27	6.12	**0.020**
	8	y = – 0.03 + 0.19 x	0.051	1,25	1.35	0.257
	16	y = – 1.22 + 1.16 x	0.463	1,14	12.09	**0.004**
Ovipositor length	2	y = 0.06 + 0.25 x	0.237	1,25	7.77	**0.010**
	4	y = 0.25 + 0.10 x	0.022	1,25	0.56	0.463
	8	y = 0.53 – 0.12 x	0.017	1,22	0.39	0.539
	16	y = 0.12 + 0.20 x	0.048	1,20	1.01	0.327

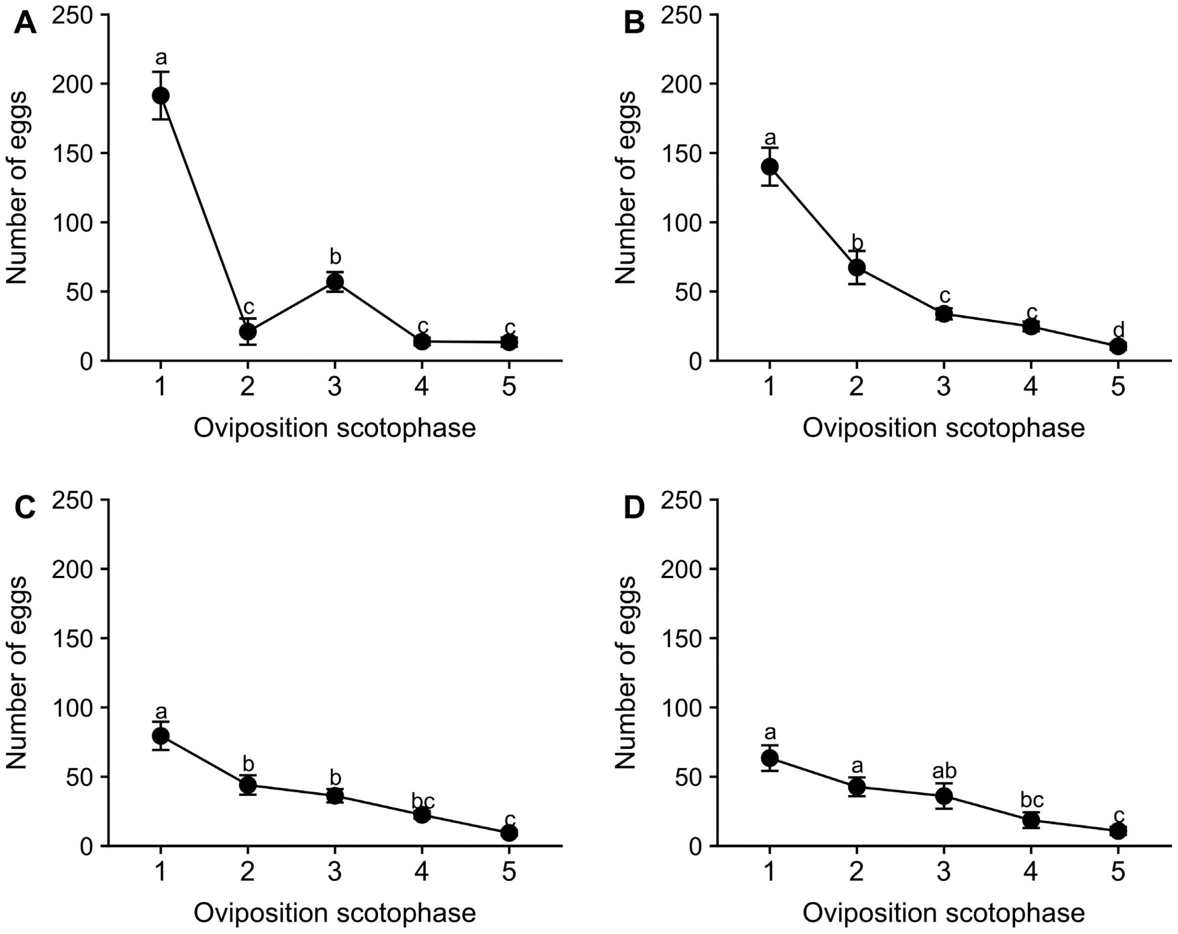

Fig. 2. Mean numbers of eggs laid in each oviposition scotophase for 5 consecutive oviposition scotophase by female *Ephestia kuehniella* reared at (A) 2, (B) 4, (C) 8 and (D) 16 larvae per g of food. In each subgraph lowercase letters above the means indicate significant different between daily oviposition ($P < 0.05$). The number eggs deposited in the sixth oviposition scotophase were not included because oviposition was observed only in three population densities (2, 4 and 8 larvae per g of food) with the number of eggs deposited < 10 at each density.

$F = 32.72$; df = 1,110; $P < 0.001$; head width: $F = 34.63$; df = 1,110; $P < 0.001$; thorax width: $F = 33.97$; df = 1,110; $P < 0.001$) (Table 2).

Unmated adult females from population densities of 8 and 16 larvae per g of food carried significantly fewer mature eggs at emergence than those from other population densities ($F = 14.78$; df = 3,76; $P < 0.0001$; Table 3). Population density had a significant effect on mean oviposition period of mated females ($F = 2.81$; df = 3,76; $P = 0.045$; Table 3), however, post hoc analysis yielded no significant differences among population densities. The daily oviposition pattern was not constant with > 80% of fecundity realized during the first-three oviposition scotophases at all population densities. Females from population densities of 2 larvae per g of food ($F = 33.45$; df = 4,80; $P < 0.0001$; Fig. 2A), 4 larvae per g of food ($F = 22.72$; df = 4,87; $P < 0.0001$; Fig. 2B) and 8 larvae per g of food ($F = 15.46$; df = 4,75; $P < 0.0001$; Fig. 2C) oviposited significantly more eggs in the first oviposition scotophase compared to subsequent oviposition scotophases. A different pattern was observed at high population density (16 larvae per g of food), at which the mean daily fecundity did not differ significantly between first, second and third oviposition scotophases but decreased thereafter ($F = 7.52$; df = 4,70; $P < 0.0001$; Fig. 2D). Neither the mean mating frequency ($F = 0.27$; df = 3,76; $P = 0.848$; Table 3) nor the adult longevity ($\chi^2 = 1.34$; df = 3; $P = 0.720$; Table 3) of mated females differed significantly among population densities.

DISCUSSION

Effects of population density on adult morphology

Here, we show that female *E. kuehniella* from high larval population density (16 larvae per g of food) had small forewings, head and thorax compared to other population densities (Table 1), consistent with the general negative affects of high population density on adult morphological traits in Lepidopteran species (Hoffmann & Loeschcke, 2006; Boggs & Niitepold, 2016). At high population density (16 larvae per g of food), last instar larvae experienced both food-limitation and crowding conditions and these factors either independently or combined reduced sizes of morphological traits. The amount of juvenile and ecdysteroid hormones released at metamorphosis determines the proliferation of the imaginal discs and size of morphological traits (Nijhout & Grunert, 2010). Starvation lowers the

Table 3. Mean (± SE) egg load at emergence of unmated *E. kuehniella* females and mating frequency, total oviposition period and adult longevity (days) of mated females reared at different population densities (2, 4, 8 and 16 larvae per g of food).

Life-history trait	Population density	Mean (± SE)
Egg load	2	16.10 ± 1.68a
	4	19.00 ± 1.51a
	8	10.20 ± 1.38b
	16	6.55 ± 1.25b
Mating frequency	2	1.75 ± 0.18a
	4	1.60 ± 0.22a
	8	1.70 ± 0.18a
	16	1.85 ± 0.22a
Total oviposition period	2	5.35 ± 0.13a
	4	5.00 ± 0.25a
	8	4.65 ± 0.25a
	16	4.55 ± 0.15a
Adult longevity	2	7.95 ± 0.18a
	4	7.50 ± 0.24a
	8	7.45 ± 0.23a
	16	7.50 ± 0.22a

Means in the same section followed by the same letter are not significantly different ($P > 0.05$).

amount of these hormones released during development leading to decreased trait size (Nijhout & Grunert, 2010).

Reduction in fecundity due to food shortage is well-documented in insects, and larval crowding, independent of nutrient limitation, lowered female reproductive output in Lepidopteran species such as the rice leaf folder, *Cnaphalocrosis medinalis* Guenee (Yang et al., 2015), beet webworm, *Loxostege sticticalis* L. (Kong et al., 2013), and the African armyworm, *Spodoptera exempta* Walker (Wang et al., 2008). These effects were attributed to physical disturbance experienced by larvae during development. In line with previous studies, we show that population density had a negative impact on abdominal depth (Table 1), which is an indicator of fecundity in *E. kuehniella* (Xu & Wang, 2010), and we conclude that high population density had a detrimental effect on fecundity.

Ephestia kuehniella adults are short-lived and do not feed (Norris, 1934) so there is no opportunity to supplement resources acquired by larvae. As expected, we found that the slope of the allometric relationship between abdominal depth and body mass was steeper for females at high population density (16 larvae per g of food) compared to other population densities (Fig. 1B), indicating investment of resources in reproduction at stressful conditions. This may alleviate some, if not all, negative effects of larval crowding on reproduction. This is similar to short-lived caddisfly, *Agrypnia deflata* Milne, which do not feed as adults; stress due to larval case removal shifted the resource allocation to abdomen (fecundity) compared to thorax (dispersal) (Jannot et al., 2007). Likewise, investment of resources to abdomen increased in relation to body mass when female Mormon fritillary, *Speyeria mormonia* Boisduval experienced food shortage as larvae (Boggs & Niitepold, 2016). In the comma butterfly, *Polygonia c-album*, the short-lived summer morph allocated relatively more resources to reproduction compared to the long-lived winter morph (Karlsson et al., 2008).

Producing more eggs may directly increase female reproductive output – and in *E. kuehniella*, and many other species, males prefer to mate with more fecund females (Bonduriansky, 2001) a higher egg load may increase female mating success. Allocation of resources to individual eggs is also a response to environmental conditions faced during early life but this varies among insect species. For example, nutrient-deprived female *Gryllus texensis* Cade and Otte field crickets increased investment in eggs compared to females that developed under normal conditions (Stahlschmidt & Adamo, 2015), while, egg size in the cabbage white butterfly, *Pieris rapae* L. (Jaumann & Snell-Rood, 2019) and egg mass in the map butterfly, *Araschnia levana* L. (Mevi-Schütz & Erhardt, 2005) was maintained irrespective of female nutrition. In some other cases, food-stressed females allocated relatively fewer resources to eggs compared with well-fed females (Yanagi & Miyatake, 2002; Bauerfeind et al., 2007).

The ovipositor is often morphologically- and developmentally- constrained as changes in ovipositor shape have to be accompanied by changes in female body size or egg morphology (Bauerfeind & Fischer, 2008; Yanagi & Tuda, 2012), and changes in ovipositor length can interfere with its normal functioning and so affect offspring survival (Menken et al., 2010; Hou et al., 2019). Consistent with this we found no difference in ovipositor length among population densities.

Adult insects that experience crowding and food stress during early life tend to move away from deteriorating habitats (Saastamoinen et al., 2010; Elliott & Evenden, 2012; Khuhro et al., 2014). In Lepidoptera, at poor conditions dispersal is facilitated through lowered wing loading or relatively large wings (Tigreros & Davidowitz, 2019). Here, we found no changes in proportion of forewing length to body mass at different experimental densities (Table 2) consistent with the response of fall army worm and monarch butterfly (Ferguson et al., 1997; Johnson et al., 2014).

A dispersal response to resource limitation may not occur in *E. kuehniella* because of time constraints on the benefits from flight versus reproduction. Previous studies have shown that flight following emergence slows egg maturation process and lowers fecundity in species that emerge with an egg load (Niitepõld & Hanski, 2013; Gibbs et al., 2018), while in others it can suppress ovarian development and delay reproduction. *Ephestia kuehniella* carry a full egg load at emergence, and flight in 1–2 day old females may directly interfere with egg maturation process. Moreover, *E. kuehniella* adults mate in the first night following eclosion, which is followed by oviposition (Calvert & Corbert, 1973). A delay in reproduction due to flight could reduce mating opportunities and increase the likelihood of female mortality without mating. A high initial egg load also imposes severe biomechanical constraints on flight (Dudley, 1999) that affects take-off angles (Almbro & Kullberg, 2012), flight frequency (Huang et al., 2019) and flight duration (Jyothi et al., 2021). Unlike long-lived insects that can compensate for pre-reproductive dispersal by foraging, short-lived capital breeders have no opportunity to replenish resources.

Effects of population density on adult life-history traits

Here, we found differences in the daily oviposition pattern between females emerged from low and high population densities (2 larvae per g of food versus 16 larvae per g of food). At high density, females laid similar numbers of eggs in the first three oviposition scotophases while females at low density laid more eggs in the first oviposition scotophase. It is possible that females at high population density (16 larvae per g of food), which deposited 50% of their eggs in the first-two oviposition scotophases had the potential to carry remaining eggs to new habitat and so reduce competition among resulting offspring. In some migratory insects such as monarch butterflies, *Danaus plexippus* L., flight is initiated after the start of oviposition (Malcolm et al., 2018), and this is considered a bet-hedging strategy favoured under unpredictable environmental conditions. Female spruce budworms, *Choristoneura fumiferana* Clemens in heavily defoliated forests engaged in migration only after depositing about 40% of treir entire egg load in the current habitat (Rhainds, 2020).

When resources are limited, trade-offs typically occur between reproduction and survival (Niitepõld, 2019) but this was not apparent in *E. kuehniella*; mated females from different population densities had similar short adult lifespans (Table 3). This might be because the smaller individuals (from high population density) had lower maintenance costs and required fewer resources to survive. Conversely, females developed at low population density (2 larvae per g of food) with the most resources had greater reproductive output and oviposited more eggs in the initial oviposition scotophases resulting in short survival periods.

In conclusion, we found a strong negative impact of high population density on adult morphological and life-history traits of *E. kuehniella.* The lack of differences in the allometric slopes of forewing and thorax sizes with body mass at different population densities suggest that dispersal to escape poor conditions, as seen in some Lepidopterans may not be an option to this species because of its short adult lifespan and lack of adult feeding. On the other hand, ovipositor length was unaffected by rearing density and females that emerged from crowded larvae had relatively deeper abdomens, which may mitigate the negative effects of high population density on reproductive potential.

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