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Some Aspects of the Natural History of *Longitarsus Subrufus* (Coleoptera: Chrysomelidae)

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SOME ASPECTS OF THE NATURAL HISTORY OF *LONGITARSUS SUBRUFUS* (COLEOPTERA: CHRYSOMELIDAE)

Andrew H. Williams[1]

ABSTRACT

This is a synthesis of historic specimen data, published information, and the results of observation and experimentation in the field and greenhouse. The primary food plant of Nearctic *L. subrufus* is *Onosmodium molle* (Boraginaceae) and the known distribution of the beetle includes most of the plant's wide midcontinental range. Adults feed on all above ground tissues except seeds; larvae feed on roots. The species is univoltine, spending winter as larvae. Daily activity patterns of adults are presented and three predators reported (*Sinea*, *Nabicula*, *Enallagma*).

Over 1992-1996, I studied *Longitarsus subrufus* LeConte (Chrysomelidae) and its primary food plant *Onosmodium molle* (Boraginaceae), resulting in my MS thesis (Williams 1996) which, as pertains to the beetle, is summarized here. Data were gathered from historic specimens, the literature, and from observation and experimentation in the field and greenhouse.

MATERIALS & METHODS

Historic beetle specimens were sought from all institutional collections in the U.S. and Canada as well as from individual U.S. collectors with a known interest in Chrysomelidae. References to *L. subrufus* were found in eight works (LeConte 1859, Horn 1889, Blatchley 1910, Duckett 1920, Craighead 1923, Fattig 1948, Wilcox 1954, Kirk and Balsbaugh, Jr. 1975) dated prior to my thesis (Williams 1996) and in three more recent references (Clark 2000, Riley et al. 2003, Clark et al. 2004).

Field work over 1992-1996 led to the collection of many *L. subrufus* specimens now in the Insect Research Collection (IRC) of the University of Wisconsin - Madison. My initial determinations of these as *L. subrufus* were confirmed by D. G. Furth and E. G. Riley. Most field work was conducted in Wisconsin.

The range-wide distribution of *O. molle* was mapped (Fig. 1) using data from 135 U.S. and Canadian herbaria and from that part of the literature vouchered by specimens. The historic distribution of *O. molle* in Wisconsin was mapped (see Williams 1996) and the discovery of current populations was made using herbarium data and botanical literature, surveying Wisconsin field botanists, and through extensive field work. Habitat information was collected from the literature, from plant specimen labels, and through field work. By talking with property owners, the land use history of each *O. molle* site was documented. The *O. molle* plants were counted and the vascular flora thoroughly surveyed on each current Wisconsin site. Most sites were visited a minimum of three times. Specimens of *O. molle* from each site were deposited in the Wisconsin State Herbarium at University of Wisconsin - Madison. To a lesser degree, I sought and studied *O. molle* sites in other states. All above ground *O. molle* fauna were studied (Williams 1999). Plant nomenclature generally follows Gleason and Cronquist (1991).

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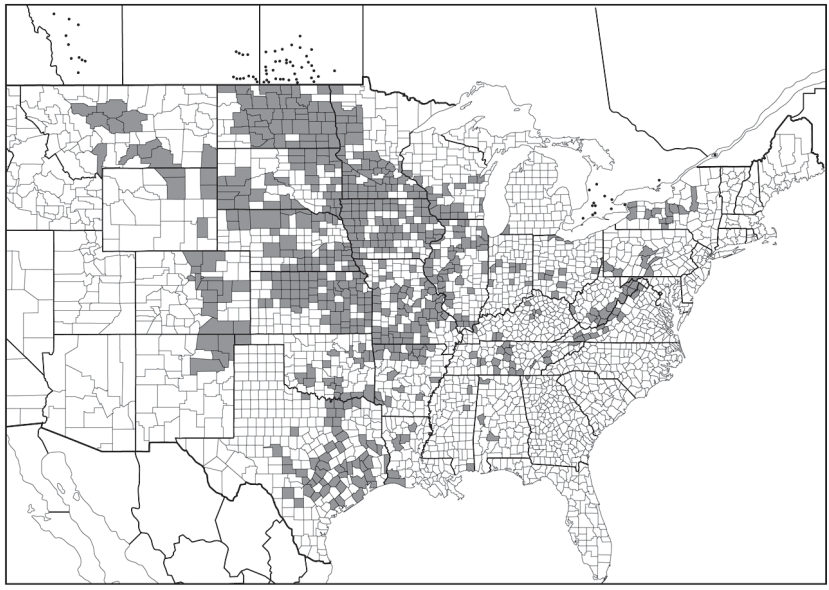

Figure 1. Specimen collections of *Onosmodium molle* in 1996. Data were contributed by 135 herbaria, listed here by herbarium codes (New York Botanical Garden 1990): ALTA, APSC, ARIZ, ASTC, ASU, AUA, BAYLU, BDI, BHO, BHSC, BUF, BUT, CANM, CHI, CLEMS, CLM, CM, COCO, COLO, CSB, DAO, DAV, DBG, DEK, DHL, DMNH, DUKE, DUL, ECH, EIU, ETSU, F, FARM, FLAS, FUGR, FWM, GFND, GH, GMUF, GRI, H, HNH, HNWU, HPC, HPH, IA, ILLS, IND, ISC, ISM, ISU, KNK, KNOX, KSP, LCDI, LLC, LSU, MASS, MICH, MIL, MIN, MISS, MMMN, MODNR, MONT, MONTU, MOR, MOVC, MSC, MT, MU, MUHW, MWI, NCBS, NCSC, NEB, NEMO, NLU, NMC, NO, NPWRC, NY, NYS, ODU, OKLA, OWU, PAC, PH, PUL, RMWC, RSA, SASK, SAT, SBSC, SCHN, SEMO, SLRO, SMU, TAES, TAMU, TENN, TER, UAM, UARK, UCHT, UCR, UNA, UNCC, UNM, US, USF, UT, UVST, UWFP, UWM, UWO, VCU, VDB, VMIL, VPI, VT, WARM, WET, WILLI, WIN, WIS (specimens collected in this study), WJC, WNC, WTS, WTU, WVA, WVW, YU, Beloit College, and University of Wisconsin - Green Bay. Data were also drawn from that part of the literature vouchered by specimens (Deam 1940, Steyermark 1963, Das 1965, Radford et al. 1965, Booth and Wright 1966, Great Plains Flora Association 1977, Mohlenbrock and Ladd 1978, Martin and Hutchins 1981, Baskin et al. 1983, New York Flora Association 1990, Ownbey and Morley 1991, Rhoads and Klein, Jr. 1993).

In addition to the results of my general field work, those of three discrete projects are presented here: two rearing experiments and a study of daily activity patterns of adults in the field.

Experiment One

The purposes of this experiment were to see whether or not adult beetles would emerge from potted and overwintered *O. molle* roots, and when.

On 29 November 1994, seven large, senescent *O. molle* plants were dug and their tops discarded. Each rootcrown was cut to 10 cm and positioned vertically in soil in its own pot that was buried that same day in a Wisconsin garden for the winter. On 21 April 1995, pots were dug up, cleaned, individually caged, and brought into the lab, where they were cared for daily under artificial light until 20 September 1995.

Experiment Two

One purpose of this experiment was to test adult female behavior. Would females oviposit in such a way that their larvae could develop using only *O. molle*? Other purposes were to show that these larvae can develop using only *O. molle* roots, to produce adult beetles from these potted plants, and to learn when the adults would appear.

On 24 May 1995, small *O. molle* plants were dug, carefully cleaned and the bare-rooted plants potted, two or three per pot. Their roots showed no evidence of larval feeding. Pots were individually caged and tended daily in a greenhouse. On 12 July 1995, 38 pairs of *L. subrufus* collected *in copula* from *O. molle* in the wild that same day were introduced to the 11 caged pots, three or four pairs per pot. These adults were removed in early August. On 11 October, these pots were buried, still caged, in a Wisconsin garden. Pots were dug up, cleaned, individually caged, and returned to the greenhouse on 11 April 1996. The daily routine of plant care was resumed through 1 October 1996.

Study of Daily Activity Patterns

To learn about adult behaviors around the 24-hour daily cycle, a field study was conducted over 13-23 August 1995. Ten isolated *O. molle* plants — five plants on each of two sites — were each observed for a two minute period once per hour. Air temperature was recorded hourly. At each site, observations were made over 00:00-11:00 hrs. on one occasion and then over 12:00-23:00 hrs. on another. Site I14 (plants 1-5) had an extraordinarily high beetle population, which could alter more usual behavior, so the study was duplicated on site GN31 (plants 6-10). I stood in the same position relative to each plant during each observation and did not handle the plants. It did not rain over the periods of observation and wind was absent to very light.

This study was designed to answer several questions. How many beetles were present at each of the 24 hourly observations? What percentage of those present were mating? When was feeding observed? Do data differ between sites?

RESULTS

Historic beetle specimens were obtained from 29 sources — museums and individuals. These data and my own, both summarized in Table 1, outline the known distribution of *L. subrufus*, which is mapped (Fig. 2). Some historic specimens could not be ascribed to counties, but 82% of those that could were collected in counties in which *O. molle* has also been collected, in some cases by the same person who collected the beetle. Blatchley collected the beetle in 1893, and the plant in 1889 (plant specimen at New York Botanical Garden), in Vigo Co., Indiana. Schwarz collected the beetle on 10 April and again on 16 April, in an unrecorded year, and the plant in April 1902 (plant specimen at Smithsonian Institution), in Victoria Co., Texas. Graenicher collected the beetle over 5-10 August

Table 1. Summary of specimen data for *Longitarsus subrufus* in 1996. Museums and individuals contributing data to this table are ANSP, Academy of Natural Sciences at Philadelphia; BCCC, University of Minnesota; CNCI, Agriculture and Agri-Food Canada; CUIC, Cornell University; DEUN, University of Nebraska - Lincoln; EGRC, E. G. Riley's collection; FGAC, University of California - Riverside; FMNH, Field Museum of Natural History; FSCA, Florida State Collection of Arthropods; INHS, Illinois Natural History Survey; IRC, University of Wisconsin - Madison (specimens collected in this study); KSUC, Kansas State University; MCPM, Milwaukee Public Museum; MCZC, Harvard University; MSUC, Michigan State University; NDSU, North Dakota State University; OSUC, Ohio State University; PSUC, Pennsylvania State University; PURC, Purdue University; SDSU, South Dakota State University; SEMC, University of Kansas; SMCC, S. M. Clark's collection; TAMU, Texas A & M University; TNSC, T. N. Seeno's collection; UAIC, University of Arizona; UICM, University of Idaho; UMMZ, University of Michigan; UMRM, University of Missouri; USNM, U. S. National Museum; and WSUC, Washington State University.

Museum	State	County	Date	Additional Label Data
MCZC				T. B. A. Co.
WSUC				U, O. S. Westcott Collection, L. s. LeC. 16033
SEMC	CO			Colo. 638
MCZC	CO	Clear Creek	1 July 1897	Liebeck Coll.
MCZC	CO	Denver		Denver 7
USNM	CO	Denver	7 July	Coll Hubbard & Schwarz
USNM	CO	Denver	5 September 1892	Denver Colo.
BCCC	IA			Otto Lugger Collection
UMMZ	IA		26 June 1940	County #12
MCZC	IA	Benton		
FGAC	IA	Benton	4 July 1928	G. P. MacKenzie Collection, 16033
UAIC	IA	Benton	4 July 1928	D. K. Duncan Collection, 16033
UMMZ	IA	Benton	4 July 1928	16033
USNM	IA	Dickinson	1 July	Miller's Bay, W. Okoboji L., *Longitarsus subrufus* LeC. 7011
IRC	IA	Marshall	24 June 1995	on *O. molle*, S. Sauer collector
IRC	IA	Story	29 July 1995	on *O. molle*, A. H. Williams collector
ANSP	IL			
BCCC	IL			Otto Lugger Collection
MCZC	IL			Liebeck Coll.
MCZC	IL			N. Ill., Frederick Blanchard Collection
MCZC	IL			C. Ill., Frederick Blanchard Collection
USNM	IL			S. Ill., Collection C. V. Riley, Collection F. Knab
UAIC	IL	La Salle	15 August 1908	Ottawa, Ill., F. G. Werner
INHS	IL	Peoria	28 June 1878	188
IRC	IL	Will	9 July 1995	on *O. molle*, A. H. Williams collector
IRC	IL	Winnebago	18 September 1994	on *O. molle*, A. H. Williams collector
FMNH	IN	Koscinsko	19 August 1917	Mineral Spgs., Mus. Exped., C. L. Hubbs col

Table 1. Continued.

Museum	State	County	Date	Additional Label Data
FMNH	IN	Lake	20 May 1906	Pine, Ind., F. Psota Coll. ex A. B. Wolcott Coll.
MCZC	IN	Tippecanoe	19-20 July 1925	Lafayette, E. M. Stirrett Collector
PURC	IN	Vigo	15 June 1893	W. S. B., 1253, Purdue Blatchley Collection
ANSP	KS			
ANSP	KS			Snow
MCZC	KS			
MCZC	KS			Snow, Liebeck Coll.
PURC	KS			Ashton Collection
ANSP	KS	Douglas		900 ft., F. H. Snow
SEMC	KS	Douglas		F. H. Snow
KSUC	KS	Riley	June	Popenoe
KSUC	KS	Riley	17 June 1895	Popenoe
UICM	KS	Riley	June	Popenoe
KSUC	KS	Riley	July	F. Marlatt
KSUC	KS	Riley	4 July	Popenoe, 91
MCZC	KS	Riley	4 July	Liebeck Coll.
IRC	KS	Riley	14 July 1994	on *O. molle*, A. H. Williams collector
MCZC	KS	Shawnee		Topeka, Popenoe
SEMC	KS	Shawnee		Topeka, Popenoe
KSUC	KS	Shawnee		Topeka, Popenoe, 1094
KSUC	KS	Shawnee	July	Topeka, Popenoe
USNM	KS	Shawnee		Topeka, Popenoe, on *Onosmodium*, Collection of C. V. Riley
KSUC	KS	Trego		
CNCI	MAN		17 July 1925	Aweme, N. Criddle
IRC	MAN		16 July 1996	on *O. molle*, A. H. Williams collector, 1 site
IRC	MAN		17 July 1996	on *O. molle*, A. H. Williams collector, 2 sites
BCCC	MN	Big Stone	? 1887	O. W. Oestlund
BCCC	MN	Traverse	? 1887	O. W. Oestlund, 46, 2373, 1335
IRC	MO	Crawford	1 August 1996	on *O. molle*, J. Sullivan collector
EGRC	MO	Holt	16 June 1979	on *Onosmodium occidentale*, Loess Prairie Habitat, 1.8 miles S. Mound City
TAMU	MO	Holt	16 June 1979	on *Onosmodium occidentale*, Loess Prairie Habitat, 1.8 miles S. Mound City
UMRM	MO	Holt	16 June 1979	on *Onosmodium occidentale*, Loess Prairie Habitat, 1.8 miles S. Mound City
EGRC	MO	Holt	2 July 1992	on *Onosmodium occidentale*, Loess Prairie Habitat, 1.8 miles S. Mound City
UMRM	MO	Jackson		Kan. C., Mo., L. s. Lec. 7011
IRC	ND	Foster	15 July 1996	on *O. molle*, A. H. Williams collector

Table 1. Continued.

Museum	State	County	Date	Additional Label Data
IRC	ND	Griggs	15 July 1996	on *O. molle*, A. H. Williams collector
IRC	ND	Nelson	15 July 1996	on *O. molle*, A. H. Williams collector
IRC	ND	Rolette	17 July 1996	on *O. molle*, A. H. Williams collector
IRC	ND	Towner	16 July 1996	on *O. molle*, A. H. Williams collector
IRC	ND	Traill	15 July 1996	on *O. molle*, A. H. Williams collector
MCZC	NE			
MCZC	NE			on *Onosmodium*, Dr. Shimer
BCCC	NE			Otto Lugger Collection
DEUN	NE		July	Pine Ridge
ANSP	NE	Fillmore		
MCZC	NE	Fillmore		
SEMC	NM	Otero	27 June 1940	Cloudcroft, L. J. Lipovsky
SEMC	NM	San Miguel	August 1882	near Hot Springs, Las Vegas, N. M., 7000 ft., F. H. Snow
EGRC	NM	Union	2 July 1989	Clayton Lake State Park, night sweep, R. S. Anderson
FSCA	OH	Greene	23 June 1947	J. A. Wilcox Collr.
TNSC	OH	Greene	23 June 1947	J. A. Wilcox Collr., from J. A. Wilcox Collection
PSUC	PA	Franklin	30 June 1922	St. Thomas, Pa., E. M. Craighead Coll.
USNM	PA	Franklin	30 June 1922	St. Thomas, Pa., E. M. Craighead Coll., Geo. M. Greene Collection
MCZC	PA	Franklin	20 July 1921	St. Thomas, Pa., E. M. Craighead Coll.
NDSU	PA	Franklin	20 July 1921	St. Thomas, Pa., E. M. Craighead Coll.
PSUC	PA	Franklin	20 July 1921	St. Thomas, Pa., E. M. Craighead Coll.
USNM	PA	Franklin	20 July 1921	St. Thomas, Pa., E. M. Craighead Coll., Geo. M. Greene Collection
SDSU	SD	Brookings	23 July 1922	White, S. D., H. C. Severin
NDSU	SD	Brookings	25 July 1968	White, S. D., V. M. Kirk, S., V. M. Kirk Collection
SDSU	SD	Custer	August 1952	State Game Lodge, H. C. Severin Coll.
NDSU	SD	Custer	9 August 1967	Wind Cave Nat'l. Park prairie dog town, E. U. Balsbaugh, Jr.
NDSU	SD	Deuel	24 July 1969	Gary, S. D., V. M. Kirk, S., V. M. Kirk Collection
SDSU	SD	Lawrence	4 August 1952	Spearfish Canyon, H. C. Severin Coll.
SDSU	SD	Lawrence	4 August 1952	East of Spearfish Canyon, H. C. Severin Coll.
NDSU	SD	Lawrence	2 August 1967	Spearfish Canyon, 2 mi. S. of US 14, E. U. Balsbaugh, Jr.

Table 1. Continued.

Museum	State	County	Date	Additional Label Data
NDSU	SD	Lawrence	5 August 1969	Higgins Gulch, Black Hills, E. U. Balsbaugh, Jr.
CUIC	TN	Madison		
MSUC	TN	Wilson	9 June 1946	Lebanon, Tenn., R. R. Dreisbach, 16033
TNSC	TN	Wilson	11 June 1946	Lebanon, Tenn, R. R. Dreisbach, from Collection of J. A. Wilcox
UAIC	TX			Tex., 7006, C. W. Leng Collection, 16033, *Longitarsus subrufus* ks 7011
USNM	TX	Bexar	23 June	S. Antonio Tex., Coll Hubbard & Schwarz
USNM	TX	Bexar	22 June 1895	S. Antonio Tex., Collection H. Soltau
USNM	TX	Bexar	23 June 1895	S. Antonio Tex., Collection H. Soltau
TAMU	TX	Brazos	18 May 1932	College Station, H. J. Reinhard
MSUC	TX	Dallas		
USNM	TX	Dallas	18 June 1906	W. D. Pierce Collector
USNM	TX	Dallas	April 1907	*Onosmodium carolinianum*, W. D. Pierce Collector
USNM	TX	Dallas	16 April 1907	on *Onosmodium carolinianum*, Schwarz & Pratt Coll.
USNM	TX	Dallas	20 April 1907	F. C. Pratt Collector
USNM	TX	Dallas	8 May 1908	C. E. Hood Collector
USNM	TX	Dallas	8 May 1908	C. R. Jones Collector
USNM	TX	Dallas	22 May 1907	F. C. Pratt Collector
USNM	TX	Dallas	11 June 1907	elder, W. D. Pierce Collector
OSUC	TX	Goliad	10 April 1950	D. J. & J. N. Knull Collrs.
TAMU	TX	Gonzales	9 April 1967	Palmetto State Park, J. C. Schaffner
TAMU	TX	Gonzales	18 April 1970	Palmetto State Park, J. C. Schaffner
TAMU	TX	Gonzales	4 May 1970	Palmetto State Park, J. C. Schaffner
TAMU	TX	Gonzales	25 April 1971	Palmetto State Park, J. C. Schaffner
USNM	TX	Victoria	10 April	on *Onosmodium bejariense*, E. A. Schwarz collector
USNM	TX	Victoria	16 April	E. A. Schwarz collector
IRC	WI	Buffalo		on *O. molle*, A. H. Williams collector, 1 site
IRC	WI	Dane		on *O. molle*, A. H. Williams collector, 6 sites
MCPM	WI	Grant	5-11 August 1911	Museum Exped., Old Cat #57512
IRC	WI	Grant		on *O. molle*, A. H. Williams collector, 19 sites
IRC	WI	Green		on *O. molle*, A. H. Williams collector, 3 sites
IRC	WI	Iowa		on *O. molle*, A. H. Williams collector, 12 sites

Table 1. Continued.

Museum	State	County	Date	Additional Label Data
IRC	WI	Lafayette		on *O. molle*, A. H. Williams collector, 1 site
IRC	WI	Pierce		on *O. molle*, A. H. Williams collector, 13 sites
SMCC	WV	Grant	7 July 1994	Cave Mountain near Laudes, S. M. Clark
SMCC	WV	Grant	2 August 1995	Cave Mountain near Laudes, S. M. Clark
MCZC	WY	Goshen	1845	Type, #4431, J. L. LeConte collector

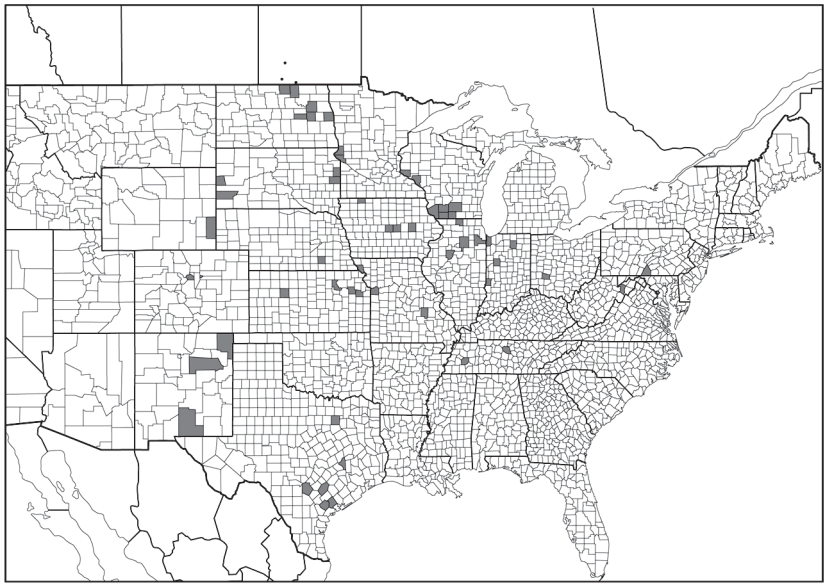

Figure 2. Specimen collections of *Longitarsus subrufus* in 1996. Data were taken from specimens included in Table 1. The 28 sources contributing data to this map are the Academy of Natural Sciences at Philadelphia, Agriculture and Agri-Food Canada, Cornell University, Field Museum of Natural History, Florida State Collection of Arthropods, Harvard University, Illinois Natural History Survey, Kansas State University, Michigan State University, Milwaukee Public Museum, North Dakota State University, Ohio State University, Pennsylvania State University, Purdue University, South Dakota State University, Texas A & M University, University of Arizona, University of California - Riverside, University of Idaho, University of Kansas, University of Michigan, University of Minnesota, University of Missouri, University of Wisconsin - Madison (specimens collected in this study), and U.S. National Museum. Also included are data from the personal collections of S. M. Clark, E. G. Riley, and T. N. Seeno.

1911 and the plant on 8 August 1911 (plant specimen at Milwaukee Public Museum), at Rutledge in Grant Co., Wisconsin. Criddle collected the beetle in 1925 and the plant in 1926 (plant specimen at Canadian Museum of Nature), at Aweme, Manitoba. Werner collected the beetle in 1908 and the plant in 1939 (plant specimen at Illinois Natural History Survey), in La Salle Co., Illinois. In Grant Co., West Virginia, the beetle and the plant were collected at one place by two people. Bartgis collected the plant in 1987 (plant specimen at West Virginia Wesleyan College). Clark, who collected the beetle in 1994 and 1995, confirmed (pers. comm.) that Bartgis' description of the plant's habitat perfectly fits that of the beetle: "dry, prairie-like pasture on Cave Mountain."

Longitarsus subrufus was described by LeConte (1859) from his own collection of the species in 1845, in Goshen Co., Wyoming. Horn (1889) wrote that this species had been collected by Snow in Kansas and that, according to Shimer, it lived on *Onosmodium*. Blatchley (1910) wrote that *L. subrufus*, "our largest species of the genus, described and known heretofore only from Kansas," was common locally on the stems and leaves of *O. molle* on 15 June in Vigo Co., Indiana. Duckett (1920) included *L. subrufus* in a list of beetles in the vicinity of College Park, Maryland. Craighead (1923) provided detailed information:

> "During July, 1921, hundreds of adults were collected by sweeping false gromwell (*Onosmodium hispidissimum* Mackenzie). Many of the adults were dissected and the females contained eggs. Egg-laying habits were not observed, but it is probable that the eggs are placed at the base of the plant on the surface or just under the ground.
>
> The larvae feed on the roots and are not very active. On examining infested roots one may find the larvae in their galleries or among the roots and when about to pupate they move a little distance away from the host.
>
> "The larva has a well-developed labrum, three-jointed maxillary palpus, ninth abdominal segment well developed, legs present, antennae two-jointed, body straight and cylindrical; 0.7 mm. to 1.2 mm. long and 0.1 mm. wide. It resembles the larva of *Diabrotica.* The larvae move around until they have formed well-defined cells in the soil and two days later pupate. Larvae remain in pupal stage from 9-15 days, averaging 10.6 days. Hibernate as larvae.
>
> "The adults feed on the leaves of *Onosmodium* and cut small irregular holes through them. Where the host was found the beetles were very abundant and by the latter part of August defoliation was complete. The adults are very active and when disturbed jump to another part of the host plant or fall to the ground where they conceal themselves under leaves. Previously recorded from Kansas and Indiana."

Fattig (1948) reported *L. subrufus* from Georgia. Wilcox (1954) wrote that *L. subrufus* had been collected on *O. molle* in Greene Co., Ohio. Kirk and Balsbaugh, Jr. (1975) included this species in a catalog of South Dakota beetles. Clark (2000) reported his own collections in West Virginia. Riley et al. (2003) simply listed the states and province where the beetle occurs. Clark et al. (2004) repeated earlier reports of this species using *O. molle* and reported for the first time that adults have been collected from *Onosmodium helleri* in central Texas.

Collections of *L. subrufus* made over the course of this study are summarized in Table 1.

Longitarsus subrufus occurred on 55 of the 59 Wisconsin sites supporting wild *O. molle* plants, but on neither of the two Wisconsin sites where *O. molle* had been introduced using seeds prior to the period of this study. In Crawford

Co., *O. molle* seeds were sown in 1987. When I visited this introduced colony, the plants were up to nine years old and *L. subrufus* was absent; the nearest beetle population was 18 miles away. An *O. molle* population in Dane Co. was started with seeds in 1962, yet *L. subrufus* was absent over 1994-1996. This site was 12 miles from the nearest beetle population. One of the four wild *O. molle* populations in Wisconsin lacking *L. subrufus* is the most disjunct, growing 125 miles from the nearest extant beetle population. This site harbored *O. molle* in 1977 (specimen at University of Wisconsin - Green Bay) and supported 187 *O. molle* plants in 1993, but despite the population's age and size, beetles were absent over 1993-1995. Beetles can colonize new *O. molle* populations, as shown by their presence on two proximal sites in Story Co., Iowa, where the plant had been introduced only by seeds, yet grows wild as close as one mile away. When I visited these Iowa sites, the oldest of these plants were in their seventh growing season.

Populations of *L. subrufus* can persist even if very few *O. molle* plants are present. Four of the 59 wild *O. molle* sites in Wisconsin harbored a single plant, yet *L. subrufus* persisted at each of them. The beetle was present at 12 of the 14 Wisconsin sites harboring fewer than nine wild *O. molle* plants.

The habitat of *O. molle*, and so of *L. subrufus*, is characterized by well-drained calcareous soils in full or partial sun, especially in areas where mammalian grazing provides disturbance. Light to moderate grazing by cattle and horses benefits *O. molle*, which is not eaten. Only when stocking levels reach the point where *O. molle* plants get routinely trampled do cattle and horses negatively impact these plant and beetle populations. I found 494 plant taxa growing with *O. molle*. These included several species in Boraginaceae: *Lithospermum incisum* (31 sites), *L. canescens* (30 sites), *Hackelia virginiana* (15 sites), *Cynoglossum officinale* (13 sites), *Lappula squarrosa* (2 sites), *Echium vulgare* (1 site), and *Lithospermum carolinense* (1 site).

Many thousands of *Longitarsus subrufus* beetles were observed over the course of this study, but only a few young adults were found feeding on plants other than *O. molle* and these others are also perennials in Boraginaceae: *Cynoglossum officinale*, *Echium vulgare*, and *Lithospermum canescens*. Whether or not the beetle can reproduce on any of these three other plants was not tested. On 26 June 1994, three beetles were found on *C. officinale*. One of these was teneral, which, given the date and the short period over which adults emerge, indicates these were young adults. *Cynoglossum officinale* is an alien pasture weed that has been in Wisconsin since at least 1849 (Lapham 1850). On 20 June 1995, one teneral beetle was found feeding on *E. vulgare*, another alien pasture weed that has been in Wisconsin since at least 1877 (Swezey 1877). On 4 July 1994, seven beetles were found mating and feeding on the native prairie plant *Lithospermum canescens* on a site adjacent to, but isolated from, an *O. molle* site. This was a steep bluff prairie above a dense belt of *Juniperus virginiana* above a pasture in which *O. molle* and *Longitarsus subrufus* occurred. *Onosmodium molle* was not found on this bluff prairie but was found in such habitat elsewhere in Wisconsin.

Longitarsus subrufus adults feed on all above ground *O. molle* tissues except seeds, leaving shot hole damage. They often enlarge existing holes, creating an array of holes of irregular size and shape. On site I13, beetles were especially abundant while, on some other sites, beetles were hard to find. Density measurements were not systematically made.

These beetles can be found in summer and autumn in Wisconsin. Adults usually begin to emerge in late June or even early July, appearing first on warmer, south-facing microsites. Typically, the plants begin to flower shortly before the beetles emerge. Mating was observed soon after adults emerged in early summer and throughout summer into autumn, as long as adults survived. Beetles can live as long into autumn as green *O. molle* tissue remains. As the leaves

blacken from frost, only the stems, which stay green a bit longer, provide food for the beetles and this is when most stem feeding occurs. Dwindling numbers of adults, as determined by the increasing difficulty of finding them, may survive even into November in Wisconsin; my latest fall collection was on 10 November.

Three predators of *L. subrufus* beetles were observed in the field: *Sinea diadema* (Fabricius) (Reduviidae), *Nabicula subcoleoptrata* (Kirby) (Nabidae), and *Enallagma carunculatum* Morse (Coenagrionidae). *Sinea diadema* adults and fourth and fifth instar nymphs fed on *L. subrufus*. This assassin bug preyed on *L. subrufus* morning, noon, and night over most of the period when beetles were present. *Nabicula subcoleoptrata* adults fed on *L. subrufus* and were twice seen to attack living beetles without success. This damsel bug was found on *O. molle* throughout the day and night during that period when beetle populations were highest. On 18 June 1994, the diurnal damselfly *E. carunculatum* snatched with its legs a beetle off the upper surface of an *O. molle* leaf. It flew to another perch, set the beetle down, landed, and sat moving its mandibles. The beetle lay on its side, barely moving. Then the damselfly flew, picked up the beetle with its legs to devour it in flight.

All above ground *O. molle* fauna were studied and pertinent to discussion of *L. subrufus* are two other beetles: *Meligethes saevus* LeConte (Nitidulidae) (Williams 2002a) and *Longitarsus melanurus* (Melsheimer) (Williams 2002b).

Experiment One

All seven rootcrowns sprouted soon after being brought into the lab on 21 April 1995. Beetles appeared on six of these caged plants over 19-31 May. The plants later died, apparently due to my poor care. The caged pots were maintained until 20 September 1995, but no more beetles emerged.

Experiment Two

After removal of the introduced adults in early August 1995, no adults were evident on daily inspections throughout that field season. Plants resprouted in only seven of the 11 caged pots that had been returned to the greenhouse on 11 April 1996. One of these soon died, leaving six pots with robust sprouts. Beetles emerged from each of these six pots over 22-31 May. Pots were checked through 1 October 1996, but no more beetles emerged. The other five pots produced no beetles. No feeding damage to leaves was observed in the absense of adults.

Study of Daily Activity Patterns

Beetles were present on each of the 10 plants at each of the 24 hourly observations. The variation in abundance by hour was more pronounced at site I14, where the beetle population was very high, than at site GN31, but the pattern of adult presence around the 24-hour cycle was similar on these two sites (Fig. 3). Beetles were least numerous on the plants during the hottest part of the day, but the nature of this correlation was not tested.

The percentage of mating beetles among those present on individual plants at each hour varied from 0-88% (Fig. 4). Mating was much reduced on both sites from 10:00-17:00 hrs. At site I14, no mating was observed from 13:00-15:00 hrs. At site GN31, no mating was observed from 11:00-16:00 hrs. Feeding was observed at each of the 24 hourly observations.

DISCUSSION

Data from historic specimens and the literature suggest the beetle's obligatory relationship with *O. molle* extends across the beetle's wide midcontinental range and my findings in the field and in the greenhouse confirm that *O. molle* is currently the only normal food plant of *L. subrufus* in Wisconsin. Young adults found feeding in Wisconsin on three other perennial borages — *C. officinale*, *E. vulgare*, and *Lithospermum canescens* — were so few in number relative to my

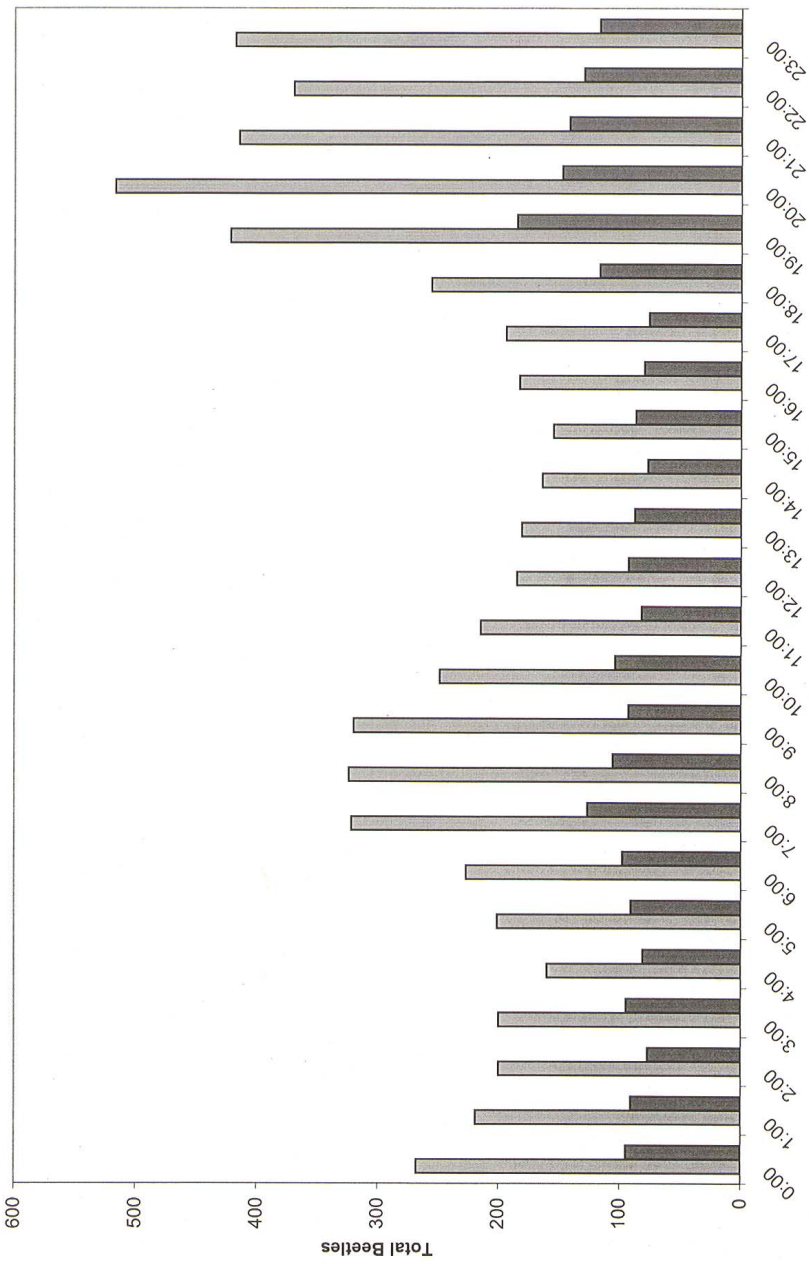

Figure 3. Hourly sum of beetles present on five plants on two sites. Left bar is site I14; right bar is site GN31.

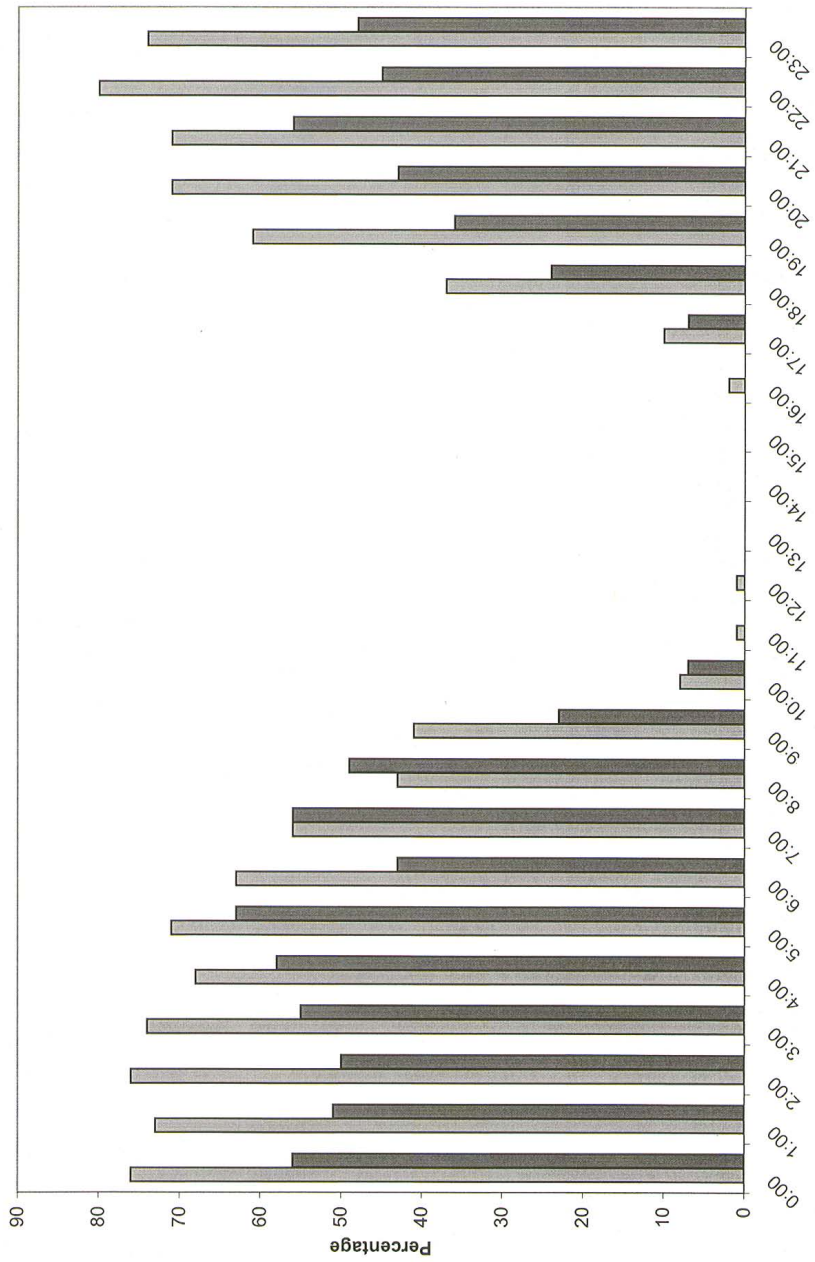

Figure 4. Average hourly percentage of beetles mating on five plants on two sites. Left bar is site I14; right bar is site GN31.

opportunities to so observe them that their behavior can only be seen as abnormal. In Texas, *Longitarsus subrufus* adults have recently been collected on *O. helleri* on which they might be presumed to develop (Clark et al. 2004).

All references to *Onosmodium* on historic specimen labels (Table 1) and in the literature except *O. helleri* in Clark et al. (2004) actually refer to *O. molle*. Probably the first specimen reference to *Onosmodium* was Shimer's, from Nebraska; another early reference is on some Popenoe specimens from Kansas. Schwarz referred to *O. bejariense* from Texas, and E. G. Riley to *O. occidentale* from Missouri. *Onosmodium carolinianum* appears on labels from Dallas Co., Texas. Craighead (1923) reported the beetle from Pennsylvania on *O. hispidissimum*. Blatchley (1910), from Indiana, and Wilcox (1954), from Ohio, reported their own collections on *O. molle*. Throughout this region, the sole *Onosmodium* is *O. molle*; *O. bejariense*, *O. occidentale*, and *O. hispidissimum* are subspecies or varieties of *O. molle* (Das 1965, Cochrane 1976, Gleason and Cronquist 1991) and *O. carolinianum* is simply misnamed — no plant bears this name. The only other plant listed on examined specimen labels is Pierce's Dallas Co., Texas, collection on elder, but Pierce also collected *L. subrufus* on *Onosmodium* in Dallas Co., earlier that same year. I deem the elder reference spurious.

Though relatively few collections of *L. subrufus* had been made prior to this study, historic specimens delineate the distribution of the species well, if we accept its obligatory association with *O. molle*. With the exception of a single specimen from Cloudcroft in Otero Co., New Mexico, this beetle has been collected only in the region where *O. molle* has also been collected, based on examined specimens. Cloudcroft is at sufficiently high elevation to support a ski resort today. Perhaps a disjunct population of *O. molle* grows there in the more moist, higher elevation along the dry western fringe of the plant's range. Perhaps *L. subrufus* also feeds on *Macromeria viridiflora* (Boraginaceae), a southwestern species that has been collected at Cloudcroft (specimen at New Mexico State University - Las Cruces). Perhaps this one beetle specimen was mislabelled.

Five of the few historic collectors of the beetle — Blatchley, Schwarz, Graenicher, Criddle, and Werner — also collected *O. molle*. Clark collected the beetle at the same site in the same habitat as Bartgis had collected the plant several years earlier.

LeConte did not refer to *O. molle* on his specimen labels or in his description of the beetle (1859), but his having collected on that same 1845 trip across our midcontinent (and described in that same 1859 paper) a second beetle that feeds only on *O. molle*, *Meligethes saevus* (Williams 2002a), suggests that LeConte encountered and collected off this plant.

Duckett (1920) included *L. subrufus* in his list of flea beetles found near College Park, in eastern Maryland. I have seen Maryland specimens determined by others as *L. subrufus*, but none of these is *L. subrufus*. Though it seems likely that the beetle lives in Allegany County, in western Maryland, as *O. molle* has been collected there and both the plant and the beetle have been collected in nearby Franklin Co., Pennsylvania, and Grant Co., West Virginia (Table 1), there is no reason to believe it lives in eastern Maryland, where *O. molle* does not occur. Duckett's (1920) report of *L. subrufus* from Maryland was almost certainly in error.

Fattig (1948) reported *L. subrufus* from Georgia, on the basis of a specimen collected by Lund and housed at the University of Georgia. I have studied the University of Georgia specimens determined as *L. subrufus*, including one collected by Lund. None of these is *L. subrufus*. Though *O. molle* has been collected in northern Georgia in Catoosa Co. (specimen at University of Tennessee - Chattanooga), and is said to occur in adjacent Walker Co. (J. R. Allison,

pers. comm.), allowing the possibility of the beetle occurring in Georgia, I have not seen Georgia specimens of *L. subrufus*. Fattig's (1948) report of *L. subrufus* from Georgia was in error.

Riley et al. (2003) reported *L. subrufus* from all of these states and Manitoba without discussion. Whether their Georgia reference is taken from Fattig (1948), which I state here is inaccurate, or from more recent, genuine collections is unclear. Louisiana, where *O. molle* occurs (Fig. 1) and so where *L. subrufus* could well be present, and the District of Columbia, where the beetle almost certainly does not occur, are also listed in Riley et al. (2003).

Some historic beetle specimens are teneral, which elucidates the beetle's phenology. Schwarz collected a series of beetles in Victoria Co., Texas, on 10 April and another series there on 16 April. The beetles of 10 April are all paler than those of 16 April. This is the most southern collection of *L. subrufus* and is essentially as far south as *O. molle* has been collected, which shows that at the southern edge of the beetle's range adults emerge in early April. In Dallas Co., Texas, a bit north of Victoria Co., Schwarz and Pratt collected a series of beetles on 26 April, several of which are teneral, suggesting that adults emerge a bit later as spring moves north. In Franklin Co., Pennsylvania, Craighead collected a series of beetles on 20 July 1921 and again on 30 June 1922, and these latter beetles were teneral. This indicates that at the northeast limit of the beetle's known range adults emerge in late June, as my collecting in Wisconsin confirms for a similar latitude.

In Texas, *L. subrufus* has been collected in April, May, and June (Table 1). North of Texas, no collections were made as early as April. The only May collection outside Texas is in Lake Co., Indiana. June specimens are more common, being collected in Texas and farther north in Missouri, Kansas, Tennessee, Illinois, Indiana, Iowa, Ohio, and Pennsylvania, as well as at higher altitude in New Mexico. July specimens don't exist for Texas but do for many states. I collected the most northern specimen on 17 July in southern Manitoba, and some specimens collected at high altitude in Colorado were collected in July. August specimens are fairly common and a single specimen was taken in early September. These collection dates suggest a wave of adult emergence from south to north and from low to higher altitude, as one would expect of a univoltine species, a fact confirmed in Wisconsin through my second rearing experiment.

In both of my rearing experiments, adults emerged over a period of a few days well after the plants had resprouted in spring and grown robust, confirming the pattern I observed in the field. In my first rearing experiment, it was shown that *L. subrufus* associated with *O. molle* roots in autumn can produce adults after exposure, at some stage of life, to winter's cold. In my second rearing experiment, it was shown that females oviposit in association with *O. molle* in such a way that larvae are able to develop, that larvae develop with only *O. molle* roots available as food and that these larvae produce adults in spring after exposure, at some stage of life, to winter. I have not shown that this cold diapause is required, but simply that it happens in Wisconsin. Craighead (1923) wrote that these larvae feed on the roots of *O. molle* and that *L. subrufus* hibernates as larvae in Pennsylvania. Both my rearing experiments yielded adults in spring only from those plants that had survived the winter and resumed sustained growth in spring, suggesting that these larvae may need to feed in spring prior to pupation. Craighead's (1923) report of average pupation time of 10.6 days in Pennsylvania, coupled with my observations of the plants having time to grow robust, usually to the point of flowering, before the emergence of adults, would allow time for larvae to feed on roots invigorated by spring.

In my second rearing experiment, adults that had been introduced into the 11 caged pots were later removed. This removal process had to be repeated over several days as beetles appeared in cages that had been purged of beetles on one

or more previous days. These hidden beetles could only have been underground. Craighead (1923) suggested that females oviposit at the bases of *O. molle* plants or just underground there. The reduced numbers of beetles present on wild plants in the hottest part of the day (Fig. 3) and the more sharply reduced incidence of mating at this same time (Fig. 4) suggest that many of the absent beetles are females and that their absence from the foliage may be explained by their ovipositing under ground.

At times when mating occurred, a higher percentage of beetles present at site I14 was mating at nearly every hour than were beetles at site GN31, suggesting that denser beetle populations support higher mating frequencies than do less dense populations.

Despite the extraordinarily high beetle population at site I13, where the noise of these tiny beetles leaping off plants when disturbed sounded like rain drops spattering adjacent plants, I did not see complete consumption of foliage as reported by Craighead (1923).

Perhaps *L. subrufus* will be shown to reproduce on *O. helleri* in Texas but, at present, it has been shown to reproduce only on *O. molle*. That may change over time, as has happened with *L. melanurus*, which once depended on *O. molle* (Williams 2002b) but which has been reported to reproduce on *E. vulgare* (Furth 1994). I reported *L. melanurus* adults feeding on *C. officinale* on sites also supporting *O. molle* (Williams 2002b). *Echium vulgare* and *C. officinale* are alien pasture weeds in Boraginaceae, perennials that have been available to *L. subrufus*, in Wisconsin, for over a century (Lapham 1850, Swezey 1877). That I rarely found teneral individuals of *L. subrufus* feeding on leaves of *E. vulgare* and *C. officinale* on sites where *O. molle* also grew suggests how these might become acceptable food plants for this beetle, as they have to some degree for *L. melanurus*, and presents a model for this process generally. My finding these beetles feeding only once in early summer on the leaves of the native *Lithospermum canescens* does not suggest this is a suitable food plant as it often grows with *O. molle* and probably has over millenia.

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