# EFFICACY OF THE AEGEAN WALL LIZARD (*PODARCIS ERHARDII)* AS A POTENTIAL BIOLOGICAL CONTROL AGENT IN MEDITERRANEAN AGROECOSYSTEMS

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# ABSTRACT

Given agriculture's outsized proportion of global land use, food production systems must be examined for their role in conservation during this era of anthropogenic global change. Central to this objective is investigating opportunities where goals of food security and biodiversity preservation are complimentary rather than incongruent. Biological control of herbivorous pests by natural enemies is one such area of focus, where accruing evidence suggests landscape complexity fosters functional diversity of predators who offer free pest control services. Despite being widespread generalist predators, reptiles have infrequently been considered for their role in suppressing invertebrate populations. In this study, we investigated an insular population of the common Mediterranean lacertid, *Podarcis erhardii* (Aegean wall lizard), for its impact on invertebrate communities and herbivory damage through field enclosure experiments. We further studied *P. erhardii's* functional response to known agricultural pests in a laboratory setting. Our field results revealed a significant negative interaction effect between lizard inclusion and time on the abundance of ground-dwelling arthropods sized 2-5 mm ($\beta = -0.017$, $SE = 0.006$, $p = 0.006$), and a marginally significant negative effect of lizard inclusion on arthropods > 5 mm ($\beta = -0.303$, $SE = 0.153$, $p = 0.052$), irrespective of time. We detected no effect of lizards on the abundance of airborne arthropods or prey < 2 mm. However, our functional response trials revealed lizards' capacity to consume copious amounts of small prey when naturally aggregated, as well as large amounts of prey biomass relative to predator body size. We found no influence of lizard inclusion on herbivory damage, potentially a result of intraguild predation by lizards on large predatory arthropods and small sample size. Our study illustrates the capacity of lizards to suppress large or naturally clumped ground-dwelling prey, especially later in the growing season when resources become scarce. We argue that biocontrol services are best realized when *P. erhardii* is among a diverse assemblage of predators, in order to maximize control of herbivorous insects over appropriate spatiotemporal scales. Accordingly, we recommend future studies involve long-term investigation of food web level interactions, including trait-mediated effects.

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## 1. INTRODUCTION

Modern practices of the industrialized farming system have resulted in land use changes whereby primary habitat is relinquished to agricultural use at alarming rates (FAO, 2009). Cropland and pasture constitute up to 40% of the global terrestrial land surface, with effects reaching far beyond the immediate area (Ellis et al. 2010; Foley et al. 205; Goldewijk et al. 2017). Of the remaining 'available' land suitable for crop production, 90% is concentrated in only a few countries in Latin America and sub-Saharan Africa (Alexandratos & Bruinsma, 2012). Once the realities of rural economies, land-scarcity in neighboring countries, and ecological constraints are accounted for (FAO, 2009), continued expansion becomes less viable. Further confronting the inefficiencies of the current food production system, where an estimated ⅓ of all food is wasted globally (Gustavsson et al. 2011), focusing efforts on efficiency and addressing *overproduction*, rather than increasing production and expansion may offer better outcomes for global food security (Perfecto & Vandermeer, 2010; Tscharntke et al. 2012).

Agriculture in and of itself is not a threat to biodiversity; rather the practice often welcomes a series of drivers leading to the decline of local species populations (Perfecto et al. 2019). Chiefly, this includes habitat loss and degradation, but may also host environmental contamination, given the prevalence of highly intensified farming regimes which rely on agro-chemical inputs. In natural systems, evolved interactions between plants, herbivorous insects, and their predators influence population levels; intensified agricultural systems ignore such biotic mechanisms in favor of a chemical-based management strategy (Singh & Singh, 2016). Despite rigorous chemical control efforts, where roughly 40 billion USD worth of pesticides are applied globally each year (Omkar, 2018), an average of 35% of potential crop yield is lost to pests and pathogens (Oerke, 2006). Biological control (biocontrol) of herbivorous pests by natural enemies, on the other hand, offers several advantages in addition to the reduction of environmental contamination, including lower developmental costs, lower risk of resistance, higher success ratios, and few (or zero) harmful side effects (Huang et al. 2016; Van Lenteren, 2012).

Wildlife dependent on natural habitats are forced into agricultural landscapes as secondary habitat, and while some drivers of biodiversity loss are more indiscriminate, use of pesticides may have greater implications for reptiles compared to other vertebrate taxa (Wagner et al. 2015). Reptiles, such as lizards, present two pathways for the bioaccumulation of pesticides: (1) through secondary consumption of contaminated prey, and (2) dermal contamination, where small-bodied reptiles are at even greater risk given their high surface area to body mass ratio (Wagner et. al 2015). Studies have found body condition is negatively correlated with pesticide exposure in lacertids, including the induction of oxidative stress response, despite being non-target organisms (Aramaral et al. 2012; Mingo et al. 2017). Regulatory agencies such as the European Food Safety Authority do not require evidence that an agro-chemical is not overly toxic to reptiles, as it does for other taxa such as aquatic organisms, bees, mammals, and birds (Amaral et al. 2012), despite the fact that 19% of all listed reptile species are classified as threatened (504 vulnerable, 514 endangered, 293 critically endangered) according to the IUCN Red List (IUCN, 2019; Mingo et al. 2017).

In this study, we aimed to further investigate the potential for positive relationships between biodiversity and agriculture, where goals of food production and conservation are not mutually exclusive. Specifically, we are interested in the role reptiles may play in reducing arthropod populations within an agroecological context in the Mediterranean Basin. In this region, landscapes are defined by a vast network of dry stone terraces, many of which date to the Bronze Age (3000 - 1200 BC) or older (Bevan et al. 2013). These terraces have been used for millennia to prevent soil erosion and allow for cultivation of steep slopes. Over the last several decades, they have been increasingly abandoned in the face of agricultural intensification (Margaris, N.S., 1992). As a result, many terraces today remain only in semi-abandoned and unmaintained use as areas for grazing livestock, mature vineyards or olive groves requiring little management (Dunjo et al. 2003; personal observation). Prior to the mid-20th century, the majority of terraces were utilized for diverse vegetable, grain, and legume production, following crop rotation practices and utilizing livestock grazing on the steepest slopes (Bevan et al. 2013).

Beyond agricultural infrastructure, however, the system of dry stone terraces provides central habitat for our focal species, the Aegean wall lizard (*Podarcis erhardii*). This species, like other wall lizards, exploits stone walls or terraces as sites for thermoregulation, resting, hiding and even hibernation; meanwhile the surrounding vegetation serves as their foraging habitat (Donihue, 2016; Mingo et al. 2017). Therefore, quality habitat is provided not only by the stone refugia, but also determined by the surrounding agricultural system's vegetation structure and diversity and the type of agricultural management. Even olive groves requiring little management differ in regard to agricultural intensification. Some systems employ agro-chemicals and/or mechanical plowing to remove the understory vegetation, thereby depleting insect communities and prey resources for higher organisms such as birds and reptiles. Low-impact olive groves maintain a mix of native understory vegetation and ruderal species, with landowners refraining from chemical and mechanical destruction of vegetation and soils. The latter agroecological practices allow for high quality habitat, including prey resources, to persist for *P. erhardii*. While wall lizards' preference for stone refugia is well documented, less is known about their impact on invertebrate communities within their habitat. As generalist insectivores, anecdotal evidence suggests *P. erhardii* may depress local arthropod populations, especially when prevalent at high densities such as surrounding stone terraces in low-input systems. However, their potential to bolster regulating ecosystem services such as biocontrol has not been determined.

Comprehensive field studies involving lizards' influence on invertebrate prey are uncommon, but generally involve their experimental removal (Borkhataria et al. 2006; Dial & Roughgarden, 1995; Pacala & Roughgarden, 1994; Spiller & Schoener, 1990; Spiller & Schoener, 1998). Removing *Anolis* lizards from rain forest canopy in Puerto Rico resulted in significant positive effects on the abundance of arthropods >2 mm in length, with significant increases in the biomass of both airborne and leaf arthropods (Dial & Roughgarden, 1995). Another enclosure experiment on St. Eustius (Lesser Antilles) found *Anolis* removal led to significant increases in arthropod abundance on the forest floor, and a 20 to 30-fold increase in the abundance of large web-building spiders. Consequently, a significant decrease in insect abundance between the forest floor and canopy was observed, illustrating cascading effects of lizard removal (Pacala & Roughgarden, 1984). The influence of lizard predation on insects has also been investigated for its additive effects, where the combined exclusion of birds and lizards resulted in the greatest increases to insect abundance within a Puerto Rican coffee plantation (Borkhataria et al. 2006).

On islands without *Anolis* populations in the Bahamas, spider abundance was found to be 10 times greater compared to islands with anoles present. Anoles' consumption of both predatory spiders and herbivorous insects was correlated with reduction of herbivory to *Conocarpus erectus* (Green buttonwood), illustrating their top-down regulation potential (Spiller & Schoener, 1990). A long-term comparative study in Exuma, Bahamas also resulted in reduced abundance, species richness, and diversity of web spiders when lizards were removed for a period of 4.5 years (Spiller & Schoener, 1998). The presence of *Crotaphytus collaris* (Eastern collared lizard) on large fragmented glades in Ozark Plateau, Missouri, was correlated with reduced arthropod richness and dominance of predatory arthropods. Only after removing the effect of *C. collaris* was glade area correlated with arthropod diversity, again showing indirect effects of reptile predation on invertebrate communities (Östman et al. 2007).

A controlled functional response experiment found *Eremias argus*, a common lizard in inner Mongolia, has the potential to control low-level grasshopper outbreaks, where *E. argus* preyed on large numbers of grasshoppers within 24 hours (Huang et al. 2016). Their feeding response followed a Holling Type III response curve, where predation rates tended to decline with increasing prey density, typical to vertebrate predators (Huang et al. 2016; Holling, 1959). Another recent laboratory experiment found *Anolis* lizards present in coffee systems in Mexico and Puerto Rico were able to reduce infestations of an economically devastating coffee pest, the Coffee berry borer (*Hypothenemus hampei*) by 49% and 83%, respectively. Lizards in this study were found at higher densities in coffee systems utilizing agroecological practices, while high-intensity sites involving pesticide usage were associated with reduced *Anolis* abundance (Monagan et al. 2017). According to surveys by Borkhataria et al. (2012), while preferences were displayed among species, the overall abundance of *Anolis* lizards in shade and sun coffee systems was indistinguishable in the absence of pesticide application, despite differences in structural diversity between plantation types.

The goal of our study was to not only understand the potential top-down effects of lizards on invertebrates in their natural environment, but also to determine whether their consumption patterns would result in reduced abundance of herbivorous pests, and indirectly to the reduction of crop damage. We used a hierarchical approach to assess the potential of *P. erhardii* as a biocontrol agent. Firstly, we investigated the impact of lizards on natural arthropod populations through a field-based study, specifically examining their preference for organisms of particular body size. This involved the experimental removal and addition of lizards in semi-natural enclosures. In order for reduction of herbivorous pests to be of economic value in an agricultural context, that reduction must be accompanied by lessened damage to target crops. To assess this indirect association, we added food crops to our study plots and assessed foliar damage by chewing arthropods. Lastly, we investigated *P. erhardii's* capacity to consume significantly large numbers of known agricultural pests. Here, we used controlled laboratory experiments to test their feeding response to two especially economically devastating insects.

## 2. METHODS

### *2.1 Study location and Focal Species*

Field work was conducted May - July 2017, in Moni, a small agricultural village in central Naxos, the largest island in the Cyclades Island cluster (Aegean Sea, Greece). Moni's landscape is characterized by a diverse matrix of olive groves and vineyards outlined by hundreds of dry stone terraces (Figure 1). The climate is characteristic of the Mediterranean hot summer regions, with mild winters and warm, arid summers allowing for an extended growing season and high crop diversity. Our study sites were located on three adjacent terraces cultivated with mature olive trees. Terraces were South-facing at an elevation of ca. 400m asl. The present olive grove had been minimally managed, allowing for understory vegetation to persist, namely ruderal species as groundcover. The combination of dry stone terraces and structurally diverse vegetation presents a heterogeneous habitat and thermal mosaic, important for proper thermoregulation in reptiles and other ectotherms (Bogert, 1959; Pafilis et al. 2016; Sagonas et al. 2017).

Our focal species, *P. erhardii* (Figures 2 & 3), is a common, medium-sized (snout-vent length 49-78 mm) lacertid lizard, widely distributed throughout Greece in a variety of open habitat types (Poulakakis et al. 2003; Valakos et al. 2008). In the Aegean region, *P. erhardii* is found at particularly high densities in areas where refugia are available, especially common along the human-built rock walls and terraces. *P. erhardii* is an opportunistic predator of arthropods, with only a very small plant matter dietary component. This species demonstrates plasticity in foraging mode, where their foraging behavior has been shown to differ according to habitat type, specifically with the presence of stone walls (Donihue, 2016). Lizards in our field and laboratory experiments were captured via noose at the field site, with over 90% caught directly from stone walls.

### *2.2 Field Enclosure Design*

A series of five sample sites were marked on three adjacent terraces. Each site consisted of three plots: paired enclosures with lizards stocked or removed, as well as a flagged control plot (no built structure), which allowed lizards from the local population to enter and exit the system freely. The presence of the control plot was designed to ascertain whether the built structures themselves presented a significant effect on arthropod abundance or lizard feeding behavior. The control plots further allowed us to investigate the influence of lizards at intermediate or natural densities. Light penetration and vegetation were assessed to match environmental conditions between plots within an individual site, while allowing for differences in temperature, vegetation density, and plant species between sites. Plots measured 3 x 2m, and enclosures were constructed using a modified design following *Anolis* enclosures described by Pacala et al. (1983). The enclosures consisted of 1m high polyethylene hardware net (mesh size 5 mm), affixed with cable ties to steel bar posts sunk at regular intervals into the ground. The bottom of the hardware net was buried 10-15 cm below ground to prevent lizards from escaping via digging. Slippery polypropylene sheeting was stapled to the top of the structures, creating a 35-cm overhang around the perimeter to prevent lizard escape or entry via climbing.

Three equally spaced stacks of 3-5 large stones were placed in each plot to serve as refugia and allow for lizard thermoregulation. We discouraged avian predation on the enclosed lizards by stringing flagging tape across the top of each enclosure plot. Entry of airborne arthropods was free over the top of the enclosures and of terrestrial arthropods through the large-eyed mesh. Lizards were collected from the local population and stocked at a density of 6 lizards (3 male, 3 female) per enclosure, according to maximum natural densities determined through personal observation in the habitat. Lizard abundance was checked daily, and individuals were restocked or removed from plots as necessary.

### *2.3 Arthropod Sampling*

Three pitfall traps were set in each plot to sample ground-dwelling arthropods. Traps consisted of plastic cups measuring approximately 12 cm deep with a 9.5 cm top diameter, buried to soil surface level. To avoid lizard mortality, a dry pitfall design was used; crumpled paper was added to the otherwise empty traps, allowing trapped lizards to escape while minimizing within-trap arthropod predation or escape. Baseline arthropod data were collected prior to stocking lizards in enclosures, including arthropod abundance, identification to insect order, and body size. Traps were kept closed with plastic lids between sampling periods to maintain arthropod populations and adequate prey for the enclosed lizards. Following the baseline measurements, traps were sampled at 9-day intervals over a 50-day period for a total of six samples including the baseline. At each sampling period, trap lids were removed for 72 hours followed by in situ assessment of trap contents. Arthropods were collected from each trap, sorted, and quantified. To maintain arthropod numbers, we released all live arthropods back into the sample plot.

To obtain a complementary measure of airborne arthropods, we used three sticky traps, also spaced 1 meter apart in each plot. Sticky traps consisted of stiff plastic cards, measured 7.5 x 13 cm and were placed on wire holders 25 cm above ground. Sticky traps followed the same sampling schedule as described above. All pitfall and sticky traps were analyzed for (1) total arthropod abundance, (2) identity of each arthropod to order (3) size of each arthropod to nearest mm in body length.

### *2.4 Herbivory Assessment*

Cucumber *(Cucumis sativus*) seedlings were obtained from a local nursery. The plants selected were grown without the use of systemic pesticides to avoid arthropod mortality and indirect toxicity to lizards. Cucumber plants were transplanted in the field on June 13, 2017, with three plants in each enclosed plot placed 1m apart. Any sun damage or herbivory on the seedlings was recorded prior to the start of the experiment, and severely damaged leaves were removed. Cucumber leaves were assessed for arthropod damage on three sampling periods: June 26, July 2, and July 11. Areas of missing leaf tissue were counted as chewing herbivory. Sucking and piercing damage was not assessed, as we found it difficult to quantify reliably. Each leaf on every plant was examined to capture the proportion of leaves damaged (# leaves with any amount of chewing herbivory / total # leaves). The extent of herbivory was also quantified by counting the number of chewed areas on each leaf.

### *2.5 Laboratory Methods*

#### *2.5.1 Functional Response: Family Aphididae*

We investigated the functional response of *P. erhardii* on aphids (Homoptera: Aphididae) under controlled laboratory conditions from June 20-June 30. Aphids are especially abundant in temperate climates, where suitable conditions may result in rapid population increases above economic thresholds (Singh & Singh, 2016). As pests, aphids have the ability to destroy many parts of a plant by sucking nutrients, leading to seedling mortality, abnormal fruit development, stunted growth, and reduction of aesthetic value (Sarwar, 2014; Singh & Singh, 2016). While we hypothesized *P. erhardii* would exhibit stronger preference for larger bodied insects in the field experiment, we aimed here to test their preference for aggregates of small-bodied prey < 2 mm.

Ten adult lizards (5 male, 5 female) were collected via noose from the field site in Moni and transported to the laboratory, where they were individually housed in plastic terraria measuring 28 x 33 x 13 cm, covered in 1-mm mesh cloth. Cardboard barriers were placed between individual terraria to eliminate visibility among individuals. Lizards were exposed to a regular 12L:12D photoperiod, and terraria included 3-4 stones to create a thermal gradient and allow normal basking behavior (Greenberg, 1978). Lizards were allowed 72 hours prior to start of the experiment to acclimate to their new surroundings and to allow for a fasting period prior to the first trial. Water was provided *ad libitum*.

Aphids were procured from an infested plum (*Prunus* sp.) branch from a nearby low-input, diversified farm. The insects were allowed to feed on cabbage (*Brassica oleracea var. capitata*) host plants inside the laboratory. Aphids were kept on cabbage leaves as substrate and introduced in the terraria immediately prior to the start of the timed trials. A randomized experimental design was used to assign individual lizards, first grouped by sex, to one of five aphid treatments: 10, 30, 50, 100, or 200 prey offered. After 8 hours, the number of aphids remaining was counted, followed by another 72-hour fasting period. Aphid treatments were again assigned randomly to the individual lizards in subsequent trials (3 total). SVL, head length, head width, and head depth of each lizard was measured, and specimens were returned to the field site following the experiment's conclusion.

### *2.5.2 Functional Response:* ***Pieris rapae***

Plants in the *Brassicaceae* family are known targets of lepidopteran pests, where damage by caterpillars results in stunted plant growth, defoliation, and fecal contamination, rendering the produce unusable (Sarwar, 2014). Similar to testing the functional response of *P. erhardii* to very small prey items, here we aimed to test their feeding response to particularly large insects. The objective was to ascertain whether lizards become satiated quickly, or if they will continue feeding so long as prey is available. A functional response trial (N = 12) was conducted using the larvae of the Cabbage white butterfly (*Pieris rapae)*, an especially common brassica pest present on cabbage crops worldwide (Embabay et al. 2015; Sarwar, 2014).

Twelve adult lizards (6 male, 6 female) were collected by noosing from the vicinity of our field site and kept under the same conditions as described above. Cabbage white larvae were procured locally, and average larvae size was 31.7±4.42 mm in length and weighed 0.306±0.091g. Each of the lizards were introduced to one of six larvae treatments: 1, 2, 3, 4, 5, or 6 prey offered inside their terraria placed on cabbage leaves. Lizards were provided with water at the time of the experiment and after 24 hours, the number of larvae remaining was counted. Lizards were returned to the field site the following day. No morphological measurements were taken.

### *2.6 Statistical Analysis*

#### *2.6.1 Arthropod Abundance*

Because previous studies (Dial & Roughgarden, 1995; Greenberg et al. 2000) had found that lizard influence may dependent on prey body size, we took this into consideration during our analyses. Arthropod abundance data were thus separated into three size classes: 1-2 mm, 2-5 mm, and > 5 mm. Due to the large number of insect orders and the corresponding small sample sizes in each group, we followed the example of Borkhataria et al. (2006) and did not consider taxonomic affiliation in our analyses. Instead we performed separate analyses for ground arthropods (captured in pitfall traps) and for flying insects (captured in sticky traps) as the ecology of each group is very different and each trapping method has its own distinct biases.

Linear mixed effect models were used to fit the change in arthropod abundance over time as a response to lizard presence. The dependent variable, number of arthropods, was log-transformed to meet the assumptions of normality of residuals and homoscedasticity. Models included treatment (lizards included, lizards excluded, control) as categorical variables, and day (of the measurement) as a continuous measurement of time. Treatment*day interactions were also included to ascertain whether the influence of lizard predation on arthropod abundance changed over the course of the study period. To address the lack of independence among observations between plots in the same site, we included site as a random effect. This model was replicated for each size class of ground-dwelling and airborne arthropods for a total of six analyses. Statistical tests were performed in R v3.4.2 using the lmerTest package. Significance was assessed at $p \leq 0.05$ using the Kenward-Rogers approximation (Kuznetsova et al. 2017).

#### *2.6.2 Herbivory Damage*

Linear mixed effect models were used to fit herbivory damage over time in the field as a response to lizard presence. Two analyses following the same model structure investigated (1) the proportion of total leaves with any chewing herbivory damage, and (2) the extent of damage (# areas of tissue loss due to chewing herbivory). For the second analysis, the number of chewed areas was log-transformed to meet the assumptions of normality of residuals and homoscedasticity. Treatments (lizards included, lizards excluded) were included as categorical variables and day as a continuous predictor. Site was included in the models as a random effect. Statistical tests were performed in R v3.4.2 using the lmerTest package. Significance was assessed at $p \leq 0.05$ using the Kenward-Rogers approximation (Kuznetsova et al. 2017).

#### *2.6.3 Functional Response:*

Linear mixed effect models and nonlinear least squares regression models were used to fit the number of prey consumed according to equations described by Holling (1959 & 1965):

$$\text{Type I: } y(N) = aN$$
$$\text{Type II: } y(N) = aN / 1 + ahN$$
$$\text{Type III: } y(N) = aN^2 / 1{+}hN^2$$

Where $y$ is predation rate (total number prey consumed), $N$ is prey density (total number prey offered), $a$ is attack rate, and $h$ is handling time. Attack rate and handling time were not measured directly in this study and were included as constants in the models (Monagan et al. 2017). Since the same lizards were used in the three aphid trials, lizard identity was added as a random effect. Trials involving *P. rapae* did not include repeated measures due to the lack of larvae we were able to obtain, and therefore were fit using nonlinear least squares regression (nls) instead of a mixed model approach. Linear mixed effect models were performed in R v3.4.2 using the *nlme* package (Pinheiro et al. 2018) and nls models were performed in the R Stats package (R Core Team, 2017). In order to assign functional response type, the $\mathrm{AIC}_C$ value of each model was used to assess performance, with the lowest value indicating the best fit to the data (Burnham & Anderson, 2004).

## 3. RESULTS

### *3.1 Field Results: Arthropod Abundance and Herbivory Damage*

First, we used a linear mixed model testing the effect of treatment, day, and treatment*day interactions on $\log_{10}$ arthropod abundance in size class 1-2 mm but found no significant effects of either of those factors (see Table 1). The same model for arthropods in size class 2-5 mm revealed day as a significant predictor, somewhat surprisingly, in a positive direction ($\beta = 0.010$, $SE = 0.00$, $p = 0.014$). While the main effect of the lizard inclusion treatment is not statistically significant, the model revealed a significant negative lizard inclusion treatment*day interaction effect ($\beta = -0.017$, $SE = 0.01$, $p = 0.006$), whereby the main effect of day on $\log_{10}$ arthropod abundance becomes negative in the presence of lizards (Table 2). For arthropods sized > 5 mm, the model revealed the lizard inclusion treatment was a significant predictor when p-value significance is assessed at $\alpha = 0.1$($\beta = -0.303$, $SE = 0.15$, $p = 0.052$) and no significant effect of day or treatment*day interaction (Table 3).

When the same linear mixed models were applied to airborne arthropods in size class 1-2 mm and 2-5 mm, we found no significant effect of treatment, time, or interaction terms (Tables 4 & 5). For arthropods in size class >5 mm, our model revealed a significant negative effect of day only ($\beta = -0.008$, $SE = 0.00$, $p = 0.033$) (Table 6).

Cucumber plants in our enclosures experienced equivalent levels of chewing herbivory damage irrespective of treatment. The linear mixed effect models revealed that the inclusion of lizards was not a significant predictor of herbivory damage, in the case of both proportional damage (*Lizards Excluded* : $\beta = -0.025$, $SE = 0.03$, $p = 0.435$; *Lizards Included*: $\beta = -0.020$, $SE = 0.03$, $p = 0.464$) and $\log_{10}$ number of chewed areas (*Lizards Excluded* : $\beta = -0.100$, $SE = 0.06$, $p = 0.091$; *Lizards Included*: $\beta = 0.005$, $SE = 0.06$, $p = 0.928$).

### *3.2 Laboratory Results: Functional Response*

$AIC_C$ comparison of the linear mixed effect models used to fit Type I, II, and III response of *P. erhardii* on aphids marginally favors the linear Type I response ($\beta$ *(attack rate±SE)* = 0.913±0.020, $p < 0.01$), as $\Delta AIC_C$ between Type I and Type II is < 3 (Table 7) (Burnham & Anderson, 2004). At the highest density of prey offered (200 aphids per leaf), lizards consumed an average of 178.2 aphids ($s = 12.0$), or 89.1% (Figure 4).

Model comparison using $AIC_C$ for the response of *P. erhardii* on *P. rapae* larvae did not distinguish between Type II and Type III response models, as $\Delta AIC_C < 1$ between the two models (Table 8). In both models, the estimate for lizard attack rate, $a$, is marginally significant when assessed at $\alpha = 0.1$ (*Type II*: $\beta = 1.517$, $SE = 0.710$, $p = 0.059$; *Type III*: $\beta = 1.083$, $SE = 0.559$, $p = 0.081$). The estimates for handling time are not significant in either model, but again were not measured directly in this study. The response curves (Figure 5) do communicate lizard satiation; however, the Type III curve is not characterized by the S-shape typical for this model, where search activity increases with prey density.

## 4. DISCUSSION

Collective results from our field and laboratory studies illustrate *P. erhardii's* capacity to impact numbers of ground-dwelling arthropods. Results from our field experiment illustrate a clear preference for larger-sized ground-dwelling prey, consistent with size preference found in studies involving *Anolis* species (Borkhataria et al. 2006; Dial & Roughgarden, 1995). Indeed, we were not able to demonstrate any effect of lizards in our study plots on the abundance of arthropods < 2 mm in length, suggesting very small-bodied invertebrates are not a favored prey source. This lack of effect was either because very small arthropod populations are abundant and mobile, or because lizards simply do not consume many small prey items when alternative, larger prey is available. Size distribution of prey in stomach contents relative to size distributions in the environment, could offer a more definitive conclusion regarding *P. erhardii's* preference or avoidance of small-bodied prey in their natural habitat. Despite the laboratory results of our functional response aphid trials, in the field our results suggest that lizards had little, if any, effect in reducing the numbers of the very smallest arthropods.

We found a significant negative interaction effect between the presence of lizards and time on the abundance of arthropods sized 2-5mm, illustrating the lizards' pressure on arthropod abundance later in the season. This interaction effect was most pronounced in the second half of the field experiment (Figure 6) and was especially apparent at the experiment's conclusion (Figure 8), suggesting that as the summer season advanced, lizards were better able to suppress arthropods of this size class. Such temporal dynamics are especially important in the context of biocontrol. Time predicts a number of environmental variables and the life cycles of plants, herbivorous insects, and their predators, ultimately influencing the strength of biocontrol services provided by natural enemies (Welch & Harwood, 2014). Deeper understanding of how temporal dependencies contribute to the structure and function of complex interaction webs may better inform implementation of biocontrol and integrated pest management schemes. For example, actions such as crop rotation, cover cropping, and sowing and harvest periods may also influence the occurrence or strength of predator-prey interactions and resulting ecosystem services (Schneider et al. 2015; Welch & Harwood, 2014; Thies & Tscharntke, 2010).

Although our results were marginally significant, perhaps because of the small numbers involved, they do communicate the ability of *P. erhardii* to consistently suppress ground-dwelling arthropods > 5 mm. Larger arthropods were found in particularly low densities in lizard inclusion plots throughout the duration of the experiment (Figure 7). Previous analysis of *P. erhardii* stomach contents at this very study location (Donihue, 2016), as well the results of an earlier study (Valakos et al. 1993), showed prevalence of larger-bodied prey such as Orthoptera and Gastropoda, a pattern that is consistent with the significant depression of the largest prey items documented in this study. Our results are consistent with a situation where lizards suppressed large insects from the very beginning of the experiment but exerted an effect on intermediately-sized insects progressively over the course of the experiment.

We did not detect a significant effect of lizards on reducing airborne arthropod populations of any size, although, we did witness at the experiment's conclusion, comparatively fewer 2-5 mm airborne arthropods in the lizard inclusion plots (Figure 9). The lack of a significant effect overall may be indicative of the lizards' preference for ground-dwelling prey, or alternatively the shortcomings of sticky card traps to detect population variation between plots of this size. Hence, plots may get - over a 72-hour period - too readily replenished with insects to discern any effect of treatment on abundance. However, it may also be possible that the physical setup of the experiment was not appropriate to truly capture an effect of lizards on flying insects: free-ranging wall lizards are typically perched and even forage on the tops of walls at much greater heights than the stones placed in their enclosures. Unless a flying insect was to land much closer to ground level, the lizards had little chance to capture airborne prey, unlike their foraging behavior in their natural habitat where they are regularly seen consuming large Diptera and Lepidoptera (CL, pers. observ.). In addition to analysis of stomach contents, larger study plots that include structural diversity of vegetation and full access to stone walls would be more appropriate to determine the influence of lizard predation on airborne arthropod populations.

Results from our functional response experiments, despite small sample size, provide evidence for the capacity of *P. erhardii* to consume copious amounts of prey. The Type I response to aphids should be interpreted with one caveat: no satiation point was detected likely because maximum prey density was not sufficiently large. While our data fits a Type I model, a true linear response is unlikely. This experiment was limited by the number of aphids we were able to procure. We recommend future trials involve significantly greater prey densities in order to determine a satiation point, especially for small, naturally clumped prey such as aphids, where very high densities are not uncommon. The fact that lizards consumed most of the prey offered, is indicative of their ability to consume insects < 2 mm when closely aggregated. Similar to experiments involving *Anolis* reduction of Coffee berry borer infestations by Monagan et al. (2017), our study offers additional evidence of large consumption of insect prey typically considered too small relative to lizard body size. This information would not have been elucidated through our field experiment alone, where no effect was detected for arthropods of this size class.

The feeding response of lizards to Lepidoptera larvae also offers insight into their ability to consume large amounts of prey biomass relative to their own body size, a positive attribute for a potential biocontrol agent. Repeated measures would certainly help to better understand *P. erhardii's* ability to suppress pest-level abundances of Lepidoptera, which are known preferred prey items (Donihue, 2016). Brassicas are a widely cultivated and economically important crop family, which are also easily contaminated by pesticides, garnering public support for chemical-free production methods (Xu et al. 2015). Beyond contamination of food crops, insecticides used on cabbage have been shown to reduce predation and parasitism of pests by natural enemies, resulting in increased damage to crops despite pesticide treatment (Bommarco et al. 2011). Our functional response trial lends support for further investigation of lizards' ability to suppress Lepidoptera larvae in low-input systems, where it is possible they *prevent*, rather than control, large-level outbreaks.

Similar to the aphid study, our sample size was limited by the number of larvae we were able to obtain. In addition to repeated measures, a more pragmatic model may also include digestion time, especially for experiments involving larger-bodied pests. Our models fit to the equations introduced by Holling (1959), which define handling time as the sum of attack time and time spent eating prey, but do not include satiation effects directly. As most predators are digestion-limited, the Steady-State Satiation Equation model introduced by Jeschke et al. (2002) may offer a more realistic prediction of the lizards' feeding response as it relates to hunger level.

We recommend that functional response trials also be conducted in semi-controlled field settings to determine how feeding response varies with the availability of alternative prey. This may also help to discern Type II and III responses, something that our model selection process was not able to distinguish. Additionally, the propensity for lizards to climb vegetation may help their ability to depress crop pests in certain systems. For example, the Cabbage white butterfly lays an egg cluster on the underside of a plant leaf. Once hatched, the small caterpillars gravitate toward the center of the plant, migrating to new, tender growth. An informative study would record the foraging behavior of lizards as it relates to plant morphology, such as height, leaf shape, size, and texture, in order to capture more realistic expectations of biocontrol services provided by lizards in managed agroecosystems.

In addition to crop species morphology, vegetation distribution of both commodity crops and semi-natural areas may influence lizard foraging behavior. A comparative study by Pitt and Ritchie (2002) found skinks captured significantly more prey in experimental arenas where vegetation was distributed in fewer but larger clumps, relative to arenas with more abundant but smaller clumps of vegetation, despite total resources remaining equal. While our functional response experiments illustrate the capacity of lizards to consume known agricultural pests, laboratory studies inherently ignore a suite of environmental characteristics which also affect predator-prey relationships, one being the spatial distribution of resources (Pitt & Ritchie, 2002). By using the optimal structure and distribution of vegetation as an asset to support natural enemies, the design and maintenance of agroecological habitats can bolster the associated contribution of predators to biocontrol services (Holland et al. 2016). Thus, a better understanding of the most advantageous mosaic of vegetation for both thermal dynamics and resource aggregation may further inform management decisions geared towards increasing the abundance of reptile predators.

Our results found no significant effect of lizard inclusion on chewing herbivory damage, which may have several explanations. Firstly, *P. erhardii* is not particularly known to glean vegetation (although they do exhibit plasticity in foraging behavior), therefore they may not consume those herbivorous insects responsible for plant damage. Furthermore, intraguild predation by lizards on predatory arthropods such as spiders may have stymied direct predation on herbivorous insects, resulting in increased plant damage. Likewise, in plots where lizards were experimentally removed, an increased abundance of predatory arthropods may have been responsible for reduction of plant damage, further masking any indirect effects of lizards on herbivory in our analysis (Pacala & Roughgarden, 1984). Future studies should investigate intraguild predation and include lizards' effect on arthropod identity, at least in the case of large, predatory arthropods.

Lastly, lizard foraging behavior may have been altered by the semi-natural enclosures. Specifically, the regular presence of human observers may have resulted in extended periods of hiding rather than engaging in foraging or exploratory behavior. The relatively high lizard stocking rate may have also prompted shifts in foraging behavior as a result of intraspecific competition or aggression, consistent with research showing adult density is correlated with variation in habitat usage in *Anolis* species (Delaney & Warner, 2017).

Lizards in our study plots were witnessed, however, interacting with the cucumber plants regularly at times of watering. Water scarcity is overcome by wall lizards through prey selection (Adamopoulou et al. 1999) and even more drastic dietary shifts, likely explaining recent records of frugivory for this species (Brock et al. 2014). Water limitation has been shown to directly reduce growth rate and activity in multiple lizard species (Lorenzon et al. 1999; Stamps & Tanaka, 1981), and water restriction is further implicated in delayed fitness response in both offspring and water-restricted *Zootoca vivipara* (European Common lizard) mothers despite no immediate effect on reproductive output (Dupoué et al. 2017). Given that water scarcity poses a serious obstacle to fitness and survival, the attraction of reptiles to irrigated crops within their surrounding habitat is not unlikely. The idea of reptiles exploiting artificial water sources is not unfounded; a recent comparative study showed *Tiliqua rugosa* (Australian sleepy lizard) populations varied in their home range area and activity levels depending on access to an artificial dam installed for grazing livestock. By late season, lizards without dam access had comparatively lower body condition (Leu & Bull, 2016). The behavior of lizards in our study poses an interesting hypothesis beyond overcoming water scarcity. The encouragement of water-limited reptiles near irrigated crops may potentially foster stronger biocontrol effects, whereby herbivorous insects avoid crops in the presence of vertebrate predators. While biocontrol is rarely implemented on the basis of indirect interactions (Chailleux et al. 2014), our observations illustrate the need for further investigation of the *combined* influence of trait-mediated effects and pairwise interactions.

This study provides basis for understanding the influence of wall lizards on invertebrate populations, where data are lacking given the widespread occurrence of this genus. Our hierarchical approach involving field and laboratory experiments, as well as consideration of indirect effects to vegetation, provides a strong starting point for future studies. We recommend future experiments be conducted over a significantly greater length of time. Our study period coincided with the tail end of the Mediterranean spring growing season, where climate becomes increasing hot and dry, inhospitable for many organisms. Lizard activity certainly slows during these months as well, therefore we were unable to fully assess temporal effects of lizard predation on invertebrate populations. Studies that straddle the entire growing season may better clarify interactions between treatment and time, offering a more holistic assessment of temporal effects. Potential top-down regulation of plant damage may fluctuate according to both arthropod and plant life stages, information germane to the efficacy of biocontrol. Year-round data collection may even elucidate potential to reduce overwintering pest populations, an area of study that has not been exhaustively researched (Tschumi et al. 2018).

Combined with existing empirical evidence, our study suggests that the efficacy of generalist predators as agents of invertebrate control is maximized under diverse predator assemblages, where the prevalence of multiple predators may bolster biocontrol services most effectively over spatiotemporal scales (Aquilino et al. 2005; Borkhataria et al. 2006; Dainese et al. 2017; Drieu & Rusch, 2017; Faria et al. 2008; Letourneau et al. 2009). Underlying the positive effects of multiple predators on biocontrol services is the ecological context in which they persist, such as structural complexity and niche complementarity (Fink & Denno, 2002; Tylianakis & Romo, 2010; Wilby et al. 2013). We argue that complementarity among functional groups is best harnessed through diverse, heterogeneous landscapes, consistent with a growing body of evidence that illustrates functional redundancy, and therefore resiliency, is best obtained through landscape complexity (Chaplin- Kramer et al. 2011; Gardiner et al. 2009; Laliberte et al. 2010). A recent meta-analysis of 552 experimental studies also confirms the role of plant diversity in promoting herbivore suppression (Letourneau et al. 2011). Results showed that enhancement of natural enemies, herbivore suppression, and reduction of crop damage were significantly stronger in diversified systems compared to monoculture or low-diversity systems (Letourneau et al. 2011). Great opportunity to maximize biocontrol services exists in agroecosystems, where the strategic maintenance of structurally and species-diverse landscapes fosters such ecosystem services.

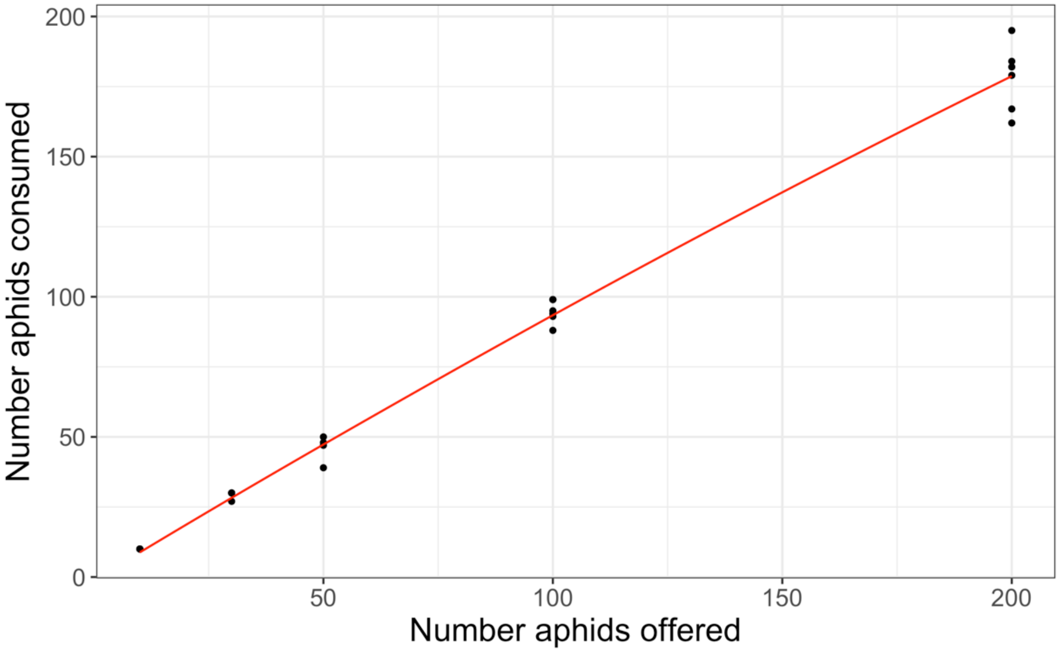
Our research question was centered around existing stone walls as an asset for promoting the occurrence of generalist predators in agricultural habitats. In the case of reptiles, habitat quality relates especially to the presence of a thermal mosaic and adequate hiding places. However, we wish to communicate more broadly the positive effects of including resource and/or structural habitat for predators, whether stone refugia or semi-natural vegetation, such as the incorporation of non-harvested hedgerows or native perennial borders (Isaacs et al. 2009; Morandin et al. 2016). Our research adds to a growing body of evidence illustrating high-quality habitat and food production spaces are not necessarily incongruent (Classen et al. 2014; Garbach et al. 2017; Vergara & Badano, 2009). By fostering biodiversity through spatial and temporal management decisions, organisms may provide free pest control among other important ecosystem services. Given its proportion of terrestrial area and impact beyond spatial boundaries, agricultural land use must continue to be investigated for its role in conservation in this era of anthropogenic global change. With under 15% of land currently under protection (World Bank, 2019), further intensification under the label ‘land sparing’ should be met with alternative strategies, where multifunctional objectives of global food security and biodiversity preservation may overlap. Further studies that pragmatically quantify ecosystem services provided by complex agricultural landscapes are urgently needed to confront a global food regime dependent on agro-chemicals at the expense of ecosystem and human health.

## FIGURES

*Figure 1.* Field site in Moni, Naxos showing stone terraces surrounded by mature olive groves and native vegetation.

*Figure 2.* Photograph of an adult Aegean wall lizard, *Podarcis erhardii,* captured from the field site in Moni, Naxos.

*Figure 3.* Adult male Aegean wall lizard, *Podarcis erhardii*, basking on the top of a dry stone wall at field site in Moni, Naxos.



*Figur*e 4. Type I functional response of *P. erhardii* on aphids. Line represents predicted responses based on the fitted Type I linear mixed effects model.

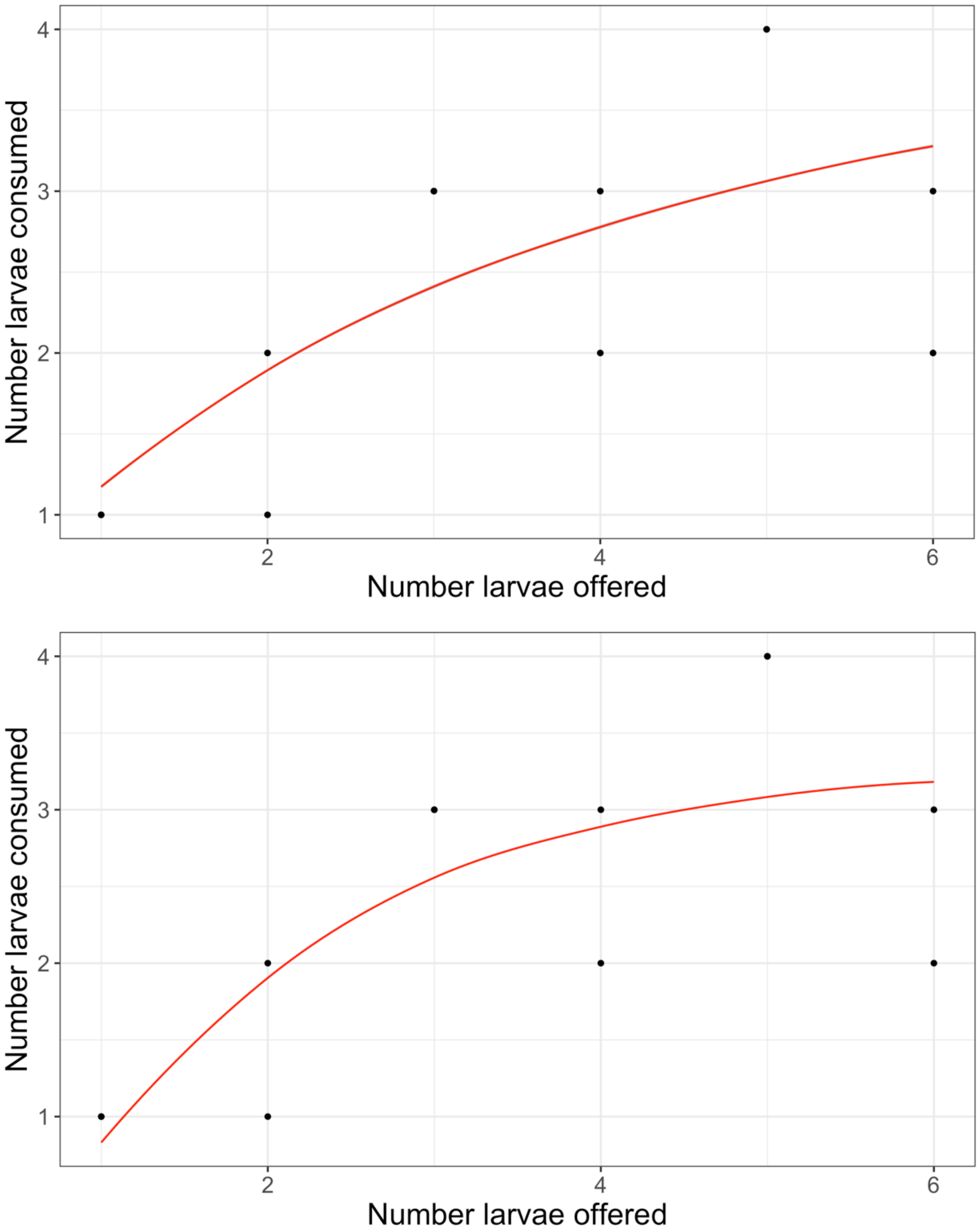


*Figure 5.* Type II (top) and Type III (bottom) functional response of *P. erhardii* on *P. rapae* larvae. Curves represent predicted values from nonlinear least squares regression models. The Type III response curve does not have the typical ‘S-shape’ indicative of greater search time (not measured in this study) but does illustrate a marginally lower satiation point.

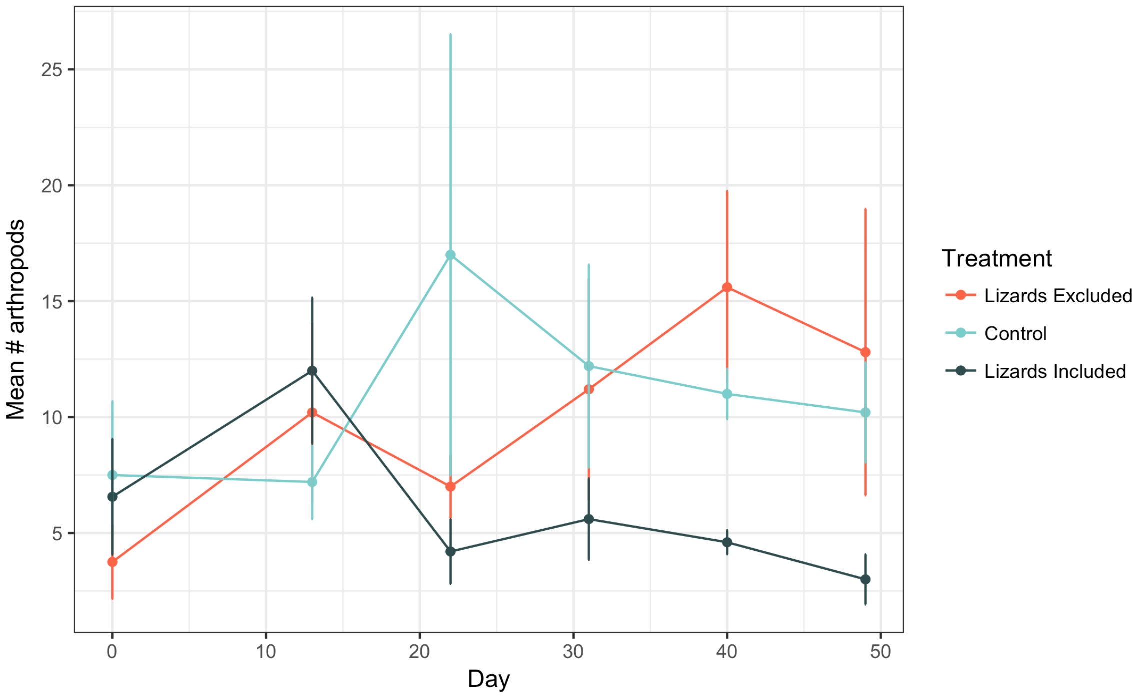


*Figure 6.* Mean abundance of ground-dwelling arthropods sized 2-5 mm over study period. Error bars represent SE.

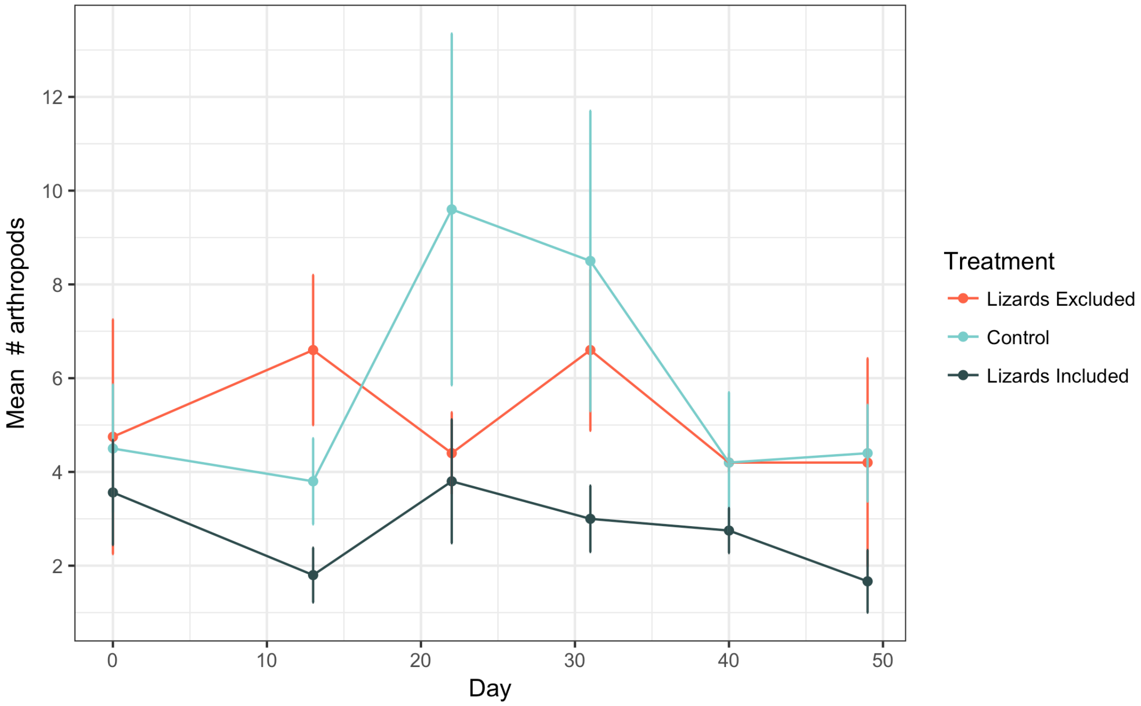


*Figure 7.* Mean abundance of ground-dwelling arthropods sized >5 mm over study period. Error bars represent SE.

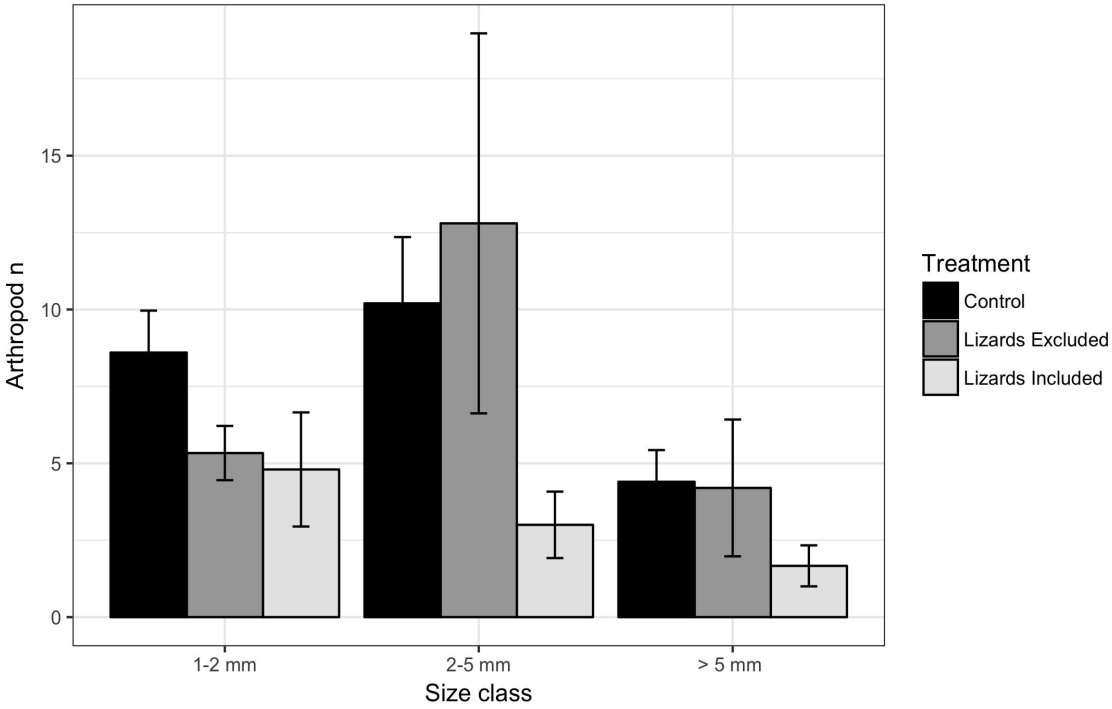


*Figure 8.* Ground-dwelling arthropod abundance at final sampling period. Error bars represent SE.

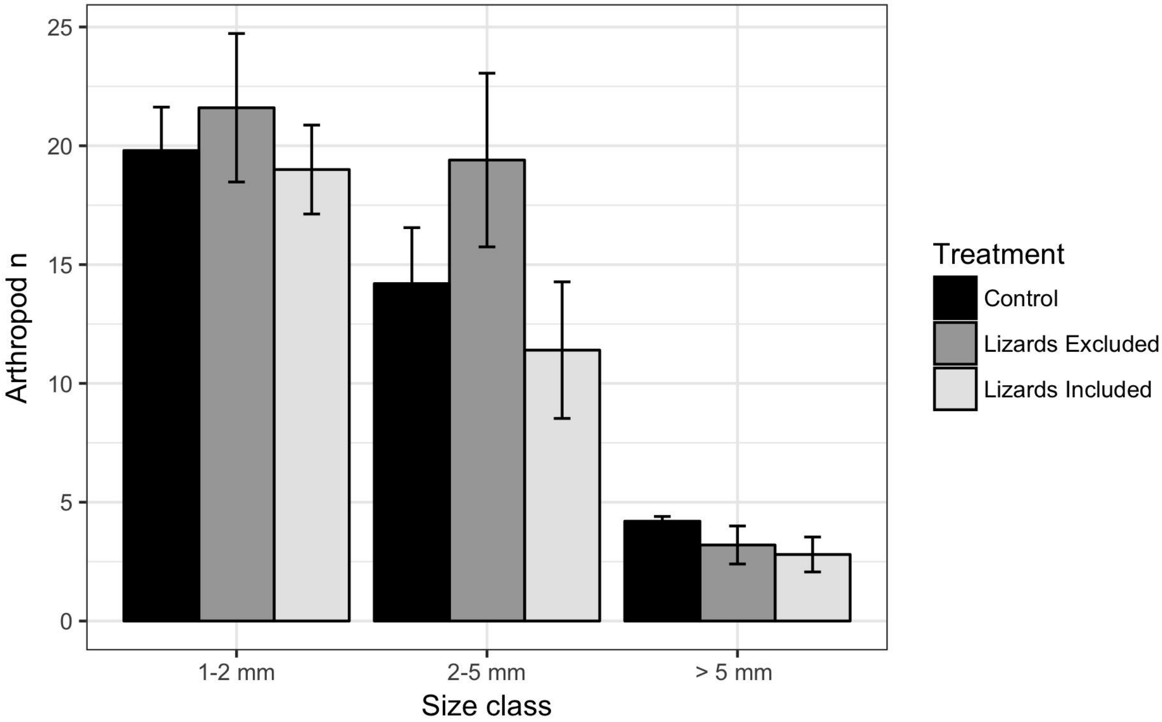


*Figure 9.* Airborne arthropod abundance at final sampling period. Error bars represent SE.

## TABLES

Table 1

*Summary of results of linear mixed effect model from pitfall trap data, arthropods size class 1-2 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | Log$_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 1.123 | 0.90 – 1.35 | 0.12 | <.001 |
| Treatment (Control) | -0.126 | -0.43 – 0.18 | 0.16 | .419 |
| Treatment (Lizards Included) | 0.199 | -0.11 – 0.51 | 0.16 | .218 |
| Day | -0.006 | -0.01 – 0.00 | 0.00 | .144 |
| Treatment (Control) * Day | 0.002 | -0.01 – 0.01 | 0.01 | .735 |
| Treatment (Lizards Included) * Day | -0.008 | -0.02 – 0.00 | 0.01 | .115 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.095 | | | |
| $\tau_{00, \text{site}}$ | 0.001 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $ICC_{\text{site}}$ | 0.014 | | | |
| Observations | 85 | | | |
| $R^2$ / $\Omega_0^2$ | .215 / .215 | | | |
| AIC | 91.797 | | | |

Table 2

*Summary of results of linear mixed effect model from pitfall trap data, arthropods size class 2-5 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | $\text{Log}_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 0.561 | 0.31 – 0.82 | 0.13 | <.001 |
| Treatment (Control) | 0.225 | -0.13 – 0.58 | 0.18 | .226 |
| Treatment (Lizards Included) | 0.266 | -0.09 – 0.63 | 0.18 | .155 |
| Day | 0.010 | 0.00 – 0.02 | 0.00 | .014 |
| Treatment (Control) * Day | -0.005 | -0.02 – 0.01 | 0.01 | .384 |
| Treatment (Lizards Included) * Day | -0.017 | -0.03 – -0.01 | 0.01 | .006 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.128 | | | |
| $\tau_{00,\ \text{site}}$ | 0.000 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $ICC_{\text{site}}$ | 0.000 | | | |
| Observations | 85 | | | |
| $R^2$ / $\Omega_0^2$ | .188 / .188 | | | |
| AIC | 114.317 | | | |

Table 3

*Summary of results of linear mixed effect model from pitfall trap data, arthropods size class >5 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | $\text{Log}_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 0.718 | 0.47 – 0.97 | 0.13 | <.001 |
| Treatment (Control) | -0.084 | -0.37 – 0.21 | 0.15 | .572 |
| Treatment (Lizards Included) | -0.303 | -0.60 – -0.00 | 0.15 | .052 |
| Day | -0.004 | -0.01 – 0.00 | 0.00 | .317 |
| Treatment (Control) * Day | 0.004 | -0.01 – 0.01 | 0.00 | .431 |
| Treatment (Lizards Included) * Day | 0.001 | -0.01 – 0.01 | 0.01 | .865 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.081 | | | |
| $\tau_{00,\text{ site}}$ | 0.018 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $\text{ICC}_{\text{site}}$ | 0.180 | | | |
| Observations | 82 | | | |
| $R^2$ / $\Omega_0^2$ | .330 / .327 | | | |
| AIC | 83.029 | | | |

Table 4

*Summary of results of linear mixed effect model from sticky trap data, airborne arthropods size class 1-2 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | $\text{Log}_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 1.913 | 1.58 – 2.25 | 0.17 | <.001 |
| Treatment (Control) | 0.046 | -0.43 – 0.52 | 0.24 | .850 |
| Treatment (Lizards Included) | -0.002 | -0.48 – 0.47 | 0.24 | .992 |
| Day | -0.007 | -0.02 – 0.00 | 0.01 | .224 |
| Treatment (Control) * Day | -0.002 | -0.02 – 0.01 | 0.01 | .824 |
| Treatment (Lizards Included) * Day | -0.002 | -0.02 – 0.01 | 0.01 | .791 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.255 | | | |
| $\tau_{00,\ \text{site}}$ | 0.001 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $\text{ICC}_{\text{site}}$ | 0.003 | | | |
| Observations | 90 | | | |
| $R^2 / \Omega_0^2$ | .079 / .079 | | | |
| AIC | 176.913 | | | |

Table 5

*Summary of results of linear mixed effect model from sticky trap data, airborne arthropods size class 2-5 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | $\text{Log}_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 1.161 | 0.94 – 1.38 | 0.11 | <.001 |
| Treatment (Control) | 0.324 | 0.04 – 0.61 | 0.15 | .038 |
| Treatment (Lizards Included) | 0.109 | -0.18 – 0.40 | 0.15 | .466 |
| Day | 0.004 | -0.00 – 0.01 | 0.00 | .250 |
| Treatment (Control) * Day | -0.007 | -0.02 – 0.00 | 0.00 | .151 |
| Treatment (Lizards Included) * Day | -0.007 | -0.02 – 0.00 | 0.00 | .168 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.093 | | | |
| $\tau_{00,\ \text{site}}$ | 0.009 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $\text{ICC}_{\text{site}}$ | 0.089 | | | |
| Observations | 90 | | | |
| $R^2 / \Omega_0^2$ | .200 / .195 | | | |
| AIC | 96.068 | | | |

Table 6

*Summary of results of linear mixed effect model from sticky trap data, airborne arthropods size class > 5 mm. Intercept represents lizard removal plot, and all other variables theoretically equal to zero.*

| | $\text{Log}_{10}$ Arthropod n | | | |
|---|---|---|---|---|
| | *B* | *CI* | *std. Error* | *p* |
| **Fixed Parts** | | | | |
| (Intercept) | 0.807 | 0.53 – 1.08 | 0.14 | <.001 |
| Treatment (Control) | 0.163 | -0.11 – 0.44 | 0.14 | .251 |
| Treatment (Lizards Included) | -0.081 | -0.36 – 0.19 | 0.14 | .570 |
| Day | -0.008 | -0.01 – -0.00 | 0.00 | .018 |
| Treatment (Control) * Day | -0.002 | -0.01 – 0.01 | 0.00 | .730 |
| Treatment (Lizards Included) * Day | 0.002 | -0.01 – 0.01 | 0.00 | .7206 |
| **Random Parts** | | | | |
| $\sigma^2$ | 0.085 | | | |
| $\tau_{00,\ \text{site}}$ | 0.049 | | | |
| $N_{\text{site}}$ | 5 | | | |
| $\text{ICC}_{\text{site}}$ | 0.365 | | | |
| Observations | 89 | | | |
| $R^2$ / $\Omega_0^2$ | .459 / .458 | | | |
| AIC | 94.073 | | | |

Table 7

*$AIC_C$ values assigned to linear mixed effect models fitting type I, II, and III functional response for P. erhardii consumption of aphids.*

| **Model** | **$AIC_C$** | **$\Delta AIC_C$** |
|---|---|---|
| *Type I* | 150.73 | 0.00 |
| *Type II* | 153.40 | 2.67 |
| *Type III* | 196.86 | 46.13 |

Table 8

*$AIC_C$ values assigned to nonlinear least squares regression models fitting type I, II, and III functional response for P. erhardii consumption of P. rapae.*

| **Model** | **$AIC_C$** | **$\Delta AIC_C$** |
|---|---|---|
| *Type I* | 36.02 | 2.84 |
| *Type II* | 34.17 | 0.99 |
| *Type III* | 33.18 | 0.00 |

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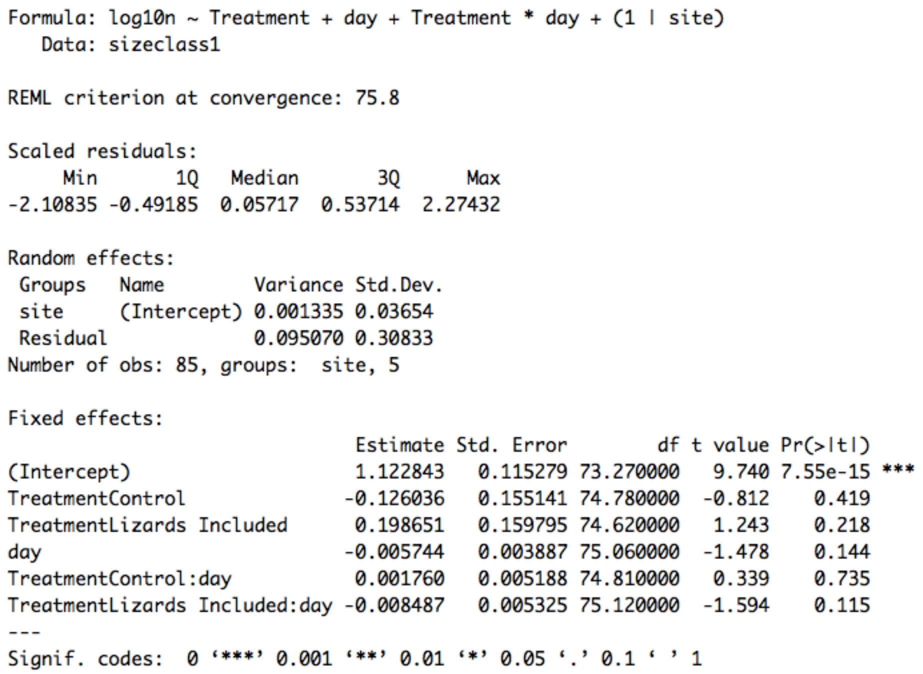
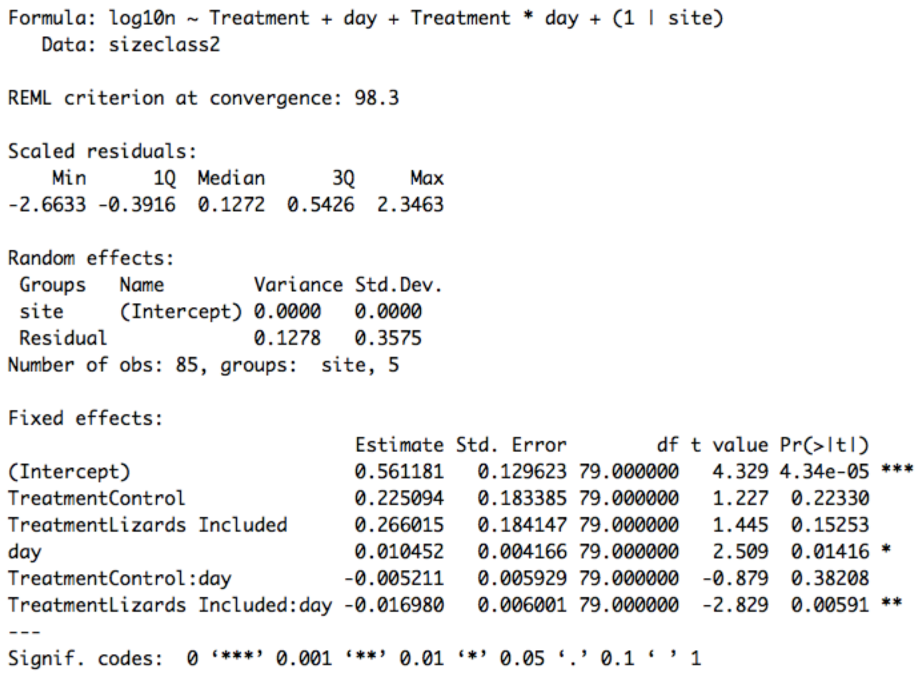
# APPENDICES

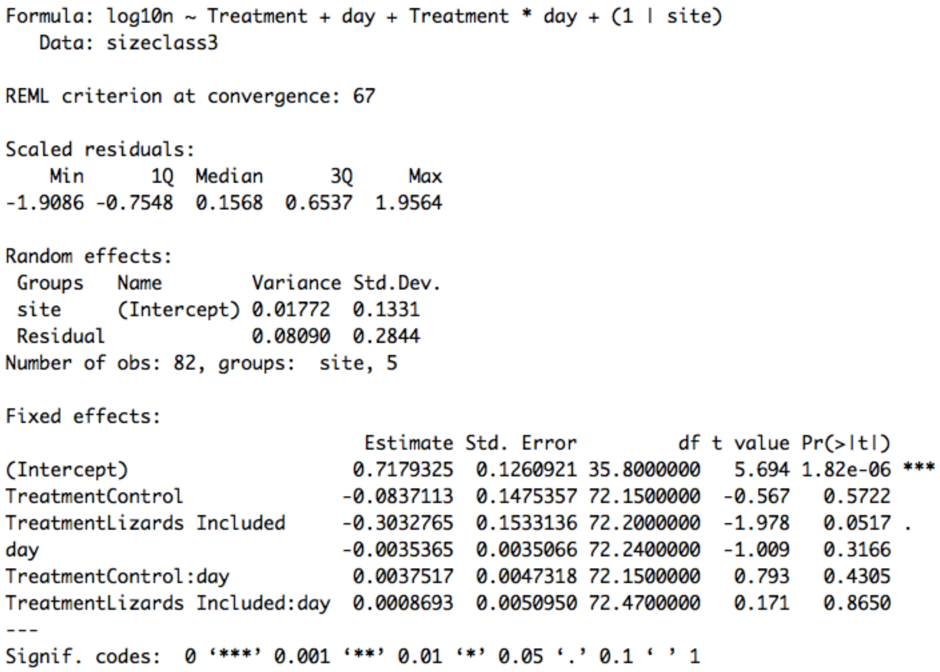
## *1. R outputs of linear mixed effect models for pitfall trap data*



```
Formula: log10n ~ Treatment + day + Treatment * day + (1 | site)
   Data: sizeclass1

REML criterion at convergence: 75.8

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.10835 -0.49185  0.05717  0.53714  2.27432 

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.001335 0.03654 
 Residual             0.095070 0.30833 
Number of obs: 85, groups:  site, 5

Fixed effects:
                              Estimate Std. Error        df t value Pr(>|t|)    
(Intercept)                   1.122843   0.115279 73.270000   9.740 7.55e-15 ***
TreatmentControl             -0.126036   0.155141 74.780000  -0.812    0.419    
TreatmentLizards Included     0.198651   0.159795 74.620000   1.243    0.218    
day                          -0.005744   0.003887 75.060000  -1.478    0.144    
TreatmentControl:day          0.001760   0.005188 74.810000   0.339    0.735    
TreatmentLizards Included:day -0.008487   0.005325 75.120000  -1.594    0.115    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

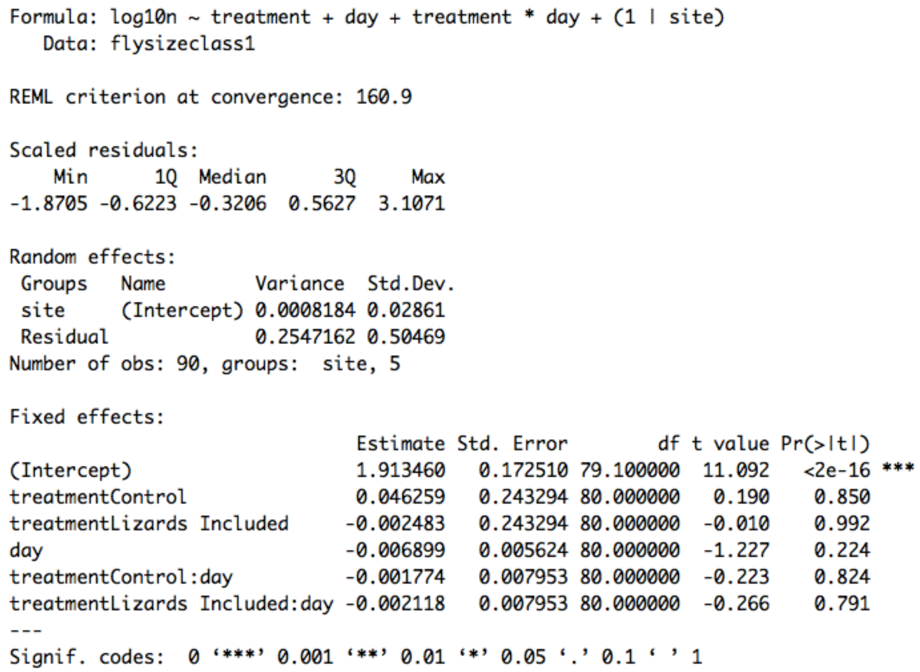


```
Formula: log10n ~ Treatment + day + Treatment * day + (1 | site)
   Data: sizeclass2

REML criterion at convergence: 98.3

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-2.6633 -0.3916  0.1272  0.5426  2.3463 

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.0000   0.0000  
 Residual             0.1278   0.3575  
Number of obs: 85, groups:  site, 5

Fixed effects:
                              Estimate Std. Error        df t value Pr(>|t|)    
(Intercept)                   0.561181   0.129623 79.000000   4.329 4.34e-05 ***
TreatmentControl              0.225094   0.183385 79.000000   1.227  0.22330    
TreatmentLizards Included     0.266015   0.184147 79.000000   1.445  0.15253    
day                           0.010452   0.004166 79.000000   2.509  0.01416 *  
TreatmentControl:day         -0.005211   0.005929 79.000000  -0.879  0.38208    
TreatmentLizards Included:day -0.016980   0.006001 79.000000  -2.829  0.00591 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

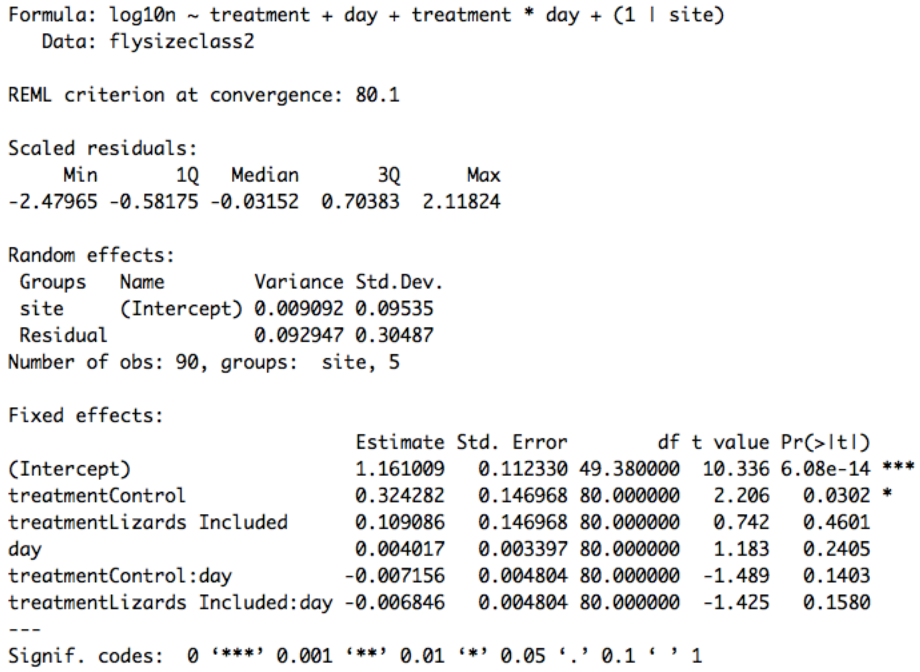


```
Formula: log10n ~ Treatment + day + Treatment * day + (1 | site)
   Data: sizeclass3

REML criterion at convergence: 67

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-1.9086 -0.7548  0.1568  0.6537  1.9564 

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.01772  0.1331  
 Residual             0.08090  0.2844  
Number of obs: 82, groups:  site, 5

Fixed effects:
                                Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)                    0.7179325  0.1260921 35.8000000   5.694 1.82e-06 ***
TreatmentControl              -0.0837113  0.1475357 72.1500000  -0.567   0.5722    
TreatmentLizards Included     -0.3032765  0.1533136 72.2000000  -1.978   0.0517 .  
day                           -0.0035365  0.0035066 72.2400000  -1.009   0.3166    
TreatmentControl:day           0.0037517  0.0047318 72.1500000   0.793   0.4305    
TreatmentLizards Included:day  0.0008693  0.0050950 72.4700000   0.171   0.8650    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

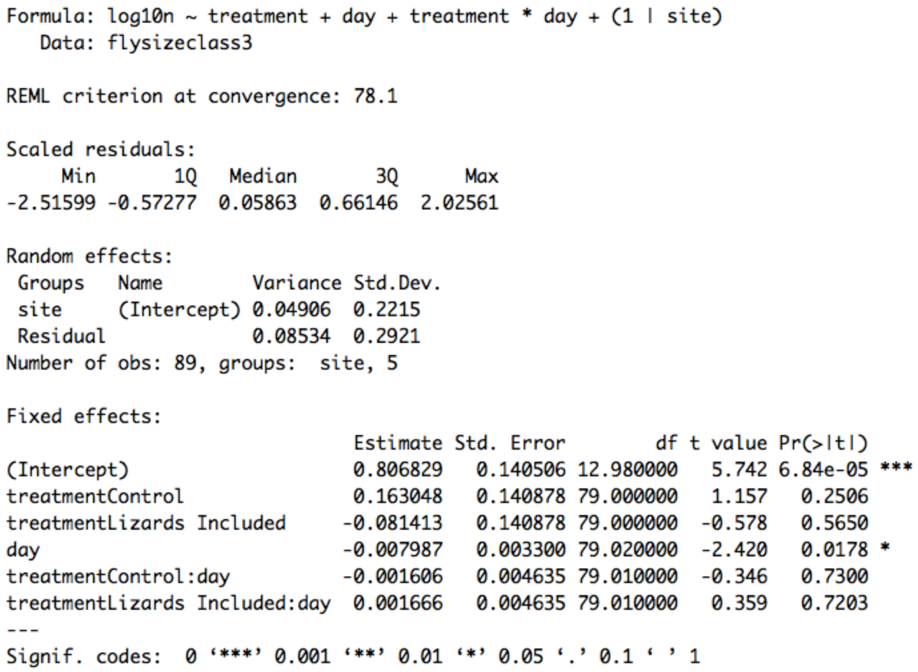
## *2. R outputs of linear mixed effect models for sticky trap data*



```
Formula: log10n ~ treatment + day + treatment * day + (1 | site)
   Data: flysizeclass1

REML criterion at convergence: 160.9

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.8705 -0.6223 -0.3206  0.5627  3.1071

Random effects:
 Groups   Name        Variance  Std.Dev.
 site     (Intercept) 0.0008184 0.02861
 Residual             0.2547162 0.50469
Number of obs: 90, groups:  site, 5

Fixed effects:
                               Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                    1.913460   0.172510 79.100000  11.092   <2e-16 ***
treatmentControl               0.046259   0.243294 80.000000   0.190    0.850
treatmentLizards Included     -0.002483   0.243294 80.000000  -0.010    0.992
day                           -0.006899   0.005624 80.000000  -1.227    0.224
treatmentControl:day          -0.001774   0.007953 80.000000  -0.223    0.824
treatmentLizards Included:day -0.002118   0.007953 80.000000  -0.266    0.791
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

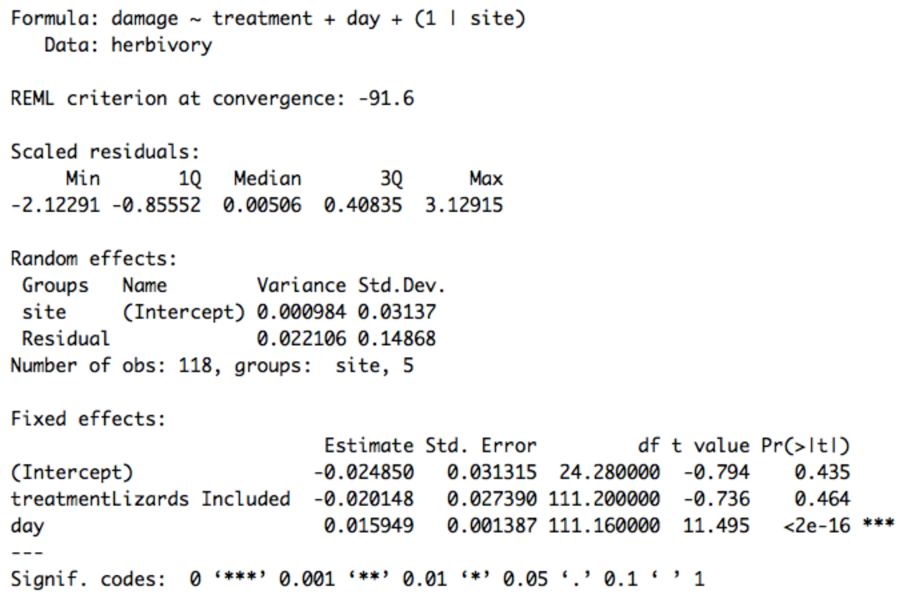


```
Formula: log10n ~ treatment + day + treatment * day + (1 | site)
   Data: flysizeclass2

REML criterion at convergence: 80.1

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.47965 -0.58175 -0.03152  0.70383  2.11824

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.009092 0.09535
 Residual             0.092947 0.30487
Number of obs: 90, groups:  site, 5

Fixed effects:
                               Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                    1.161009   0.112330 49.380000  10.336 6.08e-14 ***
treatmentControl               0.324282   0.146968 80.000000   2.206   0.0302 *
treatmentLizards Included      0.109086   0.146968 80.000000   0.742   0.4601
day                            0.004017   0.003397 80.000000   1.183   0.2405
treatmentControl:day          -0.007156   0.004804 80.000000  -1.489   0.1403
treatmentLizards Included:day -0.006846   0.004804 80.000000  -1.425   0.1580
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

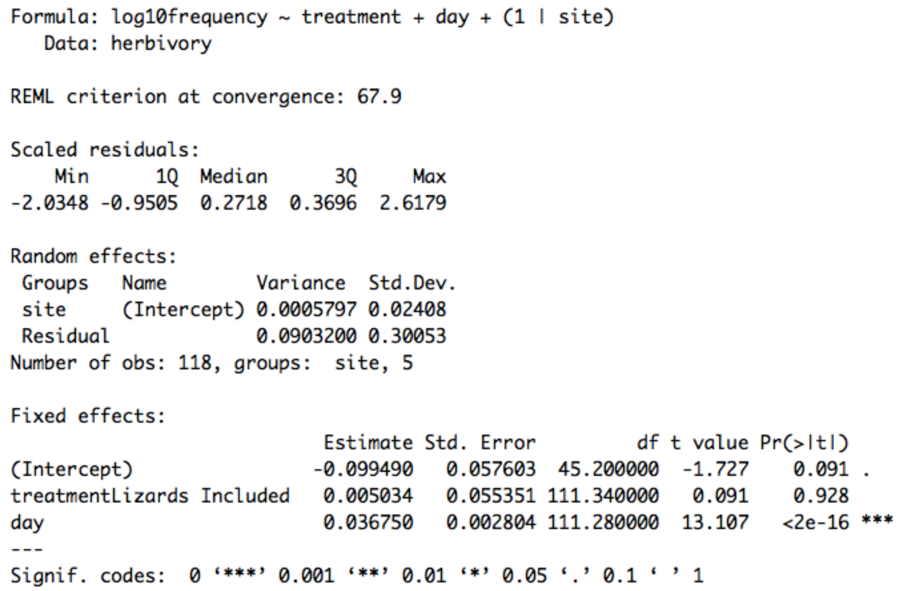


```
Formula: log10n ~ treatment + day + treatment * day + (1 | site)
   Data: flysizeclass3

REML criterion at convergence: 78.1

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.51599 -0.57277  0.05863  0.66146  2.02561

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.04906  0.2215
 Residual             0.08534  0.2921
Number of obs: 89, groups:  site, 5

Fixed effects:
                               Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                    0.806829   0.140506 12.980000   5.742 6.84e-05 ***
treatmentControl               0.163048   0.140878 79.000000   1.157   0.2506
treatmentLizards Included     -0.081413   0.140878 79.000000  -0.578   0.5650
day                           -0.007987   0.003300 79.020000  -2.420   0.0178 *
treatmentControl:day          -0.001606   0.004635 79.010000  -0.346   0.7300
treatmentLizards Included:day  0.001666   0.004635 79.010000   0.359   0.7203
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

*3. R outputs of linear mixed effect models for herbivory data.*

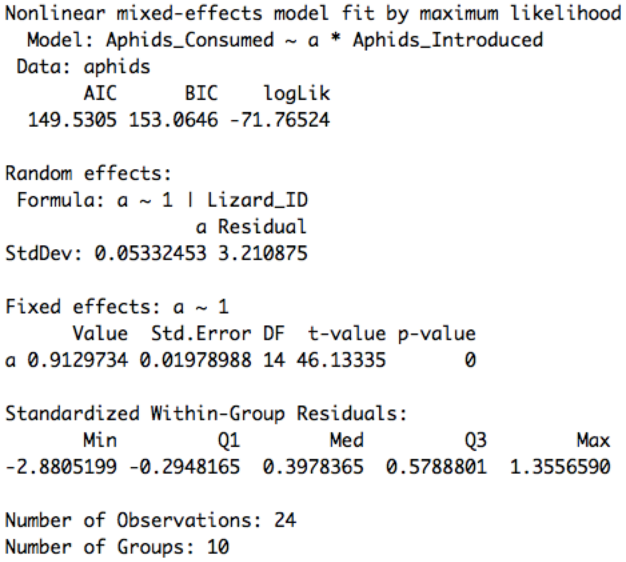


```
Formula: damage ~ treatment + day + (1 | site)
   Data: herbivory

REML criterion at convergence: -91.6

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.12291 -0.85552  0.00506  0.40835  3.12915 

Random effects:
 Groups   Name        Variance Std.Dev.
 site     (Intercept) 0.000984 0.03137 
 Residual             0.022106 0.14868 
Number of obs: 118, groups:  site, 5

Fixed effects:
                            Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)                -0.024850   0.031315  24.280000  -0.794    0.435    
treatmentLizards Included  -0.020148   0.027390 111.200000  -0.736    0.464    
day                         0.015949   0.001387 111.160000  11.495   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

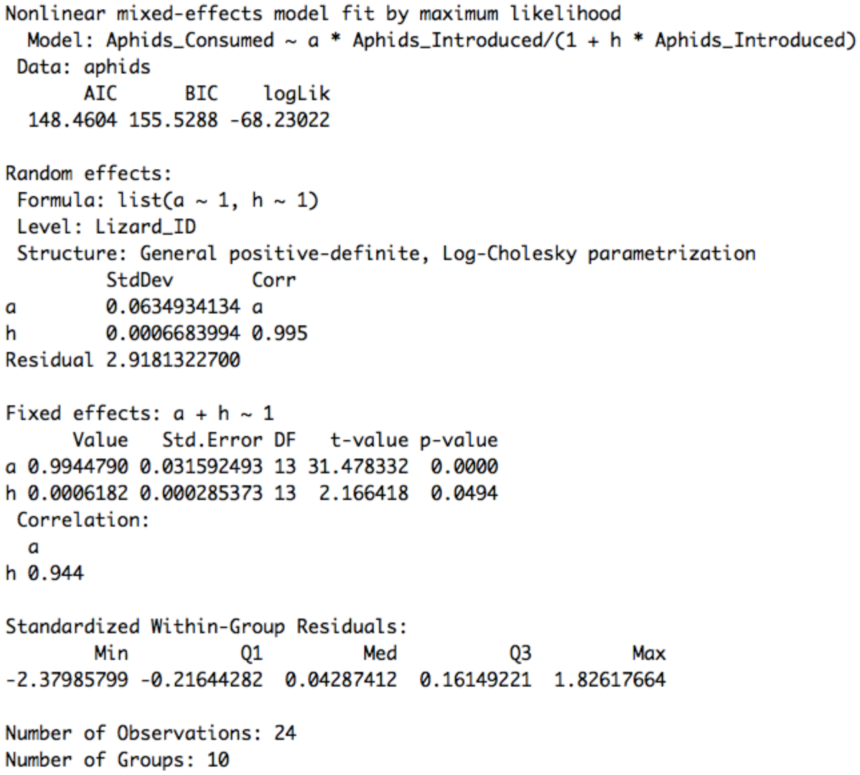


```
Formula: log10frequency ~ treatment + day + (1 | site)
   Data: herbivory

REML criterion at convergence: 67.9

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-2.0348 -0.9505  0.2718  0.3696  2.6179 

Random effects:
 Groups   Name        Variance  Std.Dev.
 site     (Intercept) 0.0005797 0.02408 
 Residual             0.0903200 0.30053 
Number of obs: 118, groups:  site, 5

Fixed effects:
                            Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)                -0.099490   0.057603  45.200000  -1.727    0.091 .  
treatmentLizards Included   0.005034   0.055351 111.340000   0.091    0.928    
day                         0.036750   0.002804 111.280000  13.107   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

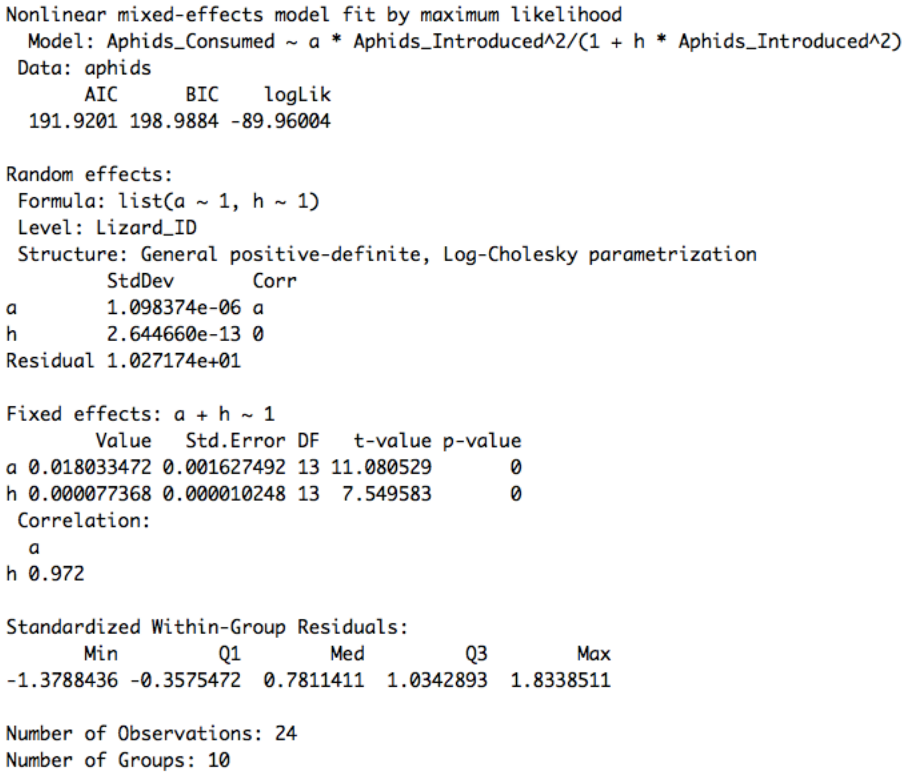
*4. R output for Type I, II, and III models used to fit aphid consumption data.*



```
Nonlinear mixed-effects model fit by maximum likelihood
  Model: Aphids_Consumed ~ a * Aphids_Introduced
 Data: aphids
       AIC      BIC    logLik
  149.5305 153.0646 -71.76524

Random effects:
 Formula: a ~ 1 | Lizard_ID
                 a Residual
StdDev: 0.05332453 3.210875

Fixed effects: a ~ 1
      Value  Std.Error DF  t-value p-value
a 0.9129734 0.01978988 14 46.13335       0

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.8805199 -0.2948165  0.3978365  0.5788801  1.3556590

Number of Observations: 24
Number of Groups: 10
```

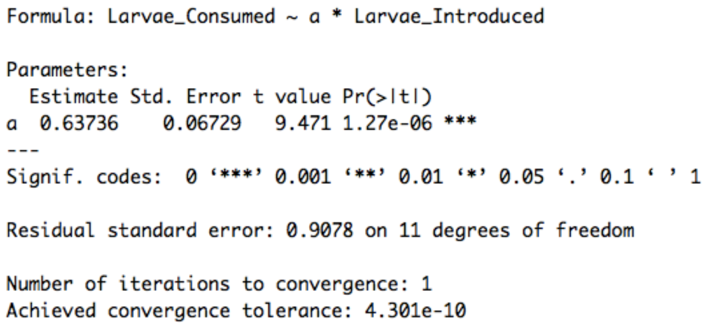


```
Nonlinear mixed-effects model fit by maximum likelihood
  Model: Aphids_Consumed ~ a * Aphids_Introduced/(1 + h * Aphids_Introduced)
 Data: aphids
       AIC      BIC    logLik
  148.4604 155.5288 -68.23022

Random effects:
 Formula: list(a ~ 1, h ~ 1)
 Level: Lizard_ID
 Structure: General positive-definite, Log-Cholesky parametrization
         StdDev       Corr
a        0.0634934134 a
h        0.0006683994 0.995
Residual 2.9181322700

Fixed effects: a + h ~ 1
      Value   Std.Error DF   t-value p-value
a 0.9944790 0.031592493 13 31.478332  0.0000
h 0.0006182 0.000285373 13  2.166418  0.0494
 Correlation:
  a
h 0.944

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.37985799 -0.21644282  0.04287412  0.16149221  1.82617664

Number of Observations: 24
Number of Groups: 10
```

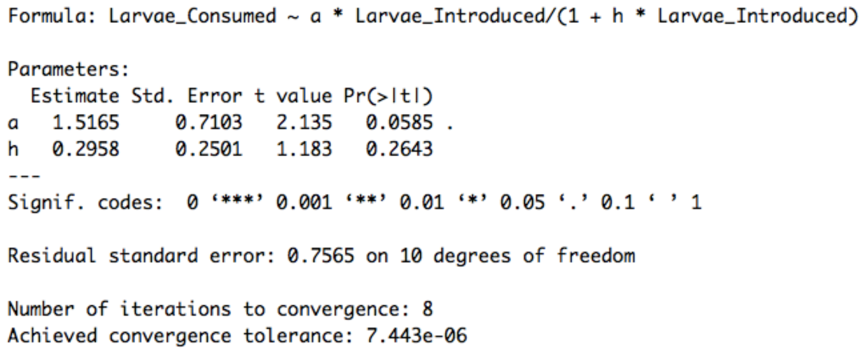


```
Nonlinear mixed-effects model fit by maximum likelihood
  Model: Aphids_Consumed ~ a * Aphids_Introduced^2/(1 + h * Aphids_Introduced^2)
 Data: aphids
       AIC      BIC    logLik
  191.9201 198.9884 -89.96004

Random effects:
 Formula: list(a ~ 1, h ~ 1)
 Level: Lizard_ID
 Structure: General positive-definite, Log-Cholesky parametrization
         StdDev       Corr
a        1.098374e-06 a
h        2.644660e-13 0
Residual 1.027174e+01

Fixed effects: a + h ~ 1
        Value   Std.Error DF   t-value p-value
a 0.018033472 0.001627492 13 11.080529       0
h 0.000077368 0.000010248 13  7.549583       0
 Correlation:
  a
h 0.972

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.3788436 -0.3575472  0.7811411  1.0342893  1.8338511

Number of Observations: 24
Number of Groups: 10
```

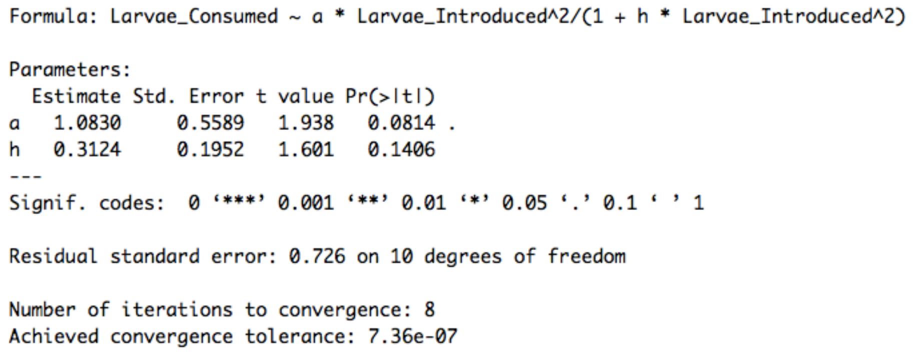
*5. R output for Type I, II, and III models used to fit Cabbage white larvae consumption data.*



```
Formula: Larvae_Consumed ~ a * Larvae_Introduced

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.63736    0.06729   9.471 1.27e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.9078 on 11 degrees of freedom

Number of iterations to convergence: 1
Achieved convergence tolerance: 4.301e-10
```



```
Formula: Larvae_Consumed ~ a * Larvae_Introduced/(1 + h * Larvae_Introduced)

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a   1.5165     0.7103   2.135   0.0585 .
h   0.2958     0.2501   1.183   0.2643
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.7565 on 10 degrees of freedom

Number of iterations to convergence: 8
Achieved convergence tolerance: 7.443e-06
```



```
Formula: Larvae_Consumed ~ a * Larvae_Introduced^2/(1 + h * Larvae_Introduced^2)

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a   1.0830     0.5589   1.938   0.0814 .
h   0.3124     0.1952   1.601   0.1406
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.726 on 10 degrees of freedom

Number of iterations to convergence: 8
Achieved convergence tolerance: 7.36e-07
```