

**BIOLOGY OF *LOPIDEA NIGRIDEA* UHLER,
A POSSIBLE APOSEMATIC PLANT BUG
(HETEROPTERA: MIRIDAE: ORTHOTYLINAE)**

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Abstract.—The basic biology of *Lopidea nigridea* Uhler is described, including details of its growth, morphology, behavior, and ecology. Distribution and abundance of this univoltine, brightly colored plant bug were studied from May through August 1985, 1986, 1987 and 1988, at 15 sites within the cirque and valley of Pike Creek, on the eastern scarp of Steens Mountain, southeastern Oregon. At Pike Creek, *L. nigridea* occurs only on the legume *Lupinus caudatus* Kellogg and feeds on the stems, undersides of leaves, flower parts and developing seeds of its lupine host plant. This paper describes the relation between *L. nigridea* and its host plant, and identifies the principal species of visually oriented arthropod predators that occur on or visit this lupine. These predators may function as operators selecting for the evolution of aposematism in *L. nigridea*, and the biology of this plant bug species is placed within the context of how protective resemblance functions in a natural community.

Lopidea nigridea Uhler (Miridae: Orthotylinae) is a brightly colored plant bug belonging to the tribe Orthotylini (Carvalho, 1958; Henry and Wheeler, 1988). Generic relationships within this large complex tribe have yet to be resolved, but *Lopidea* appears related to those genera with sericeous scalelike setae and a single tergal process on the male genital capsule (Stonedahl and Schwartz, 1986).

Lopidea is a New World genus with species occurring from Alaska to Honduras. The genus contains 103 species north of Mexico (Henry and Wheeler, 1988) and is now under review by the second author. As currently defined, *Lopidea* comprises those orthotylinines with an oblique transverse suture on the gena and a single tergal process on the right side of the anterodorsal margin of the male genital aperture. Species vary considerably in size (3.5–7.7 mm), but most display some form of red-black, yellow-black or white-black color pattern.

Lopidea nigridea Uhler belongs to a group of western species that are very similar in external morphology and general coloration. This species can be confidently distinguished from related species only by examination of the male parameres—its highly variable coloration has contributed to the creation of at least 20 synonyms (Asquith, in press). Species determination was based on examination of type material of *L. nigridea* and its synonyms at the National Museum of Natural History, Washington, D.C., and the California Academy of Sciences, San Francisco, California, with special attention paid to morphological and color variation. From our study of museum specimens and literature records (Kelton, 1980), it appears that *L. nigridea* is widely distributed in western North America (Fig. 1), extending eastward through the northern plains. *L. nigridea* is the most common species of the genus west of the Rocky Mountains and has been collected from sea level to nearly 4,000 m in elevation. Although adults occasionally are found on a variety of different plants, in the western

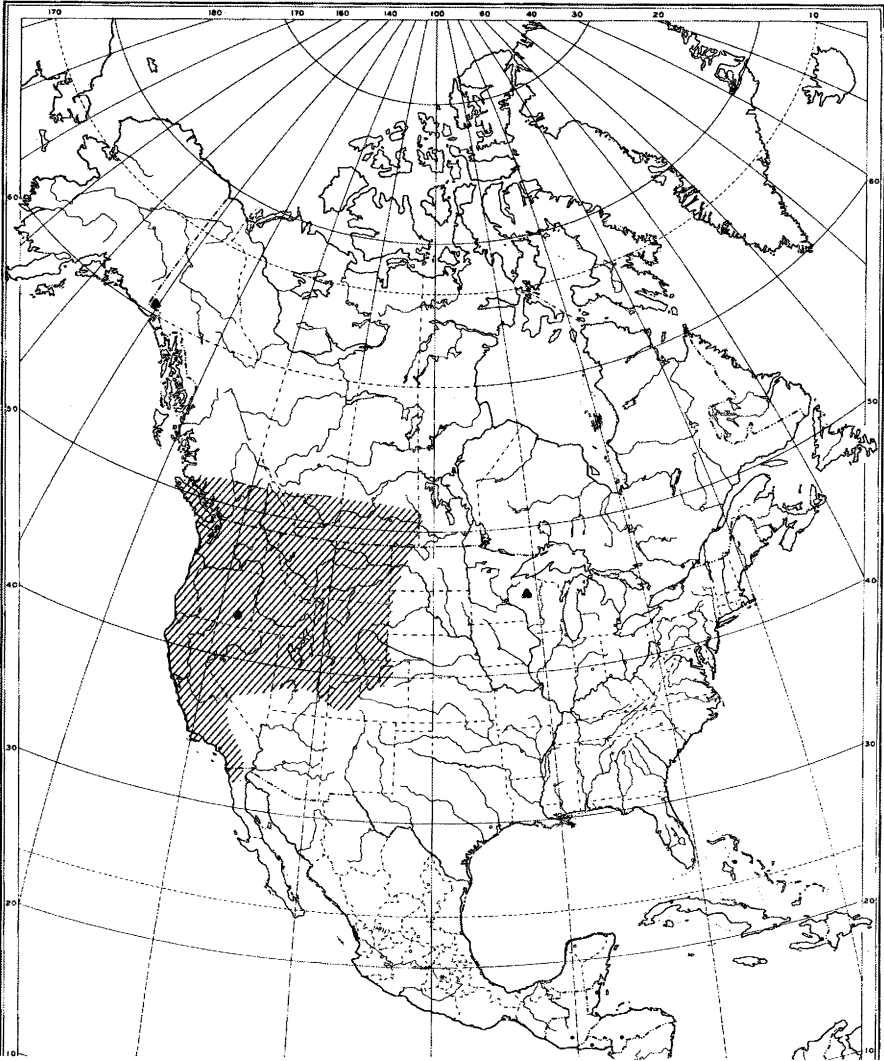


Fig. 1. Distribution of *Lopidea nigridea* Uehler; Pike Creek study area, Steens Mountain, southeastern Oregon, ●.

part of its range it is typically associated with plants of the genus *Lupinus* L., whereas in the Rocky Mountains and northern plains it more commonly occurs on species of *Astragalus* L.

At our study area in southeastern Oregon, adults of *L. nigridea* are large and robust with black calli, dark fuscous scutellum, clavus and medial aspect of the corium, with strongly contrasting red lateral margin of corium and pale red to white on the

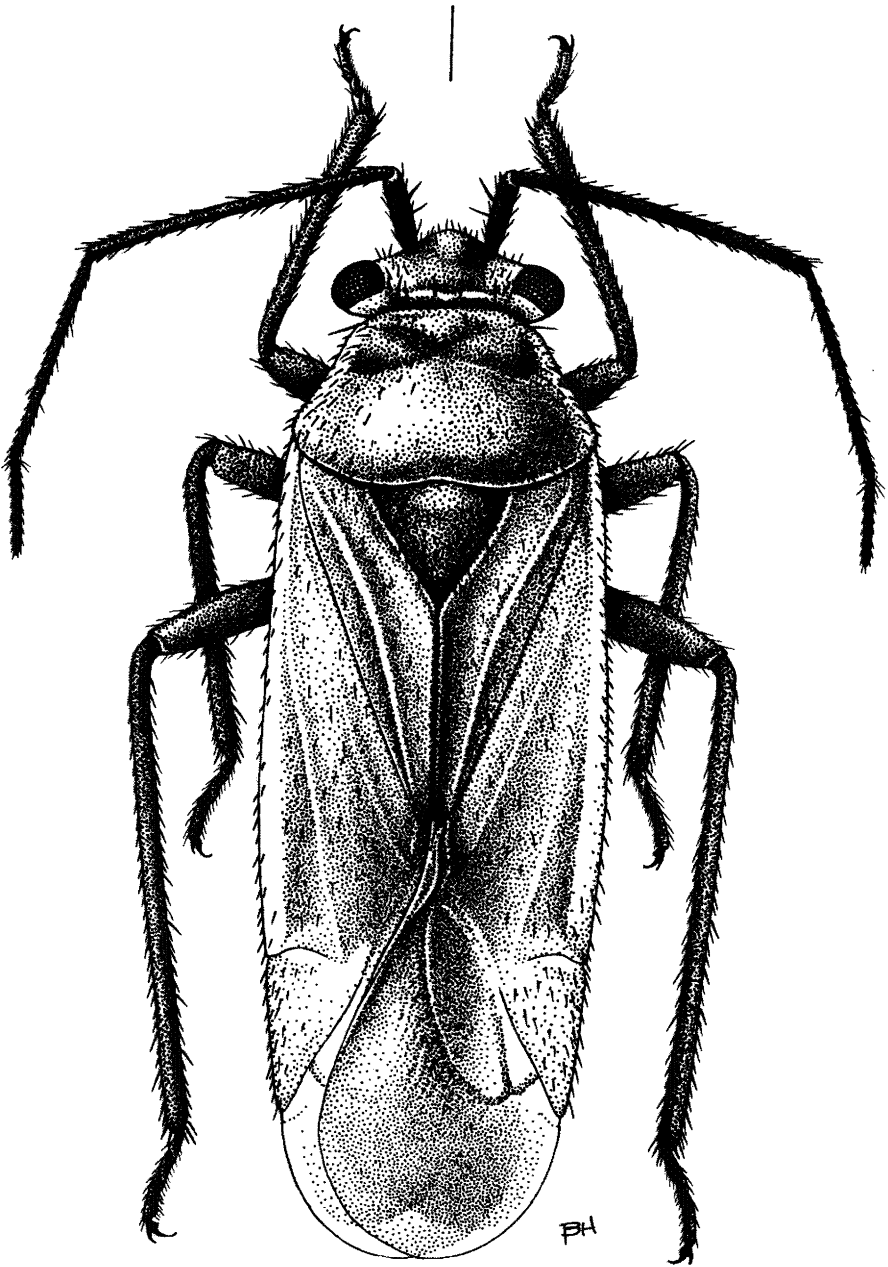


Fig. 2. Adult male of *Lopidea nigridea*, dorsal habitus.

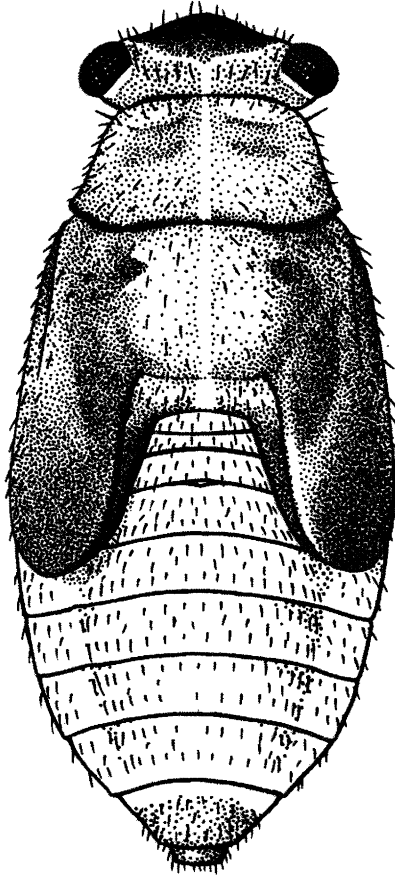


Fig. 3. Fifth instar nymph of *Lopidea nigridea*, dorsal habitus.

embolium and cuneus (Fig. 2). In other areas, this species may be almost solid bright red to dark fuscous with a bold white embolium and cuneus. The nymphs of *L. nigridea* possess similar contrasting colors, with late instars typically having a bright red abdomen with dark fuscous or black wing pads (Fig. 3).

Although many species of *Lopidea* are bright red and black, information on their basic biology, especially as it relates to aposematism, is currently unavailable. *Lopidea nigridea* is ideal for the study of aposematism because it is easy to sample, easy to maintain in the laboratory, and is specific to a single species of lupine in southeastern Oregon, allowing accurate identification of the arthropod community with which it interacts. This paper describes the biology of *L. nigridea* and identifies the common arthropod species associated with it, including potential competitors and visually oriented predators. The study will serve as a base upon which more detailed work on aposematism in *L. nigridea* will depend.

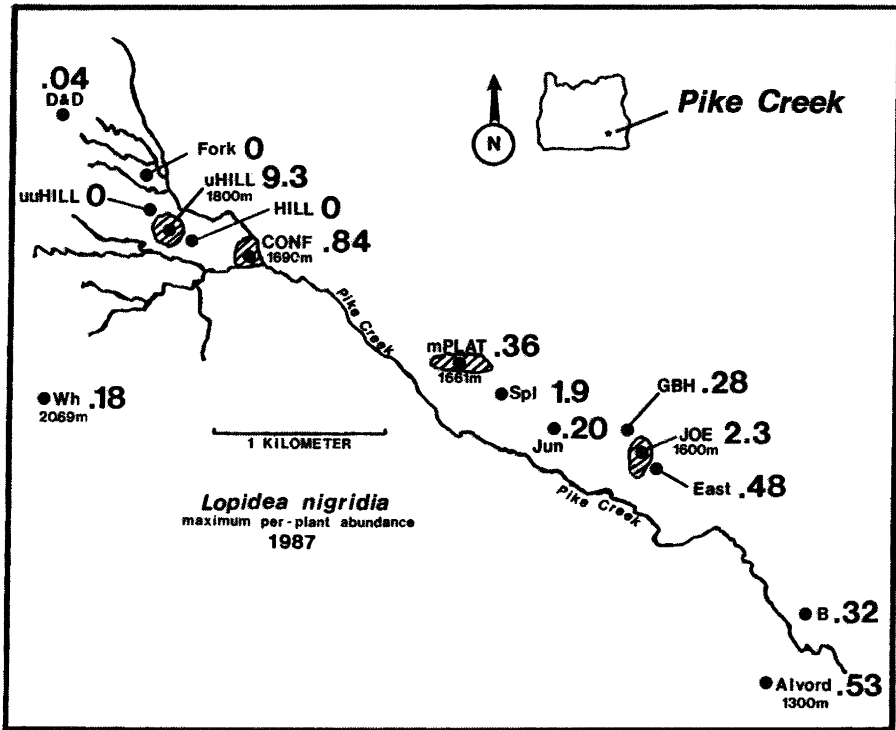


Fig. 4. Maximum average per-plant abundance of *Lopidea nigridea* in samples of 50 *Lupinus caudatus* plants at 15 sites in the Pike Creek Drainage, Steens Mountain, southeastern Oregon, May–July 1987. Hatched areas denote primary sites.

METHODS AND MATERIALS

Study area. The field research was carried out from May through August of 1985, 1986, 1987 and 1988 on the east escarpment of Steens Mountain, southeastern Oregon (118°32'30"W; 42°32'30"N). *Lopidea nigridea* populations were studied at 15 sites along an altitudinal gradient from 1,353 m to 2,286 m (4,400–7,500 ft), within the Pike Creek drainage system (Fig. 4). From these 15 sites, we chose four primary sites for intensive study (JOE—1,600 m, mPLAT—1,661 m, CONF—1,690 m, uHILL—1,800 m), and from which to collect specimens for various aspects of the research.

Plant communities of the primary sites at Pike Creek are dominated by sagebrush (*Artemisia tridentata* Nutt.) and rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britton), with a variety of other shrubs, herbs and grasses intermixed (Great Basin Province; Franklin and Dyrness, 1973). On south-facing slopes and in flat open areas, the most common herbaceous plant is *Lupinus caudatus* Kellogg (Fabaceae), the only known host plant for *Lopidea nigridea* in the northern Great Basin Desert of southeastern Oregon.

Methods. Adults and 3rd, 4th, and 5th instars of *L. nigridea* were collected in the field for description and illustration. Some of these were reared on a lupine diet for estimates of instar duration at ambient field temperatures (range of highs: 23–32°C; range of lows: 5–13°C; 5–30 June 1987). Seventeen field-collected females were dissected to obtain estimates of fecundity.

Behavioral observations were made of both nymphs and adult *L. nigridea* on their lupine host plant, and time budgets constructed for each set of observations. Casual observations were also made at irregular intervals to supplement the time budget data.

Relative abundance, expressed as frequency of individuals per sample of 50 plants, was estimated for the four primary sites at regular intervals over the active portion of *L. nigridea*'s life cycle (late April to early July 1986, 1987). To obtain a sample, bugs on each of the 50 plants were shaken onto a 0.75 × 0.75 m beating sheet, and then aged, recorded and returned to the plant. From these data, we also calculated

a "deme development index" ($\sum_{i=1}^6 n_i/N$), where i = instar; n_i = # individuals of age i ; N = total # individuals. This index provides an estimate of the effect of elevation on the speed and initiation of post-embryonic development in *L. nigridea* at Pike Creek.

Distribution of *L. nigridea* was examined on a geographic scale (using information from the literature and from museum collections), over the fifteen sites at Pike Creek (using mean 50-plant sample densities), and among individual plants at each primary site (using mean and variance of 50-plant samples). The dispersion pattern of individuals among plants within each site is described graphically, using a regression of Mean Sample Density ($\bar{x} = N/50$) against Lloyd's Mean Crowding Index ($X^* = \bar{x} + (s^2/\bar{x} - 1)$; Lloyd, 1967). This regression is then compared to the co-occurring, antimimetic plant bug *Coquillettia insignis* Uhler (Phylinae).

At five-day intervals from 29 May through 9 July 1985, 50-plant samples were taken from lupine at the CONF and mPLAT sites to identify the arthropods with which *L. nigridea* potentially interacts. Special attention was paid to other herbivores and visually oriented arthropod predators. Avian and lizard predators observed foraging on or around lupine are also reported.

RESULTS AND DISCUSSION

Life cycle. Overwintered eggs of *L. nigridea* begin to hatch during mid to late April at low elevations (<1,500 m), and early to mid May at high elevations (>1,750 m), and first instar nymphs can be found in the field until early to mid June. All instars of *L. nigridea* are active feeding stages, and development takes place during a time when host lupines are producing new growth, flowers, and seeds. Minimum time for development from early first instar to young adult is about 30 days. [Because we were unable to obtain reliable data on development in the lab, the estimate of 30 days is based on a comparison of field samples with samples taken for the sympatric plant bug *Coquillettia insignis*, for which we have good lab estimates of developmental time. The average *C. insignis* individual requires a minimum of 29.86 days to develop from early first instar nymph to adult in the lab (McIver and Stonedahl, 1987a). Since the average speed of development for populations of *C. insignis* and *L. nigridea*

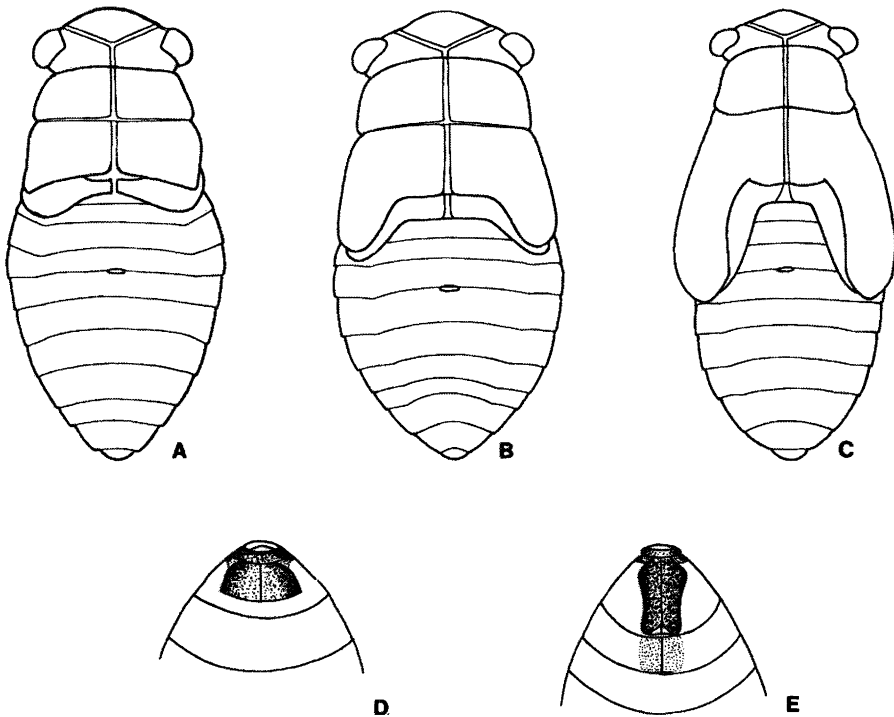


Fig. 5. Immature stages of *Lopidea nigridea*. A. Third instar nymph. B. Fourth instar nymph. C. Fifth instar nymph. D. Terminal abdominal sternites of 5th instar male. E. Terminal abdominal sternites of 5th instar female.

in the field is the same at about 11 days per nymphal stage (see Fig. 7), we can infer that the minimum time required for a *L. nigridea* individual to develop is about 30 days.]

By late June, at elevations less than 2,000 m, most individuals have reached the adult stage. Depending on plant condition, adults can be found on their host plants for nearly four weeks after the final molt. Females lay eggs from late June through most of July, usually on the same host plant upon which they developed. By early August, except in the most protected sites, lupine host plants have senesced, and the active portion of the life cycle of *L. nigridea* has ended, with the eggs overwintering to complete the life cycle.

Description of immature stages. NYMPHS (Fig. 5a-c). Nymphal descriptions and illustrations are based on alcohol-preserved specimens displaying normal growth and orientation of the various body regions and appendages. Only 3rd-5th instars are treated, as these three stages adequately represent the variation normally observed in the juvenile form. Third through fifth instar nymphs are most easily differentiated by overall size and length of the wing pads. Sex can be determined by differences in

the position and shape of the sclerotized plates on the 8th and 9th abdominal segments, and the larger size of females. All measurements are in millimeters.

THIRD INSTAR (Fig. 5a). Length 1.92–2.23; bright red; head and thoracic tergites darker red with scattered fuscous areas; dorsum with sparsely distributed black setae of various lengths; legs and antennal segments I–III also with black setae; antennal segment IV with more densely distributed, shorter pale setae. Head: subtriangular, vertical; dorsum dark red, ventral surfaces lighter; eyes large, bright red; width across eyes 0.73–0.74; only slightly broader than pronotum; vertex straight, with row of 6–8 dark setae at posterior margin; frons broad, slightly convex; antennal fossa large, situated midway between eye and base of rostrum; tylus short, darker red; jugum large, well defined, sub-rectangular, oriented vertically; lorum small, well defined; buccula short; gena well developed with oblique suture running from anteroventral base of antennal fossa to below posterior margin of eye, unpigmented. Rostrum: length 0.83–0.85, tip black, reaching past mesocoxae and almost to metacoxae. Antenna: linear, segment I slightly broader than II–IV, narrowed basally; dark red, paler at joints; length of segment I, 0.25; II, 0.49–0.53; III, 0.47–0.52; IV, 0.40–0.41. Thorax: tergites dark red with fuscous areas concentrated at lateral aspects, sternites lighter red; pronotal disk broader than long (length 0.23–0.29; posterior width 0.65–0.71), broadest posteriorly, anterior angles broadly rounded, posterior angles more acute, anterior and posterior margins nearly straight, calli indistinct; wing pads short, mesothoracic pair only slightly produced posteriorly, length 0.03–0.07. Abdomen: oblong-oval, deep red, midventral surface of sternites II–VII pale, weakly sclerotized; scent gland opening located between tergites III and IV, outlined with fuscous; abdominal sternite IX of female with dark brown sclerotized plates on either side of midline, male also with a pair of sclerotized plates on sternite IX but broader and slightly separated medially. Legs: coxae dark red with base and apex pale; trochanters pale; femora dark red with base, apex and ventral surface pale; tibia and tarsi uniformly dark red; tarsi 2 segmented, segment I much shorter than segment II.

FOURTH INSTAR (Fig. 5b). Similar to third instar except larger, and wing pads disproportionately longer. Head behind eye pale white, tylus and frons darker red, antennae closer to eye, antennal socket black; calli evident, dotted with fuscous; two plates on ventral surface of 9th abdominal segment more heavily sclerotized; coxae banded red and white, trochanters pale, femora and tibia darker, deep red to fuscous. Length 2.47–2.97. Head width across eyes 0.89–0.97. Rostrum: length 1.01–1.18. Antenna: I, length 0.30–0.33; II, 0.78–0.83; III, 0.68–0.75; IV, 0.42–0.48. Thorax: length of pronotal disk 0.39–0.40, posterior width 0.88–0.92, length of mesothoracic wing pad 0.31–0.38, reaching to anterior margin of second abdominal tergite.

FIFTH INSTAR (Fig. 5c). Similar to fourth instar except body size larger and with antennal segment II longer and wing pads disproportionately much longer. Overall darker, antennal segment IV thinner, posterior angles of pronotum more rounded, posterior margin black, wing pads divergent and darker, medial areas black. Length 3.2–4.29. Head width 1.08–1.13. Rostrum: length 1.32–1.41. Antenna: I, 0.38–0.50; II, 1.14–1.28; III, 0.99–1.05; IV, 0.50–0.56. Thorax: length of pronotal disk 0.61–0.64, posterior width 1.09–1.28; length of mesothoracic wing pad 0.85–1.02, reaching to anterior margin of fifth abdominal tergite. Abdomen: sclerotized plates on abdominal sternite IX much larger than in earlier instars, female also with well-developed plates on posterior half of sternite VIII (Fig. 5d, e).

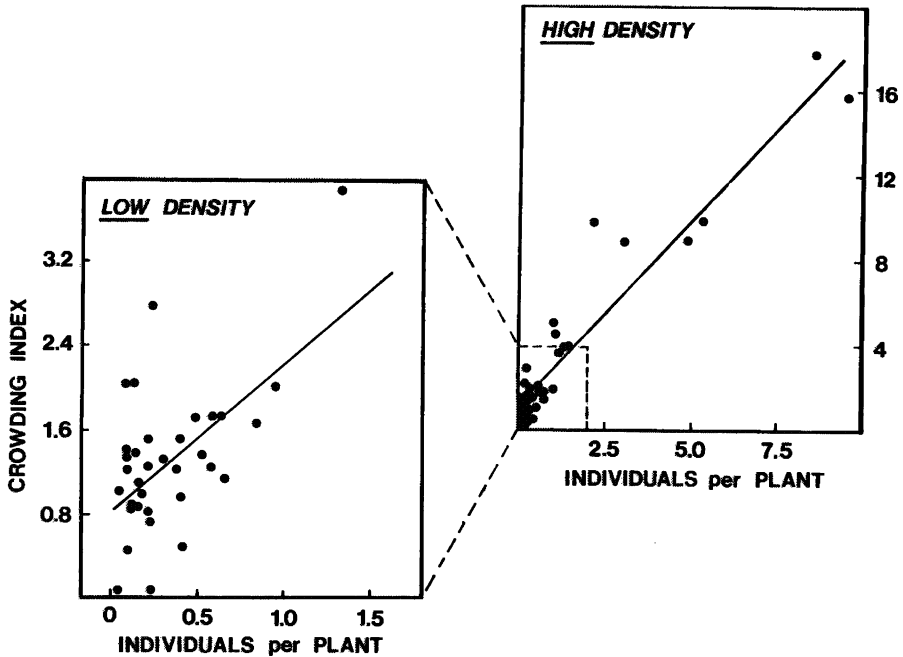


Fig. 6. Dispersion of *Lopidea nigridea* individuals among plants, at low density sites (<1.5 individuals per plant) and high density sites (>1.5 individuals per plant). Each point represents a sample characterized by a mean density (x-axis) and a mean crowding index (y-axis; $y = X^* = \bar{x} + (s^2/\bar{x} - 1)$); dashed lines represent lines of slope 1.

Fecundity estimate. A total of 17 adult females were collected at the HILL site on 18 and 26 July 1988, and dissected to determine egg load. Average egg load was 12.4 ± 5.5 SD, with a range of 3 to 26 eggs per female.

Distribution and abundance. Populations of *L. nigridea* can be found on *Lupinus caudatus* nearly everywhere the lupine grows in southeastern Oregon. At Pike Creek, *L. nigridea* is widely distributed on lupine from 1,300 to 2,250 m elevation. Among sites, however, *L. nigridea* is patchy in distribution, being very common at some localities and absent or rare at others (Fig. 4). Population density per site tends to remain constant over the years, so that a similar among-site distribution at Pike Creek was observed for all four field seasons (1985, 1986, 1987, 1988). Site constancy was extreme in some cases: at four sites within a 9 hectare area at Pike Creek, *L. nigridea* was never observed at uuHILL, HILL, and Fork, but achieved its greatest observed abundance for all four field seasons at the intermediate elevation site uHI (Fig. 4). Extreme site fidelity is probably due to a combination of factors, including the tendency for females to oviposit on the host plant upon which they develop, and the tendency for adults of both sexes to fly only short distances.

Within a typical site, *L. nigridea* individuals are also patchily distributed, especially compared to the ant-mimetic plant bug *Coquillettia insignis* Uhler (McIver and

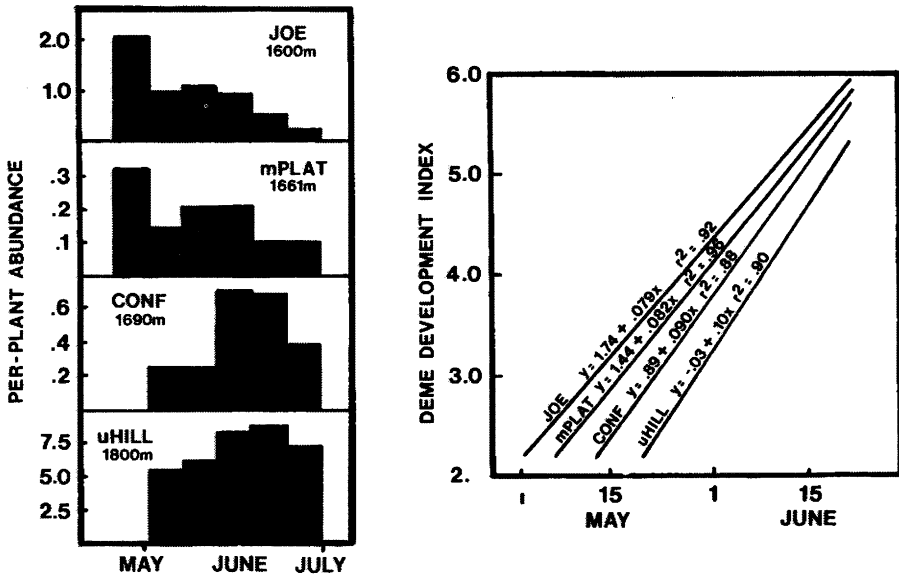


Fig. 7. a. Number of *Lopidea nigridea* individuals per lupine plant from late April to late June 1987, at the four primary sites in the Pike Creek drainage system. b. Regressions of deme development index ($\sum_{i=1}^6 n_i/N$) versus time for the four primary sites in the Pike Creek drainage, southeastern Oregon.

Lattin, in press—Fig. 3). Regressions of Lloyd's Mean Crowding Index on Density show that *L. nigridea* exhibits a wide range of densities among sites, a high average density per plant when it occurs, and a slope of density versus crowding index much greater than 1.0, all features of animals with aggregated distributions (Fig. 6). At some sites (e.g., uHILL), an average per-plant density of almost 10.0 individuals was consistently observed, nearly 10× greater than any density observed for *Coquillettia*. Such extreme aggregation of individuals may be an adaptation related to aposematism (Edmunds, 1974): interestingly, *L. nigridea* is not only brightly colored and aggregated, but is known to be distasteful to some arthropod predators (McIver, 1989; McIver and Lattin, in press).

The pattern of abundance of *L. nigridea* over time was strongly influenced by elevation (Fig. 7a). Elevation can be expected to influence temperature regimes, and so both the host plant and *L. nigridea* populations will tend to develop later at higher, cooler sites. When deme development index is regressed over time for the four primary sites, populations at higher sites clearly start later and develop faster than populations at lower sites (Fig. 7b). Presumably, this is because by the time eggs hatch at higher sites (early June at uHILL), mean ambient temperatures are higher, and so postembryonic development proceeds more rapidly compared to lower sites, where development starts much earlier (early May at JOE).

Behavior. *Lopidea nigridea* is an alert, visually oriented diurnal plant bug, the adults and nymphs of which feed on the higher stems, undersides of leaves, flower parts and developing seeds of its lupine host plant. Like many other foliage-feeding plant bugs, the feeding activity of *L. nigridea* often causes stippling and chlorosis on the upper surfaces of plant tissues (Knight, 1941). Six individuals were observed on lupine for a total of 279 minutes and five distinct behavioral activities were identified: rest = no observable movement, plant bug very responsive, body horizontal, proboscis tucked in; feed = no observable movement, bug much less responsive, body horizontal, proboscis inserted in plant tissue; groom = stereotypic grooming movements, use of mouthparts and tarsi of anterior legs to groom antennae, eyes, head, proboscis and legs with posture dependent on which body part is being groomed; run = rapid movement usually up or around stem or leaf, usually followed by rest; probe = periodic insertion of proboscis into plant tissue, usually followed by feeding. The six observed individuals spent most of their time resting (59%), followed by feeding (33%), running (6%), grooming (2%), and probing (0.4%). Compared to the sympatric ant-mimetic plant bug *Coquillettia insignis*, *L. nigridea* is much less active (McIver and Stonedahl, 1987a), and individuals tend to use a single individual host plant for much of their active lives. Although on the scale of an individual lupine plant, populations of both adult and nymphal *L. nigridea* are commonly aggregated, no social behavior (other than mating) was ever observed. After mating, females insert their eggs into stems of their host plant, in a manner similar to other plant bug species (McIver and Stonedahl, 1987b).

Predators. Three species of lizards occur at Pike Creek (collared, western-fence, side-blotched), although none was observed foraging in or around lupine. Five species of insectivorous birds often foraged on the ground in the vicinity of lupine plants (lazuli bunting, rock wren, canyon wren, sage sparrow, green-tailed towhee); the towhee commonly perch on the lower stems of lupine. As yet, there is no evidence that vertebrate predators feed on plant bugs or have a significant impact on plant bug populations at Pike Creek.

Nearly 20 species of arthropod predators forage on *L. caudatus* during the time when *L. nigridea* is active (Table 1; McIver, 1987; McIver and Stonedahl, 1987a). Most of these are visually oriented predators, some of which feed on *L. nigridea* in the field and in the laboratory. Probably the most important predators of *L. nigridea* are the flower spider *Misumenops celer* (Hentz) and the assassin bug *Sinea diadema* (Fabricius). The crab spider *Xysticus montanensis* Keyserling and most jumping spiders (*Phidippus* spp., *Metaphidippus* spp., *Sassacus papenhoei* G. & E. Peckham) typically reject *L. nigridea* after attack, presumably because of some unpleasant property (McIver and Lattin, in press). The observed distastefulness, the red and black coloration, and the tendency for populations to be highly aggregated in dispersion, all strongly indicate that *L. nigridea* is an aposematic species.

This study dealt with a population of *L. nigridea* near the middle of its geographic range and intermediate in color pattern. Comparative data are now needed on different color forms of *L. nigridea* and on populations in different areas using alternate host plants. Our future research will focus on how aposematism influences survivorship in natural populations of *L. nigridea*, with an emphasis on how host plant chemistry contributes to variation in distastefulness and coloration observed over *L. nigridea's* geographic range.

Table 1. List of arthropod species with which *Lopidea nigridea* potentially interacts, observed on *Lupinus caudatus* from 29 May to 9 July 1985; relative abundance on 3,625 plants sampled by beat sheet and sweep net; and temporal range at Pike Creek, 1,500–2,200 meters in elevation.

Taxa	Abundance on 3,625 plants	Temporal range
Herbivores		
<i>Lopidea nigridea</i> Uhler	328	early May–mid July
<i>Coquillettia insignis</i> Uhler	641	early May–mid July
Other herbivores	3,899	
Visual arthropod predators		
<i>Misumenops celer</i> (Hentz) & <i>M. asperatus</i> (Hentz)	126	mid May–late July
<i>Thanatus</i> spp. immatures	8	late May
<i>Tibellus chamberlini</i> Gertsch	7	mid May–late July
<i>Xysticus montanensis</i> Keyserling	2	early May–late July
<i>Misumena vatia</i> (Clerck)	2	
<i>Sassacus papenhoei</i> G. & E. Peckham	33	late May–late July
<i>Phidippus texanus</i> -group	2	
<i>Synageles occidentalis</i> Cutler	2	mid May–late July
<i>Oxyopes scalaris</i> Hentz	17	mid May–late July
<i>Sinea diadema</i> (Fabricius)	32	early June–early August
Reduviidae immatures	30	mid May–mid June
<i>Nabica vanduzeei</i> (Kirkaldy) & <i>Nabis alternatus uniformis</i> Harris	47	early June–early August
<i>Phytocoris</i> sp. immature	2	
<i>Geocoris</i> sp. immature	1	
Total visual predators (16 spp.)	311	
Total non-visual predators (6 spp.)	47	
Other visual predators observed since 1985: <i>Phidippus johnsoni</i> Peckham & Peckham, <i>Metaphidippus heleanae</i> (Banks), <i>Metaphidippus insignis</i> -group, <i>Tutelina similis</i> (Banks) (only in riparian area).		

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