

BIOLOGY OF AND RATES OF PARASITISM BY NYMPHAL  
AND ADULT PARASITES OF THE SALT-MARSH-INHABITING  
PLANTHOPPERS *PROKELISIA MARGINATA* AND *P. DOLUS*

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ABSTRACT

*Elenchus koebelei* (Strepsiptera) and *Pseudogonatopus arizonicus* (Dryinidae) are recorded as parasitoids of nymphs and adults of *Prokelisia marginata* and *P. dolus* in north Florida salt marshes. *Prokelisia* spp. are new host records for *P. arizonicus*. Parasitized hosts can be found year round. Average monthly levels of parasitism vary between 0 and 1% for *Pseudogonatopus* and between 0 and 20% for *Elenchus*. Both superparasitism and multiparasitism of *Prokelisia* hosts was noted. The maximum number of recorded parasites per host was four for *Elenchus* and two for *Pseudogonatopus*. Only two of 88,354 hosts were found to contain both parasites at the same time. Dryinid larvae may be hyperparasitized, but the hyperparasite responsible could not be reared out.

RESUMEN

Se registra a *Elenchus koebelei* (Estresiptera) y a *Pseudogonatopus arizonicus* (Drínida) como parasitoides de ninfas y de adultos de *Prokelisia marginata* y de *P. dolus* en saladares pantanosos del norte de la Florida. *Prokelisia* spp. es un registro nuevo como hospedero para *P. arizonicus*. Hospederos parasitados se pueden encontrar todo el año. El promedio mensual de parasitismo varía entre 0 y 1% *Pseudogonatopus* y entre 0 y 20% para *Elenchus*. Se notó el superparasitismo y multiparasitismo de hospederos de *Prokelisia*. El registro mayor de parasitismo por hospedero fue de cuatro en *Elenchus* y dos en *Pseudogonatopus*. Solo dos de 88,354 hospederos se encontraron que contenían ambos parásitos al mismo tiempo. Larvas de drínidas pudieran ser hiperparasitadas, pero el hiperparásito responsable no se pudo criar.

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*Prokelisia marginata* (Van Duzee) is a common inhabitant of salt-marsh cord grass *Spartina alterniflora* Loise on both the Gulf and Atlantic coasts of Florida (Denno et al. 1980, 1985, 1986; Stiling & Strong 1982). Nymphs and adults are attacked by two types of parasitoids, a strepsipteran, *Elenchus koebelei* Pierce, and a dryinid (Stiling & Strong 1982). We had previously reared out and identified the strepsipteran, but we had been unable to rear out dryinids from *Prokelisia* until 1989. The current paper identifies the dryinid as *Pseudogonatopus arizonicus* Perkins. We had previously thought that parasitism by either parasitoid was very infrequent in Florida, never exceeding 5% (Stiling & Strong 1982). More widespread samples in 1988 and 1989 have revealed that

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average levels of parasitism by strepsipterans may approach 20% but that parasitism from dryinids never exceeds 1%. The present paper details these results and provides information on the biology of both parasites.

It is also worth noting that what long had been known as *Prokelisia marginata* was split into two species, *P. marginata* and *P. dolus* (Wilson), in 1982 (Wilson 1982). Denno et al. (1987) have noted the presence of *P. dolus* and *P. marginata* in Florida and Atlantic marshes, and we have recently recorded both species in our north Florida study sites (unpublished). There are no major differences in life history between the two *Prokelisia* species, and the most striking ecological difference is that *P. dolus* is found in backmarsh situations, away from the seashore, whereas *P. marginata* occurs more toward the shore and less in the backmarsh (Denno et al. 1987). This paper also compares rates of parasitism between *P. dolus* and *P. marginata* nymphs and adults.

#### METHODS

We took 200 sweep samples from *Spartina alterniflora* in Wakulla County, Florida, at eight different sites every month from June 1988 through May 1989, for a total of 19,200 sweep samples. Each series of 200 sweeps was emptied into a bag, returned to the laboratory, and sorted for parasitized and unparasitized nymphs and adults of *Prokelisia*. Estimates of parasitism levels throughout the year were based on combined samples of nymphs and adults from all sites each month. Sample size was at least 1500 *Prokelisia* each month and usually many more. Statistical comparisons of parasitism levels in *P. dolus* and *P. marginata* and in male planthoppers and female planthoppers were made by means of Wilcoxon's distribution-free rank sum test (Hollander & Wolfe 1973). In addition, we reared out adult dryinids from *Prokelisia* for identification purposes, and we present some information on the biology of these parasitoids together with some new information on the strepsipterans. Nymphal or adult *Prokelisia* exhibiting dryinid sacs (defined in results section) were caged on *Spartina* leaves in the laboratory at room temperature,  $25 \pm 2^\circ\text{C}$ ,  $72 \pm 2\%$  RH. When dryinid larval development was complete, the dryinid larva exited the host, killing it. The exiting dryinid larva usually spun a cocoon on the cork stopper of the clip cage. No cocoons were spun on leaves.

#### RESULTS

We found no evidence that either *Elenchus* or *Pseudogonatopus* prefers either species of host. We examined males of 7,637 *P. dolus* and 16,044 *P. marginata* and found parasitism rates of 8.24% and 8.33%, respectively, for *Elenchus* ( $W^* = 0.015$ ,  $P = 0.492$ ) and 0.026% and 0.031% for *Pseudogonatopus* ( $W^* = 0.001$ ,  $P < 0.50$ ). We believe neither *P. arizonicus* nor *E. koebelei* discriminates between the two species of planthopper, so for the purposes of this study we have pooled data from the two hosts.

##### *Elenchus koebelei*

The adult male is free living, but the abdomen of the neotenic, parasitic female remains embedded in the host's hemocoel; only its cephalothorax protrudes to the exterior. Males mate with females while the latter are still inside their hosts. Female Strepsiptera are viviparous; eggs fill the body cavity, where they develop into minute, mobile, triungulid larvae. The larvae hatch within the female's body and reach the exterior through a brood canal. In the case of *Prokelisia* hosts, the larvae locate host nymphs and adults and bore into the body cavity. Once inside hosts, triungulids undergo hypermetamorphosis, molting into grublike, legless larvae that show sexual differenti-

ation after the second molt. Extruded male puparia are dark and most commonly appear from between host abdominal segments 7 and 8. In *Elenchus* females, the pupal stage is suppressed, and the adult becomes sexually mature after extrusion of the cephalothorax through the host's cuticle. The extrusion of the female cephalothorax is evidenced only by two small holes and is much less obvious (for examples in other host planthoppers, see diagrams by Hassan 1939, Kathirithamby 1982). Our earlier samples in 1980 and 1981 scored only male strepsipterans, and we believe this was a major reason for our low recorded rates of parasitism. Extrusion of female larvae only occurs when the host is adult, but the cephalothorax of the male is extruded from fifth- and, less commonly, fourth-instar nymphs (Table 1). Such strepsipteran extrusion patterns, in which the female parasite appears only in adult hosts, are apparently a general phenomenon in most homopterans (Hassan 1939, Williams 1957). In our study, the sex ratio of *Elenchus* was about 1:1 (2,936 males, 2,978 females). Hassan (1939) also found an even sex ratio in the strepsipterans parasitizing delphacids in England.

We recorded 173 cases of superparasitism (Table 2). The maximum number of parasites we found in a nymph was three and in an adult four (two males and two females). Where superparasitism occurs, the parasites may be extruded either on the same side of the host's abdomen or on different sides. Greathead (1970) reported that when two parasites were present they are "almost invariably" extruded on opposite sides of the host. We found just the opposite pattern (Table 3). Of a total of 54 cases in which two parasites were extruded, either in nymphs or in adults, in 47 of those cases, the parasites were extruded on the same side. We have insufficient data to say what really happens at even higher levels of superparasitism, but Greathead (1970) reports that any pattern is lost and extrusion occurs wherever there is space.

Parasitism levels of *Prokelisia* spp. by *Elenchus* varied considerably in the course of the year, from less than 4% to over 18% (Fig. 1), although this temporal variation showed no clear pattern. Some evidence of spatial variation was apparent; values between 2% and 40% were recorded at different sites at the same times (Stiling et al. unpublished data).

*Pseudogonatopus arizonicus*

Our rearing of *Pseudogonatopus arizonicus* from *Prokelisia* is a new host record for this species. Both the adult male and the adult female of *Pseudogonatopus* are free living, but only the male is winged. Females are wingless and ant-like in appearance. In addition to being parasites, female *P. arizonicus* can be voracious predators. We observed newly emerged females to attack and eat two *Prokelisia* nymphs within 10 minutes. Nymphs were lifted completely into the air and supported by the front legs and ovipositor of the dryinid.

Immature dryinid larvae are extruded in a sac from between the abdominal segments of the host. The sac, composed of cast larval skins, usually appears between segments 5 and 6. Most of the dryinid sacs observed were seen on nymphs. Of 163 sacs observed

TABLE 1. SEX RATIO OF *ELENCHUS KOEBELEI* (STREPSIPTERA) PARASITES IN THEIR *PROKLESIA* (HOMOPTERA) HOSTS.

Sex of strepsipteran	Sex of host		
	Male	Female	Nymph
male	446	593	1897
female	1581	1397	0

TABLE 2. SUPERPARASITISM AND THE FREQUENCY OF MULTIPLE STREPSIPTERAN PARASITES IN *PROKELISIA* HOSTS. TOTAL NUMBER OF HOSTS EXAMINED = 88,354.

No of parasites	n
<i>In adult Prokelisia</i>	
1 male	973
2 males	21
3 males	1
1 female	2877
2 females	38
3 females	1
1 male and 1 female	36
1 male and 2 females	1
2 males and 2 females	1
<i>In nymphal Prokelisia</i>	
1 male	1748
2 males	73
3 males	1

in the present study, 118 were visible on nymphs, 38 on adult female *Prokelisia*, and only 7 on male *Prokelisia*. Only once did an individual host support more than one dryinid sac; that host was a nymph collected in November 1989, and the two sacs protruded from opposite sides of the host's abdomen.

From dryinid cocoons, we reared out 6 adult dryinids, 1 male and 5 females. The average length of time spent in the pupal stage was 21.17 days, S.D. = 1.17. We found one dryinid larva to be hyperparasitized by three endophagous larvae, but we were not successful in rearing them out.

Percent parasitism of *Prokelisia* by *P. arizonicus* was extremely low and varied between 0% in August and September 1988 and 0.71% in June 1988. The highest parasitism recorded at any one site was only 3.49%.

TABLE 3. SUPERPARASITISM AND THE LOCATION OF MULTIPLE STREPSIPTERAN PARASITES IN ABDOMENS OF THEIR *PROKELISIA* HOSTS.

Position in host abdomen	Number and sex of strepsipterans				
	2 females	2 males	1 female and 1 male	3 males	3 females
<i>In adult Prokelisia</i>					
One same side	11	10	2	0	0
On different sides	3	2	1	1	1
<i>In nymphal Prokelisia</i>					
On same side	--	24	--	1	--
On different sides	--	1	--	0	--

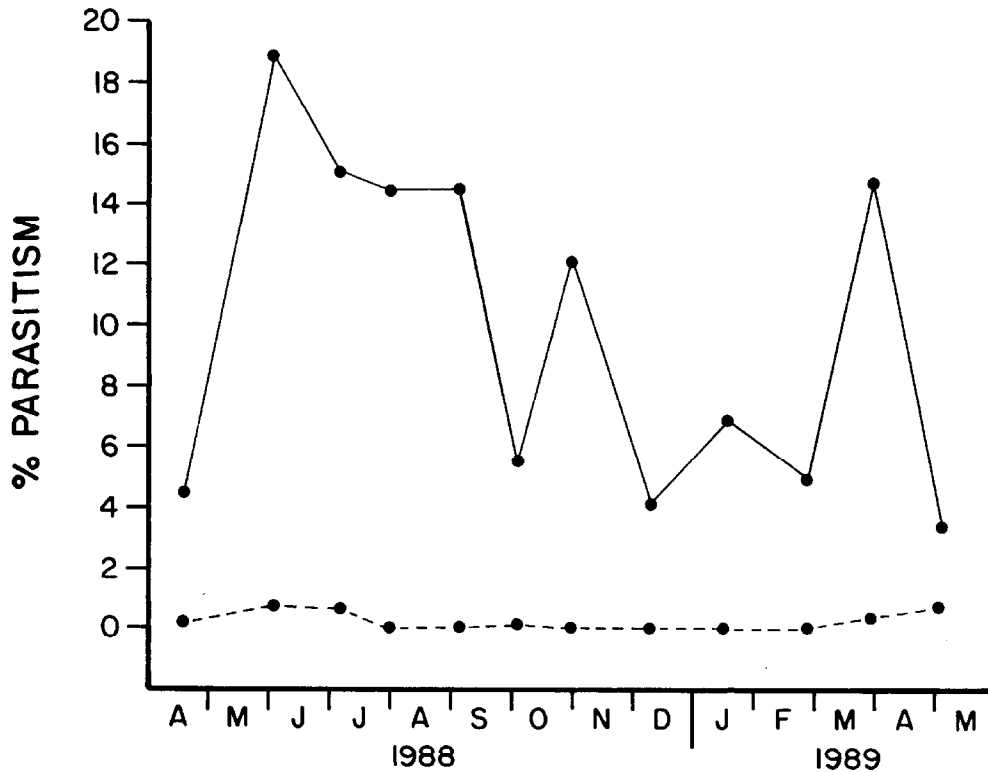


Fig. 1. Seasonal trends in parasitism rates of *Prokelisia* spp. by *Elenchus koebelei* (Strepsiptera) (solid line) and *Pseudogonatopus arizonicus* (Dryinidae) (dashed line) on north Florida salt marshes.

DISCUSSION

*Pseudogonatopus arizonicus* (Dryinidae) and *Elenchus koebelei* (Strepsiptera) are both parasites of nymphal and adult *Prokelisia* in north Florida salt marshes. This paper reports the first record of *Pseudogonatopus arizonicus* from *Prokelisia* spp., there being no record of *Prokelisia* as a host in Olmi's extensive revision of the Dryinidae (Olmi 1984). Denno (1983) swept *Haplogonatopus americanus* from New Jersey marshes and assumed that this was the species likely to be attacking *P. marginata* (Denno pers. comm.). Interestingly, Denno (1977) had earlier swept dryinids in the genus *Pseudogonatopus* from *Spartina patens* in New Jersey. Both *E. koebelei* and *P. arizonicus* can be found in hosts year round, though it is unclear how many generations the parasites pass through per year. Only 2 individuals out of 88,354 hosts examined contained both a dryinid sac and a strepsipteran larva—many fewer than would be expected by chance from our observations of 163 hosts with dryinids and 6235 with strepsipterans ( $\chi^2 = 7.52$ ,  $df = 1$ ,  $p < 0.01$ )—so the parasites do not attack the same hosts or cannot survive in the same hosts. Multiparasitism of homopteran hosts by strepsipterans and dryinids is generally not common. After extensive collections of grassland homopteran hosts in Britain over many years, Waloff (1990) recorded only one such case. However, Raatikainen (1987) recorded 207 multiparasitized individuals in 15,878 *Javasella pellucida* taken between 1958 and 1964, which is a multiparasitism rate of 1.3%.

Superparasitism was recorded in both parasitoid species, but was more commonly noted in *E. koebelei*; a maximum of four strepsipterans were found in one host. The

maximum number of strepsipteran pupae found in other Homoptera varies from three in *Ulopa reticulata* adults in Britain (Waloff 1981) to five in *Dicranotropis muiri* on Mauritius (Williams 1957) and even seven in *Poophilus costalis* in Uganda (Greathead 1970). Indeed, Greathead (1970) argues that the number of parasites per host is limited only by space, and he documents a correlation between host size and degree of parasitism. In this respect, because females are larger than males in most planthopper and leafhopper species, they may exhibit a higher degree of superparasitism (Greathead 1970) and suffer a higher overall amount of parasitism. In *Prokelisia* spp., however, we found that male and female hosts were parasitized to about the same extent (males, 8.30%,  $n = 23,681$ ; females, 7.97%,  $n = 24,795$ ;  $W^* = 0.13$ ;  $P < 0.45$ ). Williams (1957) reported no effect of host sex on the number of extruded parasites in *D. muiri* and argued that, though the abdomen of the male was smaller than that of the female, the integument allows considerable distention in both sexes.

Levels of parasitism by dryinids are extremely low and probably inconsequential to the population dynamics of the host. Dryinids may, however, affect host populations more by direct predation; females of other dryinid species have been thought to eat over 100 hosts in their lifetimes (see references given by Waloff & Jervis 1987). Levels of parasitism by *E. koebelei*, the strepsipteran, are much higher, varying, on average, between 0 and 20%. At some sites, parasitism levels may approach 40% in some months (Stiling et al. unpublished data), and *E. koebelei* may have a substantial impact on *Prokelisia* densities. These results contrast with results from New Jersey marshes, where there are three generations of *Prokelisia* per year (Denno 1983). In the first generation of nymphs in New Jersey, levels of parasitism by strepsipterans and dryinids combined may be as high as 80% (Denno 1983), but parasitism levels in the second and third generations are less than 5%. Our results suggest that parasitism of *Prokelisia* nymphs and adults may have a more consistent but less dramatic effect in Florida marshes than in those of New Jersey.

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