

# Size-Dependent Realized Fecundity in Two Lepidopteran Capital Breeders

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**ABSTRACT** Body size is correlated with potential fecundity in capital breeders, but size-dependent functions of realized fecundity may be impacted by reproductive losses due to mating failure or oviposition time limitations (number of eggs remaining in the abdomen of females at death). Post-mortem assessment of adults collected in the field after natural death represents a sound approach to quantify how body size affects realized fecundity. This approach is used here for two Lepidoptera for which replicated field data are available, the spruce budworm *Choristoneura fumiferana* Clemens (Tortricidae) and bagworm *Metisa plana* Walker (Psychidae). Dead female budworms were collected on drop trays placed beneath tree canopies at four locations. Most females had mated during their lifetime (presence of a spermatophore in spermatheca), and body size did not influence mating failure. Oviposition time limitation was the major factor restricting realized fecundity of females, and its incidence was independent of body size at three of the four locations. Both realized and potential fecundity of female budworms increased linearly with body size. Female bagworms are neotenuous and reproduce within a bag; hence, parameters related to realized fecundity are unusually tractable. For each of five consecutive generations of bagworms, mating probability increased with body size, so that virgin-dead females were predominantly small, least fecund individuals. The implication of size-dependent reproductive losses are compared for the two organisms in terms of life history theory and population dynamics, with an emphasis on how differential female motility affects the evolutionary and ecological consequences of size-dependent realized fecundity.

**KEY WORDS** cost of reproduction, eruptive population dynamics, flightlessness, life history evolution of body size, lifetime fitness

Reproductive strategies of insects can be characterized based on the nature of resources used for reproduction as either income breeding (females gain resources as adults to increase fecundity) or capital breeding (females rely strictly on larval accumulated resources for reproduction) (Stephens et al. 2009, Javoiš et al. 2011). Relationships between size and realized fecundity may be weak to nonexistent in income-breeding females, often because longevity is the main driver of lifetime fecundity and it correlates poorly with body size (Leather and Burnand 1987, Leather 1988, Ohgushi 1996, Gotthard et al. 2007). In contrast, positive relationships between the size attained by females at pupation and fecundity are ubiquitous in capital breeders (Leather 1988, Tammaru and Haukioja 1996, Sopow and Quiring 1998, Tammaru et al. 2002, Rhainds et al. 2009), and size-dependent functions of fecundity are robust across a range of environmental conditions (Miller 2005, Heisswolf et al. 2009).

Size-dependent fecundity is not equivalent to lifetime reproductive output, however, because females often fail to lay their full egg complement due (among other factors) to mating failure (Rhainds 2010) and

oviposition time limitation (premature death of females before all eggs are laid; Rosenheim et al. 2008). Relationships between body size and the magnitude of reproductive losses are generally unknown because it is difficult to quantify the effect of size on multiple components of reproductive success in field populations of insects (Moreau et al. 2006, Pekkala et al. 2011).

The most promising approach in comparative studies of size-dependent reproductive success relies on post-mortem dissections of female cadavers collected in the field (Rosenheim et al. 2008). We consolidate herein postmortem assessments of reproductive success in two species of Lepidopteran capital breeders for which replicated field data are available: the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), and the bagworm *Metisa plana* Walker (Lepidoptera: Psychidae). The two species share a combination of life-history traits (defoliation of perennial trees as feeding niche, ballooning of windborne larvae, polyphagy, pro-ovigeny, indiscriminate oviposition behavior, eggs laid in clusters, and eruptive population dynamics) but have distinct reproductive systems.

1) The spruce budworm is a univoltine moth with a geographic distribution that ranges longitudinally across much of the Nearctic boreal forest in Canada, where it is considered the most severe pest of balsam fir and

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spruce trees (Morris 1963). Within 1 or 2 d after emergence, females release sex pheromone to attract males, mate shortly thereafter, and then lay eggs in batches on the foliage of host trees (Rhainds et al. 2012). Even though females are winged, they are functionally flightless during the first 2 d of their life owing to their heavy abdomen (Rhainds and Kettela 2013). After having laid ~50% of their eggs, females often migrate over long distances by ascending above tree canopies to the atmospheric boundary layer, where they get carried downwind (Greenbank et al. 1980). Local reproduction followed by migrations in females has likely evolved as a strategy to hedge reproduction over large scales because of the short range of dispersal by ballooning larvae (Batzer 1968) and relatively low mortality of migrating females in vast (relatively homogenous) forest landscapes (Gatehouse 1997). Due to the high socio-economic impact of spruce budworms, many studies related to their reproductive ecology were conducted during the last outbreak in New Brunswick in the 1970s (Greenbank et al. 1980), including collection of females that died from natural causes on drop trays placed below tree canopies (Thomas 1978, Thomas et al. 1980). The drop tray data (most of which remain unpublished) included body size measurements (length of forewings), mating status (mated or virgin-dead, as determined by the presence or absence of a spermatophore in the spermatheca), and estimates of potential and realized fecundity (proportion of eggs laid at the time of death, as derived from the relationship between dry weight and wing length; Thomas et al. 1980). Even though collections of dead females on drop trays may not be entirely representative of local reproductive populations (because samples exclude females that emigrated or were preyed upon; Rhainds and Heard 2015), the procedure is useful for investigating the relationship between body size and parameters of reproductive output (and how these relationships may vary locally).

2) First-instar bagworms hatch from their maternal bag and shortly thereafter construct a protective bag, which is made of plant material and enlarged through development. Before pupation, last instars tightly attach the upper section of their bag to the host plant. The adults exhibit striking sexual dimorphism: males are winged moths capable of flight, whereas neotenous females (reduced body appendages and large abdomen filled with eggs) never leave their bag. Emergent females release pheromone-impregnated setae in the lower segment of their bag to attract males. Mated females lay all their eggs within their pupal case, whereas females that fail to mate die as virgins and do not oviposit; the presence or absence of eggs inside the pupal case of emerged females is indicative of lifetime mating success (Rhainds et al. 2009). Bagworms are model insects to track variation in reproductive output in natural conditions because females reproduce within a self-constructed bag (Rhainds et al. 1999; Lynch et al. 2014); for example, it is possible to estimate the potential fecundity (correlative approach based on size measurements) and mating status of thousands of field-collected females (Rhainds et al. 1999). The bagworm

under study here, *M. plana*, is a tropical species native to Southeast Asia that completes development in ~70 d and feeds on seven families of host plants (Table 1 in Rhainds et al. 2009).

In the current study, multiple sources of reproductive success (potential and realized fecundity, reproductive losses associated with mating failure and oviposition time limitation) are evaluated in relation to body size in two Lepidopteran capital breeders with distinct reproductive systems.

## Materials and Methods

**Spruce Budworm.** The study was conducted in forest stands with preferred host trees of budworms as either dominant or codominant species at two locations in 1977 (Acadia Forest Research Station near Fredericton, NB, Canada, and Heath Steele, NB, Canada; Thomas et al. 1980) and 1978 (control plots of mating disruption studies in St-Quentin, NB, Canada and Amherst, NS; Miller 1979). Females that died from natural causes were collected during the entire flight season using 1.7-m<sup>2</sup> drop trays placed below the canopy of host trees (unspecified number of drop trays at different locations); between 90 and 351 females were collected at different sites. Each individual female budworm was subjected to three measurements: 1) body size was measured as the length of one forewing (WL, in mm); 2) mating status was determined using the presence-absence of a spermatophore in the spermatheca (mated or virgin female, respectively); and 3) dry weight (DW, in mg) was determined after placing the specimens in an oven for 48 h at 65°C. The raw data from these trials were retrieved from the archives at the Canadian Forest Service – Atlantic Forestry Centre in Fredericton, NB, where they have been professionally stored for the past 35 years. A trial conducted at Acadia in 1979 (Thomas et al. 1980) was not included in this manuscript because mating status of females was not recorded.

Females collected as pupae at Acadia in 1977 were reared in the laboratory and allowed to lay eggs over different time periods to determine the potential fecundity (PF) and realized fecundity (RF = number of eggs laid at the time of death) in relation to wing length (WL) and DW.

$$PF = 61.68 WL - 465.7, \text{ and} \quad (1)$$

$$RF = 73.32WL - 13.24DW - 535.4 \text{ (Thomas et al. 1980).} \quad (2)$$

Slopes and intercepts of linear regressions between WL–DW–PF–RF did not significantly vary in relation to the location where pupae were collected (Thomas 1978, Thomas et al. 1980). Furthermore, estimates of PF and RF are robust and largely independent of the location at which pupae were collected (Rhainds and Kettela 2013). For these reasons, all estimates of PF

**Table 1.** Length of forewing (mean ± SE) of female spruce budworms collected after natural death on drop trays

Site	Year	Reproductive status		
		VIRGIN	MATED	
			OTL	SPENT
Acadia, NB	1977	11.33 ± 0.17 <sup>a</sup> (7)	11.65 ± 0.05 <sup>a</sup> (229)	11.47 ± 0.08 <sup>a</sup> (115)
Heath Steel, NB	1977	10.61 ± 0.26 <sup>a</sup> (8)	10.79 ± 0.09 <sup>a</sup> (75)	10.94 ± 0.27 <sup>a</sup> (7)
Amherst, NS	1978		11.15 ± 0.10 <sup>a</sup> (41)	11.23 ± 0.05 <sup>a</sup> (192)
St-Quentin, NB	1978	11.4 ± 0 (1)	<b>11.63 ± 0.05<sup>b</sup> (194)</b>	<b>11.14 ± 0.14<sup>a</sup> (40)</b>

Females were regrouped in three reproductive categories based on the presence (MATED) or absence (VIRGIN) of spermatophore in their spermatheca; mated females were further divided in OTL (females did not lay their full egg complement) or SPENT (females laid their full egg complement before death). For each location, bold estimated with different letter superscripts are significantly different (ANOVA followed by Student–Newman–Keuls’ test,  $P < 0.05$ ). Because only one virgin female was sampled at St-Quentin in 1978, it was not included in analysis. The outcome of ANOVA for different locations is as follows: Acadia:  $F = 2.34$ ,  $df = 2, 350$ ,  $P = 0.097$ ; Heath Steel:  $F = 0.36$ ,  $df = 2, 89$ ,  $P = 0.727$ ; Amherst:  $F = 0.32$ ,  $df = 1, 232$ ,  $P = 0.550$ ; St-Quentin:  $F = 12.95$ ,  $df = 1, 233$ ,  $P = 0.0004$ ).

and RF derived in this manuscript are based on equations 1 and 2.

Estimates of RF were constrained between 0 and PF for any value of WL and DW. The proportion of eggs laid by females at the time of death is equivalent to the ratio RF:PF, which varies between 0 and 1. The number of fertile eggs laid by females that were virgin at the time of death was set at 0, a reproductive loss that was attributed to mating failure.

Reproductive output was estimated by segregating females in three classes: 1) VIRGIN: females that did not mate as adult (RF = 0); 2) OTL = oviposition time limitations [mated females that did not lay their full complement of eggs; RF as in equation 2); 3) SPENT = mated females that laid their full egg complement (RF = PF). Reproductive losses (LOSS) were calculated as the difference between PF and RF. The wing length of females of different reproductive classes (VIRGIN, OTL, and SPENT) was compared using one-way analysis of variance (ANOVA) followed by Student–Newman–Keuls’ test (one separate ANOVA for each location). Linear regressions were used at each location to evaluate relationships between WL and RF – LOSS.

**Bagworm *M. plana*.** The source of the data originated from a study conducted in 1995 in a commercial plantation of oil palm, *Elais guineensis* Jacques (Rhainds et al. 1999), in Selangor, Malaysia. One population of *M. plana* was sampled during five consecutive generations of bagworms. For each generation, one leaf was sampled on the same 95 palms, and all pupal bags on that leaf were collected (Rhainds et al. 1999). Sampling was conducted over periods of 14–17 d for different generations, starting when >50% of females had emerged as adults.

Each pupal bag was individually measured to the nearest 0.01 mm and cut open to determine its content (Rhainds et al. 1999). In this manuscript, only data related to females that had reached the adult stage (as indicated by the presence of an anterior split in the pupal case plus pheromone-impregnated scales in the lower section of the bag;  $N > 7,000$ ) are reported. The mating status of females was determined based on the presence or absence of eggs in pupal cases (mated

and virgin females, respectively). Females that were actively pheromone calling at the time of sampling were not included in analysis because their subsequent (postsampling) reproductive fate could not be determined. The potential fecundity (PF) of females was estimated based on the length of their pupal bag ( $SIZE = x$ ) using the equation below:

$$PF = 27.2x - 182.6 \text{ (Fig. 8 in Rhainds et al. 1999).} \quad (3)$$

The realized fecundity (RF) of mated females was equal to equation 3 above, whereas RF was set as 0 for virgin-dead females. Reproductive losses associated with oviposition time limitations were set at 0, an assumption that is biologically realistic because female bagworms lay all their eggs shortly after mating.

For each generation, logistic regression was used to quantify relationships between bag length and the proportion of mated females. The relationships between  $SIZE(x)$  and  $RF - LOSS$  were solved using algebra by multiplying logistic mating probability functions with linear regressions of PF (using equation 3 to estimate PF as a function of  $x$ ):

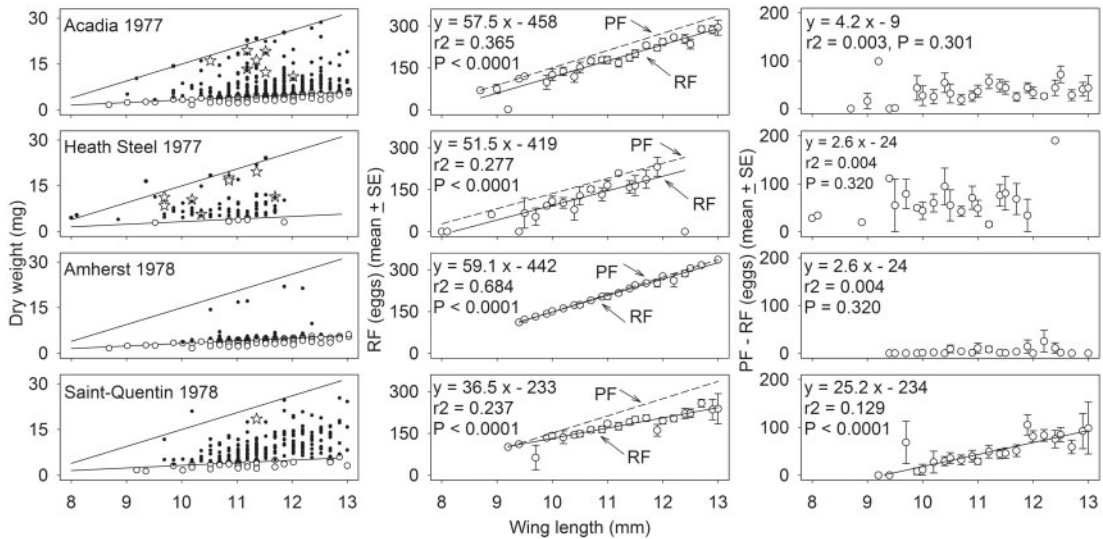
$$RF_x = [e^{(b_0 + b_1x)} / (1 + e^{(b_0 + b_1x)})] * PF_x \quad (4)$$

$$LOSS_x = PF_x - \left\{ [e^{(b_0 + b_1x)} / (1 + e^{(b_0 + b_1x)})] * PF_x \right\} \quad (5)$$

**Results**

**Spruce Budworm.** The mating success of females was high, exceeding 90% at all locations (Table 1). Logistic regression models did not disclose any significant relationship between body size and mating probabilities (Acadia: Wald  $\chi^2 = 0.75$ ,  $P = 0.387$ ; Heath Steele: Wald  $\chi^2 = 0.30$ ,  $P = 0.583$ ; only one virgin female was sampled in St-Quentin, and none in Amherst; Fig. 1).

The length of forewings did not vary for different reproductive classes, with the exception of St-Quentin in 1978, for which spent females were significantly



**Fig. 1.** Relationship between parameters related to reproductive success and body size (WL, estimated using the length of one forewing) for female spruce budworms captured on drop trays after natural death at four locations in Atlantic Canada. Left panels: Regression of dry weight of females (DW) in relation to WL. The two solid lines represent the expected weight of gravid females that did not lay any eggs (realized fecundity, or RF, is equal to 0; upper line) and of spent females that laid all their eggs (RF = potential fecundity, or PF). Equations 1 and 2 in text were used to evaluate PF and RF. Stars represent individual females that did not mate as adults. Center panels: Regression of RF versus WL (solid lines, outcomes of regression models on the upper left corner of each plot). The dashed lines represent estimates of RF assuming that all females mated during their lifetime and laid their full complement of eggs, as derived from equation 1 in the text. Right panels: Regression of reproductive loss (PF – RF) versus WL (outcome of regression models on the upper left corner of each plot).

smaller than females that did not lay their full egg complement (Table 1). The realized fecundity of females increased with body size at all locations (Fig. 1). The realized fecundity of females at Amherst in 1978 was nearly equivalent to their potential fecundity, which was because of low incidence of mating failure and oviposition time limitations. At Acadia and Heath Steel in 1977, realized fecundity was ~20% lower than potential fecundity, independent of body size (Fig. 1).

Reproductive losses due to mating failure and oviposition time limitation (PF – RF) were independent of body size at three of four sites; in contrast, reproductive losses significantly increased with the size of females at St-Quentin in 1978 (Fig. 1). Plots of residuals versus body size did not suggest any nonlinearity in the functions of reproductive losses.

**Bagworm *M. plana*.** The proportion of mated females increased with the length of pupal bag (logistic regressions,  $P < 0.0001$  for each generation; Fig. 2). The realized fecundity of females consistently increased with body size for all generations; the shape of the function was the product of a linear function (size-dependent fecundity) multiplied by sigmoid functions of size-dependent mating probability (Fig. 2). Reproductive losses due to mating failure declined with body size and were low for large females with high mating success (Fig. 2).

## Discussion

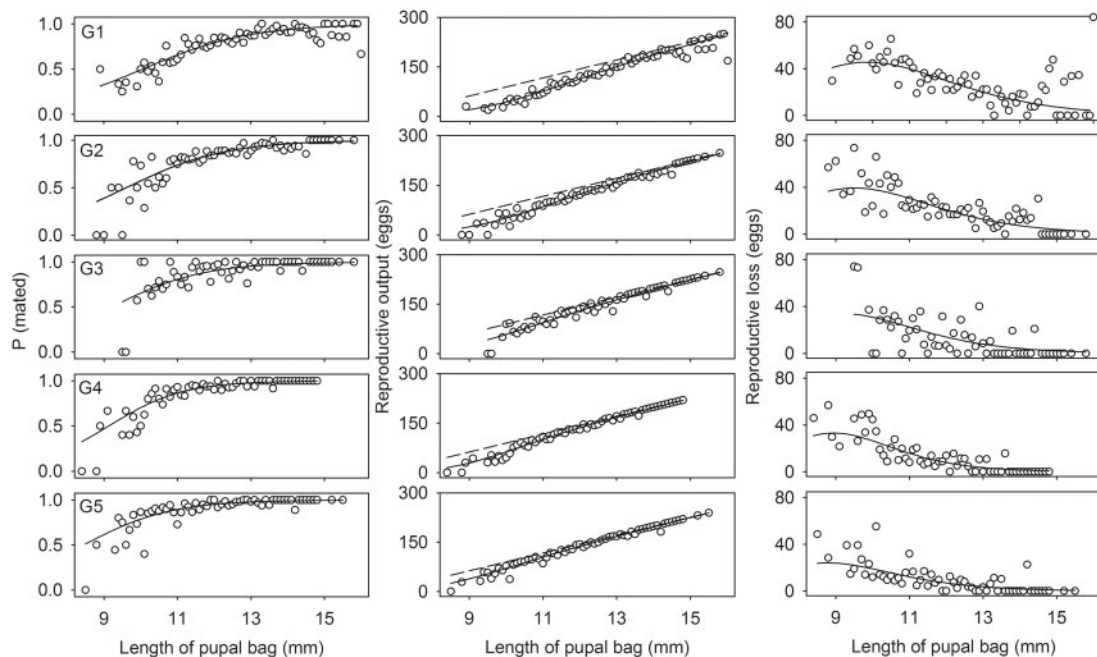
The focus of the study was to document and quantify the effect of size-dependent reproductive losses

associated with mating failure and oviposition time limitation on the realized fecundity of females in two lepidopteran capital breeders with distinct reproductive systems. Understanding the role of body size on multiple parameters of realized fecundity is important to conceptualize how phenotypic traits influence the evolution of life histories (Klingenberg and Spence 1997, de Roos et al. 2003) and to improve forecasting models of population dynamics (Tammer and Haukioja 1996, Nykänen and Koricheva 2004).

**Life-History Evolution of Body Size in Lepidopteran Capital Breeders.** In holometabolous insects, body size attained by female larvae at pupation is constrained by several parameters, including physiological size threshold below which reproduction is not viable (Callier and Nijhout 2013), trade-offs between the cost of long larval development (increased mortality) and the benefit of large size (Blanckenhorn 2000), and potential negative effects of large size-delayed emergence in terms of temporal asynchrony (availability of mates or suitable host plants; Morbey 2013). In the absence of studies comparable to the one reported here, it is unclear whether size-dependent reproductive losses that occur postemergence (mating failure and oviposition time limitation) influence the optimal size attained by female larvae at pupation.

Positive relationships between body size and potential fecundity are ubiquitous in bagworms at both intra-specific and interspecific levels (Rhainds et al. 2009). Females have vestigial body appendages and the ovarioles represent more than two-thirds of the fresh





**Fig. 2.** Relationship between parameters related to reproductive success and body size (SIZE, estimated using the length of pupal bag) for female bagworms, *M. plana*, sampled during five consecutive generations in 1995 in a commercial plantation of oil palm in Selangor, Malaysia. Left panels: Logistic regression of mating probability (y) in relation to SIZE (x) of the form  $y = e^{(\beta_0 + \beta_1 x)} / (1 + e^{(\beta_0 + \beta_1 x)})$  (solid lines). The parameters of logistic regressions for different generations G are as follows: G1:  $\beta_0 = -6.86$ ,  $\beta_1 = 0.683$ , Wald  $\chi^2 = 194.11$ ,  $P < 0.0001$ ; G2:  $\beta_0 = -7.14$ ,  $\beta_1 = 0.743$ , Wald  $\chi^2 = 117.47$ ,  $P < 0.0001$ ; G3:  $\beta_0 = -7.13$ ,  $\beta_1 = 0.780$ , Wald  $\chi^2 = 40.33$ ,  $P < 0.0001$ ; G4:  $\beta_0 = -9.64$ ,  $\beta_1 = 1.043$ , Wald  $\chi^2 = 68.50$ ,  $P < 0.0001$ ; G5:  $\beta_0 = -7.00$ ,  $\beta_1 = 0.832$ , Wald  $\chi^2 = 64.63$ ,  $P < 0.0001$ . Center panels: Regression of realized fecundity (RF) in relation to SIZE under the assumption that virgin females do not produce viable eggs; the solid line is derived by multiplying logistic regression models above with equation 3 in text. The dashed line represents the potential fecundity (PF) under the assumption that all females mated. Right panels: Regression of reproductive losses (PF – RF) in relation to SIZE. Note: data are not shown (but were included in analysis) when the sample size was one female for a given size measurement and generation.

biomass of females (Rhains and Ho 2002, Rhains et al. 2008), indicative of a highly effective reproductive energy budget (Hall et al. 1992). The benefit of neoteny (high conversion of larval accumulated resources into reproductive tissue) is apparently counterbalanced by mating cost linked to flightlessness (Bell 1982, Roff 1990, Denno 1994), resulting in high rates of mating failure (Rhains et al. 2009, Fig. 2). Size-dependent mating probability implies a double cost of small body size, both direct (reduced potential fecundity) and indirect (via low mating success), which suggests strong selective pressures to attain large size at pupation. In that context, differences in pupal size among host plants likely have fitness consequences for females (Awmack and Leather 2002, Moreau et al. 2006, Rhains et al. 2008).

In addition to potential fecundity and mating probability, body size attained by female larvae at pupation enhances other measures of fitness not reported in this study, including survival to adult stage and conversion of somatic tissue in reproductive tissue (Rhains et al. 1999, 2008). Multiple benefits of body size provide strong selective pressures favoring large size at pupation ("larger is always better," Tammari et al. 2002). This evolutionary trend is likely counterbalanced by

some unknown physiological, environmental, or genetic processes.

Neonate bagworms often remain on their natal trees where they complete development and the process is repeated over multiple generations, which likely increases genetic relatedness among individuals (Rhains et al. 2009). This poses the intriguing question as to whether natural selection operates on individual females (seeking to achieve the largest possible size) or rather acts on local groups of genetically related females (seeking to achieve large body size on average).

The potential fecundity of female spruce budworms (as evaluated by rearing field-collected pupae in the laboratory) increases with body size across a range of population densities and defoliation levels (Miller 1957, Morris 1963, Thomas et al. 1980, Robison et al. 1998). In addition, the realized fecundity of females at death (taking into account reproductive losses owing to mating failure and oviposition time limitations) also increases with body size (Fig. 1; Table 1). Most female budworms mated at the high-density sites under study [ $P(\text{mated}) > 98\%$  at three of four locations, 91.2% at Heath Steel in 1977], and body size did not affect mating success (Table 1). The latter finding is somehow surprising because positive associations between body

size and mating probabilities are prevalent in insects (Crespi 1989, Bonduriansky 2001). In contexts whereby mating of females is constrained, e.g., low-density populations (Régnière et al. 2013) or pheromone-based mating disruption (Rhains et al. 2012), body size may mediate competitive interactions among females for access to mates (Kipp et al. 1987).

Oviposition time limitation was the major factor reducing the realized fecundity of females: at three of four sites > two-thirds of females did not lay their full egg complement before death (Table 1). At St-Quentin in 1978, the proportion of eggs laid by females decreased with body size (Fig. 1), which suggests an indirect cost of being large (Gotthard et al. 2007, Berger et al. 2012). Small female spruce budworms also have low wing:load ratios and better preoviposition flight capacity than large females (Blais 1953), which suggests another potential benefit of small size in terms of long-range dispersal.

**Consequences of Body Size Variation on Population Dynamics.** In the absence of emigration or immigration, life tables of realized fecundity are ultimately conditional on the following three functions: 1) the distribution of body size within a population of females; 2) the relationship between body size and potential fecundity; and 3) the relationship between body size and reproductive losses. Ultimately, life tables and population studies that account for reproductive output need to quantify a transitive term between the number and size of females in generation  $t$  versus expected number of eggs – offspring in generation  $t + 1$ . The implementation of life tables of realized fecundity is challenging because empirical data on intraspecific size–frequency distribution are rare in the literature (Chown and Gaston 2010, Gouws et al. 2011), and it is logistically difficult to assess reproductive losses in field populations of insects (Cushman et al. 1994).

Bagworms are ideal insects to link the consequences of reproductive success at the population level due to lack of female dispersal and unusual tractability of parameters related to reproduction. In *M. plana*, the impact of mating losses on the net reproductive output at the population level may be minimal because dead-virgin females are predominantly small and least fecund (Fig. 2). In the bagworm *Thyridopteryx ephemeraeformis* Haworth, realized fecundity can be used as a predictor of extinction of local populations (Rhains and Fagan 2010).

It is ironic that life tables were originally developed in spruce budworm (Morris 1963), an insect that is ill-suited to quantify expected versus observed densities of egg masses because females migrate between oviposition bouts (Greenbank et al. 1980). The vast majority of mated females had laid >50% of their eggs at the time of death (Acadia in 1977: 319 of 344 females, or 92.7%; Heath Steel in 1977: 70 of 82 females, or 85.4%; Amherst in 1978: 228 of 233 females, or 97.9%; St-Quentin in 1978: 217 of 235 females, or 92.3%); thus, it cannot be ruled out that these females were immigrants. On the other hand, females that laid >50% of their eggs and then

migrated would have been absent from the local pool of dead females.

The ultimate nature of interreproductive migrations in spruce budworms (obligatory ontogenetic shift during adult development, condition-dependent strategy dependent on local defoliation or density of conspecifics, facultative strategy independent of local conditions—“bet hedging”) remains unknown; thus, it is impossible to delineate numerically the local pool of reproductive females and their expected fecundity. Historically, the egg to pupa ratio has been used to segregate the reproductive output of females into two components (oviposition of resident and migrant females), but the approach has limited heuristic value due to multiple unaccounted for transitions between the pupal–egg stages (survival to adult stage, body size, mating probability, proportion of eggs laid by local female before migration, proportion of females that emigrate, and fecundity of immigrant females; Morris and Miller 1954, Miller 1957, Nealis and Régnière 2004).

Body size was positively correlated with both potential and realized fecundity in spruce budworms and bagworms, yet the effect of size on reproductive losses was distinct for the two organisms. In bagworms, mating probabilities increased with body size; thus, reproductive losses owing to mating failures were most pronounced for small, least fecund females (Fig. 2). The realized fecundity of female spruce budworms increased linearly with body size, mating failures were rare, and oviposition time limitations were either size independent or declined with body size. Owing to the incidence of interreproductive migrations in spruce budworms, detailed postmortem assessments of reproductive output may not improve our understanding of population dynamics because populations are subject to waves of emigrations–immigrations, and thus the local pool of reproductive females is impossible to delineate.

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