Observations on Feeding Behavior by the Terrestrial Flatworm Bipalium adventitium (Platyhelminthes: Tricladida: Terricola) from Illinois

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ABSTRACT.—*Bipalium adventitium* Hyman, 1943, an exotic terrestrial flatworm that is predatory on earthworms, is reported from Illinois for the first time. No-choice laboratory feeding tests were performed to test the acceptability of several lumbricid earthworm species as prey for *B. adventitium* and to compare the mass gained by *B. adventitium* in feeding bouts on different species of lumbricid earthworms. All species of earthworms (*Allolobophora chlorotica* (Savigny, 1826), *Aporrectodea rosea* (Savigny, 1826), *Ap. turgida* (Eisen, 1874), *Eisenia fetida* (Savigny, 1826) and *Octolasion tyrtaeum* (Savigny, 1826)) presented to *B. adventitium* were attacked and consumed. *Allolobophora chlorotica*, *Aporrectodea rosea* and *Eisenia fetida* are added to the list of potential prey species of earthworms in North America. *Bipalium adventitium* readily attacked and fed on earthworms up to 55 times larger than themselves in mass and they gained 52% of their prefeeding live mass during feeding bouts. Prefeeding live mass of flatworms was a significant predictor of the mass gained by feeding flatworms, but prey mass was not, possibly because all flatworms fed on earthworms at least 1.9 times larger than themselves in mass. Earthworm prey species had no influence on the mass gained by feeding flatworms.

INTRODUCTION

Bipalium adventitium Hyman, 1943 is a terrestrial flatworm that, like the other members of the genus *Bipalium* Stimpson, 1857 found in North American (*B. kewense* Moseley, 1878; *B. pennsylvanicum* Ogren, 1987), is believed to be introduced (Ogren, 1984, 1987). Some 136 bipaliid species are now known in the world, all essentially endemic to East Asian and Madagascan regions of the world (Kawakatsu and Ogren, 1998). *Bipalium adventitium*, however, was first described from specimens collected in California (Hyman, 1943) and it has been found since then in Connecticut, Massachusetts, Maryland, New York, Pennsylvania, Tennessee and Washington (Hyman, 1954; Klots, 1960; Dindal, 1970; Ogren, 1981, 1984; Curtis *et al.*, 1983; Ogren and Kohn, 1989; Ball and Sluys, 1990; Ogren and Kawakatsu, 1998; Ducey and Noce, 1998; Ducey *et al.*, 1999). It is generally hypothesized that the initial introduction of *B. adventitium* to North America, and its subsequent dispersal, occurred passively through transport on the roots of plants and in soil as part of the horticultural trade (Hyman, 1954; Dindal, 1970; Ogren, 1984, 1985; Ducey and Noce, 1998).

Although some reports have suggested that *Bipalium adventitium* may feed on slugs and insect larvae (Hyman, 1954; Klots, 1960), earthworms are its favored prey. Dindal (1970) provided the first detailed description of its feeding behavior based on laboratory observations. Ducey and Noce (1998) found that *B. adventitium* attacked and fed upon all species of earthworms presented to it in laboratory tests, but it rejected the larvae of *Tenebrio* sp. and slugs. In laboratory tests, *B. adventitium* has accepted *Aporrectodea trapezoides* (Dugès, 1828), *Ap. tuberculata* (Eisen, 1874), *Ap. turgida* (Eisen, 1873), *Bimastos* sp., *Bim. tenuis*

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[=Dendrodrilus rubidus (Savigny, 1826)], Lumbricus rubellus Hoffmeister, 1843, L. terrestris Linnaeus, 1758 and Octolasion tyrtaeum (Savigny, 1826) as prey (Dindal, 1970; Ducey and Noce, 1998; Ducey et al., 1999). However, this is only a small proportion of the earthworm species found in North America.

The introduction of exotic terrestrial flatworms can lead to changes in the relative composition of earthworm communities (Blackshaw, 1995; Lillico *et al.*, 1996). Although this may be due to differences in ecological niches and the frequency with which flatworms encounter different species of earthworms (Blackshaw, 1990; Lillico *et al.*, 1996; Fraser and Boag, 1998), acceptance as prey may also influence the vulnerability of different earthworm populations to predation. One measure of this is whether or not different species will be attacked and fed upon when presented to flatworms; to date, no-choice laboratory feeding tests have demonstrated no differences in species vulnerability (Dindal, 1970; Ducey and Noce, 1998; Ducey *et al.*, 1999). Another measure might be the size of the meal taken. Flatworms may "give up" feeding after taking meals of different sizes if, for example, captured earthworms differ in nutritional quality or palatability.

The objectives of this study are to report the first observation and collection of *Bipalium adventitium* in Illinois, to test the acceptability of several lumbricid earthworm species as prey for *B. adventitium* and to compare the mass gained by *B. adventitium* in feeding bouts on different species of lumbricid earthworms.

METHODS

Flatworms were collected from beneath pieces of wood, stones and plastic bags of leaves in the yard of the author's residence in Urbana, Illinois, or at night or early in the morning following rain showers from the wet surface of the paved driveway and sidewalk in front of the residence.

Flatworms were kept in 85 mm diameter plastic petri dishes with 30 g of the 0.85–2.00 mm fraction of air dried sieved soil (silt-loam, 4% organic matter). A moistened filter paper was placed on the soil surface to provide shelter and the soil was maintained at a water content of 0.2–0.3 g g⁻¹ soil with deionized water. Flatworms were held in a dark incubator at 15 C, inspected weekly and fed small earthworms. After they had finished feeding, flatworms were transferred to a new dish of soil.

Allolobophora chlorotica (Savigny, 1826), Aporrectodea rosea (Savigny, 1826), Ap. turgida, Lumbricus terrestris and Octolasion tyrtaeum used in this study were collected from wild populations, held in moist soil in a dark incubator at 15 C and periodically fed cattle manure that was first leached to remove potentially toxic salts. Eisenia fetida (Savigny, 1826) were cultured in the laboratory at room temperature in a commercial bait box with wet coarsely shredded newspaper and regular additions of coffee grounds and kitchen scraps for food.

Using 17 *Bipalium adventitium* collected between 23 September and 26 December 1999, the vulnerability of different species of earthworms to attack by flatworms and the mass gained by flatworms during feeding bouts was determined. When collected, the flatworms used in these tests ranged in mass from 37 mg to 146 mg (93 ± 36 mg, mean \pm sD). Each flatworm was used in up to three separate tests, with a minimum period of 15 d between tests. Earthworm species used in these feeding tests were: *Allolobophora chlorotica, Aporrecto-dea rosea, Ap. turgida, Eisenia fetida* and *Octolasion tyrtaeum*. For each test, live masses of a flatworm and an earthworm were recorded before placing them together in a covered petri dish containing moist soil. The interactions of the worm and flatworm was observed for up to 1 h. Dishes were then placed in a dark incubator at 15 C and inspected again

after 48 h. Evidence of attack and feeding by the flatworm, survival of the earthworm and the live mass of the flatworm after feeding were recorded.

The mass gained by flatworms during feeding bouts (postfeeding minus prefeeding live mass) was regressed against their prefeeding live masses and the live masses of the earthworm prey by forward stepwise regression using the General Stepwise Regression module of Statistica (StatSoft, 2001). The influence of earthworm species on this relationship was tested using analysis of covariance after confirming the assumption of homogeneity of slopes (StatSoft, 2001). All hypotheses were tested at the 5% level of significance.

RESULTS

Between 50 and 60 terrestrial flatworms were discovered early in the morning of 31 October 1997 on the paved sidewalk and driveway of the author's residence in Urbana, Illinois. It had rained the night before and the pavement was still wet. In addition to the flatworms, numerous earthworms (predominantly *Aporrectodea* spp.) were crawling on the pavement. Specimens of the flatworm were tentatively identified as *Bipalium adventitium* using the key of Ball and Sluys (1990) and they matched published descriptions of the external morphology and coloration of this species (Ogren, 1984). Externally visible characteristics are sufficient to distinguish *B. adventitium* from other terrestrial flatworms, including other species of *Bipalium*, currently known from North America; however, positive identification requires microscopic examination of serial sections of the animal.

More flatworms were collected at this location by searching through the spring of 2000. During the day flatworms were often found curled up on the bare soil surface beneath stones, wood or plastic bags full of yard waste. The live mass of the flatworms collected ranged from 11 mg to 146 mg. On at least a dozen occasions, a flatworm was found within a few inches of a live but injured *Lumbricus terrestris* on the soil surface. These earthworms (all large, >2 g) were relatively inactive and appeared to have been attacked by the flatworm. They had wet lesions on their bodies and they often had terminal body segments (anterior and/or posterior) partially or completely fragmented off. It was not unusual to find the same earthworm alive and in the same place for more than 1 d.

Actively foraging flatworms glided over the soil surface in an extended position with the anterior portion of the body slightly raised above the substrate, the head moved from side to side and its leading edge gently touched to the substrate. Flatworms rapidly oriented their behavior toward earthworms upon first contacting them by crawling onto the body of the worm. Earthworms did not respond vigorously to this initial contact, but if a worm did crawl away, the flatworm often followed its trail over or into the soil. Once the flatworm had crawled onto the earthworm and began to evert its pharynx, the worm responded violently by trying to crawl away or thrash about to dislodge the flatworm. This was usually unsuccessful, and shortly the motions of the earthworm became less violent, as if it were partially paralyzed. Subsequently, liquefied tissues of the earthworm were drawn up through the pharynx of the flatworm. After feeding for approximately 1 h, flatworms withdrew from the attacked earthworm and remained curled up and inactive. Within 2–3 d of feeding the flatworms regurgitated unassimilated material.

Live masses and earthworm:flatworm live mass ratios of the worms used in laboratory feeding trials are summarized in Table 1. Representatives of all species of earthworms were successfully attacked and fed upon by flatworms in the no-choice laboratory feeding tests. The mass range of earthworms attacked and fed upon was 239–878 mg, and their range of earthworm:flatworm mass ratios was 1.9–55.4. Of 42 earthworms presented to flatworms, only three showed no evidence of being attacked or fed upon after 48 h: one *Allolobophora chlorotica* (mass, mass ratio = 71 mg, 1.7), one *Aportectodea tuberculata* (mass,

Species	Live mass (mg)				Worm:flatworm mass ratio		
	n	mean	SD	range	mean	SD	range
Allolobophora chlorotica	4	322	186	71-512	4.8	2.8	1.7-8.5
Aporrectodea rosea	23	420	143	239-878	5.2	2.7	2.0 - 11.9
Ap. turgida	2	298	70	248-347	16.5	7.4	11.3-21.7
Eisenia fetida	3	476	195	310-690	4.3	0.5	3.7 - 4.8
Octolasion tyrtaeum	10	371	128	222-609	8.7	16.5	1.9-55.4

TABLE 1.—Summary statistics of live masses and earthworm:flatworm live mass ratios for earthworms used in no-choice laboratory feeding tests of *Bipalium adventitium*

mass ratio = 453 mg, 3.3) and one *Eisenia fetida* (mass, mass ratio = 222 mg, 7.4). The mass of the *Al. chlorotica* and the *E. fetida* that escaped attack were the smallest of those tested, as was the mass ratio of the *Al. chlorotica* (Table 1). Other values overlapped with those of worms that were attacked and fed upon. Of the 39 earthworms that were attacked and fed upon during the course of testing, six were still alive at the end of 48 h. One of these, an *E. fetida*, had the largest mass ratio (55.4) of any worm in these feeding tests (Table 1); otherwise, mass and mass ratio values for earthworms attacked but still alive after 48 h overlapped with those that had died.

The prefeeding live mass of *Bipalium adventitium* explained a significant amount of the variation in the mass gained by flatworms during feeding bouts ($F_{1,37} = 43.9$, P < 0.000001), with flatworms gaining 52.2% \pm 7.9% (mean \pm sE, n = 38) of their prefeeding live mass (Fig. 1). Earthworm live mass alone did not explain a significant amount of the variation in flatworm mass gain ($F_{1,37} = 2.23$, P > 0.1), or improve the explanation provided by the prefeeding live mass of the flatworms ($F_{1,36} = 0.013$, P > 0.9) in stepwise regression. Mass gain by flatworms during feeding bouts was independent of the species of the worm attacked (ANCOVA, $F_{4,33} = 1.89$, P > 0.10).

DISCUSSION

The appearance of the flatworms collected in Urbana, Illinois (Fig. 2) matched photographs and detailed descriptions of *Bipalium adventitium* provided by Ogren (1984): body elongate, ribbon shaped, tapering at rear, length up to 70 mm when moving; head fan shaped, rounded in front and tapering back to the neck; ground body color pale yellowish or orange brown; anterior margin of head dark pigmented; dark dorsal median stripe extending from neck to the posterior tip of the body. Ogren (1984) reported that this stripe does not extend onto the head, but Ducey and Noce (1998) reported that the amount of darkness on the head and the starting point of the stripe varied among individuals collected in New York. In all of the specimens inspected in this study, the dark dorsal stripe did not extend onto the head.

This is the first report of *Bipalium adventitium* from Illinois or any other Midwestern state. It's discovery in a suburban residential area in Illinois, far separated from other parts of its known range, is consistent with the hypothesis that it's dispersal is primarily passive in the soil and roots of plants transported in the horticultural trade (Hyman, 1954; Dindal, 1970; Ogren, 1984, 1985; Ducey and Noce, 1998). Given the cryptic nature of these animals and the apparent ease with which they can be distributed through the horticultural trade, it seems reasonable to hypothesize that *B. adventitium* is much more widely distributed than is currently known. The survey reported by Ducey and Noce



Bipalium adventitium live mass (mg)

FIG. 1.—Regression of mass gains on prefeeding live masses of *Bipalium adventitium* presented single earthworms of different species in no-choice laboratory feeding tests. All flatworms were less than one-half the mass of their prey

(1998) tripled the number of New York counties with records of *B. adventitium* from five to fifteen.

In general, observations of the searching, attacking and feeding behavior of *Bipalium* adventitium compared favorably with those of Dindal (1970), Ducey and Noce (1998) and Ducey et al. (1999). Earthworms are not always immediately killed when attacked and fed upon by flatworms, and they may continue to struggle and move about during feeding (Ogren, 1995; Ducey et al., 1999). Capping, a behavior described by Ducey et al. (1999), in which the flatworm covers the anterior segments of the earthworm and significantly reduces the earthworm's escape behavior, was not observed. However, not all attacks on earthworms occurred during the initial observation period of these tests. Field observations of B. adventitium resting near live Lumbricus terrestris with missing anterior or posterior segments may result from an extension of this capping behavior if feeding is also concentrated on terminal segments. Ducey et al. (1999) noted that very large earthworms attacked at their posterior end occasionally escaped and autotomized their injured segments. In contrast, "decapitated" earthworms observed in the field were relatively inactive and made no attempt to escape. Toxins produced by the flatworms may also induce immobilization (Ogren, 1995; Ducey et al., 1999). Incapacitated earthworms could provide an easy second meal to attacking flatworms and further studies may reveal whether, by reducing the time and energy invested in searching for and capturing prey and by reducing the risk of injury, capping behavior, decapitation or toxic paralysis are advantageous.



FIG. 2.—*Bipalium adventitium* foraging in leaf litter. Extended length of this specimen, collected in Urbana, Illinois, was about 60 mm. The fan shaped head (right) is characteristic of the family Bipaliidae. *Bipalium adventitium* is distinguished from other bipaliid flatworms currently known from North America by a single dark mid-dorsal stripe that extends from the posterior end to the neck or head

Bipalium adventitium attacked and fed upon all species of earthworms presented to them. This finding is consistent with those of Dindal (1970), Ducey and Noce (1998) and Ducey et al. (1999), and it expands the range of North American earthworm species known to be accepted by B. adventitium as prey to include Allolobophora chlorotica, Aporrectodea rosea and Eisenia fetida. Flatworm predation on different earthworm species in laboratory studies, however, may not indicate their influence on earthworm populations in the field. In assessing how introduced flatworms may influence earthworm populations in Europe, Fraser and Boag (1998) noted that epigeic earthworms, which live on the soil surface in or just beneath the litter layer, and anecic earthworms, which form permanent burrows that open to the soil surface and which regularly feed on the soil surface to feed, may be more susceptible to attack by flatworms than endogeic earthworms. Endogeic earthworms form temporary burrows in the topsoil, backfill their burrows with castings and rarely come to the soil surface to feed. Of those species of earthworms reported to be accepted by B. adventitium as prey in laboratory tests, only Eisenia fetida, Lumbricus rubellus and Bimastos tenuis (and probably Bimastos sp.) are epigeic species and only L. terrestris is an anecic species. Nevertheless, observations made during this study suggest that any species of earthworm that emerges from the soil and crawls about during cool wet weather may be vulnerable to attack.

Mass gained by feeding flatworms also provided no evidence for differences in the acceptability of earthworm species as prey for *Bipalium adventitium*. Flatworms gained, on average, 52% of their body mass in feeding bouts, in contrast to the 82% mass gain reported by Dindal (1970), who weighed flatworms upon cessation of feeding. Because flatworms were not reweighed until 48 h after beginning the tests reported here, lower

mass gains may be attributable to regurgitation of unassimilated material and the elimination of waste products after feeding. Mass gained by flatworms in feeding bouts was explained well by the initial mass of the flatworms (Fig. 2). Earthworm mass did not explain mass gained by feeding flatworms, in contrast to the results reported by Dindal (1970), who found that the average mass gained by *B. adventitium* was greater when feeding on smaller earthworms than on larger earthworms. In his calculations, however, he did not take into account the mass of the flatworms, which ranged from 7 mg to 126 mg. In the trials reported here, all flatworms fed on earthworms at least 1.9 times greater in mass. Thus, all of the flatworms could have been sated without completely consuming their prey. Flatworms in these tests readily attacked and fed upon earthworms up to 55 times their own mass, the largest mass ratio tested. Ducey *et al.* (1999) tested earthworms with greater mass ratios and reported that *B. adventitium* attacked worms more than 110 times their own mass, but concluded that attacks were more successful with prey up to 10 times their own mass. Dindal (1970) reported that *B. adventitium* subdued and fed upon earthworms up to 30 times their own mass, and he observed that no earthworms recovered.

Few field studies of *Bipalium adventitium* populations in North America have been conducted thus far (Ducey and Noce, 1998), and it is not known what impact its establishment may have on earthworm populations or on the important soil processes that earthworms mediate, such as soil formation, organic matter transformations and nutrient cycling. However, the accumulating data suggest that the impact on earthworm populations could be significant. *Bipalium adventitium* is clearly an aggressive predator of earthworms, and earthworms attacked by *B. adventitium* rarely survive (Dindal, 1970; Ducey and Noce, 1998; Ducey *et al.*, 1999). Furthermore, when earthworms are readily available, it appears that feeding by flatworms is very inefficient in that they are capable of attacking and killing earthworms with a biomass much greater than they are able to ingest. Depending on how frequently and efficiently *B. adventitium* feeds, it may be capable of killing several hundred times its own biomass in earthworms each year.

Ducey *et al.* (1999) noted that the invasion by *Bipalium adventitium* in North America is ecologically similar to that occurring in Northern Europe by the New Zealand flatworm *Arthurdendyus triangulatus* (Dendy, 1895), formerly *Artioposthia triangulata*. This flatworm, accidentally introduced into Ireland in the early 1960s, and lumbricid earthworms can coexist to some degree (Fraser and Boag, 1989), but in Europe the flatworm's establishment has resulted in reductions in earthworm populations and alterations in earthworm community structure. At one site where this flatworm became established, earthworm populations dropped to below detectable levels (Blackshaw, 1990). Further studies to establish basic biological information about *B. adventitium*'s feeding and reproduction in nature, the environmental factors that may limit its distribution and the vulnerability of North American earthworm species under field conditions will help us predict whether *B. adventitium* will have a similar impact on North American earthworm populations.

Acknowledgments.—The technical assistance of Lori Soeken in maintaining flatworms and earthworms in the laboratory is greatly appreciated. Rob Wiedenmann and three anonymous reviewers provided helpful comments on early versions of this manuscript. This work was supported by the Illinois Agricultural Experiment Station.

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SUBMITTED 18 MARCH 2002

Accepted 17 June 2002