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LIFE HISTORY TRAITS AND REARING TECHNIQUES FOR FALL WEBWORMS (*HYPHANTRIA CUNEA* DRURY) IN COLORADO

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ABSTRACT. The fall webworm (*Hyphantria cunea* Drury) is a moth species native to North America and an invasive pest in Europe and Asia. *Hyphantria cunea* larvae are noted generalists, and have been recorded feeding on dozens of plant families worldwide. There appear to be at least two forms of *H. cunea* that are distinguished by the larval head capsule color: black or red. Most previous accounts of *H. cunea* in the literature focus on the black-headed form. The three goals of the research we present here are to 1) detail successful rearing techniques for the red-headed form of *H. cunea*, 2) describe life history traits of red-headed *H. cunea* in Colorado and 3) test whether female pupal mass predicts potential fecundity for *H. cunea* as well as other lepidopteran species. Our data are compiled from two years of rearing experiments in the lab. In addition, we compare measures of life history traits from our research with those of other collections of *H. cunea* from Asia, Europe, Canada, and other regions of the United States to enable a better comparison between the black-headed and red-headed forms of *H. cunea*.

Additional key words: Arctiidae, Erebidae, fitness, life history, potential fecundity

The fall webworm (*Hyphantria cunea* Drury) is a moth species native to North America and an invasive pest in Europe and Asia (Tadić 1963, Yang et al. 2008). The gregarious larvae spin extensive webs for protection (Ito 1977) and thermoregulation (Morris and Fulton 1970, Rehnberg 2002, 2006), usually on the outer branches of deciduous trees. *Hyphantria cunea* are noted generalists and have been recorded feeding on dozens of plant families worldwide (Warren and Tadić 1970). Their preferred hosts are deciduous, woody plants, but larvae have been observed on herbaceous plants like *Clematis* (Swain 1936) and even gymnosperms (Oliver 1964).

The taxonomic status of *H. cunea* is unclear. There are at least two genetically distinct 'races' or forms of *H. cunea* in North America (Jaenike & Selander 1980) capable of interbreeding to produce fertile offspring (Oliver 1964, Masaki & Ito 1977). Morphologically, the only distinguishing feature is larval coloration: a black-headed form and a red or orange-headed form. The two larval forms are also behaviorally distinct as fifth instar larvae; black-headed *H. cunea* leave the web during the ultimate instar and become solitary (Szalay-Marzso 1972), whereas red-headed *H. cunea* are reported to cluster within the communal web until pupation (Oliver 1964). Masaki and Ito (1977) noted a third form with a mottled head native to North America. Because red and mottled-headed larvae create a much thicker web that spreads to the crook of the host tree, similar to the behavior of tent caterpillars, they are sometimes referred to collectively as *Malacosoma*-type *H. cunea* (Masaki & Ito 1977). We do not distinguish between red and mottled-headed *H. cunea*, both of which may exist in Colorado, and refer to the *H. cunea* form that we study as red-headed. Within North America, the black-headed form is primarily in the east and northeast, whereas the red-headed form is mostly in the south and west, with large areas of sympatry (Masaki 1977). Voltinism is graded geographically; *H. cunea* populations in the northeastern United States and Canada are univoltine, and populations in the Gulf States and Mexico have been observed with four or more generations per year (Masaki 1977). Where red and black-headed forms co-occur in the mid-Atlantic, they are phenologically distinct, with a univoltine red-headed generation emerging between two black-headed generations (Masaki 1977). Host selection also differs between the two forms, however, there is some overlap (Oliver 1964).

Several researchers have published rearing techniques for *H. cunea* on both natural host plants and artificial media (Jasič & Macko 1961, Yearian et al. 1966, Morris & Fulton 1970,) as well as studies of larval fitness on natural host plants (Jasič & Macko 1961, Morris & Fulton 1970, Greenblatt 1978, Gomi et al. 2005, Mason et al. 2011). However, all of these studies have focused on the black-headed form, which is the only form present in Europe and Asia, and there are very few studies on the red-headed form (but see Oliver 1964, Masaki & Ito 1977). For this paper we had

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§Authors contributed equally to this research and are listed in alphabetical order three objectives. Our first objective was to provide the first published account of successful rearing techniques for red-headed *H. cunea*. Our second objective was to measure and report life history traits of *H. cunea* in Colorado and to compare them with other published accounts. Our third objective was to test whether female pupal mass predicts fecundity, and thus lifetime fitness, for *H. cunea* as well as other lepidopteran species.

MATERIALS AND METHODS

Objective 1 – Rearing techniques for red-headed *H. cunea*

Larval collection. The red-headed form of *H. cunea* is widespread in North America; in Colorado, researchers and hobbyists have recorded the moths in 15 counties (Ferguson et al. 2000). We collected wild larvae from multiple field sites near the cities of Boulder (Boulder County, 40.090013, -105.359962), Fort Collins (Larimer County, 40.5852602, -105.084423), and Idledale (Jefferson County, 39.746944, -105.210833) in Colorado (Fig. 1). The conspicuous webs were visible along roads and waterways, and we most commonly found webs in canyons dominated by deciduous woody plants and on the plains abutting the foothills. We collected larval *H. cunea* from July 21 through September 21 of 2010, after which webs that we searched were empty. Webs were distributed at heights greater than one meter from the ground on the outer branches of woody shrubs and trees. When webs were out of reach of hand clippers, we used an extendable tree pruner (4.9m Jameson poles, Marvin pruner head, Sherrill Tree, Greensboro, North Carolina) to remove the inhabited branch. After cutting down a web, we placed 12 larvae into a 0.5L clear plastic container (Fabri-Kal, Kalamazoo, Michigan) provisioned with a wet filter paper disc (7.5 cm diameter; VWR, West Chester, Pennsylvania) and a sprig of the natal host, and replaced the web within the branches of the tree of origin. We kept the containers cool and transported them to the laboratory on the same day.

Rearing larvae in the laboratory. We successfully reared both wild-caught *H. cunea* larvae in 2010 and *H. cunea* larvae hatched from eggs in 2011 (see subsections below on 'Mating adult moths' and 'Oviposition, eggs and early instar larvae') in ambient conditions in our laboratory at the University of Denver in Denver, Colorado. Depending on size, we reared larvae individually or in groups of up to six individuals in the same type of clear plastic containers that we used to collect them from the field. Large larvae were housed individually and small larvae were housed in groups, with group size decreasing as they grew larger. Early instar larvae are naturally aggregative feeders and it has been shown previously that group sizes of four to eight black-headed *H. cunea* hatchlings are necessary for establishment and survival, while later instars develop faster with less crowding (Watanabe & Umeya 1968). We stored the plastic containers with *H. cunea* larvae at room temperature on shelves with exposure to ambient light from outside a nearby window.

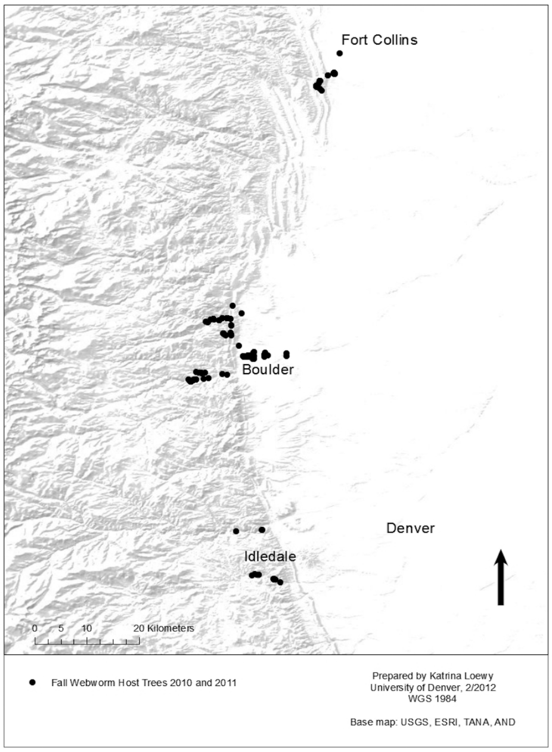

FIG. 1. Map of observed *Hyphantria cunea* webs along the Colorado Front Range during the summers of 2010 and 2011. Each dot represents the location of a host tree. Dots are allowed to overlap. The directional arrow points north.

We collected fresh host plant branches from our field sites biweekly and stored them in 49.2L plastic bags (Tall Kitchen Bags, Safeway, Pleasanton, CA) in a walk-in growth chamber (Kysor-Sherer, Marshall, MI) set at 4–10°C. For each larval container, we replaced old food plants with fresh foliage and removed frass biweekly. In 2010, we reared larvae on 5 host plant species: chokecherry (*Prunus virginiana*, n= 183), crabapple (*Malus* sp., n= 40), Lombardy poplar (*Populus nigra*, n= 20), narrowleaf cottonwood (*Populus angustifolia*, n= 167), and thinleaf alder (*Alnus tenuifolia*, n= 20); although larvae were reared on all of these host plants, any single larva was reared for the entirety of its development on the single host plant species upon

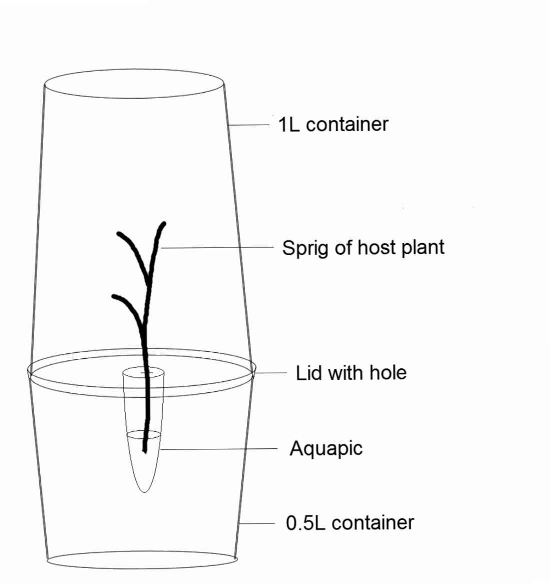

FIG. 2. Diagram of rearing chamber configuration used to rear *Hyphantria cunea* larvae in environmental chambers.

which it was discovered. During feeding, we used a spray bottle filled with tap water to remoisten the filter paper, which helped to keep the host plant material fresh and to increase ambient humidity, a function performed by the web in wild populations (Morris & Fulton 1970). When larvae reached the prepupa stage, we suspended maintenance, as pupating larvae experience higher mortality when disturbed (Morris & Fulton 1970).

Rearing larvae in growth chambers. In 2011, we moved a subset of 400 20-day-old, lab-reared larvae from the lab to environmental growth chambers (Percival Scientific, Pery, IA) set to a diurnal cycle calculated to mimic average field temperatures in Boulder, CO on August 15, 2011 (L14:D10 and 27ºC:19.5ºC). Individual larvae were housed in an inverted 1L plastic container (Fabri-Kal, Kalamazoo, Michigan) with a sprig of host plant from one of four plant species (chokecherry, crabapple, narrowleaf cottonwood and thinleaf alder); we divided the 400 larvae equally among the host plants such that there were 100 larvae reared on each host. The plant had a fresh water supply provided by an aquapic (7.6 cm recycled water tubes, Afloral.com, Jamestown, NY). We replaced sprigs of host plant and refilled aquapics with water biweekly. The aquapic was placed in a 1.5 cm diameter hole in the lid so that when closed, the host plant and larva were enclosed in the 1L plastic container (Fig. 2). The inverted 1L container was then placed on an upright 0.5 L container so that the entire apparatus could stand alone. Condensation built up quickly inside the containers, and it was especially important to remove standing water from containers with later instars, because too much water can prevent successful splitting and shedding of the final larval skin (Morris & Fulton 1970, Loewy, pers. obs.). We checked containers daily to record any larvae that had reached the prepupa or pupal stage.

Pupae. We removed hardened pupae, most of which had entered diapause, from their containers and cleaned them of debris and frass. We placed each individual pupa into a new 0.5 L plastic container that contained 2–3 cm of moist sphagnum peat (Ferti-lome peat moss, Cheek Garden Products, Austin, TX). We overwintered the containers with peat and pupae in environmental growth chambers (L0:D24 and 4 °C) for seven months, starting in early November. Morris and Fulton (1970) suggested a minimum chilling period of 6 months at 1.7 degrees C, and a maximum of 8 months, after which survival rate decreased sharply. We moistened the peat with tap water by misting the containers every two to three months to maintain ambient humidity.

Adult emergence. In the beginning of June, we cleared pupal containers of peat, misted the pupae, and placed a moistened filter paper disc under each pupa in its container. Then we returned the containers to the environmental growth chambers set to a diurnal cycle calculated to mimic average field temperatures in Boulder, CO on June 8, 2011 (L15:D9 and 23ºC:16ºC). We recorded newly-emerged adults daily, and definitively determined their sex. Male moths have pectinate antennae and tend to have smaller abdomens, while female moths have filamentous antennae and

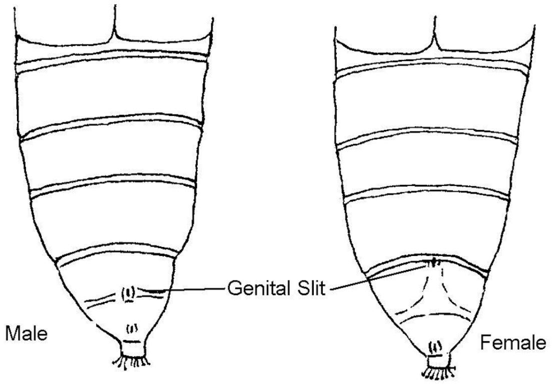

FIG. 3. Diagram of pupal sex differences in *Hyphantria cunea*, with the ventral surface of a male pupa on the left and a female pupa on the right. On female pupae, the genital slit is located on the anterior edge of the fourth abdominal segment posterior to the wing covers. On male pupae, the genital slit is located on the posterior edge of the same segment. The genital slit of both sexes sometimes appears to transect two segments.

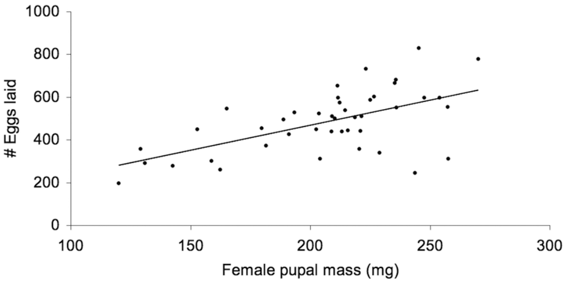

FIG. 4. The relationship between female fecundity, measured by eggs laid per female, and female pupal mass ($y=2.353x - 1.8343$; $N=43$ females, $R^2=0.34$, $t=4.59$, $P < 0.0001$) for red-headed *Hyphantria cunea* in Colorado.

larger abdomens, at times with greenish eggs visible within.

Mating adult moths. On the day of emergence, we placed a single female and one to three males into a plastic shoebox (34.6 cm × 21 cm × 12.4 cm, Sterilite Corp., Townsend, MA) lined with wax paper that served as a mating chamber, taking care that none of the females were paired with a male sibling from the same natal web to avoid potential inbreeding depression in our colony. Jaenike and Selander (1980) confirmed that black-headed larvae within a single web are full-sibs, and we assumed the same of the red-headed form. Putting the mating chambers in an environmental growth chamber with its stark transition between light and dark did not facilitate mating behavior. However, when we moved the mating chamber into the lab and exposed it to natural light, mating took place within two days. Hidaka (1977) found that mating flight is likely cued by the dim light of dawn or dusk in black-headed *H. cunea*. We did not record the precise timing of mating behavior in the lab, although we only discovered mated pairs, still in coitus, in the mornings.

Oviposition, eggs and early instar larvae. A day after copulation, we removed males from the mating chamber so that they would not disturb the ovipositing female; females were left to oviposit in the shoebox mating chamber. Oviposition began 1–3 days after mating was observed. With rare exceptions, females laid their eggs on the wax paper-lined walls of the mating chamber, rather than the floor or lid. Females slowly swung their abdomens back and forth, creating row after row of eggs, usually in a single layer. When undisturbed, most females laid all eggs in a single batch and often died with their wings covering the egg mass, a behavior also observed in wild populations by Swain (1936).

We removed egg masses from the mating chamber by cutting the wax paper around them with a X-acto knife. We kept eggs on the wax paper until hatching to avoid breakage and placed the egg masses in a new 0.5 L plastic deli container with a moist cotton ball. We kept most of the containers in the lab under ambient conditions, and moved eight into the growth chamber at 26°C. We labeled containers with information about the eggs' maternal and paternal lineage and the date that they were laid. As long as the cotton ball was moist, humidity within the container was sufficient to allow hatching. Head capsules became visible, turning the eggs dark, a day before the larvae hatched.

Once larvae began to eclose, we removed the moist cotton ball and replaced it with a moist filter paper disc. We also placed a sprig of host plant into the container. We found that if we tried to move neonate larvae to a host plant leaf with a fine paintbrush, they suffered higher mortality than neonates we allowed to locate the leaf on their own. We placed fresh leaves in the container biweekly. To minimize disturbance of delicate early instar larvae, we only removed old leaves if they started to get moldy. We misted containers lightly while introducing the fresh host plant. As the larvae grew, we divided them into smaller groups and moved them to new containers to minimize the frequency with which food needed to be replaced and make individual identification easier.

Objective 2 – Life history traits of red-headed *H. cunea* in Colorado

To better understand the life history of red-headed *H. cunea* in Colorado, in 2011 we recorded the timing of life events for larvae reared in the lab for the entirety of their development, including the dates of oviposition, eclosion, and pupation so that we could calculate total larval development time. For ease of comparison with the results from other studies, larval development times are only included for larvae that completed their development in the environmental growth chambers, not in the lab. After overwintering, we also recorded the number of days that passed from when the pupae were first exposed to spring conditions in the environmental chambers to adult emergence. For adult females, we recorded the number of days that passed from mating to the onset of oviposition.

Pupae deplete their fat stores over time, so we weighed all pupae exactly 30 days after pupation (to the nearest 0.01 mg; Mettler-Toledo XP6, Columbus, Ohio). We determined the sex of each individual by viewing the pupae under a dissecting microscope and noting the location of the genital slit (Fig. 3), similar to methods reported by Villiard (1975) and Carter and Feeny (1985). We confirmed our sex determinations after the moths emerged as adults the following spring.

Objective 3 – Pupal mass as a predictor of potential fecundity and lifetime fitness in Lepidoptera

To quantify fecundity for red-headed *H. cunea*, we photographed egg masses using the macro setting on a Cannon PowerShot SD780 IS and uploaded the pictures to a computer for counting in Paint (Microsoft, Redmond, WA). For greatest accuracy, we dotted each egg with the pencil tool and kept track of the number with a tally counter. We also reviewed the literature for other studies that have investigated the relationship between female pupal mass and fecundity. We performed keyword searches on Web of Science and Google Scholar using various combinations of the following terms: fecundity, fitness, Lepidoptera, lifetime fitness, pupa* mass and realized fitness. We then limited the results to studies that ran a regression of female pupal mass by potential fecundity. Following Awmack and Leather (2002), potential fecundity is a measure of the number of eggs an insect produces, while realized fecundity refers to the number of offspring produced.

Statistical analyses. We analyzed our results with T test and regression using JMP Pro 9.0.0 (SAS Institute Inc., Cary, NC). All means are reported ± 1 standard error.

RESULTS

Survival. We found that our rearing technique for fall webworm was quite successful. When larvae were reared on a high-quality host plant such as chokecherry (n=100), we found that 98% of the larvae successfully pupated and 74% successfully completed their development to the adult stage. Survival was lower for larvae collected from the field or reared on lower quality host plants, but this was due to mortality related to parasitism and host plant quality, rather than our rearing technique.

Sex determination. For our analyses, we identified morphological differences between male and female *H. cunea* pupae. Of the 129 pupae that we determined to be female, 125 emerged as female moths. Of the 141 pupae that we determined to be male, 139 emerged as male moths. Thus, we were able to successfully identify 99% of male pupae as males and 97% of female pupae as females. Our ability to distinguish males from females in the pupal stage allowed us to investigate whether male and female larvae differ in developmental life history traits without excluding individuals that did not reach adulthood.

Development time. We found that all eggs from a single egg mass hatched on the same day and the mean development time was 13.9 ±0.2 days (*N*=44 egg masses, range=10–16 days) in the population kept in ambient lab conditions, and 11.6 ±0.6 days (*N*=7 egg masses, range=9–13 days) in the population kept in an environmental chamber set at 26ºC. After the eggs hatched, we found that mean larval development time was 42.1 ±0.2 days (*N*=332, range=35–62 days) in the environmental chamber (L14:D10 and 27ºC:19.5ºC).

We found that female larvae took longer to develop than male larvae by 0.3 days, but the difference was not significant (t=0.9, P=0.36). Females took 42.2 ±0.3 days (*N*=167, range=36–53 days) to develop while males took 41.8 ±0.3 days (*N*=155, range=35–62 days).

After pupae were removed from the overwintering chamber, we found that it took 26.8 ±0.5 days for adults to emerge (*N*=264, range=17–52 days); of the 300 pupae that we overwintered in growth chambers from 2010–2011, 88% emerged. Females took longer to emerge than males by 1.8 days (t=1.93, P=0.055). Females emerged 27.7 ±0.7 days (*N*=125, range=17–52 days) after removal from cold storage, while adult males emerged 25.9 ±0.6 days (*N*=139, range=17–44 days) after removal from the cold.

Pupal mass. As in most Lepidoptera, female pupae were significantly larger than males (t=13, P< 0.0001). The mean mass for male pupae was 185.66 mg (±1.9, *N*=155, range=127.78–286.00 mg), while the mean mass for female pupae was 223.25 mg (±2.19, *N*=167, range=143.58–300.52 mg), which is 120% heavier than male pupae.

Adult female fecundity. An average of 2.2 ±0.2 days elapsed from when female *H. cunea* were mated until they began to lay eggs (*N*=45, range=1–5 days). Females laid an average of 484.2 ±22.4 eggs (*N*=43, range=34–830 eggs). We found a significant positive relationship between a female's pupal mass and the number of eggs that she laid during her lifetime (R^2=0.34, t=4.59, n=43, P<0.0001); for every additional mg of pupal mass, a female laid an additional 2.35 eggs (Fig. 4). Our literature review demonstrated that there is a significant, positive relationship between pupal mass and potential female fecundity for the majority of lepidopteran species for which this relationship has been investigated (Table 1).

DISCUSSION

Here we report natural history for the red-headed form of *H. cunea* for the first time; previously, all detailed published accounts of *H. cunea* natural history have focused on the black-headed form. To our knowledge, this is also the first account of successful rearing techniques for red-headed *H. cunea*. Our results suggest that much of the phenology of red-headed *H. cunea* differs from that of the black-headed form; red-headed eggs took longer to hatch and larvae took longer to develop than those in studies of the black-headed form. Additionally, red-headed pupae were heavier than black-headed pupae.

Comparison of *H. cunea* life history traits among studies is complicated because different studies have used a variety of different host plants and temperatures for rearing caterpillars. Furthermore, voltinism differs among populations with anywhere from one to more than four generations per year; *H. cunea* in Colorado has a single generation each year (pers. obs.), but black-headed populations in Maryland are bivoltine while populations in southwestern Japan are trivoltine (Gomi & Takeda 1996, Mason et al. 2011). Despite these complications, we compared our results with those of other studies to better understand how life histories may differ between red-headed and black-headed *H. cunea*. At several life stages, red-headed *H. cunea* took longer to develop than the black-headed form. European, Asian, and North American measurements of embryonic development time (the time from oviposition to hatching) for black-headed *H. cunea* range from ~7 days at 27ºC to ~23 days at 16ºC (Jasič & Macko 1961, Yearian et al. 1966, Szalay-Marzso 1972, Gomi et al. 2005). We found that red-headed *H. cunea* eggs incubated at 26 ºC took 11.6 days to hatch, which is longer than in any study of black-headed *H. cunea* eggs incubated at that temperature. Red-headed *H. cunea* larvae took longer to develop than black-headed *H. cunea* larvae in similar studies; published development times for black-headed *H. cunea* larvae range from 17–47 days depending on which host plants were used as food, the temperature at which the larvae were reared, and the sex of the larva (Jasič & Macko 1961, Yearian et al. 1966, Morris & Fulton 1970, Gomi et al. 2005). The red-headed larvae we studied took 40–70% longer to develop compared with black-headed larvae in other studies. Furthermore, Jasič and Macko (1961) recorded shorter larval development times for males than for female black-headed *H. cunea*, with 1–2 days difference between the sexes. Notably, males and females in our study both took about 42 days to develop from egg hatch to pupation, with mean male development time shorter than mean female development time by only a fraction of a day.

The pupae of female red-headed *H. cunea* tend to be much larger than the female pupae of the black-headed form studied by Jasič and Macko (1961), Morris and Fulton (1970), and Gomi et al. (2005). One complicating factor when comparing pupal masses across studies is that there is a positive relationship between rearing temperature and pupal mass such that even on the same host plant, larvae develop into heavier pupae when reared at higher temperatures (Jasič & Macko 1961). Despite the use of a different host plant, white mulberry (*Morus alba* L.), Jasič and Macko (1961) reared black-headed *H. cunea* at a similar temperature to the temperatures we used to rear red-headed *H. cunea*, differing only by about 1–2 degrees. Jasič and Macko (1961) recorded a mean pupal mass for black-headed *H. cunea* that was 24% lower than the mean pupal mass we recorded for red-headed *H. cunea*, despite rearing the larvae at a mean temperature 2.1 degrees higher than that of our study.

Intraspecific variation in insect body mass is often correlated with lifetime fitness (Slansky &Scriber 1985, Honěk 1993). Two studies have previously found a positive correlation between pupal mass and potential fecundity for *H. cunea* (Jasič & Macko 1961, Morris & Fulton 1970), but both of these studies focused only on the black-headed form. Our results demonstrate that pupal mass may be used as a predictor of potential fecundity for the red-headed form of *H. cunea* as well. Furthermore, our results support and add to the limited but growing body of literature that demonstrates a positive relationship between body size and lifetime fitness for Lepidoptera. In a thorough review of the literature, we were able to find studies for 21 lepidopteran species that investigated the relationship between female pupal mass and potential fecundity (Table 1). For 19 of these 21 species, a significant, positive relationship exists between pupal mass and female fecundity (Table 1); for the two limacodid species, the relationship was still positive, but not significant. Thus, for all of the lepidopteran species studied to date, females that gain more mass as larvae are able to produce more eggs as adults. The magnitude of the effect size may depend on the feeding behaviors of adult female moths; the mass gained as larvae may be even more critical to lifetime fitness for species that do not feed as adults (Jervis et al. 2005).

Our data on the natural history of red-headed *H. cunea*, combined with genetic and molecular analyses (Jaenike & Selander 1980, McIntee & Nordin 1983) and behavioral observations (Oliver 1964), suggest that red-headed and black-headed *H. cunea* may be two distinct species or subspecies. To better understand natural history and behavioral differences between the two forms of *H. cunea*, there needs to be consistency among studies to allow for meaningful comparisons among populations of these two host forms. Previous studies have all used different rearing temperatures and diets that reflect the local climate and habitat of the focal *H. cunea* population, but this makes it difficult to compare natural history traits for the two forms across their geographic range. In Colorado, we find only the

TABLE 1. Compilation of data that examines the relationship between female pupal mass and potential fecundity from studies of other Lepidoptera gathered from the literature. The slope represents the increase in the number of eggs per mg of additional pupal mass. Depending on the study, the number of eggs could refer to eggs laid, dissected out, matured, or any combination of the three. If a variable was not reported, it is noted as NR. Other values given in the table are the correlation coefficient r (all correlation coefficients are significant unless noted 'ns' for not significant) and the number of groups or individuals in the study (n).

Family	Species	Slope	r	n	Source
Erebidae	*Hyphantria cunea*	4.8	0.64	71	Jasič and Macko (1961)
	(black head)	4.4	0.68	86	
		4.7	0.70	20	
		3.8	0.49	167	
		3.8	0.89	30	Morris and Fulton (1970)
	Hyphantria cunea	2.35	0.58	43	Loewy et al. (this study)
	(red head)				
	Orgyia antiqua	1.12	0.93	39	Tammaru et al. (2002)
	Orgyia leucostigma	1.29	0.89	187	Tammaru et al. (2002)
	Orgyia vetusta	NR	0.69	32	Harrison and Karban (1986)
Geometridae	*Operophtera brumata*	10.5	0.92	91	Roland and Myers (1987)
		9.14	0.96	41	
	Epirrita autumnata	2.31	NR	296	Heisswolf et al. (2009)
Lasiocampidae	*Malacosoma disstria*	0.45*	0.89	12	Lorimer (1979)
		0.45*	0.82	12	
		0.45*	0.71	12	
		0.45*	0.6(ns)	9	
		0.45*	0.89	13	
		0.59*	0.81	13	
		0.59*	0.95	11	
		0.59*	0.92	14	
		0.59*	0.82	15	
	Streblote panda	0.09	0.73	55	Calvo and Molina (2005)

TABLE 1. Continued from previous page

Family	Species	Slope	r	n	Source
Limacodidae	*Acharia stimulea*	0.24	0.57(ns)	11	Murphy et al. (2011)
	Euclea delphinii	0.27	0.32(ns)	23	Murphy et al. (2011)
Noctuidae	*Mythimna convecta*	7.02	0.7	NR	Smith (1986)
	Mythimna pallens	4.36	0.61	14	Hill and Hirai (1986)
		2.29	0.57	13	
		6.05	0.83	21	
		1.97	0.53	15	
	Mythimna separata	6.24	0.9	10	Hill and Hirai (1986)
		7.99	0.92	20	
		2.46	0.39	29	
		3.43	0.51	28	
	Sesamia nonagrioides	5.73	0.49	50	Fantinou et al. (2008)
	Spodoptera exigua	11.2	0.73	NR	Tisdale and Sappington
		12.5	0.60	NR	(2001)
		16.8	0.81	NR	
Plutellidae	*Plutella xylostella*	28.0	0.78	15	Sarfraz et al. (2011)
Saturniidae	*Antheraea polyphemus*	0.05	0.88	26	Miller et al. (1982)
	Callosamia promethea	0.14	0.99	25	Miller et al. (1983)
Tortricidae	*Choristoneura conflictana*	2.09	0.2(ns)	20	Evenden et al. (2006)
		4.36	0.81	13	
		-4.7	0.3(ns)	7	
		4.07	0.65	22	
		5.37	0.73	16	
		1.91	0.5(ns)	6	
	Choristoneura fumiferana	1.1	0.4(ns)	42	Lorimer and Bauer (1983)
		1.9	0.78	40	
	Cnephasia jactatana	35.7	0.62	175	Jiménez-Pérez and Wang (2004)

[*] Slopes were obtianed by combining nine separate broods of *Malacosoma disstria* into two geographic groups

red-headed form, but in some areas of North America the black-headed and red-headed forms are sympatric, which would allow for more direct comparisons between the two forms. Investigations into ecological, phenotypic and genetic differences among black-headed and red-headed populations of *H. cunea* across the entire geographic range, both where the forms are sympatric and allopatric, would be a fruitful area of future research.

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