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**ETHOLOGY OF *LAPHRIA FERNALDI* (BACK)
(DIPTERA: ASILIDAE) IN SOUTHEAST WYOMING¹**

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Abstract.—The behavior of a western coniferous forest asilid, *Laphria fernaldi* (Back), was studied in southeast Wyoming. Prey, predominantly Coleoptera and Hymenoptera, are captured in aerial flights. No prey manipulation occurs once the asilid returns to the feeding site. Mating without prior courtship is completed on perch sites one to nine meters above the forest floor.

Described by Back (1904) as *Dasyllis fernaldi*, this species was subsequently placed in the genus *Bombomima* by Enderlein (1914). There it remained until Nagatomi (1964) synonymized *Bombomima* with *Laphria*, thus placing *fernaldi* in the latter genus. This change of status was supported by Martin (1965).

This species, like other species formerly placed in *Bombomima* and species in the genus *Mallophora*, strongly resemble bumblebees in size, shape and color patterns and have been referred to as mimics (Bromley, 1930). Toads, at least, quickly learn to associate these color patterns with stinging hymenopteran models after one error of judgment (Brower et al., 1960) suggesting that this is batesian mimicry. Waldbauer and Sheldon (1971) maintain that for *Laphria flavicollis* Say and *L. thoracica* Fabricius, insectivorous birds are the main selective agents which determine the morphology and behavior of the mimics.

A widespread distribution has been attributed to *L. fernaldi* in the western United States and Canada, specimens being cited from: Colorado (type locality) (Back, 1904; Cockerell, 1917; James, 1938, 1941); Nebraska, South Dakota (Jones, 1907); Oregon (Cole and Lovett, 1921); Utah (Brown, 1929; Knowlton and Harnston, 1938); Washington, Idaho, New Mexico, Arizona, Montana (Adisoemarto, 1967); British Columbia (Criddle, 1921) and Alberta (Adisoemarto, 1967). Because there appears to be a complex of species involved (Bullington, unpublished data), some of these records may be in error. However, comparison of specimens from our study population with specimens taken from a variety of locations in Colorado have convinced us that the specimens referred to in the present paper are definitely *Laphria fernaldi*.

METHODS

James (1938) refers to *B. fernaldi* as a coniferous forest denizen and it is within a predominantly lodgepole pine forest that our study was conducted. The study

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site was located in the Snowy Range Mts., Albany Co., Wyoming, in a moderately wooded area across the North Fork of the Little Laramie River from the USFS North Fork Campground (elev. 2577 m). The area was bisected by an old logging road which at one point expanded into a large clearing. Most recorded activities were within the forest bordering the clearing. Fallen and cut logs of various dimensions were scattered over the forest floor, but most branches and small dead trees had been removed by campers seeking firewood.

Methods of study of this population were similar to those described in Lavigne (1982) for *Neoitamus vittipes*. Additionally, individuals were marked by placing dots of various colors of Testers model airplane paint (Pla Enamel, the Testor Corporation, Rockford, Illinois) on the dorsum of the thorax. Each specimen was marked the first time it was encountered and had a specific designation, such as B₃ (= 3 blue dots). With this method we individually marked 12 specimens in 1978 (12 ♂), 3 in 1979 (2 ♂, 1 ♀) and 43 in 1981 (36 ♂, 7 ♀). A few additional observations were made on a small population at Battle Creek Campground, Sierra Madre Mts., July 25-26, 1978.

Extensive observations were made on this species in 1978 (7/25-9/9) and again in 1981 (7/16-9/20), while we were engaged in a study of male territoriality (Lavigne and Bullington, unpublished data). Incidental observations also were made during the adult flying season in 1979 (7/21-9/9) when time permitted. Specimens upon which this paper is based have been placed in the entomological collection of the Smithsonian Institution, Washington, DC as: R. J. Lavigne, Voucher Spec. #47.

Weather conditions appeared to be the dominating influence on *L. fernaldi* activities during all three years. Activities largely ceased on cloudy days and on rainy days the asilids would disappear. Intermittent rain showers or all day rains were common in August, thus limiting opportunities for the flies to feed, mate and oviposit.

Each sunny morning male *L. fernaldi* would appear on rocks or on logs between 0845 and 1005 h, whenever the log surface temperature reached ca. 27°C. In late afternoon between 1700 and 1800 h, the asilids usually would leave the logs. Followed males flew 20-25 m in interrupted flights eventually disappearing into the tree canopy, where it is presumed they spent the night. As the season progressed and the angle of the sun changed, logs would be sunlit for shorter periods and asilids would leave them at an earlier time.

FORAGING AND FEEDING BEHAVIOR

All observed *Laphria fernaldi* males foraged from sunny spots on logs (Fig. 1) which they constantly patrolled. We speculate that females foraged within the tree canopy. In only five instances over a four year period were females observed with prey in the study area; in four, the female was resting in sunlight on the surface of a log. The remaining female was found clinging to a rock in a clearing with a bumblebee as prey. The sky was cloudy. Other observed females were engaged in mating, oviposition, or resting but never foraging. Subsequent foraging data refer to male activity.

The heads of males are almost constantly in motion presumably in order to evaluate both potential prey and potential mates and/or competitors. Often the whole body is turned. Attack flights are initiated from log surfaces in response to moving insects. However, apparently particular characteristics of potential prey

are important in stimulating an attack since a great variety of insects are ignored, though obviously seen.

Once initiated, the prey capture dart may be a straight line attack or, if the potential prey, such as a syrphid or dragonfly exhibits evasive action ($N = 6$), the chase may be a long and convoluted flight. Observed foraging flights ranged from 1/3 m to 11 m. Unsuccessful flights ($N = 51$) covered the same distances, whereas successful capture darts ($N = 11$) covered 1/3 to 7 m. It is interesting, however, that the means for successful capture darts ($\bar{x} = 11.8$ m) are very close to those for unsuccessful ones ($\bar{x} = 12.3$ m). All prey were collected while airborne ($N = 20$).

Contact and capture may not mean that the prey is impaled. Six additional capture darts ended with the release of the collected item before the asilid landed.

Prey selection apparently functions on the basis of visual discrimination. On four occasions, asilids circled insects (all bees) and then returned to their perch without making an attack suggesting a learned response. Another time a male flew halfway towards a small bee and then returned to its log. Conversely, errors are made. In one case a dandelion seed was the captured item, not an insect.

Once prey are captured they are manipulated and impaled during a short hover prior to landing. The prey was usually still struggling when the asilid landed with the prey positioned (Fig. 2), facing forward, between its legs. Unlike most other asilid species, no manipulation takes place during feeding.

The length of time males spend feeding is inordinately short in comparison to that spent by other asilids whose prey are proportionately large. For example, the mean feeding time for three specimens of the cantharid, *Podabrus lateralis* LeConte, was 4 min. Complete feeding times were recorded for 13 prey, ranging from 2 to 27 min ($\bar{x} = 9.5$).

Feeding asilids were often forced to move quickly with prey impaled upon their probosces. In one instance, an ant grabbed a feeding asilid's leg who responded by flicking off the ant and flying to a new perch. In addition to foraging ants, asilids responded to moving spiders. Larger predators were also a potential disturbance. Various species of birds hawked in the vicinity of the logs and both chipmunks and squirrels used the logs as runways.

While feeding was in progress, and even afterwards, small numbers of tiny flies flitted about the asilid's proboscis. Some landed on the proboscis and others on the prey where the partially digested contents oozed from the open wound. When the harrassment was too great, the asilid would fly rapidly to a new perch.

Once feeding ceased prey were discarded in one of two ways: in flight ($N = 16$) or when the asilid pushed the prey off its proboscis with its foretarsi on site ($N = 10$). The logs from which the asilids foraged, were partially decayed and often housed colonies of carpenter ants, *Camponotus* sp. Those that didn't, usually served as roofs for nests of *Formica* sp. Both kinds of ants were constantly foraging and discarded prey were quickly collected and taken into the nests.

While male foraging activity has been observed as early as 0845 h (log surface temp. 23°C) and as late as 1729 h (log surface temp. 31°C), feeding records only cover the hours 0928 to 1649. The five female feeding records cover the time period 1120 h to 1537 h.

PREY SELECTION

Records of prey taken by bumblebee mimetic *Laphria* are few. Bromley (1930) states that this group of asilids "seem to prefer as prey, insects of the 'buzzing'



Fig. 1. One of the logsets patrolled by males in the coniferous forest habitat of *Laphria fernaldi*.

Fig. 2. Male *Laphria fernaldi* with winged reproductive *Formica* sp. as prey showing size difference between predator and prey.

rather than the 'fluttering' type of flight" and commonly take Coleoptera and occasionally Hymenoptera as prey. MacFarlane (1973) lists 17 instances where bumblebees served as prey; however, his single record for *L. fernaldi* does not occur in his listed citation (i.e. Brown, 1929).

Table I. Numbers and percentages of measured prey of different taxa captured by males and females of *Laphria fernaldi* at the North Fork study site, Medicine Bow Nat'l. For., Wyoming. This listing does not include 13 prey, which were recognized as to taxa but were carried off by asilids, or prey collected at other locations.

Taxa	Males				Females			
	No.	%	Size Range (mm)	\bar{x}	No.	%	Size Range (mm)	\bar{x}
Coleoptera	32	51.6	3.5-14.5	6.9	2	50	8.5-16.3	12.4
Diptera	8	12.9	6.7-11.1	7.4				
Hemiptera	1	1.6	3.6					
Hymenoptera	18	29.0	6.1-15.7	9.6	2	50	6.1-10.9	8.5
Lepidoptera	2	3.3	9.9-12.4	11.2				
Plecoptera	<u>1</u>	<u>1.6</u>	<u>4.8</u>	—	—	—	—	—
Total	62	100	3.5-15.7	7.8	4	100	6.1-16.3	10.5

Measured prey ranged widely in size, but were considerably smaller than the predator. Females were larger ($\bar{x} = 15.9$, $r = 15-17.4$ mm, $N = 6$) than males ($\bar{x} = 13.6$, $r = 10.1-15.4$ mm, $N = 10$), and took slightly larger prey. Prey taken by females ranged from 6.1-16.3 mm ($\bar{x} = 10.5$, $N = 4$); those taken by males ranged from 3.5-15.7 mm ($\bar{x} = 7.8$, $N = 62$). The predator to prey size ratio, based primarily on male captures, was 1.61:1 (1.74:1 for ♂; 1.51:1 for ♀).

Separation of prey records on the basis of taxa taken show that Coleoptera (51.5%) and Hymenoptera (30.3%) were favored by both sexes (Table 1). Observed recorded prey not collected by the investigators, when added to the figures in Table I increase the dominance of Coleoptera in the prey record to 43 (54.4%). The total number of Hymenoptera increases to 22 (27.7%), that of Diptera to 9 (11.4%) and Hemiptera to 2 (2.5%).

There is little doubt that male *L. fernaldi* exhibit selectivity in their choice of prey as seen by the list of prey. Additionally, on numerous occasions insects flew well within the attack range of the asilid and yet were acknowledged only by a head turn.

Following is a listing of prey taken by *L. fernaldi*. The number of observations and sex, when known, of the predator are indicated in parentheses following the prey taxa. All captures were made at the North Fork study site unless otherwise indicated. COLEOPTERA, Buprestidae: *Chrysobothris lands* VanDuzee, VIII-2-78 (♂), VIII-11-78 (♂), *Chrysobothris trinervia* (Kirby), VIII-1 1-78 (♂), *Melanophila drummondi* (Kirby), Pingree Park, Roosevelt Nat'l. For., CO, VIII-26-53 (♀) (R. H. Painter), *Melanophila lecontei* Obenb., VII-26-78 (♂), Cantharidae: *Podabrus lateralis* LeConte, VII-26-78 (3 ♂), VII-28-78 (2 ♂), VII-31-78 (2 ♂), VIII-2-78 (♂), VIII-4-78 (♂), VIII-10-78 (♂); Cerambycidae: *Acmaeopsproteus* Kirby, VIII-2-78 (♂), VIII-4-78 (♂), VIII-10-78 (♀), VIII-16-78 (♂), *Cosmosalia nigrolineata* (Bland), VII-26-78 (♂), VII-23-81 (♂), VII-29-81 (♂), *Gnathacmaeops pratensis* (Laicharting), VII-28-78 (♂), *Judolia gaurotoides gaurotoides* (Casey), The Sinks, Fremont County Youth Camp, ca. 18 mi SW Lander, VII-1-73 (♂) (R. J. Lavigne), *Leptura propinqua* Bland, VII-29-81 (♀), *Xestoleptura behrensi* (LeConte), Salmon laSac, Kittas Co., WA, VII-26-69 (♂) (C. J. Homing), undet., VII-26-78 (♂); Elateridae: *Athous pallidipennis* Mann, VIII-4-78 (♂), *Ctenicera breweri* (Horn), VIII-5-78 (♂), undet., VII-26-80 (♂); Meloidae: undet., VII-27-78 (♂); Scarabaeidae: *Aphodius*

fimentarius L., VII-25-81 (♂), *Aphodius scobriceps* LeConte, VII-25-81 (♂). DIPTERA, Asilidae: *Eucyrtopogon* sp., VIII-27-78 (♂); Bibionidae: *Bibio* sp. VIII-19-78 (♂), VIII-20-78 (♂); Muscidae: undet., Syrphidae: *Metasyrphus* sp., prob. *laponicus* Zett., VIII-1-78 (♂), HEMIPTERA, Miridae: *Lygus* sp., VIII-10-78 (♂). HYMENOPTERA, Apidae: *Bombus bifarius* Cresson, Pingree Park, Roosevelt Nat'l. For., CO, 9000', VIII-19-30 (♂) (D. A. Wilbur), *Bombus bifarius nearcticus* Handlirsch, Grassy Lake, Targhee Nat'l. For., WY, VIII-10-66 (♂), *Bombus mixtus* Cresson, VIII-1-78 (♂); *Psithyrus fernaldae* Franklin, Olga, WA, VII-14-09 (♂); Colletidae: *Colletes* sp., VII-27-78 (♂), VII-26-79 (♂), VIII-1-78 (♂); Formicidae: *Formica* sp. (winged reproductives), VIII-2-78 (♂), VIII-13-78 (♂), VIII-20-78 (♂), VIII-26-78 (2 ♂), VIII-23-81 (♂), Battle Creek Campground, Medicine Bow Nat'l. For., VII-25-78 (♂); Halictidae: undet., VII-16-78 (♀), *Halictus* sp., west of Cody, Rte. 16 overlook, North Fork, Shoshone R., VI-27-77 (♂) (R. J. Lavigne, Ichneumonidae: *Spilichneumon nubivagus* (Cresson), VIII-30-81 (♂); Pompilidae: undet., VIII-13-78 (♂), VII-22-81 (♂); Sphecidae: undet., VIII-19-78 (♂), VII-23-81 (♂); Tenthredinidae: *Tenthredo anomocera* Rohwer, VIII-10-78 (♂); Vespidae: *Vespula vulgaris* (L.), Cameron Pass, Gould, CO, VIII-8-78 (♀). PLECOPTERA, Nemouridae: undet., VIII-4-78 (♂).

MATING

As with most species of Asilidae, mating occurs without prior courtship. Males dart with equal vigor at females and other males that appear on or in the vicinity of the log patrolled by the male. Upon contact, the male grapples with the other asilid often forcing it off the log into the ground cover. If the encountered asilid is a female, copulation usually takes place. Encountered males are chased away without apparent injury.

Initial copulation is in the male atop female position, but almost immediately the pair take positions facing in opposite directions (Fig. 3). The pair then flies to a high perch somewhere within 10 m of the copulation site. Perch heights varied from 1 to 9 m ($x = 4.7$, $N = 11$). While copulating, both sexes open and close their wings intermittently as well as occasionally cleaning their eyes and then the foretarsi. Just prior to the cessation of copulation, the female arches her body and moves forward. The male relaxes his gonopods, releases the female and flies off leaving the female resting on the substrate ($N = 5$).

Initial observations of mated pairs ($N = 14$) were made between 1002 h and 1617 h, with all but three occurring between 1002 h and 1245 h. Only three matings were observed in their entirety. These copulations at 1058 h, 1112h and 1614 h lasted 121, 86 and 79 min, respectively.

A pair apparently seeks moderate temperatures for extended matings. Temperatures on log surfaces in sun at the time copulations were initiated varied from 20° to 47°C ($x = 32^\circ\text{C}$). Temperatures at heights the pair flew to varied from 22° to 31°C ($x = 26.6^\circ\text{C}$). It may well be, however, as Baker (1983) suggests, citing the example of *Scatophaga stercoraria* (L.), that males select where to take the copulated female in order to reduce the risk of being displaced by another male. Multiple matings apparently occur although this strategy was only observed once. On August 26th, at the end of a mating, the female (with frayed wings suggesting old age) was collected. She was released 15 min. later in the vicinity of an unmarked male who immediately flew in her direction, made contact and



Fig. 3. Mated pair of *Laphria fernaldi* in typical copulatory position.

Fig. 4. Female *Laphria fernaldi* ovipositing in entrance of carpenter bee burrow.

copulated with her in the grass beside the log. The male kept trying to fly while the female clung to a grass stalk. After 13 min. the male removed his gonopods from the female's ovipositor and flew. The female crawled into the shade under a pine cone and died.

Males apparently are able to distinguish between their own species and their

bumblebee model, *Bombus melanopygus* Nylander, only upon close inspection. Twice *L. fernaldi* males flew 2 m to hover 2.5 cm behind bumblebees working thistle blossoms. The bumblebees would "kick" with their hind legs at the asilids who subsequently retreated to their former perches after 10-15 sec.

OVIPOSITION

All known larvae of the Laphriinae occur in dead wood (Lavigne et al., 1978). "In *Laphria*, *Lampria* and *Bombomima* the ovipositor is short and the eggs are laid in shallow crevices of dead wood." (Bromley, 1946). Bromley was referring primarily to eastern species with which he was familiar. Similar oviposition sites were recorded for species of European *Laphria* by Melin (1923). *Laphria fernaldi* oviposition habits do not differ significantly from those previously mentioned, although no one has noted hovering prior to site selection.

Females of *L. fernaldi* were rarely seen except when they appeared on large logs for the purpose of oviposition. Typical oviposition behavior was as follows. A female would fly along a log ca. 5 cm above the surface. Intermittently she would hover 2.5-4 cm above a dark area, usually the entrance to a carpenter bee tunnel or a crack in the wood. If the site was "suitable," she would land next to the hole, reverse position and move backwards to the lip of the convexity (Fig. 4). The ovipositor would then be extruded in various directions within the hole. When extruded, it is covered with long erect hairs which presumably have a sensory function. The ovipositor is intermittently retracted and extruded while the female is in position. It may be removed from the depression any time within 15 sec to 5 min and the female will then fly outward and resume her flight along the log seeking new sites. If disturbed by an organism while ovipositing, such as a carpenter ant, the female will fly 15-20 cm down the log and, as soon as the intruder has departed, will return to the same hole. In one instance a bee was in the hole and the asilid returned 4 times to attempt to utilize the burrow. Having been chased off each time, it flew 9 m up into a pine tree and finally out of the area. Of the 58 times females were observed placing their ovipositors in potential sites, 24% were in carpenter bee holes, 20% in elongate cracks in the log surface, and 14% were under bark.

All observed females searching for oviposition sites were seen between July 27 and August 10. Mated pairs, however, were seen as late as August 26. Oviposition attempts were observed as early as 0957 h and as late as 1715 h, but the majority (12 out of 18) occurred between 1012 h and 1340 h. Temperatures on the log surface where females were ovipositing ranged from 23°C to 48°C (\bar{x} = 34.5°C). In 50% of the cases where females were searching for oviposition sites, they were accosted by males who forced them into the grass alongside the logs and attempted copulation.

EGGS

Sculpturing on asilid egg chorions was first mentioned by Melin (1923) who commented "The *Laphria* species all have oval-shaped eggs, with rounded poles, reddish brown and somewhat shiny. The shells are firm and furnished with facet-like ridges." He then proceeded to illustrate a single line drawing showing a hexagonal pattern, referring to the sculpturing on egg chorions of *L. ephippium* Fabricius, *L. flava* Linn., *L. gibbosa* Linn., *L. gilva* Linn. and *L. marginata* Linn.

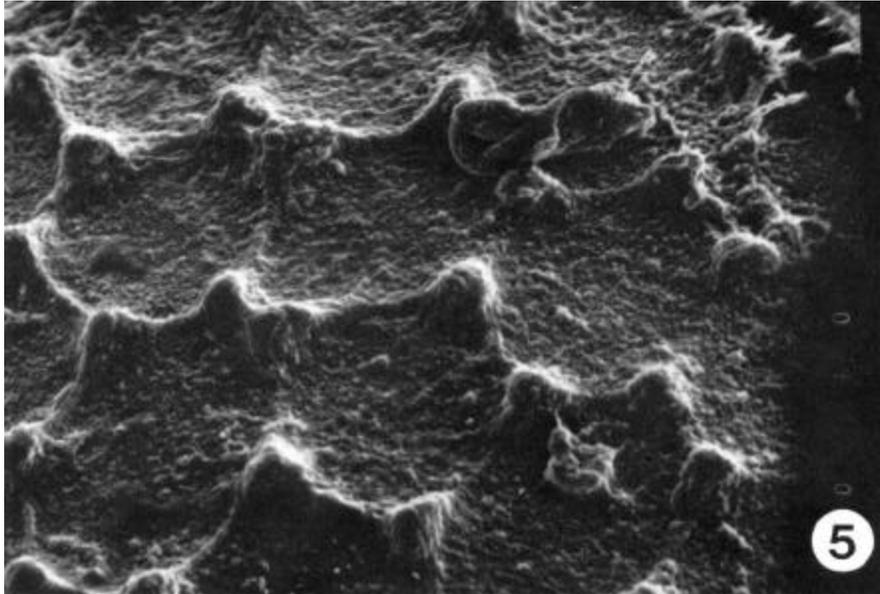


Fig. 5. Chorionic sculpturing of eggs of *Laphria fernaldi* (SEM photo, 800 x).

Eggs of *Laphria fernaldi* were dissected from the abdomens of dried pinned females. The insects were first relaxed and then a lateral slit was made between the tergites and sternites which allowed the eggs to be removed easily without destroying the specimen. The mature eggs were oval and reddish brown. They ranged in length from 0.75 to 0.93 mm ($x = 0.8$, $N = 50$) and in width from 0.55 to 0.6 mm ($x = 0.57$).

With the advent of the scanning electron microscope (SEM) a new tool became available for examination of the chorionic sculpturing on insect eggs. Musso (1981) used it successfully to produce pictures of eggs of some French asilid species. Two species of *Andrensoma* (the only Laphriinae tested) were the only ones that had the type of sculpturing he designated as "(a) pigmented eggs with a thick chorion of irregular polygon surface structure." His SEM picture of the chorionic sculpturing is somewhat similar to that which we have found on the chorion of *L. fernaldi* (Fig. 5). Dr. Fred Lawson (Entomology, University of Wyoming), who kindly took the SEM photo, agrees with us that sufficient differences exist to suggest that SEM photos of eggs could be a useful taxonomic tool in suggesting phylogenetic relationships.

LONGEVITY OF ADULTS

Because of the large size of adult *L. fernaldi* in relation to wing span and because individual males were extremely active, we were interested in adult longevity. In other words how could such large insects, that apparently fed infrequently for short time periods expend such huge amounts of energy and not expire rapidly? Marking of individuals in 1978 was initiated halfway through the season; three individuals were observed intermittently over 10 day periods and one was known

to survive 12 days. The population was practically nonexistent in 1979, but one male was found to have survived 16 days. Greater emphasis was placed on longevity in 1981 when every observed individual was marked. Despite diligent searching, only 7 individuals were recorded as surviving longer than 10 days as follows: 11, 13, 13, 16, 18, 29, 30 days ($\bar{x} = 18.5$). All were males. It is probable that these figures are a reasonable estimate of longevity for individuals, even though the seasonal distribution of this population may extend 65 days. The constraints of working in a forest combined with the flying abilities of the asilids would seem to preclude obtaining more definitive data for *L. fernaldi*. Additionally, individuals appear at odd times of the year. We have collected specimens with the following data: May 16th, June 27th and July 3rd, which fall well outside the range of dates for the population reported herein, i.e. mid July to late September.

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