



Polyandry across Behavioral Classes in Female Spruce Budworm

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Abstract Reproduction in spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is characterized by sedentary oviposition in the natal forest patch early in life (gravid females are incapable of flight due to their heavy abdomen) followed by windborne migrations among females that have laid >50% of their eggs; the nature of migrations (facultative or obligatory) remains unknown. The incidence of polyandry (females with more than one spermatophore in their reproductive tract) was evaluated for several thousand field-collected female budworms (data professionally archived at Canadian Forest Service) using an array of sampling procedures that can be delineated along four behavioral classes: (1) resident females collected on host trees; (2) in-flight females captured while foraging in forest canopies; (3) migrant females captured above tree canopies; and (4) females collected postmortem on drop trays. Overall, polyandry increased over time (reflecting the ageing of local populations) and with female body size (likely due to male mating preference for large, most fecund females). Polyandry did not increase postmortem realized fecundity of females. The level of polyandry was lowest among migrants, intermediate for in-flight and resident females, and highest for naturally dead females. Sedentary reproduction among young female budworms may limit gene flow and increase the risk of inbreeding; a low level of polyandry among migrants may thus be due to females not only seeking novel habitats for their progeny but also mating partners that are not closely related genetically.

Keywords Breeding dispersal · female mating failure · morphometrics · monandry · natal dispersal

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Introduction

Polyandry is a widespread life history trait in insects, most notably in Lepidoptera where it appears ubiquitous based on spermatophore counts among field-collected females (> 350 species in multiple families) (Burns 1968; Pease 1968; Pliske 1973; Byers 1978; Ehrlich and Ehrlich 1978; Wiklund and Forsberg 1991; Walters et al. 2012). Polyandry is most common in species where multiple mating increases the reproductive output of females (through enhanced fecundity, fertility, longevity, and/or fitness of progeny), which may result from multiple causes, including (among others): spermatophores provide nutrients to females, multiple copulations are needed to fertilize the full egg complement, females gain genetic benefits from multiple paternity, and/or polyandry reduces the negative impact of inbred copulations (Ridley 1988; Jennions and Petrie 2000; Torres-Villa et al. 2004; Cornell and Tregenza 2007; Forbes 2014). In many species, however, multiple matings are frequent among females even though they do not yield apparent benefit and may even be detrimental (Arnqvist and Nilsson 2000; Kawagoe et al. 2001; Torres-Vila et al. 2004). This evolutionary paradox may be explained, in part, by the high cost of lifetime mating failure (zero fitness) (de Jong and Sabelis 1991; Rhainds 2010) relative to the moderate cost of polyandry: multiple mating by females may thus be viewed as byproduct of low thresholds for mate acceptance that have evolved primarily to prevent mating failure (Gowaty and Hubbell 2013; Kokko and Mappes 2013). As expected within that context, the level of mate choosiness is relaxed for virgin females relative to mated females (because virgins face the risk of encountering / rejecting one single male during their life and thus not reproducing) (Kokko and Mappes 2005).

The mating system of moths that rely on female-produced sex pheromone for mate attraction provides general support to the hypothesis above. As they age, unmated females spend more time actively releasing sex pheromone, presumably to mitigate the ever-increasing risk of lifelong virginity; after copulation, in contrast, females generally reduce their investment in mate signalling (delayed onset and shorter duration of calling, lower pheromone titers) (Wedell 2005; Umbers et al. 2015). These trends suggest that mate signalling in moths has evolved primarily (although not exclusively) to ensure successful mating rather than promote polyandry.

The spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae), illustrates the extent of polyandry in a species that may be characterized as primarily monandrous. Shortly after emergence, females release pheromone to attract males and generally mate on the same day they emerge (Outram 1971; Silk and Kuenen 1988). Polyandry in female budworm is limited by several factors: sperm precedence, long duration of copulation (males mate once per night), post-copulatory mate guarding by males, strong male preference for virgin over mated females, physiological inhibition of pheromone production following mating, restricted period of sexual activity of ovipositing females, and limited benefit of multiple mating in terms of reproductive output (Outram 1971; Sanders and Lucuik 1972; Retnakaran 1974; Sanders 1975; Kipp et al. 1990; Delisle et al. 2000; Delisle and Simard 2002). Although polyandry does not increase reproductive output in budworm (unless females previously mated with a low quality male), it has no apparent cost in terms of reduced fertility (Delisle and Hardy 1997) and may thus be viewed as neutral trait that is not strongly selected against.

Polyandry has been documented anecdotally in field-collected female budworm (Outram 1968), but its incidence in natural conditions has yet to be rigorously quantified. Based on the literature, two specific trends can be predicted a priori in female budworm. (1) Polyandry is expected to increase over time, a seasonal effect that reflects the ageing of individuals in local populations (monotonic increments in number of sexual partners over a female's life) (Pease 1968; Pliske 1973; Ehrlich and Ehrlich 1978; Sims 1979; Walters et al. 2012). (2) Polyandry is expected to increase with female body size (Rutowski 1982; Gage 1998; Bergström and Wiklund 2002; Wedell et al. 2002; Jiménez-Pérez et al. 2003) due to male preference for large, most fecund females (Crespi 1989; Bonduriansky 2001).

Behavioral plasticity in female dispersal strategies may further influence the incidence of polyandry (Hirota 2004; Brom et al. 2016). Due to their heavy abdomen, gravid female budworms are not capable of flight until 50% of their eggs have been laid (Rhainds and Kettela 2013); later in life, partly spent females may (or may not) undertake windborne migrations by ascending above tree canopies to the upper boundary layer (Greenbank et al. 1980; Boulanger et al. 2017). Sedentary reproduction in the natal patch may limit gene flow and increase the risk of inbred copulations (Roderick 1996; Peterson and Denno 1998). Female budworm that undergo long-range dispersal may thus not only seek novel habitats for their progeny but also mating partners that are not closely related genetically. If true, a low level of polyandry would be expected among migrants relative to residents that reproduce locally.

Links between dispersal strategy and polyandry are challenging to validate empirically, however, as they require hard-to-gather estimates of polyandry for population subsamples segregated along behavioral classes. Despite the wealth of studies reporting spermatophore counts in feral females, field estimates of polyandry are (to the author's knowledge) rarely based on more than one sampling procedure, other than some lepidopteran pests of corn (Elliott 1977; Latheef et al. 1991). The spruce budworm represents a notable exception: during the last outbreak in Atlantic Canada in the 1970s, spermatophore counts were recorded for several thousand females collected using an array of sampling procedures that can be grouped into four behavioral classes: (1) resident females collected on host trees; (2) in-flight females collected with traps deployed in forest canopies; (3) migrant females collected above tree canopies; and (4) females that died from natural causes. The first three classes provide punctual assessments of polyandry at the time of sampling; the fourth class provides postmortem assessment of lifetime polyandry. Data on dead females include morphometric measurements (ratio of dry weight to wing length) that can be used to infer lifetime realized fecundity of females (Thomas et al. 1980). The spermatophore data, professionally archived at the Canadian Forest Service - Atlantic Forestry Centre, have never been published in any way or form.

Four hypotheses related to the incidence and fitness consequence of polyandry among feral female spruce budworms are evaluated. The proportion of polyandrous females is expected to increase over time (H1) and with body size (H2), and to be lower among emigrants than resident females (H3); in addition, polyandry is not expected to influence lifetime reproductive output of female budworm (H4).

Materials and Methods

Source of Data

Female budworms were collected in the 1970s in Atlantic Canada at multiple forest stands characterized by hosts of budworm being dominant or codominant tree species (for geographic location of different sites, see Fig. 1 in Rhainds 2013); budworm densities were high at all sites. The data originated from different research contexts, including studies on dispersal and migration behavior (Chipman, NB, 1973–1974; Juniper, NB, 1975) (Greenbank et al. 1980), as well as large-scale trials aimed at interfering with budworm reproduction by killing adults (aerial applications of insecticide; Acadia, NB, 1977; Heath Steel, NB, 1977) (Thomas et al. 1979, 1980) or suppressing mating with pheromone disruptant (St.-Quentin, NB, 1978; Amherst, NS, 1978) (Miller 1979); in the latter two cases, only data from control (untreated) plots are included. Females were collected with several sampling procedures (see below), generally over periods exceeding 8 days. Females were dissected to determine the number of spermatophores by macerating their genitalia in heated potassium hydroxide (Robinson 1976).

Sampling Procedures

Female budworms were collected using several sampling procedures (Miller 1979; Thomas et al. 1980; Greenbank et al. 1980; Hurley and Titus 1987) that can be grouped in four behavioral classes:

- (1) Resident - ovipositing females were collected on tarpaulins deployed below host trees that had been fogged with pyrethrins and piperonyl butoxyde. Although it is possible that some females collected on host trees were migrants, as a whole the behavioral class of ‘residents’ includes more females that can be unambiguously labeled as local than any other sampling procedure (young virgin – gravid females unable to fly / migrate due to heavy abdomen) (Rhainds 2013; Rhainds and Kettela 2013).
- (2) In-flight adults captured with malaise traps and light traps deployed in tree canopies are classified as foragers seeking suitable oviposition sites. In-flight females are on average physiologically older than resident females as indicated by their low wing load (ratio of dry weight to wing length characteristic of spent females that have laid more than half their eggs; Rhainds and Kettela 2013) and mating status (samples include no virgins; Rhainds 2013).
- (3) Migratory females were collected with sweep nets while ascending above tree canopies, in the atmospheric boundary layer using aircrafts, or shortly after immigration in early morning on the runways of airport (tarmac) isolated from forest stands; the tarmac was inspected the evening before to ensure that no moths were present. The physiological age of in-flight and migrant females appears similar based on wing load and mating status (Greenbank et al. 1980).

- (4) Dead females were collected using drop trays placed below the canopy of host trees, where postmortem assessments provide lifetime estimates of polyandry.

Postmortem Assessment of Lifetime Realized Fecundity

Postmortem morphometric measurements of monandrous and polyandrous females collected on drop trays [wing length (WL), recorded to the nearest 0.167 mm; dry weight (WT) recorded to the nearest mg, following a 48 h exposure at 65 °C] were available at three sites: Acadia, Heath Steel, and St.-Quentin. The proportion of eggs laid by each female was inferred using site-specific baseline equations describing relationships between WL and WT for gravid and spent females using the procedure described below (Thomas et al. 1980).

Female pupae were collected from branches of host trees at each site and monitored daily in the laboratory to determine timing of emergence. Emerged females were divided in two groups. (1) Gravid females (g) were killed shortly after emergence (realized fecundity = 0) to determine relationships $WT_g = \beta_{g-0} + \beta_{g-1} WL$. (2) Spent females were allowed to copulate with one male then introduced in a Petri dish with foliage of host plants to oviposit until death, to determine the relationship $WT_s = \beta_{s-0} + \beta_{s-1} WL$; these functions estimate the weight of female “skeletons” after all eggs are laid. Site-specific equation parameters for WT_g and WT_s are reported in Table 1.

For each field-collected female i with known WL and WT, the proportion of eggs laid at the time of death (P_{laid-i}) was estimated using the equation:

$$P_{laid-i} = 1 - [WT_i - \{\beta_{s-0} + (\beta_{s-1} WL_i)\}] / [\beta_{g-0} - \beta_{s-0} + \{(\beta_{g-1} - \beta_{s-1}) WL_i\}] \quad (1)$$

Estimates of P_{laid-i} were constrained between 0 and 1. P_{laid} can be viewed as the WT to WL ratio of a given female relative to known ratios for spent females that laid their

Table 1 Parameters of linear regressions characterizing the relationship between wing length (estimated to the nearest 0.167 mm) and dry weight (estimated to the nearest mg) of female spruce budworms collected as pupa at three locations (Acadia, NB, 1977; Heath Steel, NB, 1977; St-Quentin, NB, 1978) and allowed to emerge in the laboratory

Location	♀ status	N	β_0	β_1	r^2	P
AC-77	Gravid	568	-42.15 ± 2.13	5.640 ± 0.190	0.610	0.0001
	Spent	509	-6.04 ± 0.65	0.955 ± 0.058	0.347	0.0001
HS-77	Gravid	108	-29.51 ± 3.58	4.543 ± 0.333	0.637	0.0001
	Spent	99	-4.77 ± 1.43	0.839 ± 0.133	0.292	0.0001
SQ-78	Gravid	99	-34.82 ± 5.54	4.760 ± 0.448	0.538	0.0001
	Spent	56	-3.26 ± 1.58	0.749 ± 0.128	0.389	0.0001

The females were either killed shortly upon emergence (gravid females) or allowed to oviposit until death (spent females). The equations as derived for different locations were used to infer the proportion of eggs laid by females at death (Eq. 1 in text)

full egg complement ($P_{\text{laid}} = 1$) and gravid females that have not yet oviposited ($P_{\text{laid}} = 0$) (see Fig. 2 in Rhainds and Kettela 2013).

Statistical Analysis

Analyses were conducted using SAS statistical package (SAS Institute, Cary, NC). The proportion of polyandrous females (with >1 spermatophore) was computed for each sampling procedure and site. The data set is similar to that described in Rhainds (2013), with the exception of sites for which an estimate of polyandry was only available for one behavioral class; these sites were deleted from analysis, because one of the main research objectives was to document polyandry across behavioral classes.

The data set used in the first analysis (proportion of polyandrous females, independent of sampling date) included 29 female collections (each collection refers to a given sampling procedure at a given site and year) (Table 2). Because the structure of the data was unbalanced (empty cells for 20 of 49 possible observations), separate analyses were conducted on a per site basis to evaluate how the incidence of polyandry (poly / total) varied in relation to sampling procedure (method, defined as class variable) [proc sort; by site; proc. logistic; class method; model poly / total = method].

For each of five sites at which the date of female collection was known, data were grouped into three time periods, each containing approximately the same number of females. The incidence of polyandry at each site was evaluated in relation to method and time (the latter defined as a continuous variable) with logistic regression model [proc logistic; class method; model poly / total = method time method*time]. Nonsignificant two-way interactions were deleted from final models.

For the three sites at which postmortem morphometric measurements were available, wing length and proportion of eggs laid by females (Eq. 1, using site-specific parameters reported in Table 1) were compared across sites and mating status (monandrous versus polyandrous females) using two-way ANOVA.

Results

Monandrous females outnumbered polyandrous females by a factor of 2.2 (5478 versus 2530 females). Most (88%) polyandrous females had mated only twice ($N = 2228$), versus 12% that had mated three or four times ($N = 302$); no female had more than four spermatophores in their reproductive tract.

The proportion of polyandrous females at different sites varied significantly (and consistently) across sampling procedures: polyandry was most common among females that died from natural causes, and least common among migrant females (Table 1).

The incidence of polyandry increased over time for most locations and sampling procedures, with the possible exception of dead females collected on drop trays. The interaction between time and sampling procedure was statistically significant at Amherst and St.-Quentin, due to a lack of temporal variation in polyandry among dead females (Fig. 1).

Wing length of females collected postmortem varied significantly among sites ($F = 42.17$, $P < 0.0001$): females collected at Heath Steel were considerably smaller than those at Acadia or St.-Quentin (Fig. 2). Polyandrous females were larger than monandrous females at all sites ($F = 24.85$, $P < 0.0001$) (Fig. 2).

Table 2 Proportion of polyandrous female spruce budworms collected at multiple sites (see Fig. 1 in Rhainds 2013 for geographic location of experimental sites)

Site - Year	Procedure	N	P (polyandry)	Wald χ^2	<i>P</i>
CH – 1973	FOG	420	0.340	15.19	0.0017
	LT	473	0.258		
	PTF	158	0.196		
	AIR	9	0.111		
CH – 1974	FOG	225	0.284	27.93	0.0001
	LT	138	0.210		
	PTF	404	0.158		
	AIR	815	0.151		
	TAR	198	0.116		
JU – 1975	LT	111	0.369	30.08	0.0001
	PTF	87	0.149		
	TAR	38	0.079		
	AIR	51	0.020		
	DEAD	91	0.143		
AC – 1977	FOG	900	0.232	100.87	0.0001
	LT	195	0.195		
	MAL	269	0.390		
	DEAD	315	0.511		
HS – 1977	FOG	565	0.492	49.15	0.0001
	LTC	172	0.180		
	MAL	58	0.517		
	DEAD	81	0.481		
AM – 1978	LT	340	0.244	100.12	0.0001
	MAL	400	0.463		
	PTF	144	0.299		
	DEAD	605	0.567		
SQ – 1978	LT	171	0.409	33.79	0.0001
	MAL	221	0.271		
	DEAD	349	0.521		

Different sampling procedures were used to collect females, which procedures are categorized in four behavioral classes: (1) Resident females were collected by fogging host trees with insecticides (FOG); (2) In-flight females foraging within forest stands were collected either using light traps (LT) or malaise traps (MAL); (3) Migrant females were collected while ascending above forest canopies (observation platform, or PTF), in the upper boundary layer with airplanes (AIR), or on tarmacs in early morning (TAR); and (4) naturally dead females were collected on drop trays (DEAD). For each site, proportions of polyandrous females were compared across sampling procedures using logistic regression models

Postmortem realized fecundity of females (assessed using proportion of eggs laid) varied significantly among sites ($F = 57.20$, $P < 0.0001$): females at Acadia had laid more than 90% of their eggs compared with approximately 70–75% at Heath Steel and St.-Quentin (Fig. 2). The realized fecundity of monandrous and polyandrous females did not vary significantly ($F = 0.88$, $P = 0.3480$) (Fig. 2).

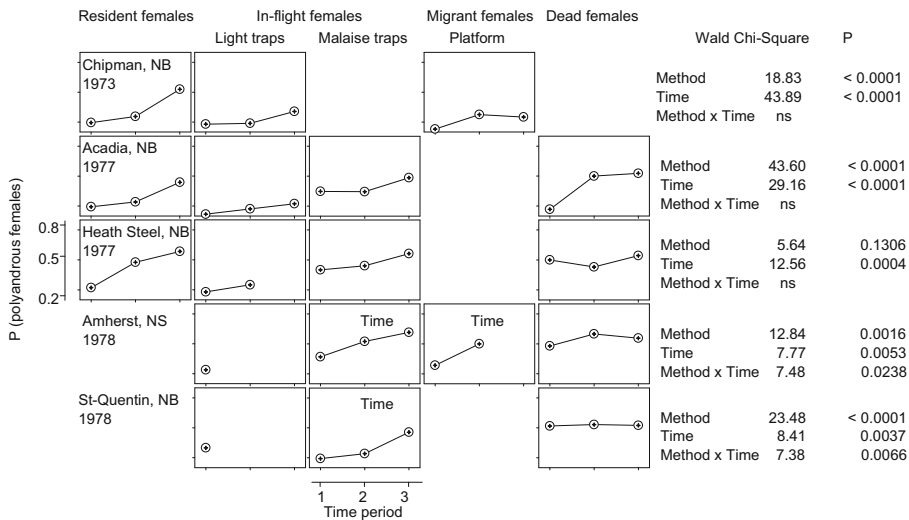


Fig. 1 Proportion of polyandrous female spruce budworms collected at multiple sites (see Fig. 1 in Rhainds 2013 for geographic location of experimental sites). Different sampling procedures were used to collect females, which procedures are categorized in four behavioral classes: (1) Resident females were collected by fogging host trees with insecticides; (2) In-flight females foraging within forest stands were collected either using light traps or malaise traps deployed in tree canopies; (3) Migrant females were collected while ascending above forest canopies (observation platform); and (4) naturally dead females were collected on drop trays. For each site, data were divided into three time periods with approximately the same number of females [Chipman: (1) 1–6 July: 270 ♀; (2) 7–9 July: 336 ♀; (3) 10–12 July: 444 ♀. Acadia: (1) 5–13 July: 678 ♀; (2) 14–17 July: 437 ♀; (3) 18–28 July: 556 ♀. Heath Steel: (1) 9–18 July: 190 ♀; (2) 19–24 July: 172 ♀; (3) 25–29 July: 193 ♀. Amherst: (1) 7–18 July: 363 ♀; (2) 19–21 July: 477 ♀; (3) 22–31 July: 313 ♀. St-Quentin: (1) 5–11 July: 305 ♀; (2) 12–14 July: 131 ♀; (3) 15–22 July: 134 ♀. [NOTE: analyses in Amherst and St-Quentin excluded light trapping because it was conducted only during a short 4-day period in early season] The effects of method and time (set as class and continuous variable, respectively) were evaluated for different sites using logistic regression models; whenever nonsignificant, the interactions method x site were deleted from analysis

Discussion

Lifelong mating failures are rare among female spruce budworm, as indicated by the high mating success of females collected postmortem (>98%; Rhainds 2013). Mating constraints are thus unlikely to suppress the reproductive output of females and affect population dynamics, with the possible exception of low density populations (mate-encounter Allee effect; Régnière et al. 2013). Higher levels of polyandry in females that died from natural causes than among females collected while still alive (residents, in-flight, migrants) are expected due to the old age of dead females. In absolute terms, however, the high proportion of protandrous females at death (nearly 50% on average; Table 1) is unexpected, considering that polyandry does not affect lifetime realized fecundity (Fig. 2). Unless polyandry enhances unknown fitness parameters not recorded in this study (i.e., sperm insurance; Delisle and Hardy 1997), female budworm may mate more than once during their life to reduce the cost of male harassment in high density populations (Forsberg and Wiklund 1989). Indirect support for this hypothesis is provided by density-dependent shift in male behavior. At low population density, nocturnal males orient toward individual pheromone sources of calling females; at high density, in contrast, males are active during the day (when females are *not* releasing

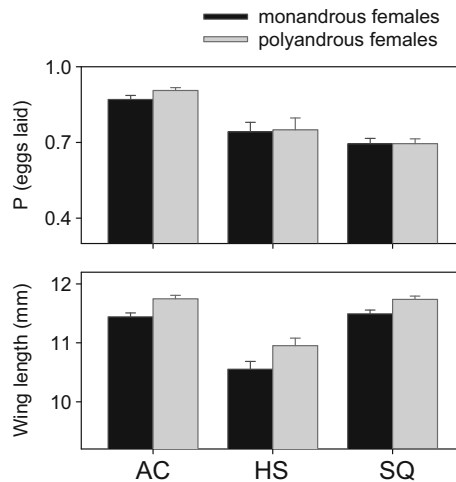


Fig. 2 Wing length and proportion of eggs laid (mean values \pm SE) by female spruce budworms collected postmortem on drop trays at three sites (AC: Acadia, NB, 1977; HS: Heath Steel, NB, 1977; SQ: St-Quentin, NB, 1978). The proportion of eggs laid was estimated for each female using Eq. 1 in text, with site-specific parameters reported in Table 1. Females were classified as monandrous or polyandrous based on the number of spermatophores in their reproductive tract (1 versus >1)

pheromone) and seek sexual partners by hovering (‘buzzing’) around tree crowns (Sanders and Lucuik 1972; Greenbank et al. 1980; Liebhold and Volney 1984; Kipp et al. 1995), a density-dependent behavior that may increase harassment of ovipositing females.

The incidence of multiple mating is highly variable at the interspecific level, thus species are often categorized as primarily monandrous or polyandrous based on proportions of females that mate more than once (using, for example, thresholds of $<25\%$ and $>40\%$ for monandrous and polyandrous species, respectively; Torres-Vila et al. 2004). Comparison of polyandry levels across sampling procedures reveals potential biases in assessing ‘true’ estimates of polyandry in natural conditions. For example, estimates of polyandry based on females captured at light traps (an approach that is very common in applied entomological research) may systematically underestimate the true incidence of polyandry in spruce budworm. In contrast, data comparable to those reported here in two lepidopteran pests of corn (*Ostrinia nubilalis* Hubner, *Heliothis zea* Boddie) reveal that polyandry among females collected at light traps does not differ from that observed with sweep net collections (Elliott 1977; Latheef et al. 1991).

The level of polyandry in spruce budworm increased over time for resident, in-flight, and migrant females (Fig. 1), a trend that reflects the ageing of local populations and increments in the number of sexual partners during the course of a female’s life (Pease 1968; Pliske 1973; Ehrlich and Ehrlich 1978; Sims 1979; Walters et al. 2012). Interestingly, polyandry among females collected postmortem was largely invariable in relation to time, with the possible exception of Acadia (Fig. 1); in that case, the apparent low level of polyandry in early season may be due to low sample size (one of six polyandrous females, representing $<2\%$ of 312 females collected on drop trays).

Body size of female budworm mediates competitive interactions for access to mates in ecological contexts where limited availability of males restricts reproductive success i.e., large size of mated females (relative to virgins) in plots treated with pheromone disruptant (Kipp 1987). Because multiple mating has no apparent effect on the reproductive output of females, it seems unlikely that size-dependent polyandry in budworm reflects the outcome of mating contests among females. Rather, it suggests that males preferentially mate with large females, a behavior that is highly adaptive due to tight linkages between body size and fecundity across a wide range of population densities and defoliation levels (Miller 1957; Morris 1963; Thomas et al. 1980; Rhainds 2015).

Natal dispersal from the emergence patch before the onset of reproduction (Johnson and Horvitz 2005) is rare to nonexistent in budworm: gravid females have limited mobility due to their heavy abdomen and are incapable of sustained flight before oviposition (Rhainds and Kettela 2013). Later in life, females may (or may not) undergo long-range migrations (breeding dispersal, defined as dispersal movements away from the natal patch after some reproduction took place; Lakovic et al. 2015). Females actively in-flight in forest canopies or undergoing long-range migrations (breeding dispersal) have laid >50% of their eggs, which means they are at least 2 d old based on the schedule of oviposition (Harvey 1977; Greenbank et al. 1980; Delisle and Hardy 1997). It is unknown whether breeding dispersal in budworm is obligatory (ontogeny shift in partly spent females) or conditional upon high density of conspecifics or host tree defoliation (Rhainds 2015). Assuming that migrant females seek not only novel habitats for their progeny but also mating partners that are not closely related (sedentary reproduction early in life may lead to inbreeding pressures), multiple paternity (polyandry) may reduce the incidence / benefit of migrations (Hirota 2004); this hypothesis remains to be formally validated.

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