

Grazing of *Utetheisa pulchelloides* Larvae on its Host Plant, *Argusia argentea*, on Coral Cays of the Great Barrier Reef¹

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ABSTRACT

The foraging behavior and grazing intensities of *Utetheisa pulchelloides* (Lepidoptera: Arctiidae) larvae were examined on its host plant, *Argusia argentea*, a prostrate shrub commonly found on coral cays of the Great Barrier Reef. Larval abundance was greatest during summer (January–February), just after the major flush of *Argusia* leaves. The larvae were host specific, consuming approximately 2.9 cm² leaf area/day (annually 2–5% *Argusia* leaf production of One Tree Island), and exhibited significant preferences for windward, shade leaves. Their diurnal activity was comprised of 53 percent feeding, 8 percent moving, and 39 percent resting. Displacement experiments showed greatest nonrandom tendency to relocate the host plant when navigating westward, but nonetheless involved a large time and energy investment. The turnover of *Argusia* leaf biomass through the grazing pathway is not high; presumably predators, physical environment, or factors other than food supply limit the *Utetheisa* populations on coral cays.

ALTHOUGH HERBIVOROUS LARVAE ARE COMMONLY ASSOCIATED WITH FOREST COMMUNITIES, the dispersal and feeding behavior of individuals are difficult to determine in this habitat due to the logistic problems associated with the structural complexity and inaccessibility of the canopy. Because of these problems encountered in the field, most studies on feeding behavior of insect herbivores have been confined to the laboratory (Cates and Orians 1975, Scriber and Feeny 1979). Most defoliation studies rely on both controlled conditions and simulated grazing methods (e.g., Lee and Bazzaz 1980, Lowman 1982a). However, the isolation of individuals from their natural surroundings may influence feeding and development.

The coral islands of the Great Barrier Reef provide isolated patches of vegetation that are rather simple both structurally and floristically. In particular, One Tree Island (23°30'S latitude, 152°08'E longitude), has 21 permanent plant species (Heatwole *et al.* 1981) including approximately 128 shrubs of *Argusia argentea*, a prostrate, continuously-leaving shrub whose distribution extends throughout the Indo-Pacific from East Africa to the East Indies. On One Tree, *Argusia argentea* is the host plant to a monophagous Lepidopteran larva of the moth *Utetheisa pulchelloides* (Arctiidae). The caterpillars are abundant, albeit with some seasonality, with cohorts staggered throughout the year.

Argusia establishes on open beaches, usually just above the high tide line although sometimes extending into the island interior. This tendency to grow on exposed island edges may be a consequence of its oceanic seed dispersal (Guppy 1891). In fact, salt water exposure appears to be a prerequisite to germination (Lesko and Walter 1969).

The most critical factor affecting the survival of *Argusia* appears to be the physical environment: salt and wind exposure, and availability of fresh water and nutrients. No studies, however, have been conducted to quantify aspects of its biological environment or to examine the consequence of its plant-animal interactions.

Sydney University operates a research station on One Tree Island, which provides an ideal outdoor laboratory for studying herbivory on *Argusia* shrubs. The prostrate growth form of *Argusia* bushes creates an almost two-dimensional system, conducive for behavioral studies of herbivores on their host plant, that are not logistically feasible in three-dimensional forest ecosystems. In this study, several aspects of the life history, feeding rates, and foraging behavior involved in this plant-insect relationship were examined:

1. What are the abundance and feeding rates of *Utetheisa* larvae on *Argusia* bushes?
2. What is the range of foraging patterns of the herbivores?
3. What are the implications to growth and biomass of coral cay vegetation?

METHODS

FIELD OBSERVATIONS OF *UTETHEISA* LARVAE.—Aspects of larval behavior were observed under field conditions over five trips to One Tree Island between 1979–1981. During each trip the following data were recorded: phenology of *Argusia* shrubs; number of larvae in 20 one-meter³ plots; and defoliation damage of different samples of leaves. For assessments of defoliation damage, groups of 30 leaves were picked to represent young and old ages, sun and shade light regimes, and windward and leeward sides of the island; leaf area, proportion of leaf missing to herbivores, and fresh and dry weights were measured.

¹ Received 24 November 1982, revised 7 June 1983, accepted 26 June 1983.

Leaf areas were calculated with a Lambda portable area meter (model 3000), and the leaf holes were masked with tape to calculate the area of leaf eaten (see Lowman 1982b). Additional leaf samples were collected from five other coral cays in July 1982, and similarly assessed for grazing damage. Sweep sampling (100 sweeps per cay) was also conducted with nets (38 cm diameter) to census *Utetheisa* larvae and other insects. The abundance of larvae was compared to leaf damage levels.

FEEDING RATES AND FORAGING BEHAVIOR.—Several field and laboratory experiments were conducted to observe the feeding behavior of *Utetheisa* larvae. First, larvae were placed in glass cylindrical chambers (on sprays of leaves whose branches were immersed in water baths) to measure feeding rates and determine host plant preferences. Amounts of leaf area eaten and number of frass pellets produced were counted daily. Different plant species were offered to test larval food preferences.

Second, thirty larvae were marked in the field with drops of colored nail polish on their dorsal sides. They were observed at hourly intervals during morning (0500–1100 hr), midday (1100–1700 hr), and evening (1700–2300 hr) to determine the amounts of time allocated to different activities. During each hour, larval behavior was noted every minute and recorded as movement, feeding, or resting. In addition, 10 of the larvae were tracked for up to 19 days, and observed for home ranges, distance travelled, and rosettes visited (the remaining 20 disappeared).

Third, larvae were tested for ability to navigate back to a host bush after displacement, as would happen when wind or bird movements dislodge them from a leaf. Twenty larvae were selected, and each larva was placed in black bag to block out any light-related directional senses, and then removed and placed one m away from the base of its bush, either N, S, E, or W from the original location. At one minute intervals, the direction in which the larva travelled was recorded to determine whether larval orientation was random.

RESULTS

PHENOLOGIES OF ARGUSIA AND UTETHEISA.—Both flowering and leafing in *Argusia* peak in approximately October–November (Fig. 1, adapted from Heatwole *et al.* 1981). The leaf fall exhibits no such peak, but rather fluctuates throughout the year. The numbers of *Utetheisa* larvae in *Argusia* bushes peak during January–February, approximately 2–3 months after the major leaf flush. This pattern probably ensures the larvae of maximum availability of new, fully-expanded leaves since most leaves have flushed and expanded. Leaf flushing, flower production and larval numbers all decline during late summer and winter. *Utetheisa* larvae are present in *Argusia*

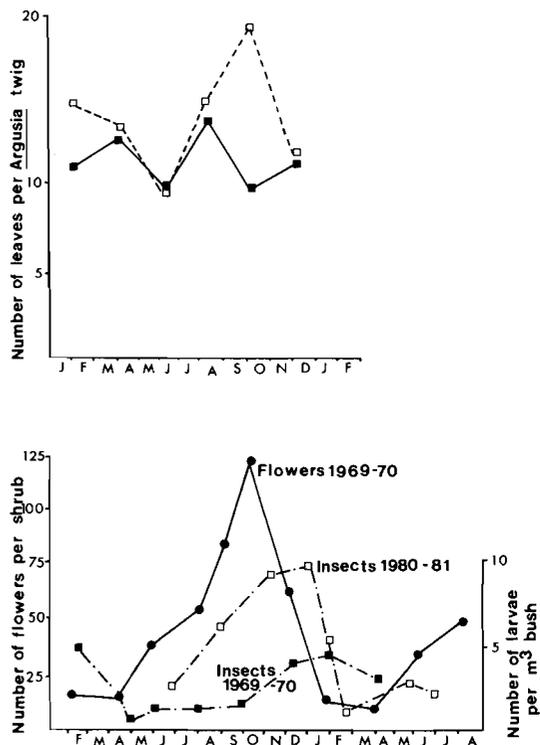


FIGURE 1. Phenology of *Argusia argentea*, showing peak periods of leafing, leaf fall, and flowering in relation to relative abundance of *Utetheisa pulchelloidea* larvae from censuses during 1969–1970 and 1980–1981. (Plant phenological events represented by circles; insect numbers by squares.) Data from 1969–1970 are from Heatwole *et al.* (1981).

shrubs throughout the year, albeit fluctuating in abundance. Their numbers decline during times of lower leaf flush, but cohorts are staggered throughout the year. Similarly, *Argusia* shrubs are continuously leafing, thereby providing an abundant food supply for the host-specific larvae.

GRAZING OF UTETHEISA LARVAE ON ARGUSIA SHRUBS.—Host specificity of *Utetheisa* larvae was confirmed by placing 25 larvae in isolated chambers containing fresh branches, five on each of: *Argusia*, *Pisonia grandis*, *Melanthera biflora*, *Scaevola taccada*, or *Sesuvium portulacastrum* (all naturally occurring on One Tree). In all cases, larvae did not feed on any species except *Argusia* and died if offered any other food choice alone.

Once the species-specificity of *Utetheisa* larvae on *Argusia* was established, further tests for preference of leaves within *Argusia* shrubs were conducted. Leaf samples were collected with regard to different biological factors (light, age, wind, time) and were analyzed for grazing damage (Table 1). Data were transformed to $\log(x + 1)$ to obtain

TABLE 1. *Insect herbivory in Argusia canopies on One Tree Island. N = 30 leaves per sample.*

Leaf sample	Month (1980)	ALA* (SE) cm ²	Per-cent loss (SE)	
Old	Windward	Jan	62.5 (2.1)	7.0 (0.6)
Young	Windward		49.9 (2.2)	1.4 (0.8)
Old	Leeward	April	51.8 (2.0)	1.9 (0.5)
	Windward		38.3 (1.8)	6.0 (1.8)
Young	Leeward		38.9 (1.3)	0.3 (.09)
	Windward		28.2 (1.2)	0.6 (.29)
Old	Leeward	June	58.1 (1.6)	1.0 (0.3)
	Windward		45.2 (3.7)	2.1 (0.8)
Young	Leeward		57.1 (1.6)	0.4 (0.2)
	Windward		38.6 (1.0)	0.3 (0.2)
Old	Leeward	Nov	79.3 (8.1)	1.0 (0.2)
Young	Leeward		45.7 (3.5)	0.7 (.15)
Mean			49.5	1.9

* ALA is 'actual leaf area' remaining after insect grazing.

homogeneity of variance (Snedecor and Cochran, 1967). Approximately two percent of the leaf area was grazed throughout *Argusia* canopies. Larvae exhibited significant preferences for windward leaves ($F_{1,118} = 3.5$, $P < 0.05$), and shade leaves ($F_{1,42} = 17.9$, $P < 0.01$). Old leaves had higher grazing damage than young leaves ($F_{1,118} = 40.5$, $P < 0.001$); this is more likely to represent cumulative greater herbivory as leaves age rather than a distinct feeding preference, since the grazing losses are low in all leaves and make a conservative increase from 1.3 percent loss to 2.9 percent loss as the leaves age.

Previous studies on One Tree Island showed slightly higher grazing of 5–10 percent for *Argusia* (Heatwole *et al.* 1981) during 1969–1970, and sampling of other coral cays in this study also showed grazing losses of 5–10 percent with an average loss of 7.8 percent leaf area (Table 2). This indicates that the larvae may have been in lower abundance relative to available food on One Tree during 1980–1981, or that additional herbivores may have existed in previous years and on other cays. (Damage patterns were noted on some leaf surfaces of other cays and appeared to be of orthopteran origin. This remains to be confirmed.)

An overall assessment of grazing on the major plant species of six coral cays on the Great Barrier Reef revealed consistent leaf area losses of approximately six percent. The numbers of herbivores collected in sweep net samples did not correlate at all with grazing losses measured ($r^2 = 0.07$, $P < 0.1$), indicating that herbivore populations probably fluctuate temporally and spatially over the duration of an entire year, and the cumulative damage of 2–10 percent leaf area loss did not correspond to numbers of insects at only one point in time.

TABLE 2. *Herbivory losses on several coral cay islands of the Great Barrier Reef.*

Island	No. species sampled* (N = 30 leaves/species)	Percent leaf area loss of all species	Percent leaf area loss for <i>Argusia</i> ^b
Bell	7	7.0	17.8
Frigate	5	1.5	5.3
Gannet	2	2.2	
Heron	5	8.7	8.7
One Tree	10	7.8	2.0
Riversong	2	10.9	
\bar{x}		6.4%	7.8%

* Plant species: *Boerhavia diffusa* (Riversong, Frigate, Gannet, Bell), *Coronopus integrifolia* (Frigate, Gannet), *Cakile edentula* (Bell), *Ipomoea pes-caprae* (Bell), *Salsola kali* (Bell), *Sphenotaphrum micranthum* (Frigate), *Thuarea involuta* (Bell, Riversong), *Triumfetta procumbens* (Frigate), *Tribulus cistoides* (Bell). For Heron and One Tree Islands, see Heatwole *et al.*, 1981.

^b No. herbivores captured correlated to grazing losses: $r^2 = 0.07$.

Grazing losses on One Tree fluctuate temporally with higher losses in summer during both 1969–1970 and 1980–1981 (Fig. 2a). The highest grazing losses occurred during summer (November–January) when new leaves were most plentiful (Fig. 1a) and insects were abundant (Fig. 2b). Grazing damage was lower during autumn and winter, when insect numbers declined. The temporal patterns in grazing losses of *Argusia* leaves were similar to the changes in numbers of insects found on *Argusia* foliage (Fig. 2b). These data may also include some insects other than *Utetheisa* larvae, although *Utetheisa* was by far the most abundant grazer.

LARVAL FORAGING AND FEEDING BEHAVIOR.—On a diurnal basis larvae allocated their time as follows: 53 percent feeding, 8 percent moving, and 39 percent resting (Table 3). Since larvae were consistently resting after dark, no nocturnal data (2300–0500 hr) are presented. Within the span of one day, feeding was the major activity during morning and midday (60%), and resting was the main evening activity (54%). During a 10-day span (the mean lifespan of a larva), larvae moved approximately 5.4 m (SE = 0.81) on average which included a mean of 8.6 rosettes (SE = 0.42) and 3.4 (SE = 0.21) bushes. They often remained on one leaf for an entire day, feeding in patches, more often in the leaf interior rather than along the leaf edges. When a larva moved, it often travelled over several leaves and rosettes before selecting a new leaf for grazing, and it rarely selected a leaf that already had grazing holes.

BIOMASS OF ARGUSIA DEFOLIATED ON ONE TREE ISLAND.—The amount of *Argusia* leaf material on One Tree was

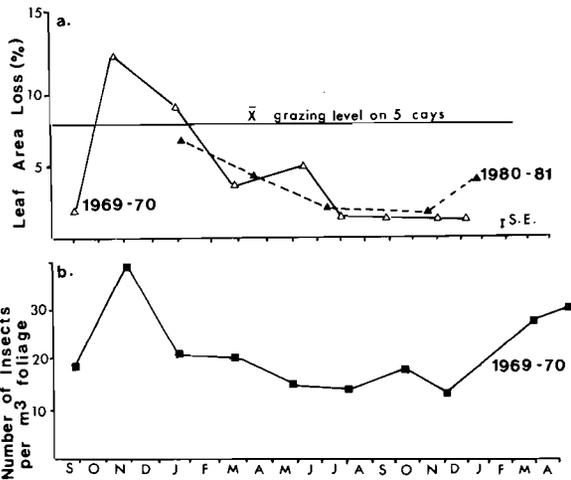


FIGURE 2. Seasonal variation in herbivory on *Argusia* leaves (a) as compared to abundance of insects on *Argusia* foliage (b). Herbivory measurements calculated as proportion leaf area missing (%) from samples of leaves ($N \geq 30$) collected during different months of 1969–1970 and 1980–1981. Data from 1969–1970 are from Hearwole *et al.* (1981).

determined by calculating mean leaf areas (Table 1) and dry weights, and counting the number of leaves per rosette, number of rosettes per bush, and number of bushes on the island. One hundred and twenty eight bushes on One Tree had 227,082 leaves, or 1146 cm² leaf area (160.9 kg dry weight). Since 1.9 percent of the leaf material is grazed, 21 m² or 3 kg leaf material (dry wt.) are removed.

DISCUSSION

For host-specific herbivores, the necessity to remain on or near the host plant is imperative. Few studies have reported on larval behavior in forest canopies but beetle larvae in beech trees literally “rain” out of the canopies during winds or disturbance (Selman and Lowman 1983). Larvae are generally sedentary, and presumably feed on leaves located within a restricted area. The event of falling from a branch, particularly with mature forest canopies, would most likely result in larval desiccation or mortality by predators on the ground.

This study, albeit conducted in shrub canopies where leaves are distributed on a notably smaller spatial scale than forest canopies, showed that Lepidopteran larvae did not range far in their grazing activities, but travelled only up to one meter per day, usually a journey from one rosette of leaves to the next. If the larvae became dislodged from the host plant by wind or disturbance, their navigational abilities appeared poor: they travelled an average of 30 m over 30 minutes to relocate *Argusia* (at their normal rate of travel, it should require only two

TABLE 3. Larval behavior in *Argusia shrubs*.

Activity	Time allocated to activity (percent)			Diurnal (percent)
	Morning	Midday	Evening	
Feed	36 (60)	56 (60)	52 (38)	53
Move	22 (7)	9 (10)	17 (8)	8
Rest	41 (33)	35 (30)	31 (54)	39
				100%

minutes). Such apparently random movements suggest that larval mortality due to storms, or perhaps even birds foraging through the shrubs, is high.

Observations on Heron Island indicate that silvereyes forage extensively for insects through *Argusia* shrubs, preferring vegetation with a leeward exposure (Catterall 1979). The greater abundance of *Utetheisa* larvae on windward leaves may be a consequence of silvereye predation, as well as dislodgement due to the physical movements of birds through shrubs, causing death from desiccation or starvation on the beach.

The larvae also exhibited preferences for shade leaves over sun leaves, which may be an additional consequence of predation pressures since larvae on sun leaves are more exposed to birds. In addition, the food quality of sun versus shade leaf tissue may be highly variable: sun leaves tend to be more sclerophyllous and toxic than shade leaves; similarly, leaves in windy conditions are more sclerophyllous and hence less palatable than sheltered leaves (reviewed in Larcher 1980, Lowman and Box 1983). This implies that *Utetheisa* larvae should prefer leeward, shade leaves, which, however, is not entirely the case. Studies of leaf chemistry and nutritive levels of *Argusia* would be of interest to assess larval feeding preferences. There may be a combined interaction of both predation and leaf food quality that has resulted in the observed preference for windward, shade leaves.

The larvae consumed an average of 2.9 cm² leaf tissue daily during their 10 days of existence. The numbers of *Utetheisa* larvae appear relatively low in relation to the apparent abundance of *Argusia* leaves. This may be a consequence of several factors. First, although food supply does not appear limiting, variability in food quality among different types of *Argusia* leaf tissue may render some leaves less palatable. The fact that larvae almost never fed upon leaves with evidence of previous grazing may even implicate the mobilization of toxins (Carroll and Hoffman 1980). Second, the physical rigors of surviving on *Argusia* bushes, situated on the perimeters of reef islands and thus subject to high winds and salt spray, may cause high larval mortality, thereby rendering physical environment (rather than food supply) a more critical limiting factor. And third, the bird predators on cays may

severely limit the abundance of insects, especially on leeward shrubs where they tend to forage most extensively. Heron Island is situated close to One Tree, but has a much higher silvereye population and fewer *Utetheisa* larvae, evidence of strong predation pressures (Catterall 1969, Lowman, pers. obs.). And fourth, in addition to physical constraints and predation, the low herbivory on *Argusia* bushes may also be related to limitations of sampling methods. The calculation of leaf damage in this study involved discrete leaf collection and analysis of missing leaf area, a sampling procedure that does not account for leaves totally missing (Lowman 1982b). Although complete defoliation of *Argusia* leaves was never observed during field or laboratory work nor by other researchers (Heatwole *et al.* 1981), it is a possibility that could only be confirmed by marking leaves and monitoring their grazing damage continuously over time.

The grazing losses to *Argusia* leaves were low, especially in comparison with other Australian vegetation: up to 75 percent for eucalypts (Journet 1981), up to 30 percent from some coral cay herbs (Heatwole *et al.* 1981) and 15–30% in rain forests (Lowman 1982b); and lower even than the 7–10 percent for most world vegetation (reviewed by Bray and Gorham 1964). The turnover of photosynthetic tissues to the primary consumer pathway of nutrient cycling is consequently low, and herbivory is obviously not a major component of the nutrient turnover in this ecosystem. Approximately 95–98 percent of *Argusia* undergoes natural senescence and the leaf material enters into the decomposition pathway, as compared to

only 2–5 percent leaf area cycling as insect frass via the grazing pathway. The herbivores on *Argusia*, albeit inconsequential to the nutrient cycling in terms of their grazing activities, may influence island nutrient cycling and productivity indirectly simply by their attraction of birds, who forage and defecate heavily around the shrubs. Studies on bird guano show that it represents a significant nutrient input to coral cays (Heatwole *et al.* 1981).

Coral cays provide ideal laboratories for studies of behavior under natural conditions that are impossible in bigger, more complex ecosystems. This study of feeding of *Utetheisa* on *Argusia* bushes not only quantified the plant-animal relationships for these two organisms, but also provided a natural experimental situation, conducive for investigation of larval behavior in general.

ACKNOWLEDGMENTS

I am grateful to Dr. Peter Sale for permission to work on One Tree Island, to Dr. Peter Myerscough and Professor Michael Pitman for departmental support of research at the reef, and to Professor Harold Heatwole for his organization of the 1982 Swains Reef Expedition. Patti Schmitt kindly assisted in 'caterpillar-watching', and many other marine biology students contributed discussion useful to designing this study: Bruce and Anna Marie Hatcher, Peter Doherty, Karen Scott, Glen Burns, and Dave Lowman. Financial support from Sydney University (Postgraduate Scholarship) and ARGC (Research Grant to H. Heatwole and MDL) is greatly appreciated. Andrew Burgess offered supportive criticism of the final draft, and Sandra Pont miraculously typed it.

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