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Geographic differences in the body sizes of adult *Romalea microptera*

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Abstract

We compared adult body size among six populations of the flightless lubber grasshopper *Romalea microptera* from south Florida, USA. The most distant populations were 113 km apart. We tested whether size differences among populations are correlated with local mean precipitation or temperature, and specifically investigated whether smaller average size is correlated with climate-related short-growth season, as has been shown for other grasshoppers. We found significant size differences among the populations for both males and females. Mean body size of *R. microptera* was greatest for a central population at Shark Valley South, declined toward the northwest, and less strikingly, toward the south. *R. microptera* females had a greater mean size at sites with high precipitation in May and low precipitation in November, suggesting that earlier onset of the wet season is positively associated with mean size. Further, mean size increased with increasing mean minimum temperature in January. These differences in adult size of *R. microptera* suggest that differences in local environments lead either to evolution of local differentiation in adult size or local differences in growth and development that result in differential expression of phenotypic plasticity in adult size.

Key words

lubber grasshopper, local population differentiation, seasonal constraints, climate, body size, biogeography, Acrididae

Introduction

Body size is correlated with most physiological and ecological characters, including metabolic rate, development time, reproductive investment, fecundity, longevity, and vagility, (Peters 1983, Schmidt-Nielsen 1984, Rowe & Ludwig 1991, Abrams *et al.* 1996, Klingenberg & Spence 1997, Telfer & Hassall 1999, Blanckenhorn 2000, Tammaru *et al.* 2002, Berner & Blanckenhorn 2006). Further, individual size influences species interactions and community patterns (Pearson 1980; Juliano & Lawton 1990a,b; Messina 2004). Geographic variation in body size is of interest, because it suggests local environmental constraints or local adaptation (Stearns 1993, Telfer & Hassall 1999, Berner & Blanckenhorn 2006). Geographic variation in size provides an opportunity to investigate the factors that both determine body size over evolutionary time and control body size within single generations.

Romalea microptera (Beauvois) (Orthoptera: Acrididae) (Eastern Lubber Grasshopper) is an ideal species in which to investigate spatial variation in adult body size, and the processes leading to that variation. These large, univoltine, grasshoppers are flightless and relatively sedentary, with a mean lifetime displacement ~ 75 m (Whitman, unpub.). Such limited mobility suggests that local

population differentiation, and possibly local adaptation, may be likely in this species. Across south Florida, local populations of *R. microptera* exist in habitats that differ greatly in soil, vegetation composition and structure, hydroperiod, natural enemies, and proximity to water (Rehn & Grant 1961, Capinera *et al.* 1999, Lamb *et al.* 1999, Lodge 2005). In south Florida, nymphs typically hatch between January and late March (Stauffer & Whitman 1997, Capinera *et al.* 1999). In our south Florida study region, populations from the northwest usually hatch and reach adulthood 1 to 2 weeks before populations from the southeast (Whitman, unpub.). Nymphal growth and development proceeds through the spring and adults first begin to appear in late April (Whitman, unpub.). Adults are most abundant June to August, but some may be found from May through January (Rehn & Grant 1961, Capinera *et al.* 1999).

Across its range from south Florida to North Carolina to east Texas (*i.e.*, spanning ~1850 km and 10° latitude), the life history of *R. microptera* shows evidence of strong seasonal constraints on development period, longevity, and reproductive tactics (Rehn & Grant 1961, Hatle *et al.* 2002, Gunawardene *et al.* 2004). In contrast, patterns of local-scale variation are unknown. We investigated spatial patterns of mean adult body size of *R. microptera* within a relatively small geographic area in south Florida (spanning ~113 km, <1° latitude and ~3 m elevation). We analyzed variation in body size of males and females at six sites sampled within one year.

Our focus on variation among local populations in a subtropical climate limits the potential influence of major differences in macroclimate (*e.g.*, length of the frost-free period – Gunawardene *et al.* 2004), because our six adjacent populations are similar in latitude and elevation. Seasonal constraints (Rowe & Ludwig 1991) on body size and development time of grasshoppers seem to be commonly associated with geographic variation in adult size, with adult size greater in locations where the season suitable for growth is longer (*e.g.*, Telfer & Hassall 1999, Berner & Blanckenhorn 2006). South Florida's subtropical climate is seasonal, with a prominent rainy season from approximately June to November (*i.e.*, the hurricane season) and a dry season from December to May (Chen & Gerber 1990). Seasonal constraints (Rowe & Ludwig 1991, Telfer & Hassall 1999, Berner & Blanckenhorn 2006) on development and body size due to precipitation or temperature could be related to mean body sizes of adult *R. microptera*, if some sites are characterized by a shorter season suitable for grasshopper growth and development. It is such short-season sites at which we would expect small adult body size (see Telfer & Hassall 1999, Berner & Blanckenhorn 2006). We test for such variation using long-term mean precipitation and temperature data from the weather station sites in south Florida that are closest to our six sample sites.

Materials and Methods

Geographic variation.— In 2005 we measured body size of adult *R. microptera* at six low-elevation sites (≤ 4 m above sea level) located in south Florida (Fig. 1). All sites were sampled within 1 week during early June. Adult males and females at a site were collected by hand, as they were encountered in the field. Individuals were held for a few minutes while we measured them, and then immediately released at the site of capture. We used digital calipers (Mitutoyo, Inc., Model CD-6 inch CS) to record the length of the prothorax along the dorsal midline, and the mean length of the hind femora, to the nearest 0.1 mm. Two different researchers measured each grasshopper independently; when there was a discrepancy, a third or fourth person measured the grasshopper, until a consensus was reached.

Data were analyzed using MANOVA on thorax length and mean femur length, testing for effects of site, sex, and interaction. We used standardized canonical coefficients (SCCs) to evaluate the contribution of each variable to significant MANOVA effects (Scheiner 2001, Hatle *et al.* 2002). For all MANOVA analyses, when there were significant effects we further compared groups using multivariate pairwise contrasts (Scheiner 2001, Hatle *et al.* 2002), employing a Bonferroni adjustment for multiple tests. Raw data met assumptions of normality and heterogeneity of variances, hence we did not transform the data for analysis.

Seasonal precipitation and temperature.— To investigate local variation in seasonal climate, we obtained 30-year (1971-2000) mean monthly precipitation and temperatures for six sites in the southernmost counties of Florida (Collier, Miami-Dade, and Monroe)

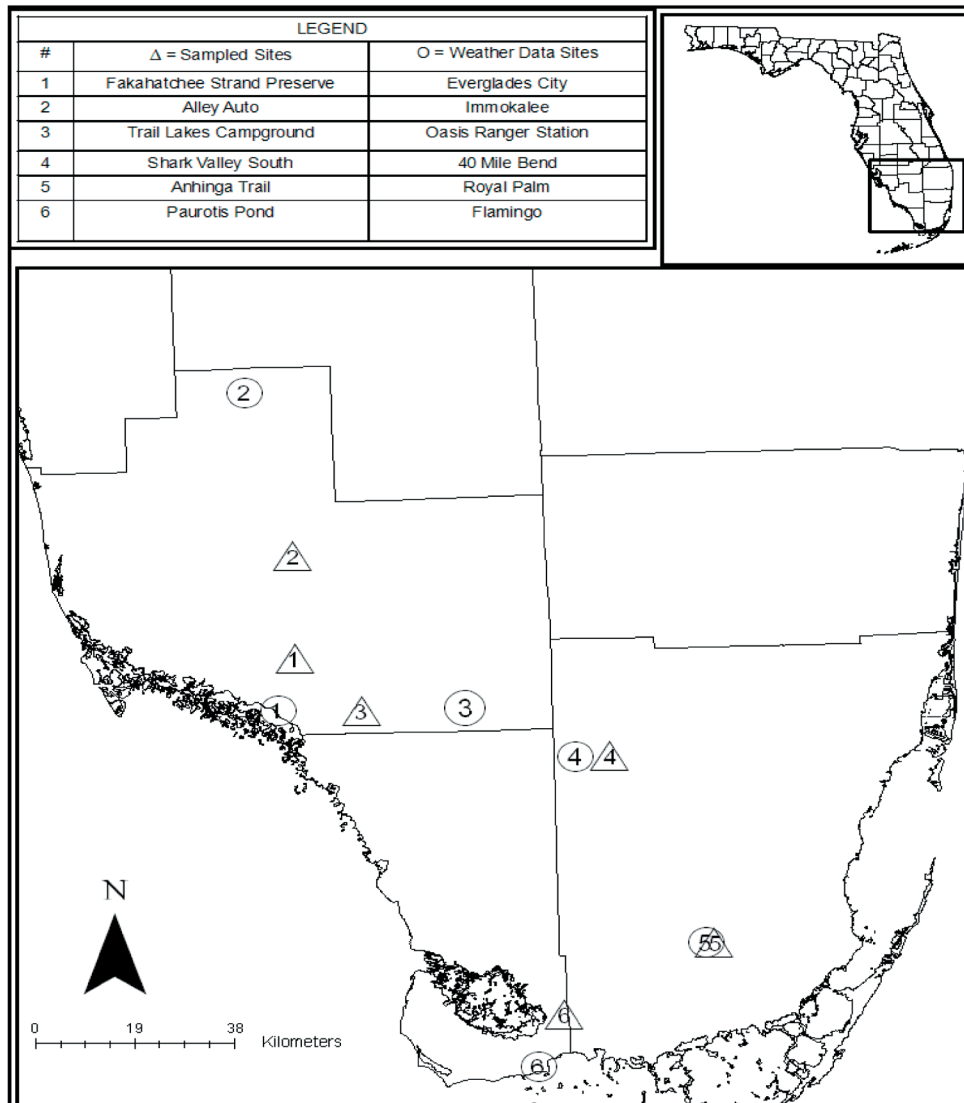


Fig. 1. Sample sites for populations and associated sites for weather data (from the Southeast Regional Climate Center). Locations given to the nearest minute; elevations to the nearest meter. Triangles = Sample sites: 1 = Fakahatchee Strand Preserve (long $25^{\circ} 57'N$, lat $81^{\circ} 21'W$, elevation 2 m); 2 = Alley Auto (long $26^{\circ} 09'N$, lat $81^{\circ} 21'W$, elevation 4 m); 3 = Trail Lakes Campground (long $25^{\circ} 51'N$, lat $81^{\circ} 15'W$, elevation 2 m); 4 = Shark Valley South (long $25^{\circ} 45'N$, lat $80^{\circ} 46'W$, elevation 2 m); 5 = Anhinga Trail (long $25^{\circ} 23'N$, lat $80^{\circ} 35'W$, elevation 1 m); 6 = Paurotis Pond (long $25^{\circ} 15'N$, lat $80^{\circ} 52'W$, elevation <1 m). Circles = Weather data sites. 1 = Everglades City (long $25^{\circ} 51'N$, lat $81^{\circ} 23'W$, elevation <1 m); 2 = Immokalee (long $26^{\circ} 28'N$, lat $81^{\circ} 26'W$, elevation 9 m); 3 = Oasis Ranger Station (long $25^{\circ} 51'N$, lat $81^{\circ} 02'W$, elevation 3 m); 4 = 40 Mile Bend (long $25^{\circ} 45'N$, lat $80^{\circ} 50'W$, elevation 2 m); 5 = Royal Palm (long $25^{\circ} 23'N$, lat $80^{\circ} 36'W$, elevation 1 m); 6 = Flamingo (long $25^{\circ} 09'N$, lat $80^{\circ} 55'W$, elevation <1 m).

geographically nearest our six sample sites (Fig. 1). Data were obtained from the Southeast Regional Climate Center (http://www.sercc.com/climateinfo/historical/historical_fl.html).

We tested for a relationship of adult size and seasonal precipitation by running stepwise multiple regression of mean femur length *vs* mean monthly precipitation. We expect that if seasonal precipitation affects body size, it will do so by affecting the season suitable for growth by nymphs (*i.e.*, February – June). Thus we predict that mean female femur length should be positively related to mean monthly precipitation during the spring. We also ran similar stepwise multiple regressions of mean female femur length *vs* mean monthly maximum temperature, and mean monthly minimum temperature, in order to test whether mean body size is related to seasonal variation in temperature. For all stepwise regressions we used SAS PROC REG (SAS Institute Inc. 2004), with the stepwise option and $\alpha \leq 0.15$ for entry or retention of an independent variable in/to the model.

Results

Geographic variation.— MANOVA on mean femur length and thorax length yielded significant effects of Site, Sex, and Site \times Sex interaction (Table 1). For interaction, thorax length made the major contribution to the significant effect (SCCs, Table 1), indicating that sex-specific differences among sites derive mainly from differences in thorax length. Though males and females show similar patterns of inter-site differences in bivariate means (Fig. 2), patterns of significant pairwise differences among sites differed between the sexes (Fig. 2). For females, sites fell into three groups: sites with large females (Shark Valley South, Anhinga Trail), medium females (Paurotis Pond, Trail Lakes), and small females (Alley Auto, Fakahatchee Strand) (Fig. 2). For males, groupings of sites with distinctly different body sizes were less clear, but the sites followed the same progression of body sizes (small to large from Alley Auto to Shark

Valley South – Fig. 2). In general, mean sizes declined from east to west and from north to south (compare Figs 1 and 2).

Seasonal precipitation and temperature.— Long-term means of precipitation for the months of May and November were significant ($P < 0.05$) predictor variables for mean female femur length (MFFL) in stepwise regression. The final regression equation ($\pm s_{\bar{x}}$ for each parameter) was:

$$\text{MFFL} = (31.61 \pm 7.01) + (0.30 \pm 0.06)(\text{May precipitation}) - (0.71 \pm 0.22)(\text{Nov. precipitation})$$

with $R^2 = 0.908$. Thus, *R. microptera* females were larger at sites with high precipitation in May and low precipitation in November. Comparison of site data (Fig. 3A) shows that Royal Palm, Oasis Ranger Station, and 40 Mile Bend were the sites with the wettest month of May, and these sites are associated with Anhinga Trail, and Trail Lakes, and Shark Valley South, respectively — the sites with the largest adult grasshoppers (Fig. 2). Sites with greater precipitation in May also tended to have greater precipitation in October (Fig. 3A).

For stepwise regressions of MFFL *vs* means of monthly minimum temperatures, two variables (January and June means) entered into the model, but only the parameter for January mean minimum temperature was a significant ($P < 0.05$) predictor of mean female femur length. The final regression equation ($\pm s_{\bar{x}}$ for each parameter) was:

$$\text{MFFL} = (51.61 \pm 20.60) + (3.70 \pm 0.71)(\text{Jan. min. temp.}) - (3.15 \pm 1.18)(\text{June min. temp.})$$

with $R^2 = 0.907$. Thus, *R. microptera* females were larger at sites with higher January minimum temperatures. The western sites (Everglades City and Immokalee) had the lowest minimum temperatures

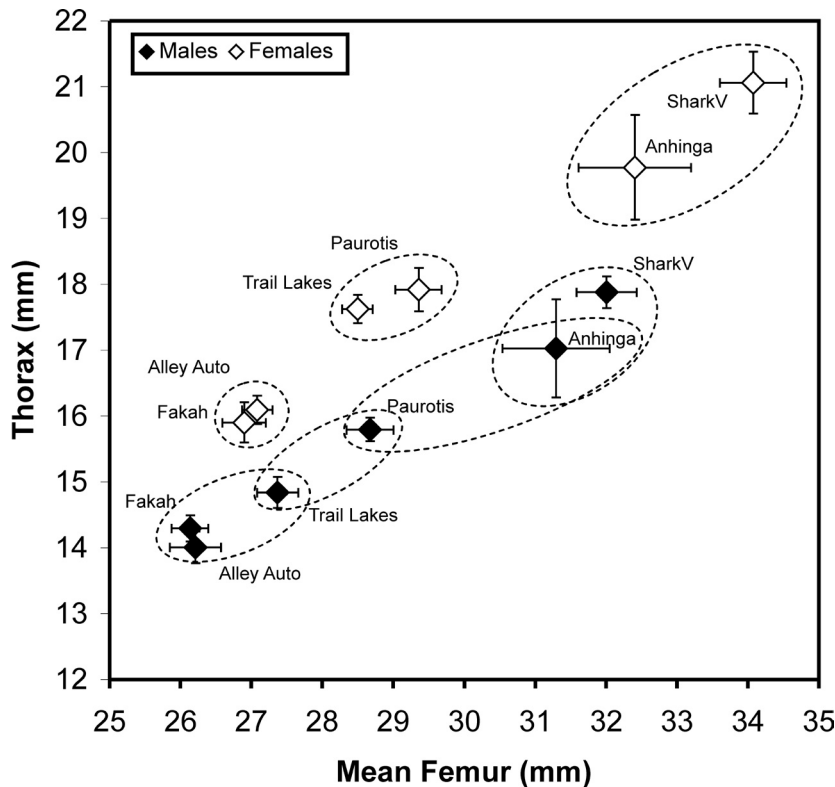


Fig. 2. Bivariate means for males and females from six populations in 2005. Bivariate means within each sex enclosed in the dotted ellipses are not significantly different at (experimentwise) $\alpha = 0.05$. Abbreviations: Fakah=Fakahatchee Strand, SharkV=Shark Valley South, Paurotis=Paurotis Pond. For analysis see Table 1.

Table 1. MANOVA for *R. microptera* males and females collected at six sites in 2005. Standardized canonical coefficients quantify the contributions of the two original variables (mean femur length and thorax length) to the significant multivariate differences detected in the analysis. For means and $s_{\bar{x}}$ of the original variates, and for results of pairwise bivariate contrasts among sites within each year, see Fig. 2.

Source	Pillai's Trace	F (df,df)	P	Canonical variates			Standardized Canonical Coefficients	
				Variate number	Percent variation	P	Mean Femur Length	Thorax Length
Site	0.347	24.49 (10, 354)	0.0001	1	0.97	0.0001	0.967	0.839
				2	0.03	0.0731		
Sex	0.610	137.37 (2, 176)	0.0001	1	1.00	0.0001	-1.829	3.123
Site × Sex	0.113	2.12 (10, 354)	0.0222	1	0.600	0.0229	-0.002	1.862
				2	0.400	0.0793		

in January (Fig. 5B) and were associated with populations with the smallest adult females (Fig. 2, Fakahatchee Strand and Alley Auto, respectively). In contrast the eastern sites (40 Mile Bend and Royal Palm) had the highest minimum temperatures in January (Fig. 3B) and were associated with populations with the largest adult females (Fig. 2, Shark Valley South and Anhinga Trail, respectively). Long-term means of monthly maximum temperature were not significantly related to female femur length.

Discussion

Our results show considerable spatial variation in mean adult body size for *R. microptera* within a short distance of 113 km and identical altitude. Body size is largest at Shark Valley South, and tends to decline with distance away from this site, both to the northwest and the south (Figs 1, 2). We would not expect major differences in macroclimate or seasonal temperatures over such short distances, in contrast to other cases of geographic variation in grasshopper size (Telfer & Hassall 1999, Berner & Blanckenhorn 2006), because of limited differences in latitude and altitude over this local geographic area. Indeed climate data (Fig. 3) suggest that differences in precipitation and temperatures among these 6 sites are rather small.

Weather data associated with the sample sites indicate that mean female size is positively associated with sites that, on average, have a wet May and a dry November. This relationship suggests that larger females occur at sites that have a slight shift of the wet season to earlier times in the year. This shift is not associated with earlier hatching, opportunity for prolonged development, and associated greater body size, because hatching and adult eclosion actually take place 1-2 weeks earlier in the smaller, northwestern populations (Whitman, unpub.). In addition, hatching occurs well before May; hence the impact of this precipitation on growth period is unclear.

We did not anticipate finding a greater body size associated with greater January (more generally, winter) minimum temperature. In January, virtually all individuals in these *R. microptera* populations reside in the soil as eggs. Because larger populations experiencing higher winter minimum temperatures actually hatch later than smaller populations (Whitman, unpub.), it does not appear that this temperature difference affects body size via earlier hatching and an extended growth period.

All of these associations with long-term mean climate must be taken only as a preliminary evaluation of one possible mechanism favoring larger or smaller body size in local populations of this grasshopper. Indeed, our six sites vary dramatically in soil, vegetation, parasite load, and timing and degree of hydroperiod (Lamb *et al.* 1999, Lodge 2005). It is clear that data on hatching dates,

nymphal growth and development, mortality schedules of nymphs, adult eclosion, fecundity, and survivorship at these (and other) sites in South Florida would be useful to evaluate these correlations with subtle variation in climate. Further, determining how these fitness-related traits are related to body size at each site would be valuable for understanding the causes of local size variation in this grasshopper.

If these associations with long term average climate are robust, they suggest that local climate has selected for differences in development and life history and that local variation in adult body size is simply one manifestation of those differences. Our data do not allow us to evaluate alternative explanations for local variation in body size – namely that other factors such as local variation in food plants, natural enemies, or sexual selection may have influenced body-size evolution, or that size is influenced by phenotypic plasticity in response to weather or diet within a single season.

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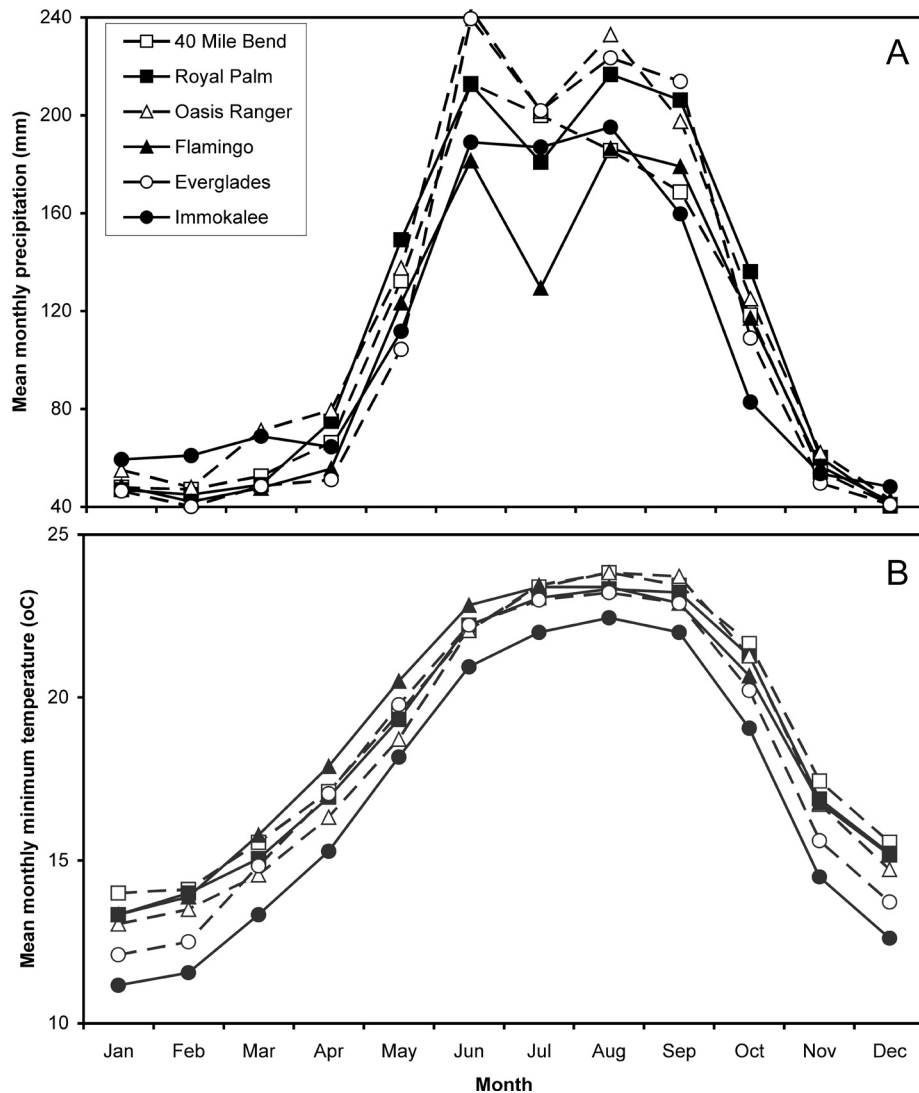


Fig. 3. Mean (1971-2000) monthly precipitation (A) and low temperature (B) for weather stations near each collection site. Sites are arrayed in the legend in order of largest to smallest grasshoppers. 40 Mile Bend nearest Shark Valley S.; Royal Palm nearest Anhinga; Oasis Ranger nearest Trail Lakes; Flamingo nearest Paurotis Pond; Everglades nearest Alley Auto; Immokalee nearest Fakahatchee Strand. Data from SERCC (http://www.sercc.com/climateinfo/historical/historical_fl.html)

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