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Tests of aggregative preferences of wandering salamanders (*Aneides vagrans*)

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Abstract Plethodontid salamanders usually exhibit territorial spacing patterns and behaviors. Previous works suggest that plethodontids from Vancouver Island, Canada lack strong territoriality. In one Vancouver Island species, *Aneides vagrans*, salamanders may even be found in the field in small aggregations. We investigated preferences of *A. vagrans* for occupied vs unoccupied cover objects and for cover objects occupied by conspecifics of different age/size classes. We also tested *A. vagrans* preferences for conspecific vs heterospecific salamanders in an attempt to determine if the lack of territoriality by *A. vagrans* is species-specific and perhaps related to habitat segregation. *A. vagrans* did not avoid occupied cover objects or exhibit a preference for occupied vs unoccupied sites. Age class did not affect cover object choice. *A. vagrans* did not avoid heterospecifics that exhibit the highest degree of resource overlap (*Plethodon vehiculum*), which we believe might be attributable to a benign and resource-rich habitat, although alternative explanations exist. *A. vagrans* did avoid syntopic newts (*Taricha granulosa*), though this is probably due to toxic newt skin secretions.

Keywords *Aneides vagrans* · Plethodontidae · Territoriality · Behavior

Introduction

The spatial distribution of individuals is a function of both environmental heterogeneity and behavioral interactions (Brown and Orians 1970; Parrish and Edelstein-Keshet 1999). It is the former that has usually been invoked as the explanation for the patchy distribution of caudate amphibians (Heatwole 1960; Alvarado 1967; Spotila 1972). Within patches of suitable habitat though, the distribution of salamanders depends strongly on behavioral interactions (Mathis et al. 1995). In the lungless salamanders (family Plethodontidae), the preponderance of species that were investigated exhibits nonrandom spacing and a variety of territorial behaviors (Cupp 1980; Jaeger et al. 1986; Mathis 1989; Gergits and Jaeger 1990; Verrell and Donovan 1991; Anthony 1993). On Vancouver Island, Canada, the two plethodontid species studied to date exhibit relatively reduced territorial behavior (Ovaska 1987, 1988, 1993; Ovaska and Davis 1992; Davis 2002a). Of these two, the wandering salamander *Aneides vagrans* (ne: the clouded salamander, *Aneides ferreus*; see Jackman 1998) arguably exhibits the fewest signs of territoriality.

A. vagrans can exhibit agonistic behaviors typical of other plethodontids, but at much reduced frequencies and intensities (Davis 2002a). Experimental investigations of spacing patterns indicate that *A. vagrans* is not territorial (Davis 1991) and wandering salamanders do not use fecal pellets as territorial markers, unlike many other plethodontids (Jaeger et al. 1986; Ovaska and Davis 1992). Although individuals do exhibit strong cover site fidelity, they are often found in small aggregations of several individuals (Davis 2002b; T. W. J. Garner, personal observation) under the bark of downed trees or within crevices formed by fractures in downed and solid woody debris (Davis 2002b; Jackman 1998; Fellers and Drost 1994; Davis and Gregory 1993). Syntopes either occur under, rather than within, cover objects or within cover objects of advanced decay stages not frequented by wandering salamanders (Davis and Gregory 1993). Resource partitioning with syntopic plethodontids and salamandrids on Vancouver Island therefore occurs, and

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even though diet overlap is strong among syntopic plethodontids (Harestad and Stelmock 1983; Nussbaum et al. 1983), differential utilization of cover sites could be preventing strong competitive effects.

It was suggested that other habitat factors have contributed to the relative absence of territoriality and agonistic behaviors exhibited by Vancouver Island plethodontids. Ovaska (1987, 1988) concluded that the lack of territoriality in *Plethodon vehiculum* could be attributed at least in part to mild seasonality and a concurrent increase in food availability without resource partitioning. Davis (2002a) also attributed *A. vagrans*' relatively innocuous behavior to mild climate and plentiful food resources, but because cover sites used by *A. vagrans* are more patchily distributed than those for *P. vehiculum*, site tenacity is strong, females attend clutches, and single adults are commonly found sharing cover with juveniles. Davis (2002a) posited that lowered aggression among individuals within a log might be more a matter of inclusive fitness. Research showed that salamanders avoid inbreeding and can therefore discriminate among individuals of differing levels of relatedness (Garner and Schmidt 2003) and kin recognition was detected in several species of caudate amphibians (Blaustein and Walls 1995).

These scenarios generate several testable hypotheses regarding expected spacing behavior and individual recognition of wandering salamanders. If *A. vagrans* is truly a nonterritorial salamander, then it should show no preference for unoccupied vs occupied cover objects, nor select occupied cover sites on the basis of the age status of occupants. Lastly, if there is no opportunity for interspecific competition among syntopic species found on Vancouver Island, then *A. vagrans* should show no preference for cover objects occupied by conspecifics over those occupied by heterospecifics. We tested these hypotheses using field captured *A. vagrans* of different age classes. We also tested preferences of individual wandering salamanders for conspecifics of one of two heterospecific caudate species that cooccur with *A. vagrans*, the western red-backed salamander, *P. vehiculum*, Family Plethodontidae, and the rough-skinned newt, *Taricha granulosa*, Family Salamandridae.

Materials and methods

We collected salamanders at Rosewall Creek Provincial Park on Vancouver Island, British Columbia, Canada (see Davis 2002a). In addition, *P. vehiculum* and *T. granulosa* were collected at this location and at two others (Lake Cowichan and Goldstream Provincial Park) also on Vancouver Island. We assigned collection numbers and measured the snout-to-vent length (SVL) of each salamander. Individual salamanders were maintained until use in experiments in environmentally controlled chambers located at the University of Victoria, Canada under standards approved by the University's Animal Care Committee. We kept salamanders in 1-l glass jars with mesh cloth lids. Jars contained moss and leaf litter and were

kept moist at all times. Salamanders were held at 4°C under a 12-h light:12-h dark photoperiod and plethodontids were fed with *Drosophila* ad libitum and, when available, with termites (*Zootermopsis angusticollis*) once a week. Newts were fed earthworms on a similar schedule. Because of noticeable mass loss, newts were switched to a room temperature environment with no fixed photoperiod (diet maintained) during the early months of 1994 where they thrived. Each animal was returned to its respective point of capture after experiments were completed.

We performed all experiments in the aquatic facility of the University of Victoria. This facility is on a fixed photoperiod (12 h light:12 h dark), but has skylights that allow twilight to enter: This lighting approximated the amount of twilight encountered under a forest canopy at night. We set up trials at or just after sundown and salamanders were allowed to select cover objects undisturbed throughout the night. We checked replicates before sunup the next day, and the position of the selector was recorded at this time. All trials were carried out during the winter of 1993 through the spring of 1994.

The experiments were performed using test chambers designed by Ovaska (1993). Test chambers were three plywood cages, each divided by 2-cm-wide plywood barriers into four separate 16×100×6 cm channels. Cage edges and dividers were topped with 0.75×2 cm foam tape, providing an escape-proof seal that prevented salamanders from squeezing into adjacent channels during the course of the evening. Each cage was sealed for the duration of the test by paired, clear glass sheets. The tight fit of the dividers and the thickness of the plywood made the likelihood of chemical communication between test channels extremely low: Therefore, trials in adjacent channels were treated as independent. Between sets of replicates, all cages, cover objects, and glass sheets were washed with warm, soapy water and then were rinsed with clean water to eliminate potential residual chemical cues left by salamanders. All foam tape, paper towel, mesh cloth, and duct tape (see below) were discarded between runs as a further measure of chemical cleanliness.

Cover objects of approximately 10×10 cm were cut from pieces of alder bark (*Alnus* spp.) as *A. vagrans* is commonly found under the bark of downed alders. Cover objects were placed at either extreme end of each channel. Occupants or surrogate salamanders (pieces of rolled, wet paper towel), depending on the treatment, were retained under cover objects by placing them under fine mesh cloth and by taping the edges of the mesh cloth in place with duct tape. Mesh cloth restrained occupants while allowing limited visual and almost unlimited chemical communication between occupants and site-selecting salamanders. To prevent desiccation, we placed occupants on a wet piece of paper towel before being taped in. Once occupants and surrogates were in place, we covered them with wet cover objects, leaving about 2 cm of space for site-selecting salamanders to access. We lined the remainder of each channel with wet paper towel up to the duct tape under each cover object and up to the lip of each channel. By maintaining a moist surface, we hoped to avoid any bias in

cover object selection attributable to environmental (moisture) heterogeneity.

Finally, we placed glass sheets on top of the cages, leaving a small gap at the middle of each cage (approximately 50 cm from either end of the channels) so we could introduce site-selecting salamanders into the relevant channels. Because site-selecting salamanders were introduced in every case into each channel immediately after cover site set-up, we considered handling stress to be standardized. We placed introduced salamanders into channels so that nose-to-tail orientation was across the width of each channel, so as to limit selection bias. At sunup the next day, we recorded the position of the selector relative to the nearest cover object.

We performed a total of four different experiments. Experiment 1 investigated the effect occupancy had on site selection. In this experiment, one cover object was occupied by a single, randomly selected *A. vagrans*, while a surrogate salamander occupied the other cover object, which we assigned randomly, as in all experiments, to ends of the runs. The site-selecting salamander was a randomly chosen *A. vagrans*. Experiment 2 investigated the effect of reproductive status and age class of the occupant on cover object selection. In this experiment, one occupant was a juvenile or subadult *A. vagrans*, while the other was a sexually mature *A. vagrans*. Due to the limited availability of adult *A. vagrans*, only juveniles or subadults were selectors. We allocated individuals to age/reproductive status categories using the color and pattern criteria of McKenzie and Storm (1971). Furthermore, age classes can be distinguished by size, as adults are 58.2±4.8 mm (mean±SD) SVL, subadults are 41.3±4.7 mm (mean±SD) SVL, and juveniles are 24.0±3.8 mm (mean±SD) SVL (McKenzie and Storm 1971).

The last two experiments investigated the potential for interspecific territoriality. In experiment 3, occupants were a randomly selected *A. vagrans* and a randomly selected *P. vehiculum*, while in experiment 4 the heterospecific occupant was a randomly selected *T. granulosa*. In both experiments, the selector was a randomly selected *A. vagrans*. We used all animals only once in one experiment, and no animal was used in more than one experiment: Thus, availability limited sample sizes. For all four experiments, we analyzed all data using a two-tailed binomial test (Zar 1984). In all analyses, cover site selection was tested against random ($p=0.5$, no preference) at a significance level of 0.05.

Results

We found site-selecting salamanders in close association with a cover object at the end of every trial (sunup). No selecting salamander was found in the middle of a channel or more than a few centimeters from a cover object when trials were concluded. Although we found more than two thirds of the selecting salamanders in experiment 1 associated with the occupied cover object, cover object preference was not significantly different from random (Table 1 for this and all other results). Sexually immature

Table 1 Results from experiments testing cover object preferences of *Aneides vagrans*

Experiment #	O1	O2	N	X	P (X)
1	Occupied	Surrogate	19	13	0.167
2	Juv/subadult	Adult	16	7	0.804
3	<i>Aneides vagrans</i>	<i>Plethodon vehiculum</i>	19	10	1.000
4	<i>Aneides vagrans</i>	<i>Taricha granulosa</i>	13	12	0.0034

See text for explanation of experiment number
O1 Occupant type for cover object one, *O2* occupant type for cover object two, *N* number of replicates for each experiment, *X* number of times occupant type *O1* was chosen by site-selecting salamander, and *Juv* juvenile

salamanders showed no preference for the different age classes of occupants. Similarly, wandering salamanders showed no avoidance or preference for conspecifics and *P. vehiculum* occupants. Selecting *A. vagrans* did exhibit a preference when confronted with a choice between conspecific occupants and sites occupied by *T. granulosa*. We scored 12 out of 13 selectors in association with sites occupied by conspecifics and the one selector that we found near a *Taricha*-occupied cover object was located on top of the cover object.

Discussion

Our findings provide further evidence that wandering salamanders are nonterritorial, a relatively rare behavioral pattern among the species of the family Plethodontidae. Previous work showed that *A. vagrans* does not use indirect and typical plethodontid chemical cues to assess retreat site occupancy, or at least ignores these chemical cues (Ovaska and Davis 1992). Our work clearly shows that when confronted with direct evidence of cover site occupancy, wandering salamanders do not avoid conspecific confrontations. In addition, Davis (1991) also found that spacing patterns of unrestrained animals did not meet expectations of territoriality.

Age class of occupants also did not affect cover object selection in this species, at least when smaller and sexually immature animals were selecting between age/size classes. If adults defend retreat sites for the purposes of mate attraction, adults should pose the greater threat to intruders (Cupp 1980; Jaeger et al. 1982; Mathis 1990). However, our selectors showed no avoidance of adults. Jaeger et al. (1995) discovered that adult red-backed salamanders do tolerate the presence of juveniles under certain ecological conditions, a result extended to other conditions by subsequent research (Faragher and Jaeger 1997), so it is possible that selection may only favor avoidance behavior in adults. We have preliminary data that when adult *A. vagrans* are used as selectors and different age/size classes are used as occupants, again no preference for occupant is expressed by the selector ($n=6$ trials, two-tailed binomial test, $p=0.22$), suggesting that age/size status plays no role

in the lack of territoriality we detected in experiment 2. As is the case with any experiment investigating territoriality in salamanders, experimental design may influence the observed patterns. In our experiments “resident” animals might not have been afforded sufficient time to establish territories (Jaeger et al. 1982) and residents were unable to actively defend cover objects. Still, given the evidence of Davis (1991, 2002a) and Ovaska and Davis (1992), *A. vagrans* does not actively defend cover sites, lending credence to our results that failed to detect either occupant avoidance or preference.

Wandering salamanders are often found in small groups under bark, and these groups commonly involve a single adult animal and one or more juveniles in close proximity. Jaeger et al. (1995) hypothesized that adult red-backed salamander’s tolerance of intrusion by juveniles might involve kin discrimination and inclusive fitness, which was implicated in *A. vagrans* (Davis 2002a). While none of our experiments tested this directly, we again have preliminary data that animals previously found in groups in the wild do not prefer cover objects occupied by familiar conspecifics over those occupied by unfamiliar ones ($n=7$, two-tailed binomial test, $p=1$). Although preliminary evidence against Davis’s (2002a) hypothesis of inclusive fitness, these findings are in no way conclusive evidence against extended parental care or kin recognition in this species. Until the genetic or genealogical relatedness of field aggregations is investigated, we can only conclude that the patterns of aggregation detected in the field may not be behaviorally maintained under laboratory conditions. Further investigations assessing the genetic relatedness of clustered animals relative to those from other logs at the molecular level are certainly warranted.

Of the two heterospecifics used in this study, *P. vehiculum* exhibits the strongest degree of habitat overlap with *A. vagrans*. Even so, *A. vagrans* does not appear to avoid cover sites occupied by western red-backed salamanders. This result is in agreement with both the hypothesis that habitat segregation precludes competition for food and the hypothesis that Vancouver Island is a habitat that imposes little in the way of food restriction on salamander species. However, *P. vehiculum* does not exhibit strong territorial behavior (Ovaska 1987, 1988) even though typical chemical cues can be used to distinguish between occupied and unoccupied cover sites (Ovaska and Davis 1992). Furthermore, when confronted with an “occupied” retreat site, individual *P. vehiculum* do not avoid such sites and exhibit similar levels of aggression when exposed to fecal pellets and dummy controls (Ovaska and Davis 1992). This is in sharp contrast to a congener with a geographic range near, but not including, Vancouver Island (Ovaska and Davis 1992). These and our results, plus those of Davis (1991, 2002a), are more supportive of the hypothesis of a benign environment and excess food availability rather than habitat segregation due to differential use of cover sites. Other alternative explanations are also feasible: historical processes involved in the founding of the species on Vancouver Island (Jackman 1998) may have led to the loss of agonistic behaviors expressed in

sister taxa. Staub (1993) has described agonistic behavior in *Aneides flavipunctatus* and recorded scarring on 32% of field-collected *A. ferreus*, the sister taxon to *A. vagrans*. If these scars are the result of intraspecific encounters involving biting, as suggested by Staub (1993), then the possibility exists that founder effects, rather than ecological influences, led to a reduction in territoriality in *A. vagrans*.

Wandering salamanders do avoid cover objects occupied by rough-skinned newts. It is possible that rough-skinned newts are predators of juvenile or at least small *A. vagrans*, as *T. granulosa* is a relatively robust salamander that utilizes prey items within the size range of a smaller *A. vagrans* (Nussbaum et al. 1983). However, we find this explanation unlikely because adult *A. vagrans* avoided cover objects occupied by *T. granulosa* as did juveniles and subadults. A more plausible explanation is that the potent neurotoxin, tetrodotoxin (Brodie 1968) secreted by *T. granulosa*, is hazardous to *A. vagrans* (Brodie et al. 2002). Although newts from Vancouver Island lack tetrodotoxin (Brodie and Brodie 1991), *A. vagrans* represents a recent (approx. 100 years) anthropogenic introduction from California where newts can exhibit some of the highest levels of tetrodotoxin (Jackman 1998; Brodie et al. 2002). Sufficient toxin may still be secreted by Vancouver Island newts as to pose a threat to animals exposed to ingested or absorbed newt skin secretions. Further, newts secrete toxins other than tetrodotoxin that could harm *A. vagrans*. Conversely, wandering salamanders may retain avoidance behavior historically selected for in source California populations.

In summary, *A. vagrans* exhibits little in the way of intraspecific avoidance behavior. Furthermore, avoidance of a heterospecific that could potentially compete directly for food resources appears to be absent. Overall, our results support the hypothesis that Vancouver Island represents a relatively benign environment for terrestrial salamanders that has selected for reduced territoriality and aggressive behavior, but alternative explanations should be considered. Avoidance of rough-skinned newts by *A. vagrans* is likely not due to habitat overlap or territorial behavior in either species. Instead, wandering salamanders probably avoid newts to eliminate the chance of exposure to toxic newt skin secretions.

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