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Body Size, Age, and Disease Influence Female Reproductive Performance in *Choristoneura conflictana* (Lepidoptera: Tortricidae)

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ABSTRACT We determined the effect of body size and adult female longevity on the realized fecundity and fertility of the large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), an outbreaking forest lepidopteran. We examined these relationships from an ecological perspective and included the impact of age at pairing and infection with a microsporidian pathogen in our analyses. The relationship between body size, as measured by pupal weight and forewing length and area, and realized fecundity and fertility was best for healthy females that were paired immediately after eclosion. A delay in age of pairing or sublethal pathogen infection eroded these relationships. A delay in age of pairing resulted in a lower percentage of females that produced fertile eggs and a significant reduction in the number of eggs laid. Although sublethal pathogen infection indirectly disrupted the body size-realized fecundity and fertility relationship, infection did not directly decrease egg production. Wing area was the best predictor of total and fertile egg production. The relationship between pupal weight and wing area was correlated, but females eclosing from small pupae had proportionately larger wings than females from large pupae, which may indicate a cost of large body mass in this actively dispersing species. Longevity of females did not predict the total or fertile number of eggs laid by females. There was no consistent relationship between pairing treatment and longevity of female moths, suggesting that there is no trade-off between longevity and reproductive fitness in this species. Sublethal pathogen infection significantly decreased female moth longevity, but this decrease was not reflected in reduced fecundity of infected females. Our data illustrate that although body size is an important determinant of realized fecundity and fertility in *C. conflictana*, these relationships are mediated by several factors that may vary greatly under field conditions and at varying population densities.

KEY WORDS large aspen tortrix, body size, reproductive performance, microsporidia

In many insect species, large or long-lived females exhibit greater fecundity than small or short-lived females (Leather 1988, Honěk 1993). However, this relationship is affected by an array of ecological and physiological factors (Leather 1988). In the Lepidoptera, variation in temperature (Carroll and Quiring 1993, Kamata and Igarashi 1995), larval nutrition (Danthanarayana 1975, Thomas et al. 1980), adult nutrition (Tammaru et al. 1996, Tisdale and Sappington 2001), and disease load (Bauer and Nordin 1989) can influence the body size and longevity–fecundity relationships. In addition, intrinsic factors such as age at mating (Proshold et al. 1982, Torres-Vila et al. 2002) and genetic variation (Lorimer and Bauer 1983) can alter the correlation between body size, adult longevity, and fecundity. In some outbreaking forest Lepidoptera, body size and fecundity have been positively correlated with population density (Myers and Kuken 1995), whereas in other species the correlation is negative (Klemola et al. 2004, Nealis and Régnière 2004). Regardless of the relationship, factors that influence body size or longevity of adult moths and in turn fecundity may contribute to the observed population fluctuations in outbreaking species of forest Lepidoptera.

The large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), is a native defoliator of trembling aspen, *Populus tremuloides* Michx., throughout its range in North America. Periodically, *C. conflictana* populations increase to outbreak levels that persist for 2–3 yr over large areas of aspen forest (Cerezke 1992). Natural enemies of *C. conflictana* include many parasitoids (Prentice 1955, Torgersen and Beckwith 1974) and eight identified pathogens (Burke and Percy 1982) that contribute to population collapse in this species (Cerezke 1992). Of the pathogens, three microsporidian (Protozoa: Microsporidia) species have been identified from field-collected populations (Wilson and Burke 1971, Burke and Percy 1982), and a microsporidium was found in

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C. conflictana from a laboratory rearing facility (van Frankenhuyzen et al. 2004). Sublethal microsporidian infection in other forest Lepidoptera has been linked with decreased body size, longevity, and fecundity (Thomson 1958, Wilson 1977, Bauer and Nordin 1989) and therefore may significantly impact any body size and longevity–fecundity relationships that may exist in *C. conflictana* and potentially impact population dynamics of this outbreaking species.

Here, we test the influence of female body size and longevity, two factors that are likely to change with population density as food resources become depleted, on female *C. conflictana* reproductive potential. However, we consider these relationships in conjunction with other ecological and physiological factors and include the impact of female age and sublethal infection with a microsporidian pathogen in our analyses.

Materials and Methods

Insect Origin. *C. conflictana* were collected from a declining outbreak population as eggs or larvae from field sites located in the Rocky Mountain foothills of western Alberta between Drayton Valley (53° 13′ N, 114° 59′ W) and Rocky Mountain House (52° 22′ N, 114° 55′ W). Insects collected as larvae were fed aspen leaves and the offspring of the resulting moths were used in the study. Insects collected as eggs were allowed to emerge, and first instars were fed a wheat germ-based synthetic diet (spruce budworm diet, BioServ, Frenchtown, NJ) and provided with cheesecloth squares as overwintering substrate. All study organisms were held as diapausing, second instars at 2–4°C for 20 wk before the initiation of the study. Voucher specimens have been deposited in the Strickland Museum, University of Alberta.

Insect Handling. Diapausing second instars were removed from overwintering conditions and allowed to emerge from hibernacula for a 5-d period. Larvae were individually transferred with a sterilized no. 1 artist's brush to a 30-ml cup containing synthetic wheat germ-based diet (BioServ) with 200 ppm Benomyl (Sigma-Aldrich, St. Louis, MO) according to the protocol used at the Insect Production Laboratory, Canadian Forest Service (Great Lakes Forestry Centre, Sault Ste. Marie, Ontario, Canada). Although benomyl is used in this rearing procedure to prevent the buildup of microsporidian parasites, our studies (M.L.E. and B.A.K., unpublished) have indicated that this treatment does not impact disease status of microsporidian-infected large aspen tortrix. Larvae were held at 24°C under a photoperiod of 16:8 (L:D) h and transferred to fresh diet as necessary throughout larval development. Insects were examined daily, and pupae were separated by sex (Jennings and Acciavatti 1975) and weighed (Mettler-Toledo XS105DU, Mettler-Toledo, Greifensee, Switzerland) on the first day of pupation. Pupae were held individually in 150-ml (BioServ) translucent cups and observed daily until eclosion. Moths were provided with 10% sugar solution via a cotton wick.

Pairing Treatments. Females aged 0, 2, and 4 d old were paired individually with a 2- to 3-d-old male in a 450-ml cardboard container with a transparent lid and held under the same conditions as the colony. There were 24, 28, and 18 pairs established for 0, 2, and 4-d-old females, respectively. Pairing occurred ≈1 h before the onset of scotophase and was conducted over a period of 8 d. The fourth treatment consisted of a female moth alone ($n = 19$). Moths were checked daily, and pairs remained together until death. After death, the length and width of the right forewing of each female moth was measured using an ocular micrometer attached to a dissecting microscope. At the completion of the experiments all females were examined for microsporidian infection by diluting the contents of each female's abdomen in 100 μl of sterile water and observing the contents of a 25-μl droplet of the suspension at 400× magnification for the presence of spores. For each female sample, 10 frames were observed and infected females were categorized on a relative scale from lightly infected (containing 1–10 spores per frame) to heavily infected (containing >100 spores per frame). The spores present in our dissections morphologically resembled *Cystosporengenes* spp., a microsporidian parasite recovered from *C. conflictana* in an insect rearing facility (van Frankenhuyzen et al. 2004). However, this species has never been recorded from *C. conflictana* in the wild, and we have retained specimens for further identification of the causative agent(s) of infection in our collected individuals.

Egg Mass Measurements. All egg masses laid by individual females were labeled and allowed to develop to determine fertility by the appearance of black head capsules. The total number of fertile eggs laid by each female was quantified by scanning each "black-headed" egg mass (HP Scanjet 3970) and counting individual eggs on the resulting enlarged digital image. Realized fecundity of each female was determined by adding the fertile eggs laid to infertile eggs laid that were patchily distributed and counted directly under a dissecting microscope.

Statistical Analyses. Linear regression analysis (PROC REG, SAS Institute 1996) was conducted to test the hypothesis that female body size, as measured by pupal weight, forewing length, and area was related to realized female fecundity (total eggs laid) and fertility (fertile eggs laid). Individual regression analyses were conducted for individuals paired at 0 and 2 d that produced fertile eggs. Because few females paired at 4-d-old produced fertile eggs, regression analyses were not conducted for this treatment. Additional regression analyses were conducted on subsets of individuals that were determined to be infected or healthy.

Linear regression analyses were conducted to test the hypothesis that female moth longevity was predictive of realized fecundity and fertility. Individual regression analyses were conducted for individuals paired at 0 and 2 d that produced fertile eggs. Regression analyses also were conducted to determine whether pupal weight was predictive of female lon-

Table 1. Summary statistics of body size parameters, longevity, and egg production of female *C. conflictana*

Parameter	Females used in summary	n^a	Mean + SE	Range^b
Pupal wt (mg)	All	85	120.56 + 2.54	63.71–173.78
	Healthy	52	117.59 + 2.99	73.44–163.93
	Infected	27	126.72 + 4.66	80.06–173.78
Forewing length (mm)	All	75	12.88 + 0.09	11.16–14.66
	Healthy	46	12.77 + 0.11	11.16–14.66
	Infected	24	13.06 + 0.16	11.50–14.50
Forewing area (mm^2)	All	75	68.83 + 1.08	49.07–93.31
	Healthy	46	67.25 + 1.29	49.07–90.37
	Infected	24	70.86 + 2.03	53.62–93.31
Longevity (d)	All	84	11.70 + 0.30	6–18
	Healthy	52	12.04 + 0.37	7–18
	Infected	26	10.92 + 0.42	7–15
Fertile eggs^c	All	50	286.5 + 26.64	0–705
	Healthy	35	299.89 + 34.73	0–705
	Infected	14	273.50 + 34.15	0–531
Total eggs	All	85	263.26 + 19.06	0–829
	Healthy	52	276.38 + 24.92	10–705
	Infected	27	270.85 + 33.21	0–829

[a] Total number of females may not equal the sum of the healthy and infected females because infection status could not be determined for all individuals.

[b] Range of all females may be different than the range of healthy plus infected females because infection status could not be determined for all individuals.

[c] Counts of fertile eggs produced from 0- and 2-d-old females.

gevity and whether pupal weight was correlated with wing area in any of the four pairing treatments. For these final series of regressions, all females in all treatments were used even if they did not produce fertile egg masses.

The effect of age at pairing on the proportion of paired females that produced fertile eggs was tested using chi-square analysis (PROC FREQ, SAS Institute 1996). The total number of eggs laid by paired females was compared by factorial analysis of variance (ANOVA) that incorporated age, infection status, and an infection × age interaction term into the model (PROC GLM, SAS Institute 1996). A similar model was used to compare the number of fertile eggs produced by females, but in this case only eggs laid by 0- and 2-d-old females were analyzed. Inclusion of the number of fertile eggs laid by 4-d-old females resulted in non-normally distributed data (PROC UNIVARIATE, SAS Institute 1996). Female longevity was compared among females in various pairing treatments by a factorial ANOVA with infection status and an infection × pairing treatment interaction term in the model (PROC GLM, SAS Institute 1996).

Results

Some females (27/89) were infected by a microsporidian with similar morphology to *Cystosporengenes* spp. (van Frankenhuyzen et al. 2004). Infection of a proportion of the females allowed us to directly compare the impact of sublethal microsporidian infection on the reproductive parameters studied here (Table 1). We were unable to incorporate the level of microsporidiosis into our analysis because most infected females examined (20/27) were highly infected.

Body Size and Fecundity–Fertility Relationship. The influence of female body size on the realized fecundity and fertility of *C. conflictana* varied depending on age at pairing and infection status of females (Tables 2 and 3). The relationship between pupal weight and the total and fertile number of eggs laid was best for healthy females that were paired immediately after eclosion (0 d) (Table 2). Pupal weight of females paired 2 d after eclosion was a significant predictor of realized fecundity and fertility when all individuals were pooled and when only healthy females were included in the analysis (Table 2). Pupal weight was not predictive of the total or fertile eggs laid for females infected with the microsporidian pathogen, regardless of female age at pairing (Table 2).

In general, forewing area as a measure of body size was a better predictor of realized fecundity and fertility than forewing length. However, as observed for pupal weight, this relationship varied depending on the age at pairing and infection status of the female. When all females were pooled for analysis, neither forewing length nor area predicted realized fecundity

Table 2. Linear regression analyses of pupal weight on the realized fecundity (total eggs) and fertility (fertile eggs) of mated female *C. conflictana*

Dependent variable	Females used in analysis	Female age^a	n	R^2	P	F	Regression line equation^b
Total eggs	All	0	20	0.0586	0.1569	2.18	$y = 199.54 + 2.09x$
	Healthy	0	13	0.6572	0.0005	24.01	$y = -42.59 + 4.36x$**
	Infected	0	7	−0.107	0.3776	0.94	$y = 1{,}079.4 - 4.71x$
	All	2	22	0.4284	0.0006	16.74	$y = -205.31 + 4.07x$**
	Healthy	2	16	0.5262	0.0009	17.66	$y = -349.49 + 5.37x$**
	Infected	2	6	0.2732	0.1650	2.88	$y = 27.61 + 1.91x$
Fertile eggs	All	0	20	0.0740	0.1299	2.52	$y = 172.23 + 2.03x$
	Healthy	0	13	0.6793	0.0003	26.42	$y = -89.45 + 4.67x$**
	Infected	0	7	0.0345	0.3206	1.21	$y = 749.95 - 2.88x$
	All	2	22	0.3139	0.0039	10.61	$y = -183.2 + 3.74x$**
	Healthy	2	16	0.4138	0.0043	11.59	$y = -334.24 + 5.13x$**
	Infected	2	6	0.1672	0.2298	2.00	$y = 54.32 + 1.44x$

[a] Age (days) of female at time of pairing.

[b] Equations marked with double asterisk (**) indicate a significant linear regression relationship at $P \leq 0.01$

Table 3. Linear regression analyses of wing dimensions on the realized fecundity (total eggs) and fertility (fertile eggs) of mated female *C. conflictana*

Dependent variable	Independent variable	Females used in analysis	Female age[a]	n	R^2	P	F	Regression line equation[b]
Total eggs	Wing length	All	0	19	−0.0224	0.4472	0.61	y = 3.86 + 33.57x
		Healthy	0	12	0.4957	0.0064	11.81	y = −960.04 + 108.54x**
		Infected	0	7	0.1139	0.2406	1.77	y = 2,439.4 − 147.06x
	Wing area	All	0	19	0.0013	0.3257	1.02	y = 233.61 + 3.07x
		Healthy	0	12	0.7150	0.0003	28.60	y = −151.81 + 9.15x**
		Infected	0	7	0.2142	0.1654	2.64	y = 1,510 − 13.99x
	Wing length	All	2	22	0.0963	0.0871	3.24	y = −477.9 + 59.63x
		Healthy	2	16	0.0857	0.1432	2.41	y = −576.37 + 68.36x
		Infected	2	6	0.1058	0.2757	1.59	y = −371.92 + 48.89x
	Wing area	All	2	22	0.0832	0.1038	2.90	y = −86.83 + 5.39x
		Healthy	2	16	0.0469	0.2085	1.74	y = −95.47 + 5.69x
		Infected	2	6	0.3168	0.1426	3.32	y = −135.64 + 5.65x
Fertile eggs	Wing length	All	0	19	0.0013	0.3258	1.02	y = −87.19 + 37.67x
		Healthy	0	12	0.4827	0.0073	11.27	y = −1,028.5 + 112.81x**
		Infected	0	7	0.0888	0.2637	1.58	y = 1,411.7 − 77.50x
	Wing area	All	0	19	0.0239	0.2464	1.44	y = 191.91 + 3.14x
		Healthy	0	12	0.6807	0.0006	24.45	y = −181.87 + 9.41x**
		Infected	0	7	0.1133	0.2412	1.77	y = 868.92 − 6.69x
	Wing length	All	2	22	0.0544	0.1529	2.21	y = −411.35 + 52.98x
		Healthy	2	16	0.0599	0.1837	1.96	y = −563.17 + 66.26x
		Infected	2	6	0.0013	0.3725	1.01	y = −217.88 + 34.55x
	Wing area	All	2	22	0.0259	0.2265	1.56	y = −29.18 + 4.28x
		Healthy	2	16	0.0072	0.3103	1.11	y = −56.43 + 4.91x
		Infected	2	6	0.1651	0.2313	1.99	y = −55.98 + 4.06x

[a] Age (days) of female at time of pairing.

[b] Equations marked with double asterisk (**) indicate a significant linear regression relationship at $P \leq 0.01$.

or fertility of 0-d-old females (Table 3). However, both forewing length and area were significant predictors of realized fecundity and fertility in the subset of healthy 0-d-old females but not for infected females (Table 3). Neither forewing length nor area accounted for significant variation in realized fecundity or fertility for 2-d-old females, regardless of infection status (Table 3).

Longevity and Fecundity–Fertility Relationship. The number of days that female moths lived was not predictive of the total or fertile eggs laid by females, regardless of age at pairing and infection status of females (Table 4). Pupal weight was not predictive of adult female longevity, regardless of pairing treatment (0-, 2-, and 4-d-old or virgin) or infection status.

Pupal Weight and Wing Area Relationship. The two measures of body size, pupal weight and wing area were significantly correlated. However, females eclosing from small pupae had proportionately larger wings than females eclosing from large pupae (Fig. 1).

Effect of Delayed Pairing and Infection Status on Egg Production and Female Longevity. The proportion of females that produced fertile eggs was dependent on age at pairing ($\chi^2 = 21.73$, $P < 0.0001$). More than 80% of females paired at 0 and 2 d old produced fertile eggs compared with 23% of females paired at 4 d old (Fig. 2a). The number of total and fertile eggs laid by females paired immediately after eclosion was significantly greater than those produced by females paired 2 d posteclosion (Fig. 2b). The total number of

Table 4. Linear regression analyses of female longevity on the realized fecundity (total eggs) and fertility (fertile eggs) of mated female *C. conflictana*

Dependent variable	Females used in analysis	Female age[a]	n	R^2	P	F	Regression line equation
Total eggs	All	0	20	0.0326	0.2165	1.64	y = 261.34 + 17.72x
	Healthy	0	13	−0.0800	0.7448	0.11	y = 410.23 + 5.67x
	Infected	0	7	0.1553	0.2067	2.10	y = −114.5 + 56.10x
	All	2	21	0.0565	0.1609	2.14	y = 96.06 + 16.25x
	Healthy	2	16	0.0140	0.2892	1.21	y = 116.71 + 14.83x
	Infected	2	4	0.2039	0.3149	1.77	y = 18.42 + 21.79x
Fertile eggs	All	0	20	−0.0457	0.6855	0.17	y = 12.61 − 0.01x
	Healthy	0	13	−0.0276	0.4279	0.68	y = 9.55 + 0.02x
	Infected	0	7	−0.0207	0.3917	0.88	y = 15.84 − 0.04x
	All	2	21	0.0198	0.2547	1.38	y = 105.54 + 14.02x
	Healthy	2	16	−0.0261	0.4447	0.62	y = 142.65 + 11.45x
	Infected	2	4	0.6666	0.1181	7.00	y = −44.58 + 24.79x

[a] Age (days) of female at time of pairing.

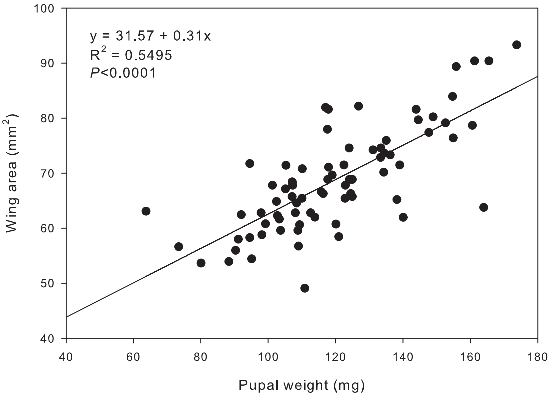

Fig. 1. Relationship between pupal weight and wing area of female *C. conflictana* used in all four pairing treatments.

eggs laid by females paired at 4 d old was equal to the number of eggs laid by unpaired virgin females (Fig. 2b). There was no influence of infection status ($F = 0.35$, $P = 0.5564$; $F = 0.35$, $P = 0.5536$) and no infection status × age interaction effect ($F = 0.01$, $P = 0.9214$; $F = 0.84$, $P = 0.4743$) on the number of fertile and total eggs produced by paired females, respectively. Female longevity was not influenced by pairing treatment ($F = 4.49$, $P = 0.8313$). However, infection significantly reduced female longevity ($F = 4.49$, $P = 0.0376$) (Table 1), and there was a marginal infection status × age interaction effect ($F = 2.54$, $P = 0.06307$).

Discussion

We assessed factors that influence the realized fecundity and fertility of female *C. conflictana*, an outbreaking species of forest Lepidoptera. Our results demonstrate that the generalized relationship of increased fecundity with increased body size seen in many insect species (Honěk 1993) is applicable only for young and healthy *C. conflictana.* Pupal weight accounted for 65.7 and 52.6% of the variation in realized fecundity of healthy female *C. conflictana* paired at 0 and 2 d posteclosion, respectively (Table 2). The proportion of females producing fertile eggs and the number of fertile and total eggs oviposited by female *C. conflictana* were severely reduced with increased age of pairing, so that few females laid fertile eggs when paired at 4 d posteclosion (Fig. 2). Similar studies on other tortricids have shown that a delay in mating reduces the fitness of female moths by reducing both the total and fertile eggs laid (Knight 1997, Fraser and Trimble 2001, Torres-Vila et al. 2002, Jiménez-Pérez and Wang 2003). For other Lepidoptera in which fitness is negatively affected by a delay in mating, the body size–fecundity relationship also eroded with increased female age at mating (Proshold et al. 1982, Torres-Vila et al. 2002). In our experiment, this is probably because of physiological factors such as the cessation of oocyte production (Proshold et al. 1982), insufficient quantities of eupyrene sperm in the spermatheca to stimulate oviposition (Proshold et al. 1982, Proshold 1996), or reabsorption of eggs by older females (Proshold et al. 1982, Leather and Burnand 1987). Although mating success also decreases with age in other *Choristoneura* species (Outram 1971, Delisle 1995), this cannot account for the reduced body size–fecundity relationship with age seen here, because only females that produced fertile eggs were used in these regression analyses (Table 2).

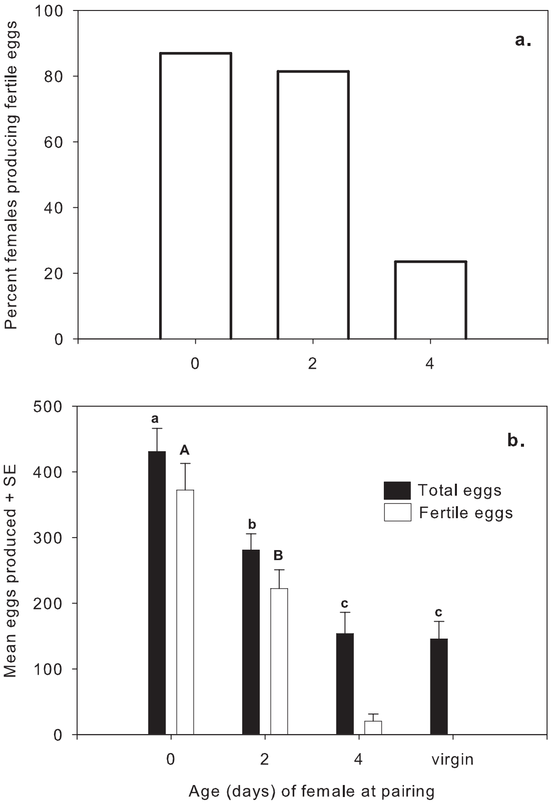

Fig. 2. (a) Effect of pairing age on percentage of females producing fertile eggs (percentages based on $n = 23$ pairs [0 d], 27 pairs [2 d], and 17 pairs [4] d). The percentage of females that produced fertile eggs was dependent on age at pairing ($\chi^2 = 21.73$, $P = 0.0001$). (b) Mean number of eggs produced by females in various pairing treatments. Black bars indicate the mean number of eggs laid, and white bars indicate the mean number of fertile eggs laid. Comparisons were made among all treatments for total eggs laid, and only 0- and 2-d-old pairs for fertile egg comparison. Similarly colored bars with different letters are significantly different (LSMEANS; $P < 0.05$).

Pupal weight explained the most variation in the number of fertile and total eggs laid when the females were healthy (Table 2). In contrast, pupal weight of *Choristoneura fumiferana* (Thomson) (Lepidoptera: Tortricidae) females infected with *Nosema fumiferanae* (Protozoa: Microsporidia) in the laboratory explained more variation in subsequent female fecundity than pupal weight of healthy females (Bauer and Nordin 1989). These authors suggested that an upper level of egg production is imposed on infected females, resulting in a tighter correlation between pupal weight and realized fecundity (Bauer and Nordin 1989). In our experiment, we found no effect of infection status on the number of total or fertile eggs produced (Table 1). However, our sample size of infected females was low (Table 1) and increased sampling may indicate a significant impact of sublethal infection on female fecundity and fertility. Field-collected insects naturally infected with microsporidia generally exhibit reduced sublethal effects on the reproductive potential of their host compared with insects artificially inoculated in the laboratory. *C. fumiferana* infected with *N. fumiferanae* in the laboratory have a greater reduction in fecundity (50%) than infected insects collected from the field (25%) (Thomson 1958). Nealis and Régnière (2004) found only a weak effect of microsporidian infection on the fecundity of *C. fumiferana* females from field populations. Sublethal impacts of infections because of vertically transmitted microsporidia may be limited in nature, as the pathogen would be predicted to go extinct because of negative effects on host fitness (Lipsitch et al. 1995). Despite the lack of a direct effect of microsporidian infection on body size or eggs produced (Table 1), removal of infected females from regression analyses resulted in a significant body size and fecundity–fertility relationship. It is possible that the lack of pupal weight and fecundity–fertility relationship in infected insects is the result of a diversion of reserves toward microsporidian growth and reproduction (Bauer and Nordin 1988, Rath et al. 2003).

A similar trend in the relationship between body size and fecundity-fertility was observed when forewing dimensions were used as the independent variable (Table 3). Forewing area accounted for 71.5% of the variation in the total number of eggs laid by healthy females paired immediately after eclosion (Table 3). It is possible that wing dimensions are a better measure of optimum body size for insects that actively disperse as adults and for which large body mass may be costly (Blanckenhorn 2000). We found that small *C. conflictana* females have proportionately larger wings (Fig. 1), which would translate into a lower wing loading on smaller individuals. A similar relationship between pupal weight and wing area was found for *C. fumiferana* and smaller females with a lower wing loading were more likely to fly than large females (Sanders and Lucuik 1975). Interestingly, for moth species in which females are functionally flightless, the pupal weight–fecundity relationship is highly correlated (Tammaru et al. 1996, Tammaru et al. 2002, Thurston and MacGregor 2003), and there does not seem to be any cost associated with large size (Tammaru et al. 2002).

Leather (1988) claimed that adult moth longevity and factors directly influencing longevity should be the most important factors impacting fecundity in the Lepidoptera. Indeed, in several lepidopteran species, adult life span or oviposition period accurately predicts fecundity (Danthanarayana 1975, Proshold et al. 1982, Leather and Burnand 1987, Torres-Vila et al. 2002). However, for *C. conflictana*, the number of days that female moths lived did not predict the total or fertile eggs laid (Table 4). These results suggest that female fitness is severely constrained by age at reproduction for *C. conflictana*, and living longer does not add significantly to female reproductive potential. In other studies in which *C. conflictana* female age was not recorded, a range of 198–398 mature eggs was dissected from female ovaries (Prentice 1955), and realized fecundities of 86.7–250.4 eggs per female were recorded (Beckwith 1970). In our experiment, females paired immediately after eclosion laid a mean of >400 eggs ranging from 0 to 705 total eggs per female (Fig. 2b). Our findings demonstrate that attracting a mate early is crucial for female *C. conflictana* to realize their reproductive potential. The likelihood of pairing upon eclosion will vary with population density and significantly impact female fecundity and potentially the development or continuation of outbreak densities. Female mating success has been shown to decline in other moth species at low (Sharov et al. 1995) or high population densities (Rhainds et al. 1999).

In many tortricids, there is an observed trade-off between reproductive performance and longevity (van der Kraan and van der Straten 1988, Vickers 1997, Torres-Vila et al. 2002). However, in our study no such trade-off was observed for *C. conflictana.* There was no effect of pairing or age at pairing on the longevity of females. Our results are consistent with a similar study on the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in which delayed mating had a severe impact on fecundity and fertility but no effect on female moth longevity (Proshold 1996).

Our data illustrate that although body size is an important determinant of realized fecundity in *C. conflictana*, this relationship is mediated by several factors that may vary greatly under field conditions (Leather 1988). In our study, measures of body size, including pupal weight and forewing dimensions, were good indicators of realized fecundity only when females were healthy and paired immediately after eclosion. The body size–fecundity relationship eroded as the result of delayed pairing and microsporidian infection. These are factors that are likely to be prevalent at high population densities during outbreaks of *C. conflictana* and may contribute, along with other ecological factors, to the population dynamics of this outbreaking forest defoliator.

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