Resource quality affects the agonistic behaviour of territorial salamanders

CAITLIN R. GABOR & ROBERT G. JAEGER

Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70504, U.S.A.

Abstract. Previous studies suggest that territories of red-backed salamanders, *Plethodon cinereus*, function as exclusive feeding areas, because prey are limited in availability during rainless periods. To test this idea, males were paired in laboratory chambers under three feeding conditions: (1) termites, a high-quality food resource, (2) ants, a low-quality resource and (3) ants plus termites. Termites are a superior food because they pass through the digestive tract significantly faster and yield significantly higher digestion efficiencies than do ants. Both territorial residents and intruders showed significantly more aggressive behaviour when higher-quality food had previously been fed to the resident than when lower-quality food had been fed to the resident. These data provide evidence that *P. cinereus* defends feeding territories and that the quality of a territory may be a function of the value of available food resources.

Territoriality is the non-random spacing of site-tenacious organisms as a result of agonistic behaviour employed by an individual (resident) that keeps others (intruders) out of a certain site. An organism involved in such a contest should act in ways that maximize fitness by weighing the costs of defence against the benefits of obtaining the contested resource (Maynard Smith & Parker 1976; Parker & Rubenstein 1981).

The quality of the limiting resource should be one of the most important factors in assessing the benefits of owning a territory. For example, if the quality of prey in an area is too poor for the individual to maintain a net positive energy budget, then that area is not worth defending as a feeding territory. While it has been shown that food resource quality benefits the inhabitant's fitness in terms of access to mates (Miller et al. 1969; Walls et al. 1989) and habitat quality affects agonistic behaviour (Itzkowitz 1979), there has been less documentation of the influence of food quality on agonistic behaviour (but see Gill & Wolf 1975; Powers 1989). We hypothesized that the quality of a food resource is one of the dominant factors affecting agonistic behaviour for terrestrial salamanders. We studied the red-backed salamander, *Plethodon cinereus*, because its aggressive defence of sites is well documented in the laboratory (Jaeger 1981, 1984; Jaeger et al. 1982) and in the natural habitat (Gergits & Jaeger 1990; Mathis 1990).

The red-backed salamander is completely terrestrial, found under rocks and logs, and in leaf litter on forest floors of eastern North America. Both males and females appear to establish territories (Jaeger et al. 1982) in defence of limited prey against conspecific and congeneric competitors (Gergits 1982; Jaeger et al. 1982) during courting and non-courting seasons (Mathis 1989). Although red-backed salamanders forage on a wide variety of invertebrate prey (Jaeger 1972), prey are limited in availability between rainfalls (Jaeger 1980, 1990), and individuals maintain territories during such periods (Mathis 1989).

A salamander would benefit from attempting to obtain a territory with high-quality food resources for two reasons: (1) on a daily basis, most 'floating' salamanders (those lacking territories) maintain lower energy budgets than territorial owners (Jaeger et al. 1981; Mathis 1991), and (2) gravid females prefer to associate with males having high-quality prey (termites) in their faeces, and thus in their territories (Walls et al. 1989; Jaeger & Wise 1991). Thus, we expected a salamander's agonistic behaviour to be affected by the quality of food available in a territory.

We predicted that prey quality is in part a function of digestion efficiency and gut-passage time for salamanders. A prey item that passes through a salamander's digestive tract faster than another type of prey item would allow a salamander to begin foraging again sooner. For

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example, prey items that are highly chitinous pass through the digestive tract of red-backed salamanders much slower than less chitinous prey items (Bobka et al. 1981; Jaeger & Barnard 1981).

We examined the relationship of food quality to territorial quality for *P. cinereus* in laboratory experiments. Based on Walls et al. (1989), we used termites, *Reticulitermes*, as a high-quality food resource and ants, *Solenopsis molesta*, as low-quality food items. Walls et al. (1989) used termites and ants because they represent extremes in the chitinous content of prey types. In our first experiment, we attempted to determine the relative 'qualities' of these two prey types based on digestion efficiency and gut-passage time for salamanders. In our second experiment, we looked at the influence of food quality on the agonistic behaviour of salamanders.

Our experimental hypotheses were as follows. (1a) Salamanders will pass termites through their digestive tracts in significantly less time than ants and (1b) will have a significantly higher digestion efficiency when eating termites than when eating ants. (2a) Territorial residents and (2b) intruders will show significantly more aggressive behaviour when the residents had (previous to the contest) access to a higher-quality food resource relative to one of lower quality.

METHODS

We collected 70 non-tail autotomized adult males of *P. cinereus* on 17 September 1991 at Hawksbill Gap, Shenandoah National Park, Virginia. Salamanders were stored individually in jars and placed in coolers with ice for 1 day before being transferred to individual petri dishes (14·5 × 1·5 cm). Each petri dish was lined with one sheet of damp filter paper and maintained in an environmentally controlled chamber at $15 \pm 5°C$ on a 12:12 h light:dark cycle. We measured the snout–vent length of each salamander from the snout to the anterior end of the cloaca.

Experiment 1: Gut Passage and Digestion Efficiency

From 5 to 16 December 1992, we determined gut-passage time and digestion efficiency of 40 randomly selected males fed ants or termites. We did not feed the salamanders for 2 weeks prior to

testing them. Gut-passage time for ants takes less than 2 weeks for *P. cinereus* (Merchant 1970), so we assumed that the salamanders' guts were cleared of any residual faeces by this time. We dried glass test-tubes for 48 h at 50°C and weighed them to 0·1 mg using a Sartorius balance to obtain their dry masses before faeces were placed in the test-tubes.

First, we randomly designated whether ants or termites were to be fed to each salamander. Then we placed 10 termites or 20 ants into each salamander's petri dish. To ensure that the stomachs of all of the salamanders were equally filled, we used twice as many ants as termites, because the dry mass of ants was half that of termites (Appendix). After 1 h, we counted how many insects were ingested; then we removed the filter paper lining and any uneaten food and placed new filter paper in the chamber. In all tests, each salamander that did not ingest the prey within 1 h or ate less than two termites or four ants was considered unresponsive and was removed from the data set. Of the 40 salamanders, 23 ate termites and 11 ate ants. We recorded the starting time for gut passage. We also determined the dry mass of insects eaten by multiplying the number ingested with the dry mass that we previously determined per ant (0·2 mg) and per termite (0·4 mg) (Appendix). On the third day, we began recording the final gut-passage time (when the faeces were released) in 0·5-h increments. We placed the faeces in pre-weighed glass test-tubes, wrapped them securely around the top with parafilm wax and stored them in a freezer (− 20°C). We dried each sample at 50°C for 48 h, weighed the faeces in the test-tubes, and calculated the dry mass of the faeces for each salamander. Data were analysed using Mann–Whitney *U*-tests at $\alpha = 0·05$ (Siegel & Castellan 1988); tests were one-tailed because we predicted that ants would be more difficult to digest than termites (Jaeger & Barnard 1981).

Experiment 2: Aggression

Our experimental design consisted of three experimental and three control conditions. In the three experimental conditions, each resident was paired by snout–vent length with an intruder. In the three control conditions, each resident was paired with a surrogate. A surrogate was a piece of moist paper towel rolled into approximately the size of a salamander. A surrogate was used to occupy the

space that would otherwise be occupied by the intruder and as a point of focus towards which behavioural displays could be directed in the control tests. For the experimental and control conditions, the residents were fed termites in condition A and ants in condition B. In condition C, one-half of the normal amount of both termites and ants was provided. All intruders were fed *Drosophila virilis*. We tested 29 residents under five of the conditions, 28 residents in the experimental termite condition and 27 intruders with the residents in the experimental conditions. We tested most of the intruders in all three experimental conditions; 174 tests, each 0·5 h in length, were performed: 87 were experimental and 87 were controls.

We randomly chose salamanders to be either intruders or residents throughout the experiment. We randomly assigned intruder/resident pairs for each condition. No two individuals were paired together in more than one test and paired individuals did not differ in snout–vent length greater than 2·0 mm. Future residents and future intruders were placed in their own separate chambers (31·5 × 17 × 1·4 cm) lined with two sheets of moist paper towels for 5 days prior to testing. This allowed the residents to mark (via pheromones: Jaeger 1986) and thus establish their territories (Jaeger 1981), and allowed both the resident and the intruder to become familiar with the chambers. We maintained individuals in the room where testing was conducted to acclimatize them to the ambient temperature (16–20°C). Testing was performed on the sixth day. We conducted tests from approximately 1400 to 1600 hours, from 14 December 1991 to 23 March 1992.

We maintained the salamanders on positive energy budgets so that the profit of owning a territory might outweigh the costs of territorial defence. We determined food quantities based on each salamander's body size. We fed future residents either (1) 12–14 termites, (2) 24–26 ants, or (3) six to seven termites plus 12–13 ants (see Appendix for calculations). We fed future intruders 16–18 *D. virilis* each (Appendix). These calculations provided only a rough estimate of a positive energy budget. We fed individuals on day 1, between days 3 and 4, and in the morning before being tested on day 6. Once placed within chambers, none of the termites, ants, or flies escaped.

On the sixth day, we removed any food left in the resident's chamber before testing, but did not change the substrate nor remove faecal pellets. We

removed the intruder from its chamber and placed it in the resident's test chamber. We handled the resident equally to prevent handling bias. We placed the intruder and the resident randomly under separate clear habituation chambers (5·5 × 1 cm) at opposite ends of the test chamber for 15 min to allow for habituation (Jaeger & Gergits 1979). We released the salamanders simultaneously, and recorded the behaviour of both resident and intruder for 30 min using a stopwatch.

We focused on two patterns of threat behaviour previously defined by Jaeger (1984): all trunk raised (ATR) and biting. During all trunk raised behaviour, the four legs of the salamander are extended down, lifting the salamander's head and entire trunk off of the substrate (the tail may or may not be raised); this is a typical 'look big' threat posture (Jaeger 1981; Jaeger & Schwarz 1991). When biting, a salamander grasps another with its mouth.

After each experiment, we placed the salamanders in their individual petri dishes until the next testing session. We tested each resident in random order, once in each of the three experimental and three control conditions, allowing at least 1 week between tests.

We used two-tailed Wilcoxon matched-pairs signed-ranks tests to analyse the results (Siegel 1956). Based on Bonferonni's inequality (Snedecor & Cochran 1980), we reduced alpha because each data set was analysed three times: $\alpha = 0.05/3 = 0.017$. For example, we compared the behaviour of a resident in the experimental condition fed termites with its behaviour in the two other experimental conditions and with the termite control condition.

RESULTS

Experiment 1

The mean ($\pm$ SD) gut-passage time for salamanders that ate termites was 97.2 ± 28.4 h ($N=23$), and for those that ate ants was 152.2 ± 57.4 h ($N=11$). Ants took significantly longer to pass through the gut than termites (Mann–Whitney U, $z=3.32$, $P<0.0005$). The mean digestion efficiency for salamanders fed termites was $73.3 \pm 19.1\%$ ($N=23$), and for those that ate ants was $43.1 \pm 22.0\%$ ($N=11$). Salamanders digested significantly more from termites than from ants (Mann–Whitney U, $z=3.01$, $P<0.0013$).
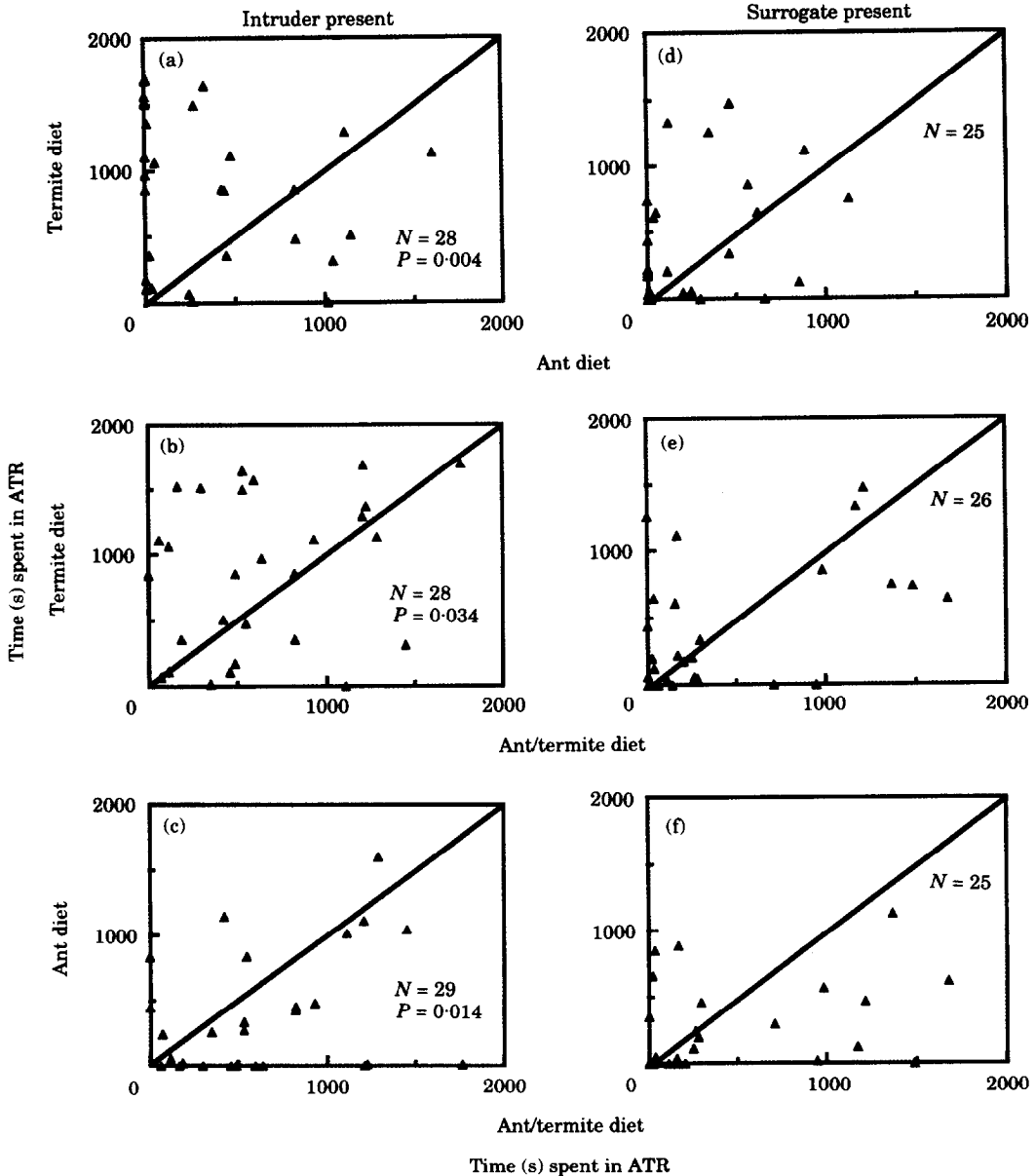
Figure 1. The amount of time residents spent in an all trunk raised (ATR) position with and without an intruder present: when fed (a, d) termites in one test versus ants in a second test, (b, e) termites versus ants plus termites and (c, f) ants versus ants plus termites. The diagonal line represents the equiprobable response line.

Experiment 2

Results from this experiment are presented on equal probability graphs (Figs 1–3). The diagonal line is the equiprobable response line. Any one point represents the amount of behaviour exhibited, as noted on the abscissa and the ordinate, by an individual. Only those salamanders that bit first in the contests were used in data analysis because we were interested in only aggressive, not defensive, behaviour.
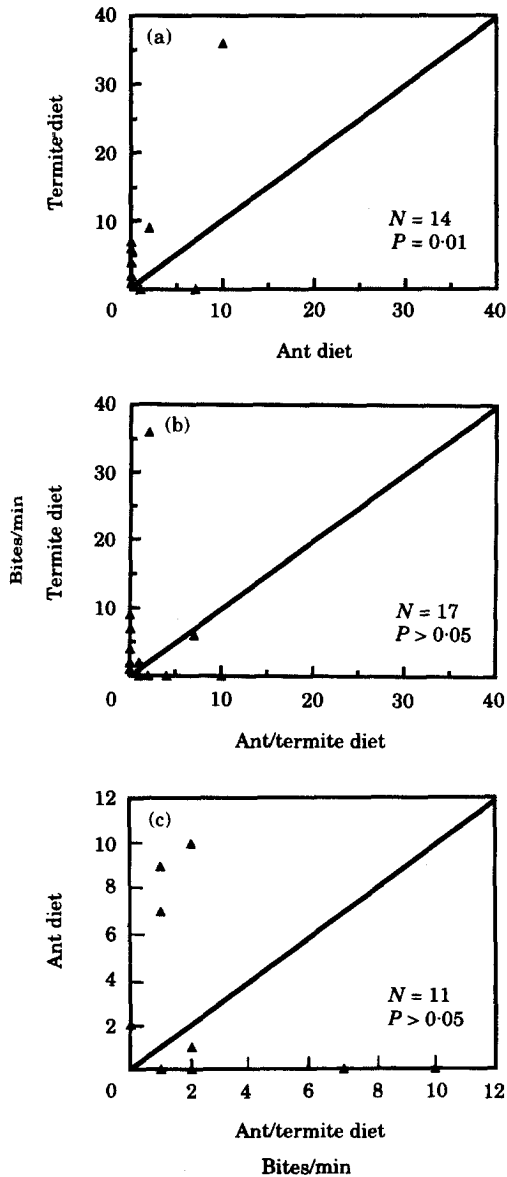
Figure 2. The number of times a resident bit an intruder when the resident was fed (a) termites in one test versus ants in a second test, (b) termites versus ants plus termites and (c) ants versus ants plus termites.

Residents

There was a significant difference in the amount of time residents spent in an all trunk raised posture towards conspecific intruders when the resident had previously been fed termites ($\bar{X}_{ATR} = 864 \cdot 3$ s), ants (366·4 s) and ants plus

termites (615·5 s; Friedman test, $F_r = 14 \cdot 07$, $N = 28$, $P < 0 \cdot 001$; Fig. 1a–c). When an intruder was present (experimental condition), residents previously fed termites spent significantly more time in an all trunk raised posture than those previously fed ants (Wilcoxon matched-pairs signed-ranks test, $z = 2 \cdot 86$; Fig. 1a). The amount of all trunk raised behaviour performed by salamanders previously fed termites did not differ significantly from those previously fed ants plus termites ($z = 1 \cdot 68$; Fig. 1b). Residents previously fed ants plus termites were in all trunk raised posture significantly more frequently than those fed ants alone ($z = 2 \cdot 45$; Fig. 1c). There was no significant difference in the amount of time residents spent in all trunk raised posture towards a surrogate (in the control conditions) when the resident had previously been fed termites ($\bar{X}_{ATR} = 390 \cdot 7$ s), ants (244·1 s) and ants plus termites (405·0 s; Friedman test, $F_r = 5 \cdot 08$, $N = 29$, $P > 0 \cdot 05$; Fig. 1d–f).

There was a significant difference between the number of first bites residents directed towards conspecific intruders when the resident had previously been fed termites ($\bar{X} = 3 \cdot 86/30$ min), ants (2·18/30 min) and ants plus termites (2·21/30 min; Friedman test, $F_r = 8 \cdot 49$, $N = 17$, $P < 0 \cdot 05$; Fig. 2a–c). Residents previously fed termites bit intruders first significantly more frequently than residents perviously fed ants (Wilcoxon matched-pairs signed-ranks test, $T = 14 \cdot 5$; Fig. 2a). Residents previously fed termites did not bite first significantly more frequently than residents previously fed ants plus termites ($T = 56 \cdot 5$; Fig. 2b); nor did residents previously fed ants bite first significantly more frequently than residents previously fed ants plus termites ($T = 30 \cdot 5$; Fig. 2c).

Intruders

There was a significant difference in the amount of time intruders spent in all trunk raised posture towards conspecific residents when the resident had previously been fed termites ($\bar{X}_{ATR} = 643 \cdot 0$ s), ants (315·6 s) and ants plus termites (391·7 s; Friedman test, $F_r = 7 \cdot 20$, $N = 23$, $P < 0 \cdot 05$; Fig. 3a–c). Intruders were in all trunk raised posture significantly more often when the resident had previously been fed termites than when the resident had been fed ants (Wilcoxon matched-pairs signed-ranks test, $T = 56 \cdot 5$; Fig. 3a). Intruders were not in all trunk raised posture significantly more often when the resident had previously been
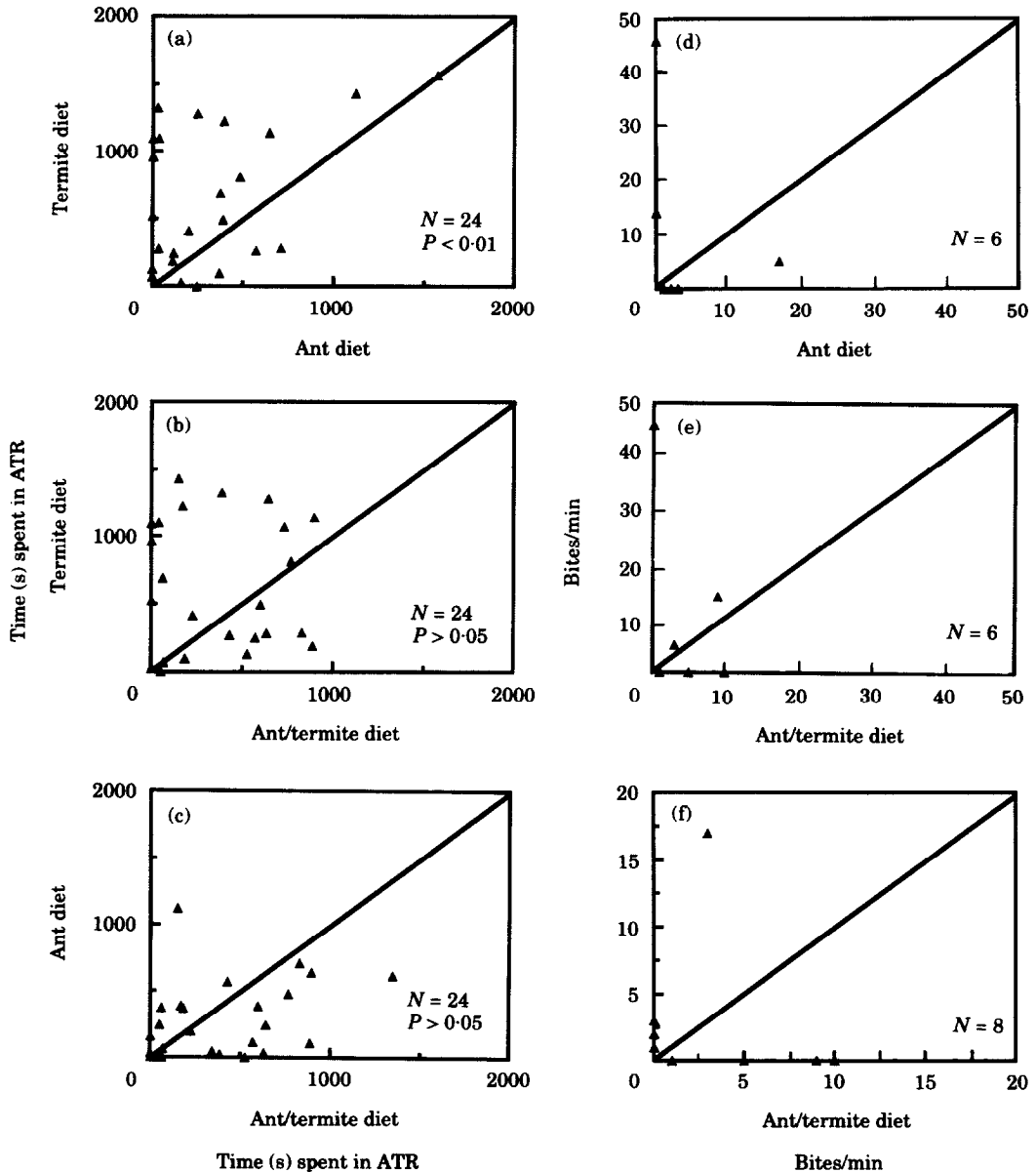
Figure 3. The amount of time intruders spent in an all trunk raised (ATR) position when paired with a resident previously fed (a) termites in one test versus ants in a second test, (b) termites versus ants plus termites and (c) ants versus ants plus termites. The number of times an intruder bit the resident when the resident was previously fed (d) termites versus ants, (e) termites versus ants plus termites and (f) ants versus ants plus termites.

fed termites versus ants plus termites ($T=90\cdot0$; Fig. 3b) nor when residents had previously been fed ants versus ants plus termites ($T=89\cdot0$; Fig. 3c).

There was no significant difference between the number of first bites intruders directed towards conspecific residents when the resident had previously been fed termites ($\bar{X}=3\cdot85/30$ min), ants ($1\cdot52/$

30 min) and ants plus termites (1·17/30 min; Fried-man test, $F_r = -5·06$, $N=8$, $P>0·10$; Fig. 3d–f).

DISCUSSION

Jaeger (1990) found that red-backed salamanders in their natural habitat tend to eliminate hard-bodied prey items from their diets during superior (wet) foraging periods and specialize on soft-bodied prey. One benefit of eating less chitinous prey is that in a given period of time, a salamander can pass a greater volume of these prey through its digestive tract in less time than one that eats highly chitinous prey. We found that termites passed through the digestive tract of salamanders faster than ants and that salamanders had a higher digestion efficiency when they ate termites than when they ate ants. We infer, then, that termites are a higher-quality prey resource than ants. Therefore, our research on territorial con-tests demonstrated that both residents and in-truders showed more aggressive behaviour when a higher-quality resource (termites) had been fed to the resident than when a lower-quality resource (ants) had been fed to the resident. Because prey were not available at the time of the encounters we infer that the behaviour of the resident was a result of territorial defence rather than direct competition over the prey items. These data sup-port the assumption (Jaeger 1972, 1980; Jaeger et al. 1982; Mathis 1989, 1990) that territorial males of *P. cinereus* defend feeding areas.

Maynard Smith & Parker (1976) pointed out that in asymmetric contests, one individual (e.g. the territorial intruder) may have less information about the asymmetry and, thus, about the costs and benefits involved in contesting the territory. In our experiment, residents fought harder for termites than for ants possibly because they were able to determine the value of the territory. Intruders may also have been able to determine information about the value of the territories, through the chemical odours (pheromones) of the residents on the substrate (Jaeger & Gergits 1979) or on faecal pellets (Walls et al. 1989), because they, too, fought harder for territories previously provisioned with termites. This increase in aggres-sion by the intruder, however, may also have been in response to the level of aggression exhibited by the resident. Yet, based on the fact that intruders were in the all trunk raised posture significantly

more often when residents had been fed termites than when they had been fed ants (Fig. 3a), we infer that both contestants were informed about the feeding asymmetries and thus that intruders were more aggressive in their attempts to obtain higher-quality territories.

From the control conditions (Fig. 1d–f), we infer that the resident's behaviour was affected by the presence of the intruder. When no live intruder was present, the resident's behaviour did not differ significantly between the three conditions.

Overall, our research demonstrates that the quality of the food resource in a territory affects the agonistic behaviour of the residents, and pos-sibly the intruders, and that territorial quality for *P. cinereus* is a function of the value of the food resource. This suggests that the territorial disper-sion of adult red-backed salamanders of various sizes found by Mathis (1990) reflects the patchy distribution of soft-bodied invertebrates on the forest floor; that is, bigger salamanders have territories with better quality prey.

APPENDIX

Measurements and Calculations

The volume of food necessary to maintain each salamander on a positive energy budget was deter-mined separately for each food resource being used. First we found the dry mass of termites and ants by drying 10 cups of 10 termites and 10 cups of 10 ants for 48 h at 50°C. Then we weighed each cup to determine the dry mass. We found that the average (± SD) dry mass of 10 termites was $4·1 ± 1·1$ mg, which was approximately twice the dry mass of 10 ants ($2·1 ± 0·7$ mg). We also deter-mined the cylindrical volume (Fraser 1976; Jaeger 1980) of 30 termites and 30 ants. The average volume was $3·32 ± 0·91$ mm^3 for termites and $0·466 ± 0·118$ mm^3 for ants.

We determined the volume of termites needed for feeding using information from Jaeger (1980), who determined the volume of *Drosophila melanogaster* (using an average cylindrical volume/fly) to be $1·59$ mm^3. We divided this num-ber by the cylindrical volume of an average ter-mite ($1·59$ mm^3/$3·32$ mm$^3 = 0·48$). Jaeger (1980) determined the volume of flies needed to maintain a salamander at 15·5°C at a zero net increase or decrease in body mass to be $0·25$ mm^3 of flies/mm salamander/day. The volume of termites/mm of

salamander/day necessary to maintain the salamanders at a zero net body mass is $0.48 \times 0.25 = 0.12$. The number of termites/day/salamander was determined by multiplying the snout–vent length of each resident salamander by 0.12 and dividing this value by the volume of a termite (3.32 mm^3). For example, if the salamander being tested had a snout–vent length of 42.6 mm, then the number of termites/day would be equal to $42.6 \times 0.12 = 5.1 \text{ mm}^3$ termites/day divided by 3.32 mm^3, or 1.5 termites/day. The final value was multiplied by four to create a positive energy budget for each salamander (1.5 termites/day $\times 4 = 6$ termites/day).

For ants, we computed the number of termites/day needed for each individual resident and then doubled the number to determine how many ants should be fed to the resident because the dry mass of termites was twice that of ants. For salamanders fed ants plus termites, we used half of the predetermined number of termites and ants.

We fed each intruder the volume of flies necessary to maintain a positive energy budget by multiplying the number of flies as determined by Jaeger (1980) for zero net energy gain by four, as above.

Finally, we doubled the number of termites, ants, ants plus termites (for residents) and the number of flies/day/salamander (for intruders) needed to maintain a positive energy budget because we performed feedings every second day.

ACKNOWLEDGMENTS

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