

Contrasts in Reproductive Ecology Between Temperate and Tropical Populations of *Jadera haematoloma*, a Mate-Guarding Hemipteran (Rhopalidae)

SCOTT P. CARROLL¹

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ABSTRACT Field studies of the effect of climate and host-plant phenology on reproductive patterns of the seed-feeding *Jadera haematoloma* Herrich-Schaeffer were undertaken in Oklahoma and Florida. In Oklahoma, most reproduction is confined to August and September, when seeds of the sapindaceous host trees, *Sapindus saponaria* L. var. *drummondii* (Hooker & Arnett) (Benson) and *Koelreuteria paniculata* (Laxman), are mature, and is followed by a reproductive diapause in winter. The proportion of females becoming reproductive in their natal year declined from August to September. Diapause occurred while food was still available and is probably photoperiodically induced. In Florida, most reproduction occurred in April–May and November–January, when seeds of the sapindaceous vine, *Cardiospermum corindum* L., were available. Diapause here occurred when seeds were unavailable. Bugs in Florida are larger, take longer to mature, and produce larger eggs, at a slower rate, that take longer to hatch, than those in Oklahoma. Greater mortality of females as overwintering adults and as nymphs in summer contributed to a strong male-bias in the adult sex ratio of Oklahoma aggregations, whereas sex ratios in Florida were not male-biased. It was therefore predicted that Oklahoma males might guard their mates from other males, whereas those in Florida would not. However, males in both populations were found to prevent females from mating with other males by remaining in copula from the time of intromission until oviposition. Contact guarding continues during oviposition and the pair may recouple afterwards. Postinsemination guarding, although not predicted by Florida sex ratios, may occur there because of greater last-male sperm precedence in that population than in Oklahoma.

KEY WORDS Insecta, *Jadera*, geographic variation, life history

Jadera haematoloma Herrich-Schaeffer is a widespread member of the Rhopalidae, occurring from the United States to northern South America (Blatchley 1926). Like other members of the subfamily Serinethinae, it specializes upon the seeds of Sapindales for development and reproduction (Schaefer & Mitchell 1983, Carroll & Loye 1987), and often forms large aggregations on its host plants. In the United States, it shows a major distributional disjunction, occurring on the soapberry tree, *Sapindus saponaria* L. var. *drummondii* (Hooker & Arnett) (Benson) in the southwestern and south-central states, and on the balloon vine, *Cardiospermum corindum* L. in peninsular Florida (Fig. 1). Aggregations also occur on *Serjania brachycarpa* (Gray) in far southern Texas, and on introduced sapindaceous plants: the golden rain tree, *Koelreuteria paniculata* (Laxman), in the southwestern and central states, *Koelreuteria elegans* ssp. *formosana* (Hayata) F. G. Meyer in Florida, and *Cardiospermum halicacabum* L. in Mississippi (Carroll & Loye 1987). Sapindaceous hosts were also recorded when the bug was introduced to Hawaii (Davis 1969, Gagné 1971). *S. saponaria saponaria* L. (Benson) is a member of the West Indian flora that, like *C. corindum*, occurs disjunctively in southern Florida;

but in contrast to the western variety of this species, it does not serve as a host plant for *J. haematoloma*, perhaps due to protective modifications of the fruit coat (Carroll & Loye 1987).

Populations of *J. haematoloma* in the American southwest and in Florida differ greatly in the patterns of thermal seasonality and host plant phenology to which they are exposed. This paper compares the reproductive ecology of *J. haematoloma* on its native and introduced host plants in Oklahoma and in Florida.

Materials and Methods

Field observations in Oklahoma were made from 1981 to 1985, on aggregations on *K. paniculata* and *S. saponaria* var. *drummondii* in Cleveland, Cotton, Oklahoma, and Woodward Counties. Field observations in the Florida Keys were made in 1984 and 1985 of aggregations on *C. corindum* in Dade and Monroe Counties. The reproductive condition of the plants was recorded, 50 seeds per plant were opened to determine the proportion with intact embryos, and adult and juvenile bugs were counted to measure aggregation size and age structure. "Mean instar," the mean age class of sampled nymphs weighted by the number of individuals in each instar (1–5), was calculated for Florida ag-

¹ Dep. Biology, Univ. Utah, Salt Lake City, UT 84112.



Fig. 1. North and Central American distributions of *J. haematoloma* (dark circles) and its sapindaceous host plants (stippled). The soapberry, *S. saponaria* var. *drummondii*, occurs in the southwestern United States and southward to Argentina. The balloon vine, *C. corindum*, occurs in Florida and from central Mexico southward. *Serjania* spp. occur from extreme southern Texas, southward to South America.

gregations. Nymphs could not be sexed in either study area.

The population dynamics of a single aggregation on *K. paniculata* in Cleveland County, Okla., were recorded by counting all adults on and under the tree from 15 April to 15 October 1981. Censuses were conducted weekly in April, May, and June, and daily thereafter. A step ladder was used to census the canopy, which was 6 m above the ground. To study reproductive behavior of individual bugs at this site, 544 adults on a *K. paniculata* were marked on the pronotum with color dots of Tek Pen inks during August–September 1981. The marked individuals were censused daily to observe whether they were mating, and, if female, how gravid they were on an arbitrary scale (0, abdomen not expanded beyond its conformation at the time of the molt to adulthood; 1, expanded ventrally but not laterally; 2, moderately expanded ventrally and laterally; 3, maximally expanded dorsally, ventrally, and laterally). Focal observations were made

of individual males and mating pairs during mate searching and oviposition, and the movements of marked individuals between aggregations were also recorded.

In censuses of aggregations in which individuals were not marked, the reproductive condition of adults in the field was assessed in two ways. First, the gravidness of a sample of females was recorded on the scale described. Second, because pairs remain in copula for many hours and most females in a reproductively active aggregation are in copula at any given time (Carroll 1983), the presence or absence of mating pairs was also used to judge whether the aggregation was in reproductive condition.

Body lengths of adults in the wild were measured from the clypeus to the posterior tip of the folded elytra, using dial calipers (± 0.01 mm).

Fecundity, age of first oviposition, egg size, incubation time, and development time were measured for bugs in captive populations maintained

at 30°C, with seeds of *K. paniculata* and water provided ad libitum. Colonies of *J. haematoloma* were housed in plastic storage boxes ca. 20 by 30 by 10 cm high, with mesh inserts in the lids for ventilation, and an absorbent substrate of plaster of paris with coconut charcoal mixed in. On the day of their terminal molt, females were isolated with like-aged males in plastic freezer boxes (10 by 10 by 6 cm high) with mesh bottoms and mesh tops. Any eggs produced fell through the mesh bottom into another, closed-bottom freezer container placed below it. The floor of this lower container was lined with absorbent filter paper. Eggs were counted and removed daily, after 1600 hours. Fecundity is reported as the number of eggs laid per day, from the day of first oviposition for ca. 30 d or until the female died. Only data from females laying 200 or more eggs are reported. Egg size is reported as the average weight per egg taken from measures of entire clutches on a Mettler electronic balance (± 0.0001 g). Eggs declined in weight over time, and all reported weights are from clutches weighed within 3 d of oviposition. Incubation time is reported as the interval between the day of oviposition and the day of hatching. The viable eggs in a clutch hatched within a few minutes of one another, and clutches were checked for hatching once each day, after 1600 hours.

To measure development time, cohorts of siblings were collected each day from newly hatched eggs. Groups were isolated in freezer boxes with filter-paper bottoms and mesh lids. Advanced cohorts were monitored daily, and any newly molted adults were recorded and removed. Development time is reported as the number of days required to develop through the five instars to adulthood after hatching. In groups of more than about 30 individuals, development time was found to be protracted, and adult body size decreased. Only data from groups of 10–30 individuals, in which >50% survived, are reported. The numbers of males and females that matured in such groups are also reported.

The survivorship of eggs in cold conditions was examined by placing 20 clutches collected from the field in September 1981 in a cold chamber at 5°C. Eggs were contained in 25-cm³ closed plastic containers, with paper toweling added to absorb any condensed moisture. Every 2 d, two of the clutches were removed and subsequently maintained at 25°C, and any development was noted.

Copulation duration for Oklahoma bugs in captivity was measured for pairs in two groups of 24 adults each. In these groups, a total of 34 males and 14 females was used to mimic natural sex ratio conditions (ca. 2.5:1 males/females). The bugs were collected as fifth instars in Cotton County, Okla., and were allowed to molt to adulthood in captivity, when they were individually marked with colored, numbered apicultural identification disks affixed to the pronotum with balsam gum. Each group was housed and observed in an enamel pan (60 by 25

by 6 cm high) with a hard substrate of plaster of paris with ground coconut charcoal mixed in. A 13.5:10.5 (L:D) photoperiod, with Daylight fluorescent tubes, matched the concurrent outdoor conditions (August 1982). Laboratory temperatures averaged $33 \pm 2^\circ\text{C}$ during the day and $28 \pm 2^\circ\text{C}$ at night. *K. paniculata* seeds and water were provided ad libitum. The mating status of each individual was recorded at 2-h intervals, six times a day during daylight hours, for 10 consecutive d in one group and 16 consecutive d in the other.

Additional data on the reproductive phenology of *C. corindum* were taken from herbarium specimens at the University of Florida, Gainesville, and the Fairchild Tropical Gardens, Miami. Specimens of *S. saponaria* and *S. saponaria* var. *drummondii* in the herbarium of the University of California, Berkeley, were used to examine geographic variation in the seed-coat morphology of that genus.

Larval lepidopteran seed predators of *C. corindum* were collected and reared to adulthood for identification.

The geographic distribution of *J. haematoloma* was determined from locality records in the National Museum of Natural History, Washington, D.C., and in the American Museum of Natural History, New York. Host plant distributions are from Vines (1960), Standley (1961), Shreve & Wiggins (1964), Brizicky (1964), and Little (1976).

Statistical analyses used are the Mann-Whitney *U* test (Siegel 1956) and χ^2 tests of independence and *G* goodness-of-fit tests (Sokal & Rohlf 1969). Means are given with ± 1 SD. The $\alpha = 0.05$ level was chosen for statistical significance.

Specimens of *J. haematoloma* from Oklahoma and Florida have been deposited in the Entomology Collection of the Utah Museum of Natural History, University of Utah.

Results

J. haematoloma develops entirely on the seeds of its sapindaceous hosts. Females were larger than males in all major body dimensions, and bugs in Florida were larger than those in Oklahoma (Table 1). Mean adult development time was also greater for the Florida Keys population, but did not differ between the sexes within populations (Table 1). Florida females produced fewer eggs per day than those from Oklahoma, and Florida eggs were significantly larger and took longer to hatch (Table 1).

Ecology in Oklahoma

Phenology. *J. haematoloma* in Oklahoma aggregate on the introduced *K. paniculata* and on the native *S. saponaria* var. *drummondii*. Both plants are unusual in not flowering until May or June, which is later than most other trees at this latitude. Seeds of *K. paniculata* ripen in late July and August, and those of the soapberry ripen from

Table 1. Comparisons of body length and reproductive characters of male and female *J. haematoloma* from Oklahoma and Florida

| Character | Okla. | Fla. | U^a | P |
|---|-------------|--------------|-------|--------|
| Body length (mm) | | | | |
| Male (20, 20) ^b | 11.0 ± 0.5 | 11.9 ± 0.7 | 57.0 | 0.001 |
| Female (20, 20) | 12.4 ± 0.7 | 14.0 ± 0.8 | 31.0 | 0.001 |
| U | 30.0 | 36.0 | | |
| P | 0.001 | 0.001 | | |
| Development time (d) | | | | |
| Male (88, 13) | 29.3 ± 4.1 | 45.3 ± 5.0 | 6.5 | 0.0001 |
| Female (85, 14) | 29.3 ± 4.4 | 42.5 ± 4.4 | 9.0 | 0.0001 |
| U | 3,672.5 | 60.5 | | |
| P | 0.42 | 0.07 | | |
| Average no. eggs/d (9, 10) ^c | 13.2 ± 2.6 | 6.4 ± 2.4 | 2.5 | 0.0001 |
| Egg wt (mg) (14, 12) ^d | 6.30 ± 0.66 | 7.35 ± 0.55 | 63 | 0.0001 |
| Incubation time (d) (14, 5) ^e | 9.25 ± 0.72 | 10.05 ± 0.59 | 370 | 0.01 |

^a Mann-Whitney U test.^b Sample sizes for Oklahoma and Florida, respectively.^c Numbers of mothers; analyses based on totals of 3,103 and 472 eggs, respectively.^d Numbers of mothers; analyses based on averages from 119 and 30 clutches, respectively.^e Numbers of mothers; analyses based on averages from 85 and 19 clutches, respectively.

mid-August to late September. Both trees ripen up to several thousand seeds.

Fig. 2 shows the adult composition of an aggregation on *K. paniculata* in Cleveland County in April–October 1981, using biweekly averages. No bugs overwintered at this site in 1980–81. A few adults arrived in early April, and fed and reproduced on fallen seeds from the previous year. The adult population declined in May and June as seeds were exhausted, and nymphs were present in late April and May, but not in June. During the remainder of the summer the aggregation increased in size, initially by the addition of males that arrived in early July, before the new seeds ripened, and then from females that arrived in mid-July, as the seeds ripened. The initial pulse of adults was followed by a period of cool and wet weather during which numbers declined. When hot, dry conditions resumed in late July, the population again grew rapidly, mainly from recruitment of nymphs that developed within the aggregation. Mating and oviposition continued until early October (Fig. 2).

Diapause began with a switch from mating behavior to feeding behavior, and then quiescence. Table 2 shows this transition for adults in an aggregation on a *K. paniculata* in Cleveland County in September–December 1982. The abdominal cavities of 10 adult males and 10 adult females collected from this aggregation on 20 October 1982 contained large quantities of adipose tissue, a condition never observed in mature adults dissected during the reproductive season ($n = 20$ males and 20 females).

In addition, the proportion of females that did not become reproductively active in their natal season, measured at an adjacent *K. paniculata*, in-

creased from August to September 1981. Of the 43 females that were marked as teneral virgins before 27 August, and observed again at least once, 39 (90.1%) became gravid or had mated. Of the 26 virgin females marked in September and observed again at least once, only 14 (53.8%) became gravid or had mated. This increase in the incidence of reproductive diapause in females molting to adulthood late in the season is statistically significant ($\chi^2 = 12.35$; $df = 1$; $P < 0.001$).

Nymphs and adults form dense clusters in leaf litter and on and between stone and wood surfaces from October to February. They are inactive and in physical contact with other individuals, but when temperatures rise above about 10°C they move into direct sunlight and cluster there. No feeding or reproduction has been observed in numerous surveys of overwintering populations in late October, November, or December. Nymphs continue to molt to the next instar or adulthood during these months. The earliest that mating has been observed to resume is 11 January (1983), and adults have been attracted to feed at manually opened seeds in January. I have noted oviposition in February, but the earliest oviposition observed to give rise to nymphs that did not subsequently disappear during development was 13 March 1983.

I attempted to break diapause by subjecting field-collected diapausing adults (200 collected in the field in Cleveland County in November 1982, and 200 in Woodward County on 20 October 1985) to a 14-h diel cycle and 28°C temperatures in captivity with ample food. In daily observations for 21 d after collection, no individuals were observed to mate or feed. Instead, they behaved in an agitated fashion, walking nearly continuously in their con-

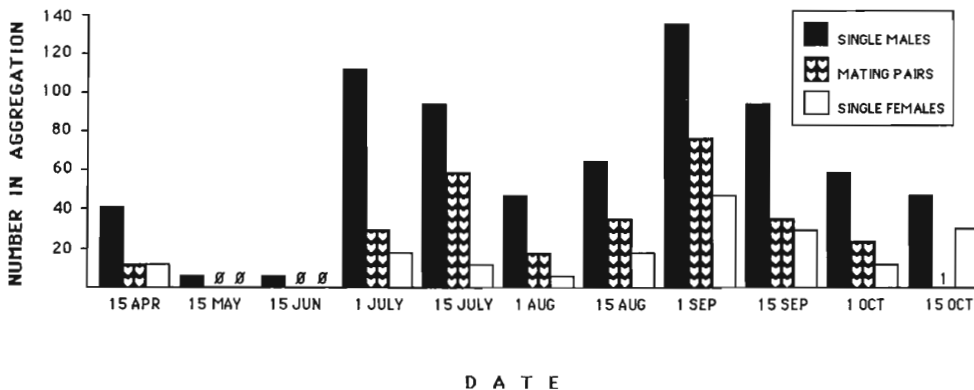


Fig. 2. Adult composition of an aggregation of *J. haematoloma* on *K. paniculata* in central Oklahoma, 1981. Values are for single samples April–June, and are averages of daily samples July–October. Dark bars show numbers of single males, hearts show mating pairs, and cross-hatching shows single females.

tainers with unusually great speed, and attempting to fly. A low, dry “churring” sound, accompanied by a very slight vibration of the proximal elytra region, has been observed only in such captive diapausing adults.

By late winter, few seeds remain intact. Fewer than 5% of *K. paniculata* seeds sampled from 10 trees, and <10% of *S. saponaria* var. *drummondii* seeds sampled from six trees, survived until March. Reproductive aggregations of more than 100 mating pairs were observed in March and early April 1983 at two *K. paniculata* in Cleveland County, but no reproductive aggregations were observed in at any of 10 trees in May or June 1981–83 (Fig. 2).

Sex Ratio. Single males outnumber both mating pairs and single females in almost all censuses (Fig. 2). Most females are mated at any given time, whereas the majority of males are not mated. Sex ratios from counts of the total adult population at 27 aggregations in central Oklahoma are presented in Fig. 3. The male bias is greatest during the aerial colonization phase in the early summer, and declines to near unity by winter. The mean sex ratio for the 21 of 27 aggregations in which adults were reproductively active was 2.73 ± 0.95 males per female. The mean sex ratio of the six diapausal aggregations was significantly lower: 1.33 ± 0.33 males per female ($U = 4$; $P < 0.001$; $n_1 = 21$, $n_2 = 6$; Mann-Whitney U test).

To examine whether sex ratios might be male biased at the time of oviposition, groups of nymphs that hatched on the same day in captivity were reared to adulthood. The sex ratios of the captive-reared groups do not differ from 1:1 (Table 4).

Environmental effects during development in the wild are therefore the probable source of male-biased ratios (excluding the unlikely possibility of sex change during development). No predation or parasitoidism of eggs, nymphs, or adults has been

observed, so these agents cannot explain the male bias in sex ratio. At least two factors do appear to be responsible, however. First, during the summer reproductive period (on seeds of the year), significantly more males develop to adulthood than do females. In 12 samples of teneral individuals in the field, there were a total of 766 males and 604 females. This differs significantly from the expected 1:1 male/female ratio, indicating that nymphal males survive at a greater rate than nymphal females ($G = 19.2$; $df = 1$; $P < 0.01$; G goodness-of-fit test).

Second, a late winter sample of diapausing adults showed that adult males were overwintering more successfully than adult females. This was determined by counting the number of living and dead adults in an overwintering aggregation in leaf litter on 19 February 1982, while they were still sessile. At this time the aggregation consisted of 38 live males and 32 live females, plus 41 dead males and 65 dead females. Because the bugs are inactive during the winter, it can be calculated that 52% of the males survived the 4.5 mo of diapause, whereas only 33% of the females survived. These rates differ significantly from the hypothesis of equivalent survivorship ($G = 4.2$; $df = 1$; $P < 0.05$; G goodness-of-fit test).

Differential recruitment of adults from nymphs is unlikely to have influenced the sex ratio of overwintering survivors, because few nymphs have ever been observed to survive into the winter, and advanced nymphs usually molt to adulthood during the late fall at a reduced size. In addition, reproduction is apparently not possible in Oklahoma in the winter: in the experiment in which eggs were held at 5°C, I found that no embryos survived exposures of more than 2 d duration.

The difference in overwintering survivorship of adults may account for part of the male bias in new arrivals during the initial stages of host colo-

Table 2. Mating and feeding frequencies of adult *J. haematoloma* during the transition to diapause

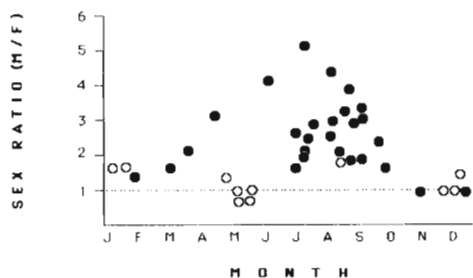
| Date | % mating | | % feeding | |
|-------------------------------|----------|---------|-----------|---------|
| | Males | Females | Males | Females |
| 20 Sept. 1982 (310 adults) | 34 | 70 | 3 | 12 |
| 28 Sept. 1982 (346 adults) | 11 | 25 | 5 | 11 |
| 3 Oct. 1982 (286 adults) | 6 | 11 | 37 | 41 |
| 20 Oct. 1982 (210 adults) | 0 | 0 | 3 | 3 |
| 7 Dec. 1982 (101 adults) | 0 | 0 | 0 | 0 |

nization in early summer. However, the glossy, newly molted appearance of many males arriving at this time suggests that some are products of the small spring generation that develops on the left-over seeds from the previous year. No survivorship data are available for nymphs or adults during this period.

Philopatry, Lifespan, and Dispersal. Of 400 bugs given individual marks when teneral, 76% (171/225) of the males and 65% (114/175) of the females were observed at the same site on at least one later date. Although bugs were active on foot within aggregations, they were rarely observed to fly, even when disturbed manually. For these 171 males, the average duration from the time of marking to the last sighting was 21.5 ± 9.5 d (range, 2–52 d). For the 114 females, this duration averaged 25.3 ± 10.1 d (range, 2–59 d). Twelve marked individuals were found at host plants other than the one at which they developed, and, of these, 11 were male. Eight of the migrants were at the closest adjacent host (ca. 40 m distant). Two males were found at a tree about 600 m distant, and presumably flew there. Eight of the male immigrants and the single female immigrant were observed mating in their new aggregations.

Ecology in Florida

Phenology. Two main environmental differences between the regions are the rarity of temperatures below which the bug is forced to be inactive (i.e., below 5–10°C) in south Florida, and the more continuous production of seeds by the Florida Keys host plant, the balloon vine. In addition, this host produces far fewer seeds at a given time than the host trees in Oklahoma (usually no more than several hundred). This plant grows in clearings and in openings in wooded areas, either sprawling across low vegetation or clambering into the canopy. Seeds are produced at the centers of inflated, spherical capsules about 2.5 cm in diameter; the wall of the sphere retards access by the bug to the seeds, and the beaks of *J. haematoloma* in the Florida Keys are significantly longer than

**Fig. 3.** Sex ratios of aggregations of *J. haematoloma* in Oklahoma (dark circles) and Florida (open circles).

those in Oklahoma (Carroll & Loye 1987). The capsules develop in about 2 wk after fertilization and hang in clusters from the vines. Field observations and examination of herbarium specimens showed that *C. corindum* flowers and produces seeds at all times of year. However, seed production is greatest in May and in November–December, when more individual plants have capsules and there are many more capsules per plant.

Table 3 shows the reproductive conditions of host plants and the reproductive status of *J. haematoloma* at five times of year on Key Largo and Plantation Key. Plants sampled in early and mid-December had recently completed fruiting, as evidenced by the presence of many old fruiting capsules, or were in the process of ripening new capsules. Thus seeds from one crop had recently become unavailable to the bug, and another crop was not yet available. Adults were not mating, and most nymphs were advanced instars.

In late January, only fallen, dry capsules, devoid of seeds, were present, apparently the artifacts of a late December seed crop. The age structure and reproductive condition of the bug population was similar to December, but more younger nymphs were present, and many more adults were present (Table 3). The majority of bugs were not directly on the host plants, but instead clustered on adjacent leafy vegetation <0.5 m above the ground. Two hundred fifty bugs (estimated to be about one-fourth of the total number of adults present) were handled individually; all 250 had shiny and malleable exoskeletons, indicating that they had molted to adulthood within the previous 3 d (the exoskeleton of *J. haematoloma* becomes rigid and loses much of its shine within 72 h of the final molt [Carroll 1983]). No older or reproductive adults were observed.

In late April and in May the development of large seed crops on numerous plants was observed. Female bugs in particular began to feed on the seeds once they became full-sized and began to darken, and mating increased in frequency as more seeds ripened (Table 3). Most nymphs observed during this period were early instars (Table 3), indicative of ongoing reproduction. Of a sample

Table 3. Effect of *C. corindum* phenology on aggregation composition and reproduction of *J. haematoloma* in the Florida Keys

| Observation | Date | | | | |
|------------------------------|--|---------------------------|---|--|----------------------------|
| | Dec. | Jan. | Apr. | May | Aug. |
| No. plants examined | 22 | 15 | 43 | 22 | 7 |
| Plant reproductive condition | Mainly immature ^a & old ^b capsules | Old capsules, few flowers | Mainly maturing ^c capsules & flowers | Mainly mature ^d & maturing capsules | Flowers, immature capsules |
| No. plants with seeds | 12 | 1 | 24 | 18 | 0 |
| No. capsules/plant | 77.4 ± 67.8 | 8 | 36.3 ± 22.1 | 151.8 ± 85.7 | 6.7 ± 10.2 |
| No. plants with bugs | 11 | 0 | 23 | 15 | 3 |
| No. adults | 160 | 1,000 ^e | 215 | 189 | 39 |
| Adults mating? | No | No | 5.9% | 31.7% | No |
| Adults feeding? | No | No | 18.1% | 35.5% | No |
| No. nymphs | 490 | 143 | 46 | 45 | 2 |
| Nymphs feeding | 1/490 | 1/143 | Yes | Yes | No |
| Mean instar | 4.04 | 3.49 | 2.28 | 2.53 | 4.50 |

^a Seeds green, capsules < ½ full size.

^b Capsules dry, shrivelled, usually fallen to ground with seeds absent.

^c Seeds green, capsules > ½ full size.

^d Seeds black, capsules full size.

^e Value estimated; see text.

of 50 seeds taken from a large balloon vine, 47 had bug feeding scars, and powdery destroyed embryos.

In August, fewer mature plants were found, and most had fewer than five capsules. Capsules and bugs were especially rare in mid-August samples, but by the third week in August, adults were observed on vines that were beginning to develop capsules.

In addition to seed predation by the bug, the larvae of two species of butterfly feed on the immature seeds: the maesites hairstreak, *Chlorostymon maesites* Herrich-Schaeffer, and the Miami blue, *Hemiargus thomasi* Clench. More than 50% of the seed crops of the four plants examined were found to be consumed by these predators in April-May observations.

Aggregation and Sex Ratio and Dispersal. Florida aggregations tended to be smaller than those on soapberry trees in Oklahoma, consisting of from about 10 to a few hundred adults per plant, and up to several hundred nymphs. Adult sex ratios from 11 aggregations averaged 1.14 ± 0.26 males per female, much closer to unity than in the 27 Oklahoma samples ($U = 18$; $P < 0.001$; $n_1 = 27$, $n_2 = 11$; Mann-Whitney U test; Fig. 3).

Reproductively quiescent bugs were found in Florida aggregations in which seeds had been exhausted, but two kinds of evidence indicate that they often move between host plants. First, even

small vines hundreds of meters from other vines, bearing mature seeds, were occupied by bugs. Second, the absence of any adults older than about 3 d in the late January observations described, suggests that the bugs were immigrating from these sites at which no seeds were available once their exoskeletons became sufficiently rigid to permit flight.

Reproductive Behavior

All reproduction takes place within the close confines of the aggregation, where reproductive females are concentrated and hundreds of males may be seeking mates simultaneously. Except where noted, the following reproductive data are for bugs observed in Oklahoma.

Searching for Mates and Copulation. Single males far outnumber single females in Oklahoma aggregations, and to a lesser extent in Florida aggregations. Males search for mates by moving actively on foot within the aggregation, or waiting until other individuals approach within a few centimeters and then running up to them. Detection appears to be visual. Encountered individuals, most commonly other males, are mounted, and their genitalia are examined with the antennae.

When the mounted individual is another male, he is dismounted in about 1 s; mounts on single females of mating pairs are of longer duration and may last for many minutes (unpublished data). In ca. 1,000 observations of males mounting females, the following pattern was observed: approaching from any direction, the male climbs atop the female, aligns his body with hers, slips his aedeagus posteriorly along her abdomen, and attempts intromission. Intromission occurs if the female is not already mated and is not resistant, and the male then swings his body 180° so that the pair mates in a tail-to-tail position.

Table 4. Numbers of captive-reared *J. haematoloma* emerging as male or female adults

| Site | No. groups | Males | Females |
|----------|------------|-------|---------|
| Oklahoma | 13 | 140 | 134 |
| Florida | 17 | 219 | 218 |

Data from groups in which <50% of the original hatchlings survived were excluded.

Age of First Mating and Oviposition. Captive adults of both sexes have been observed to resume feeding about 24 h after the terminal molt, and to begin mating 48 h later. Of 80 males marked in the field as general virgins and observed again at least once, 39 were not observed to mate. Of the 41 that were observed to mate, the average adult age of the first mating was 8.9 ± 4.7 d (range, 3–20 d; four males were observed mating at 3 d). Of 60 females marked as general virgins in August–September 1981 that were observed again at least once, 26 were not observed to mate. However, of these 26, 10 became gravid, suggesting that 44 of the 60 females (73%) became reproductively active. Of the 34 that were observed to mate, the average adult age of the first mating was also 8.9 ± 4.7 d (range, 3–23 d; three females were observed mating at 3 d).

The age of first oviposition, recorded for 19 captive females that became reproductive within 30 d, was 7.1 ± 2.9 d (range, 4–16 d).

Mate Guarding and Oviposition. Copulation lasted as long as 128 h in captive pairs (mean = 20.5 ± 24.5 h; range, 0.33–128 h; $n = 78$ pairings). This was considerably longer than the few hours needed to complete sperm transfer (unpublished data).

In Oklahoma, eggs are usually deposited in a hole that the female digs in dry, fine soil near the base of the host tree. Digging begins with the pair still coupled, and is accomplished by rapid longitudinal movements of the forelegs, using the tarsi to scoop and throw the soil posteriorly. When the hole is about half completed, at ca. 1 cm deep, the female stops digging until the male withdraws, and then completes the hole after an overall total of 2–3 min of digging ($n = 12$). The male climbs to the top or side of his mate, facing in the same direction, and holds his aedeagus less than 1 mm from the female's vulva while she lays eggs. Clutch size was 14 ± 4.1 eggs (range, 1–20 eggs; $n = 12$ ovipositions). Eggs are laid at intervals of 30–150 s. When ovipositing pairs were interrupted by searching males that attempted to copulate with the female, the guarding male quickly recopulated with his mate, preventing the intruding male from doing so ($n = 14$ intrusions experienced by 18 pairs in early July 1981). The displacement of a guarding male by an intruder during oviposition has only been observed in 2 of 145 observed attempts. The displacement of a guarding male in copula has been observed in 1 of ca. 1,100 attempts. (Experiments in mating females to two males have shown that a second male fertilizes about 50–70% of the subsequent ova laid [unpublished data].)

When oviposition was completed, or terminated by mate guarding, the female moved about the hole, covering the clutch with soil with a sweeping motion of the forelegs. Once the hole is filled to the level of the surrounding dirt, she tamps the soil with her forelegs. When oviposition was completed without interruption by another male, the guarding

male recopulated while the eggs were being covered ($n = 43$ of 45 ovipositions).

After guarding his mate through oviposition and copulating again, a male may depart within 2 h and resume searching, or remain with her for additional ovipositions. In 60 pairings of captive bugs from Oklahoma, 42 terminated after one oviposition. Thirteen lasted for two ovipositions, four lasted for three, and one lasted for four. The duration of copulatory associations has not yet been measured directly for Florida bugs. However, short-term observations of Florida captives have shown that copulations may last for at least 5–10 h, and that the mating pattern cannot be readily distinguished from that of Oklahoma bugs.

In Florida, oviposition occurs in the ground, in hollow grass stems, or in the capsule of the balloon vine itself, through the emergence holes of the butterfly larvae. Nymphs from eggs laid inside a capsule may develop up to at least the fourth instar on the seeds therein. Similarly, Oklahoma females on *K. paniculata* oviposit in this host's capsules when the soil is moist. However, unlike the capsules of the balloon vine, those of this tree are open at the bottom, and the eggs simply fall through to the moist ground below.

After oviposition, females resume feeding, remaining with the same male, or acquiring a new mate if he has departed. Most females remained gravid with little change in abdomen size from one observation to the next ($n = 37$, for which two or more observations of gravidness were recorded). Oviposition by marked females in the wild was not observed frequently enough to estimate its frequency; however, because captive Oklahoma females produced an average of 13 eggs per day, and the mean clutch size observed in the field in Oklahoma was about 14 eggs, it is suggested that at least some females deposit a clutch each day.

For periods ranging from 20–40 d, nine captive Oklahoma females laid from 213–510 eggs (mean = 368 ± 113 eggs). Maximal lifetime fecundity in the field probably reflects these values (ca. 400–800 eggs, based upon a 60-d maximal reproductive life span). Total fecundity for Florida Keys females cannot yet be estimated, and the expected life span in the wild is not yet known.

Discussion

The life history of *J. haematoloma* differs between Oklahoma and Florida in annual phenology of reproduction and diapause, and in dispersal, body size, rate of egg production, egg size, and development time. Differences are related to the timing and duration of food availability, and the thermal climate, both of which differ between the regions.

In Oklahoma, bugs mature faster and produce smaller eggs at a greater rate than do bugs in Florida. The primary breeding season in Oklahoma is limited to August and September, by late summer maturation of the host's seeds (Carroll & Loye 1987),

and by the onset of diapause in early October, before seeds are exhausted. Rapid growth and reproduction increase the rate at which the seed resource may be exploited, allowing the production of two summer generations before diapause. Because seeds are very abundant during the summer reproductive period, bugs do not compete for food, and efficient use of time should be the primary "resource" for which life histories in this population have competed in evolutionary time. By producing offspring rapidly, females increase the amount of time available to offspring for development and reproduction before the onset of diapause. This seasonal constraint may also be responsible for the observed decline in the proportion of females initiating reproduction late in the season, which further indicates that there may be a tradeoff between reproduction and the probability of surviving over winter.

In contrast, bugs in Florida feed on a seed resource that is available more frequently during the year, but is more likely to be exhausted at any one site. Year-round mild temperatures mean that the bugs can feed on the seeds whenever they are encountered. The host vine produces far fewer seeds than do the host trees in Oklahoma, and the combination of continual seed predation by the bug, and additional predation by two species of lepidopteran larvae, means that competition among individuals for food may be intense. This circumstance could select for a decrease in development time, such that the period during which competition might be experienced would be reduced. On the other hand, it might select for increased body size (and therefore increased development time or propagule size) to increase ability to compete for food (MacArthur & Wilson 1967), or to increase starvation resistance and migratory ability (Dingle 1972, Dingle & Arora 1973). Large size may increase a bug's ability to feed on a seed upon which many individuals are feeding simultaneously, but no observations of exclusion from a seed have been made. However, patchy seed production was related to both reproductive and developmental diapause in three of the five Florida study periods, as well as immigration from a site where no seeds were available in January, and emigration to vines that were producing new seed capsules in August.

The apparent absence of a photoperiodically induced diapause in Florida bugs seems in contrast to the pattern observed in the ecologically similar lygaeid, *Oncopeltus fasciatus* (Dallas), in Florida by Miller & Dingle (1982). In that species they report that reproductive activity diminishes in midwinter, and the authors suggest that this diminution may be cued by seasonal changes in photoperiod or ambient temperature. However, they also observed a decline in food availability that might explain the pattern as well.

Additional life history contrasts occur between *J. haematoloma* and patterns observed in several species of *Dysdercus* (Pyrrhocoridae) by Dingle &

Arora (1973) and Derr et al. (1981). These authors found that large body size was typically linked with rapid egg production and long-distance migration between hosts. In the present study, large body size (Florida) is coupled with migration between hosts, and although bugs in Oklahoma occasionally move between hosts, most migration is probably confined to the period of seed exhaustion in the spring before a new crop is produced. Large body size in Florida is not, however, linked to rapid egg production. The large species studied by Dingle and his associates were migrants between trees that produce abundant seed crops that are predictably available for a few months' duration. Thus, in terms of the pattern of food availability, *J. haematoloma* in Oklahoma, which do produce eggs comparatively rapidly, may be more similar to the large *Dysdercus* spp.

Reproductive aggregations in Oklahoma are characterized by a male bias in adult sex ratio and prolonged copulatory mate-guarding. The observed patterns of greater female mortality both over winter and during summer development explain part of the male bias. If males of the small spring generation that feeds on the remnant seed crop survive at a similarly greater rate, it would explain part of the extreme male bias during initial colonization. This slight bias towards males (55.9%) in the adults produced in situ during the summer is consistent with the observed decline in the extent of the male bias during the summer, after the initial aerial colonization by a preponderance of males in late June and early July. A possible source of greater developmental mortality in females may be costs associated with growing more rapidly than males (they grow to a larger size during a developmental period of similar duration).

The concentration of females at the feeding and oviposition sites, plus the male bias in sex ratio, cause direct, extreme competition among males for matings. This is particularly true in Oklahoma, where unmated females are rare, and an unguarded female is likely to be remated before all of an initial male's sperm are used for fertilization. Post-insemination copulatory mate-guarding, as practiced by male *J. haematoloma*, can only be accomplished at a cost to time that could be spent searching for additional matings (Parker 1974). Nonetheless, guarding also occurs in the Florida Keys population, where the sex ratio is close to 1:1, and a male's chances of finding multiple matings should be greater than in Oklahoma. Preliminary results indicate that greater last-male sperm precedence in Florida than in Oklahoma may provide an additional selective advantage to guarding in Florida (unpublished data).

Prolonged copulatory mate guarding has been described for other aggregating hemipterans, including the lygaeid, *Lygaeus equestris* (L.), in which the last male to mate fertilizes ca. 90% of the ova (Sillen-Tullberg 1981); the pentatomid, *Nezara viridula* (L.) (Harris & Todd 1980, McLain 1980);

and in many species of *Dysdercus* (e.g., Meyers [1927], Van Doesburg [1968], although without being interpreted as mate guarding for this genus). These species appear to guard from intramission until withdrawal is required for oviposition. *J. haematoloma* is unusual in that guarding continues through oviposition, and observations in Oklahoma showed that males sometimes remain with the same female for several ovipositions. The scarcity of females in these aggregations may account for the prolonged guarding of the mate, rather than shorter-term guarding of a single clutch.

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