Am. Midl. Nat. 141:305–314

Lumbricid Prey and Potential Herpetofaunal Predators of the Invading Terrestrial Flatworm Bipalium adventitium (Turbellaria: Tricladida: Terricola)

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ABSTRACT.—*Bipalium adventitium* Hyman, an exotic terrestrial planarian invading North America, is an aggressive predator on earthworms. The spread and ecological impact of this flatworm will be determined in part by the its interactions with potential predators and prey. In laboratory trials, we tested the ability of *B. adventitium* to prey upon earthworms of different species and sizes. We also tested the predatory responses of six salamander species and two snake species to the flatworms. *Bipalium adventitium* attacked and ate members of all earthworm species offered and attacked earthworms over 100 times their mass. However, flatworm predatory success was related to the relative size of the prey. The largest prey eaten in our study was 12.1 times the mass of the flatworm that killed it. When attacking, *B. adventitium* often used a previously undescribed behavior of capping the anterior end of the earthworm, causing subdued escape behavior. None of the amphibians and reptiles tested as predators treated *B. adventitium* as a regular prey item. Only a few salamanders (2%) struck and ate a flatworm, with most salamanders and all snakes showing little interest in the planarian. Salamanders that consumed flatworms showed no apparent long-term ill effects.

INTRODUCTION

Bipalium adventitium Hyman, 1943 (Turbellaria: Tricladida: Terricola) is an exotic terrestrial planarian that feeds on earthworms (Dindal, 1970; Ogren, 1981) and is invading North America (Hyman, 1954; Ogren, 1984; Ducey and Noce, 1998). Because earthworms are important components of native and agricultural ecosystems (Hendrix, 1995), the impact of this flatworm invasion could be significant. *Bipalium adventitium* is believed to have been transported from Asia to the United States during this century (Hyman, 1943, 1954; Ogren, 1984), first reported from California in 1943 (Hyman, 1943) and subsequently from New York (in 1947; Hyman, 1954), Tennessee (in 1982, Curtis *et al.*, 1983), Pennsylvania (in 1980, Ogren, 1981), Massachusetts (in 1950s, Klots 1960) and Washington (in 1989, Ogren and Kohn, 1989). The species is now widespread within New York State, and is most abundant in suburban and urban gardens and lawns (Ducey and Noce, 1998). The spread of *B. adventitium* appears to be primarily passive, with adults and eggs being transported with the roots of shrubs, trees and sod grasses (Ogren, 1984; Ducey and Noce, 1998). Dispersal into forested areas has been slower (Ducey and Noce, 1998), but it is not known whether this reflects the flatworm's limited ability to actively disperse, the presence of forest predators, the absence of prey in forests or some combination of these factors. More information concerning *B. adventitium*'s predator–prey relationships is needed to predict the geographical extent and ecological impact of the invasion.

Although they may eat snails or slugs (Klots, 1960), *Bipalium adventitium* feed primarily on earthworms (Dindal, 1970; Ogren, 1984; Ducey and Noce, 1998). Ogren and Sheldon (1991) found that the very similar *B. pennsylvanicum* Ogren also feeds mainly on earth-

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worms. Because different habitats support different earthworm species (Steinberg *et al.*, 1997), the dispersal of *B. adventitium* into certain habitats may depend on their ability to feed on a variety of earthworm species. Although *B. adventitium* will attack earthworms up to 80 times their own mass (Dindal, 1970; Ducey and Noce, 1998), quantitative studies documenting differential survival of earthworms during encounters with *B. adventitium*, based on either earthworm size or species, have not been reported.

The extent of the flatworm invasion will also depend in part on the response of local predators. Salamanders are among the most abundant vertebrates in eastern forests (Burton and Likens, 1975; Hairston, 1987) and are important predators of soil invertebrates (Pough, 1983). They are possible predators of *Bipalium adventitium* because they share microhabitat preferences and already eat a variety of soft-bodied organisms. Like *B. adventitium*, many terrestrial salamanders frequent moist cool microhabitats, spend most of the time beneath the ground or cover objects and move within the leaf litter and on the forest floor on rainy nights (Bishop, 1947). Salamanders feed on a variety of elongate soil invertebrates (Bishop, 1947) and can tolerate mucus secretions released by earthworms and slugs. Several species of snakes also inhabit these microhabitats and feed on invertebrates with mucus secretions. In particular, members of the genus *Storeria* regularly prey on slugs and earthworms (Judd, 1954; Rossman and Myer, 1990), foraging in moist areas beneath cover objects where *B. adventitium* may be found.

We examined predation by *Bipalium adventitium* on local earthworms by testing whether predation success of *B. adventitium* differed with earthworm species or size. We also examined predation on *B. adventitium* by testing the ability of members of six abundant salamander species (*Ambystoma laterale-jeffersonianum, A. maculatum, Desmognathus fuscus, D. ochrophaeus, Plethodon cinereus, P. glutinosus*) and two snake species (*Storeria dekayi, S. occipitomaculata*) to prey upon *B. adventitium*.

METHODS

Flatworms were captured as adults from sites throughout central and southern New York State. We housed them individually in covered plastic containers (10 × 10 × 6.5 cm or 10 × 10 × 8.5 cm) filled with moistened paper towels. We kept all animals at 18–23 C with a light cycle matching that of central New York in May through July.

BIPALIUM AS PREDATOR

We used three different experiments to examine *Bipalium adventitium* predation on earthworms. Test chambers were covered plastic containers (13.5 × 21.5 × 5 cm) lined with a single layer of moist paper towels. We measured the mass of each earthworm and flatworm 1 h before each trial. Trials were run at 19–22 C under low indirect light with the observer 0.5 m from the test subjects. For each trial, a *B. adventitium* was moved gently from its housing container into a test chamber and placed beneath an opaque glass dish to acclimate for 5 min. An earthworm was then added to the chamber 2–3 cm from the flatworm and the opaque dish was removed. Predator and prey were allowed to move freely in the chamber while observations were made of behavior of each. In each trial, if the flatworm did not contact the prey within 10 min the trial was scored as "no contact" and not used in statistical analyses.

Experiment 1.—We tested 18 *Bipalium adventitium* (mass mean, range = 0.16, 0.10–0.20 g) for their predatory behavior toward four species of earthworms common in central New York: *Aporrectodea trapezoides* (Duges, 1828) (mass mean, range = 0.55, 0.28–0.89 g), *A. tuberculata* (Eisen, 1874) (mass mean, range = 0.58, 0.32–0.91 g), *Lumbricus rubellus* Hoffmeister, 1843 (mass mean, range = 0.64, 0.22–0.87 g), and *L. terrestris* Linnaeus, 1758 (mass mean, range = 1.01, 0.45–2.12 g). Each flatworm was tested separately with individuals of each earthworm species presented in random order, with one week between repeated trials of an individual flatworm. No earthworm was used more than once. Escape success was compared among earthworm species using Conchran's Q test (Siegel and Castellan, 1988).

Experiment 2.—We tested 20 *Bipalium adventitium* (mass mean, range = 0.14, 0.06–0.21 g) for their predation success on *Aporrectodea tuberculata* (mass mean, range = 0.58, 0.30–0.86 g) of different sizes. Each *B. adventitium* and earthworm was used only once. Using a Mann-Whitney test (Siegel and Castellan, 1988), we compared earthworm mass/flatworm mass ratios between trials in which earthworms were eaten and trials in which earthworms were contacted but escaped alive.

Experiment 3.—We tested 30 *Bipalium adventitium* (mass mean, range = 0.15, 0.05–0.24 g) for their predation success on *Lumbricus terrestris* (mass mean, range = 2.45, 0.74–5.51 g) of different sizes. Each *B. adventitium* and earthworm was used only once. Statistical comparisons were done as for Experiment 2.

BIPALIUM AS PREY

We tested adults of six species of salamanders (*Ambystoma maculatum,* n = 12, from Cortland Co.; *A. laterale-jeffersonianum* complex, n = 12, Cortland Co.; *Desmognathus fuscus,* n = 17, Cortland Co.; *D. ochrophaeus,* n = 14, Cortland Co.; *Plethodon cinereus,* n = 20, Cortland Co.; *P. glutinosus,* n = 11, Allegany Co.) and from two species of snakes (*Storeria dekayi,* n = 5, Onondaga Co.; *S. occipitomaculata,* n = 8, Chenango Co.) from central New York for their predatory responses to *Bipalium adventitium.* Salamanders were housed individually in plastic containers (31 × 15 × 9 cm or 31 × 22 × 8 cm) and were maintained on a mixed diet of live crickets (*Acheta domestica*), mealworms (*Tenebrio* sp.), earthworms (*Lumbricus* spp.) and *Drosophila melanogaster.* We collected salamanders as adults and kept them in the laboratory less than 30 d before testing. Testing chambers for salamanders were 31 × 15 × 9 cm chambers lined with moist paper towels and containing tunnels under which salamanders could hide. We tested all salamanders with earthworms (*Lumbricus rubellus,* mass mean, range = 0.29, 0.08–0.50 g), mealworms (*Tenebrio* sp.; mass mean, range = 0.08, 0.04–0.11 g) and *B. adventitium* (mass mean, range = 0.22, 0.04–0.40 g) in random order with repeated trials separated by 24 h. Mass of each prey item was measured before testing. Flatworms were reused as prey only if they were not contacted by a predator during a trial. For each trial we placed a salamander within the test chamber at least 10 min before releasing the potential prey within 3 cm of the salamander's head. Observations were made of the behavior of predator and prey for 10 min. Observers were farther than 1 m from the test chamber, motionless and in dim light. To detect possible toxic effects of flatworm consumption, we monitored the health of each predator for 24 h following a trial. For each salamander species separately we compared the numbers of individuals eaten among prey types using Cochran's Q test (Siegel and Castellan, 1988).

Because very few salamanders ate *Bipalium adventitium* during the predation trials, we subsequently ran separate tests to examine the toxicity of *B. adventitium.* We trained four *Ambystoma laterale-jeffersonianum,* four *A. maculatum,* and one *Plethodon glutinosus* to eat mealworms and earthworms moved at the end of a pair of forceps. After being in captivity at least 50 days, each salamander was offered *B. adventitium* moved at the end of forceps. We recorded the salamanders' responses, their subsequent behaviors for 5 min, and their health at 1 h, 2 h, and 24 h after feeding.

TABLE 1.—Predation by *Bipalium adventitium* (N = 18) on members of four earthworm species. Shown are the number of trials (%) for each species in which the earthworms were not contacted, contacted but escaped or eaten

Earthworm species	Trial outcome			
	No contact	Contact & escape	Eaten	Total
Aporrectodea trapezoides	2 (11)	2 (11)	14 (78)	18
A. tuberculata	1 (6)	1 (6)	16 (89)	18
Lumbricus rubellus	0 (0)	2 (11)	16 (89)	18
L. terrestris	1 (6)	6 (33)	11 (61)	18

RESULTS

BIPALIUM AS PREDATOR

General description of predation behavior.—During an attack, *Bipalium adventitium* moved its head over the integument of an earthworm, shifting the head from side to side and periodically undulating its anterior edge. The flatworm would crawl onto the earthworm until most of its length was in contact with the body of the prey. Up to this point, earthworms did not show any reaction toward the predator. The flatworm would begin to unfold its pharynx, then, based on the violent movements of the earthworm, appeared to release digestive enzymes onto the prey. Earthworm struggling, including crawling, spinning and writhing, continued for 10 s to 5 min. If the movements were particularly vigorous and the earthworm sufficiently larger than the flatworm, the flatworm might be thrown off, abandon the attack or contract its pharynx and continue to hold on. The attachment of the flatworm to the prey appeared to be based on both muscle contractions and adhesive secretions. In some cases during an earthworm's struggles, *B. adventitium* crawled anteriorly on the earthworm and "capped" the prey's prostomium, peristomium and anterior segments with its own head and anterior body. This capping was quickly followed by the cessation of violent struggling by the earthworm. When an earthworm became subdued, the flatworm expanded its pharynx further and began to feed. The integument of the earthworm lost visible segmentation as it was turned to a pink viscous mass beneath and near the pharynx. The liquid was drawn into the flatworm causing the flatworm to take on a reddish hue. This would continue for 10 to 40 min, with small earthworms being completely consumed and larger earthworms losing large portions of their bodies and later dying. On a few occasions a very large earthworm was attacked on its posterior end and managed to dislodge the flatworm after a short period of tissue digestion had occurred. In these cases the earthworm autotomized the affected body segments and crawled away.

Experiment 1.—*Bipalium adventitium* attacked and ate members of each earthworm species offered (Table 1). There was no significant difference among earthworm species in escape success following initial contact (Q = 2.33, df = 3, NS). During trials, several earthworms scored as "eaten" were only partially consumed and later died (3 *Ambystoma trapezoides,* 2 *A. tuberculata,* 1 *Lumbricus terrestris,* 1 *L. rubellus*).

Experiment 2.—Five *Ambystoma tuberculata* were not contacted within the trial time, 11 were eaten (73% of those contacted), and 4 escaped following contact. Those earthworms that escaped did so during trials in which the earthworm mass/*Bipalium adventitium* mass ratios were significantly higher (Fig. 1; trials with escapes, ratio mean, range = 8.63, 5.4–14.3; trials with earthworm consumption, ratio mean, range = 4.12, 2.4–8.5; U = 48, $P < 0.02$).

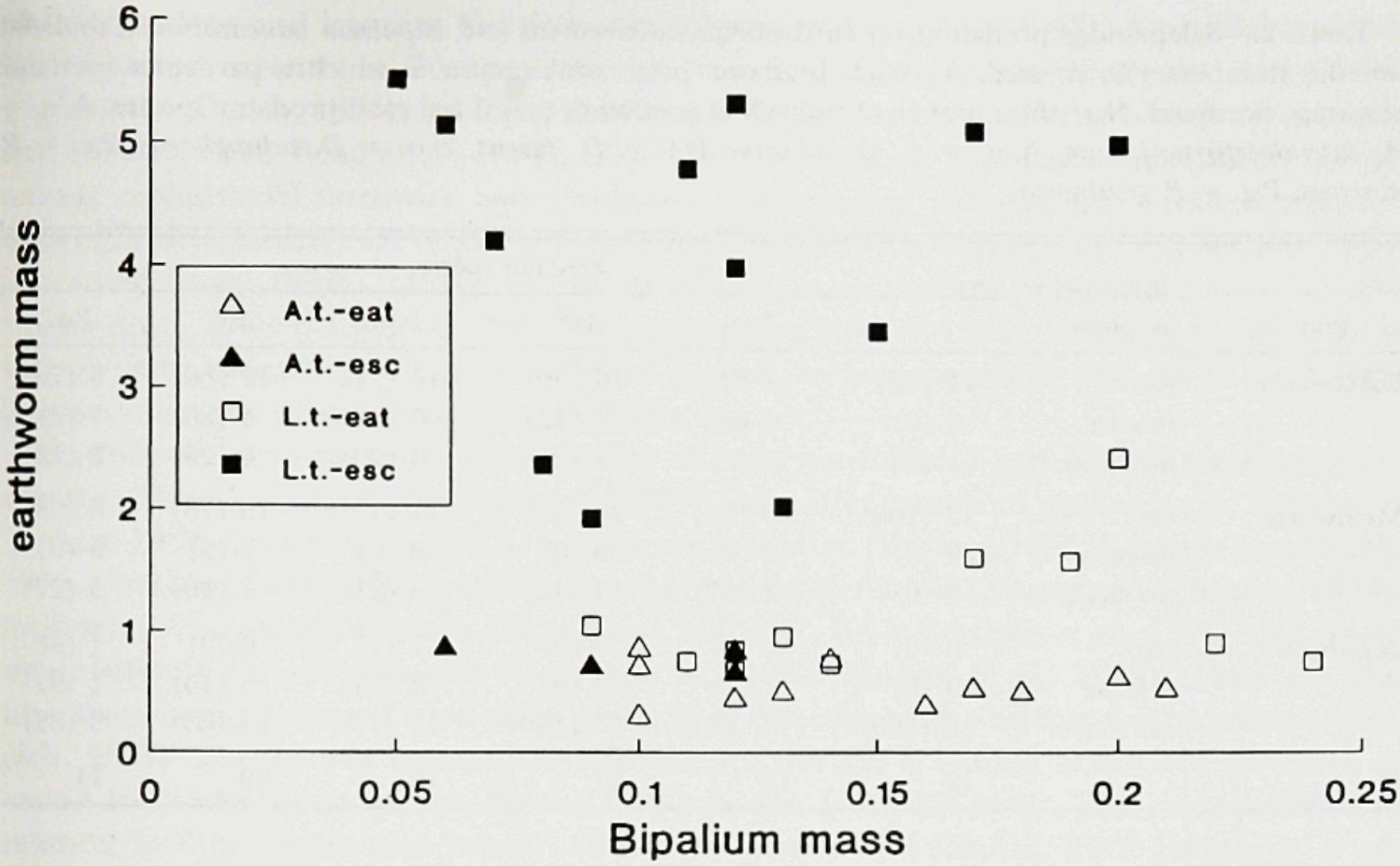

FIG. 1.—Outcomes of trials with *Bipalium adventitium* preying upon two species of earthworms in relation to predator and prey mass. A.t. = *Aporrectodea tuberculata*; L.t. = *Lumbricus terrestris*; esc = contacted by predator but escaped; eat = killed and at least partially consumed

Experiment 3.—As with *Ambystoma tuberculata,* the survival probability for *Lumbricus terrestris* during encounters with *Bipalium adventitium* was greater the larger the earthworm was relative to the flatworm. Seven *L. terrestris* were not contacted, 12 were contacted but escaped and 11 were eaten (48% of those contacted). The earthworm mass/*B. adventitium* mass ratios were significantly higher in those trials in which earthworms escaped (ratio mean, range = 43.4, 15.5–110.2) than in trials in which they were eaten (ratio mean, range = 7.32, 3.1–12.1; $z = 4.03$, $P < 0.001$; Fig. 1).

BIPALIUM AS PREY

None of the herpetofaunal species we tested treated *Bipalium adventitium* as a potential prey item (Table 2). During our salamander predation trials, only one *Plethodon glutinosus* and one *Desmognathus ochrophaeus* consumed a *B. adventitium.* Few (27%) salamanders showed even preliminary predatory interest in the flatworms. Although some members of each species briefly tracked a moving *B. adventitium* with movements of their heads or by actually walking toward the flatworm, most (90%) of the salamanders never struck at a flatworm. Eleven salamanders touched the tips of their snouts onto a flatworm, but only two of these subsequently struck at the prey. Seven salamanders (3 *P. cinereus,* 2 *D. ochrophaeus,* 1 *Ambystoma maculatum,* and 1 *P. glutinosus*) struck at and then immediately released a *B. adventitium,* with the salamander rubbing the side of its head on the substrate following release. Members of each of the salamander species ate significantly fewer *B. adventitium* than mealworms or earthworms (Table 2; *A. laterale-jeffersonianum,* $Q = 22.2$, $P < 0.001$, *A. maculatum,* $Q = 17.1$, $P < 0.001$, *D. fuscus,* $Q = 15.2$, $P < 0.001$, *D. ochrophaeus,* $Q = 14.0$, $P < 0.001$, *P. cinereus,* $Q = 21.0$, $P < 0.001$, *P. glutinosus,* $Q = 9.8$, $P < 0.01$).

TABLE 2.—Salamander predation on earthworms, mealworms and *Bipalium adventitium*. Tabulated are the numbers (%) of trials for each predator/prey combination in which a particular predator response occurred. N = the number of individual predators tested for each predator species; A.l-j. = *A. laterale-jeffersonianum*, A.m. = *A. maculatum*, D.f. = *D. fuscus*, D.o. = *D. ochrophaeus*, P.c. = *P. cinereus*, P.g. = *P. glutinosus*

Prey	Predator response	Predator species: A.l-j.	A.m.	D.f.	D.o.	P.c.	P.g.
Earthworm	eat	11 (92)	11 (92)	10 (59)	10 (71)	12 (60)	8 (73)
	release	0 (0)	0 (0)	2 (12)	0 (0)	4 (20)	1 (9)
	no strike	1 (8)	1 (8)	5 (29)	4 (29)	4 (20)	2 (18)
Mealworm	eat	12 (100)	10 (83)	10 (59)	11 (79)	15 (75)	8 (73)
	release	0 (0)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)
	no strike	0 (0)	2 (17)	7 (41)	3 (21)	4 (20)	3 (27)
Bipalium	eat	0 (0)	0 (0)	0 (0)	1 (7)	0 (0)	1 (9)
	release	0 (0)	1 (8)	0 (0)	2 (14)	3 (15)	1 (9)
	no strike	12 (100)	11 (92)	17 (100)	11 (79)	17 (85)	9 (82)
N		12	12	17	14	20	11

All habituated salamanders that were offered *Bipalium adventitium* on forceps struck and seized the flatworm. In every case the salamander's mouth was quickly filled with copious amounts of mucus, probably produced by both the salamander and the flatworm. Three salamanders (33%; 1 *Ambystoma laterale-jeffersonianum* and 2 *A. maculatum*) rejected the flatworm within five sec and the rest (67%; 3 *A. laterale-jeffersonianum*, 2 *A. maculatum*, and 1 *P. glutinosus*) swallowed the prey within 20 sec. All of the salamanders subsequently rubbed the sides of their heads on the substrate several times within the first two min and all opened their mouths in yawn-like movements at least once. No ill effects were noticed after this time, and all salamanders fed on earthworms the next day.

No individuals of either species of snake struck at or ate a flatworm, but 100% of the *Storeria dekayi* and 75% of the *S. occipitomaculata* ate slugs before or after flatworm trials. One *S. dekayi* and three *S. occipitomaculata* moved toward a moving *Bipalium adventitium*, tongue flicked directly on the flatworm, then turned away. Two additional *S. dekayi* and three additional *S. occipitomaculata* tongue flicked directly onto a moving *B. adventitium* as it passed close to them but did not show any predatory movements. The remaining four snakes showed no predatory responses even though the flatworms moved about the test chamber within 5 cm of the snakes' heads. All flatworms responded immediately to tongue-flick contacts by dramatically constricting their bodies and stopping all movements for 5–15 sec.

DISCUSSION

Bipalium adventitium is invading North America with apparent success at least in the Northeast (Klots, 1960; Dindal, 1970; Ogren, 1984; Ducey and Noce, 1998). Presently they appear to be more abundant in suburban lawns and gardens than in forested or less disturbed areas (Ducey and Noce, 1998). This may be the result of their initial dispersal in the United States being passive, with flatworms and eggs being transported among residential areas with shrubs, trees and sod grasses (Hyman, 1954; Ogren, 1984; Ducey and Noce, 1998). The related and ecologically similar species, *B. pennsylvanicum*, is also being spread among gardens and lawns in Pennsylvania (Ogren and Sheldon, 1991). A parallel invasion has occurred recently in Europe with the New Zealand terrestrial flatworm, *Artioposthia triangulata* (Dendy, 1894), invading the United Kingdom and the Faroe Islands (Blackshaw and Stewart, 1992; Boag *et al.*, 1994). Like *B. adventitium, A. triangulata* was initially spread among commercial nurseries and residential gardens and subsequently invaded adjacent agricultural or natural areas (Stewart and Blackshaw, 1993; Christensen and Mather, 1995; Jones and Boag, 1996), having significant effects on earthworm populations (Mather and Christensen, 1993; Blackshaw, 1995; Christensen and Mather, 1995). Whether *B. adventitium* will (or has) spread into agricultural and natural areas depends in part on its ecological interactions with existing predator and prey species.

Earthworms are important components of most natural and agricultural terrestrial ecosystems (Haimi *et al.*, 1992; Hendrix, 1995). They affect nutrient cycling (*e.g.*, Binet and Trehen, 1992; Gorres *et al.*, 1997), breakdown leaf litter (Darwin, 1896; Edwards and Heath, 1975; Cheshire and Griffiths, 1989), enhance soil oxygenation (Zhang and Schrader, 1993), facilitate soil water movements (Zhang and Schrader, 1993; Edwards *et al.*, 1995) and create microhabitats for soil bacteria (Gorres *et al.*, 1997; Tiunov *et al.*, 1997). They are also important components of food webs, being prey to arthropods and many vertebrates (Reynolds, 1977). Earthworm communities in the northeastern United States are mixtures of exotic and indigenous species (Olson, 1940; James, 1995; Reynolds, 1995) which differ in relation to forest types and human land uses (Shakir and Dindal, 1997; Steinberg *et al.*, 1997). Therefore, an exotic earthworm predator would have to be able to feed upon a variety of earthworm species in order to spread among different habitats.

We found that *Bipalium adventitium* fed on all earthworm species offered. They were very aggressive, attacking earthworms over 100 times their own mass. However, their predation success was dependent on relative earthworm size and the largest earthworm killed was 12.1 times the mass of its attacker. Flatworm predation success was high on all earthworms less than 10 times the flatworm's mass. Although there were some differences in escape behavior and success among earthworm species, the four species we tested did not differ significantly in survival. The lack of any escape behavior by the earthworms during initial contacts with *Bipalium* (an observation also made by Dindal, 1970), when escape success would have been highest, supports the hypothesis of a recent invasion of North America by *B. adventitium.*

Our observations on the predatory behavior of *Bipalium adventitium* generally agree with those of Dindal (1970) and Ogren (1995). We additionally noted the unusual capping behavior of *B. adventitium,* wherein the flatworm covered the anterior end of an earthworm, resulting in significantly subdued escape behavior. In our experiments, we could not determine whether *B. adventitium* produced a venom to control earthworm struggling, and we agree with Ogren (1995) that this issue needs further study.

In its invasion of Northern Europe, *Ambystoma triangulata* similarly preys upon many species of earthworms (Blackshaw and Stewart, 1992; Lillico *et al.*, 1996). Although attack frequency of *A. triangulata* may depend in part on flatworm mass (Blackshaw, 1991), experimental studies of the relationship between predator size and earthworm size have not been reported. Because *A. triangulata* is usually larger than its earthworm prey (Blackshaw and Stewart, 1992) and much larger than *Bipalium adventitium,* we expect that earthworm escape success and predator-prey dynamics in general may differ between the two invasions. However, the observation that earthworm species may differ in their vulnerability to predation by *A. triangulata* based on their soil depth and burrow dimensions (Blackshaw and Stewart, 1992; Lillico *et al.*, 1996) suggests that similar experiments should be conducted for *B. adventitium* and its prey.

The success of *Bipalium adventitium* may also be due to a paucity of local predators. None of the vertebrates we tested appears to be a predator on *B. adventitium* in nature. Most salamanders and members of both snake species did not respond toward a moving *B. adventitium* with predatory behavior, suggesting that its gliding movements are not sufficiently similar to the movements of any usual prey species to warrant further investigation. Some salamanders and snakes rejected *B. adventitium* based on chemoreception; salamanders after tapping the snout onto the prey (Arnold, 1976) and snakes following contacting the prey with their flicking tongue.

The result that a few salamanders did pursue and strike flatworms, but then did not eat them, suggests that the secretions of *Bipalium adventitium* may be distasteful to these predators. Head rubbing by salamanders following strikes at *B. adventitium* supports this. However, the sticky mucus and distasteful secretions of the flatworms were not sufficiently noxious to prevent some members of three salamander species from consuming some of the artificially presented *B. adventitium* without ill effects.

The continuing spread of *Bipalium adventitium* in North America, and in particular its dispersal into forested or agricultural areas, appears unlikely to be halted by either a lack of edible species of earthworms or the presence of herpetofaunal predators. However, lower earthworm densities in forests compared with suburban areas (Steinberg *et al.*, 1997) may slow *B. adventitium* dispersal into some forests. Additionally, there are many other potential predators (vertebrate or arthropod; *e.g.*, Gibson *et al.*, 1997), thus far untested, that could limit flatworm populations in these areas.

Acknowledgments.—Brian Rivest, Eduard Izraylovski, Brenda Petrie, Carmen Ferriero and Sean Poppe contributed important ideas, literature references and field work. Field work and/or laboratory assistance were also provided by K. Cameron, S. Ducey, W. Leung, D. Munson, H. Saso, B. Thomas and S. Thomas. The study was partially supported by grants from the SUNY Cortland Faculty Research Program (to PKD) and the New York State Museum (to SN).

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SUBMITTED 3 DECEMBER 1997 ACCEPTED 29 MAY 1998