Migratory and Local Flights in Mole Crickets, *Scapteriscus* spp. (Gryllotalpidae)[1]

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ABSTRACT To study between-habitat and within-habitat flights of *Scapteriscus acletus* Rehn and Hebard and *S. vicinus* Scudder at Gainesville, Fla., we trapped those landing at synthesized conspecific calls at paired stations—one in an infested field and the other in a nearby wood (where mole crickets do not breed). Since mole crickets end their flights (long or short) at conspecific calls, the proportion of flying mole crickets that were migrating could be estimated as follows: number ending (migratory) flights in the wood divided by number ending (migratory and trivial) flights in the field. Since this ratio may be biased by unknown details of flight or phonotactic behavior, it should be treated as an index of migration rather than an accurate estimator. During 3 years at one pair of stations, the index for *S. acletus* ranged between 0.12 and 0.18, and for *S. vicinus*, between 0.39 and 0.46. During 1 year at two other pairs of stations, the index for *S. acletus* was 0.09 and 0.14, and for *S. vicinus*, 0.64 and 1.24. Males of *S. vicinus* were migratory in a significantly higher proportion of their flights than females. Paired trapping stations can be used to study trivial and migratory flights in other insects if traps catch individuals engaged in both types of flight.

Insect flights may be functionally classed as migratory (= inter-habitat; relatively long range) or local (= intra-habitat; relatively short range). In the former, the insect leaves one habitat that is suitable for breeding (or dormancy) and flies across unsuitable areas to another. In the latter, sometimes called "trivial" flights, the insect remains within a suitable habitat, and its flights are generally concerned with feeding, mating, or oviposition (Southwood 1962, Johnson 1969, Baker 1978).

Both local and migratory flights are important to two mole cricket species that are major pests in southeastern United States. *Scapteriscus acletus* Rehn and Hebard and *S. vicinus* Scudder breed in open areas, especially in cultivated fields, turf, and pastures. Some flights are local, as revealed by recapturing marked mole crickets at the same flight traps on successive nights (Ngo and Beck 1982). These flights function in finding mates and new, nearby sites for oviposition (Forrest 1983). Some flights are migratory, as revealed by recapturing marked mole crickets up to 3.8 km from the point of release (Ulagaraj 1975, Rod Kepner and T. J. Walker, unpublished data) and by the rapid infestation of newly cleared fields. Perhaps the best evidence of migratory flights is the rapid spread of *S. acletus* and *S. vicinus* from their ports of accidental introduction in 1899 to 1925 to their present extensive ranges in southeastern United States. *S. abbreviatus* Scudder, a third species of *Scapteriscus* accidentally introduced at several ports more than 60 years ago, is flightless and has spread very little (Walker and Nickle 1981).

The development of "sound traps" for flying mole crickets made possible the easy quantification of mole cricket flights (Walker 1982, Walker et al. 1983). The idea developed in this paper is that sampling mole crickets flying over woodland (unsuitable for mole cricket breeding) estimates the density of migrants, whereas sampling mole crickets flying in fields estimates the density of local flights plus the density of migratory flights. If paired trapping stations are operated simultaneously in woods and fields, the catch of the woods station divided by the catch of the field station (W/F ratio) estimates the proportion of mole cricket flights that are migratory.

The two species we studied have similar seasonal life cycles, but their peak flights occur at different times during the spring (Walker et al. 1983). We were, therefore, interested in determining differences in seasonal trends in propensity to migrate as well as seasonwide differences between the two species.

Materials and Methods

Three pairs of standardized sound-trapping stations (Walker 1982) were operated in township R19E T9S, west of Gainesville, Fla. One station of each pair was in an open, grassy area (infested with *S. acletus* and *S. vicinus*), and the other was at least 150 m into a nearby woods (unsuitable for mole cricket breeding). Each station consisted of two calling-song-emitting units (one *S. acletus*, the other *S. vicinus*), centered over two 1.5-m-diameter wading pools partially filled with water and 2 m apart. Every evening at sunset, a timer turned on the synthetic calls for the 2 h during which *S. acletus* and *S. vicinus* fly (Ulagaraj 1975). Mole crickets landing in the pools swam on the water's surface until collected. They were then identified, sexed, and counted, and were never released. Sound units emitted calls at 106 dB (at 15 cm), compared with 70 to 90 dB for naturally calling males. Catches from the two traps at each station were pooled, since ca. 17% of *S. acletus* captured and 21% of *S. vicinus* captured land in the heterospecific trap (Walker et al. 1983).

One pair of stations was operated at site "PT" (NW quarter of section 31), 1 July 1979 to 30 June 1982. One station was in a 5-ha bahia- and bermudagrass pasture. The other was 200 m into the surrounding woods. Two pairs of stations were at site "OH" (S half of

section 9), a 200-ha experimental area containing a patchwork of grassy fields, wooded lots, vegetable crops, and ornamentals, all surrounded by extensive woods. The two OH field stations were 240 m apart in a 5-ha bahiagrass field; the corresponding woods stations were 120 m apart and about 150 m into the forest that encompassed the experimental area. The stations at site OH were operated from 8 October 1980 to 30 May (pair A) or 18 June (pair B) 1981.

On nights when one station of a pair failed to operate (e.g., from timer or power failure) or was raided by a predator (e.g., fox, opossum), data from the other station were of no use in estimating the proportion migrating and were disallowed for that purpose (e.g., Fig. 1b). In calculating seasonal changes in numbers flying (e.g., Fig. 1a), missing data were estimated from the catches at that station during the remainder of the week. Both stations of a pair generally operated properly more than 95% of the nights. The worst series of mishaps occurred to pair B at site OH, yielding a reliability of ca. 85% during spring 1981.

Data were analyzed for seasonal trends by grouping at weekly, monthly, and semiannual intervals. Since mole crickets flying in the fall are of the same generation as those that fly the following spring, we added the fall flights of one year to the spring flights of the next to obtain figures applying to an entire generation.

Results

As estimated by W/F ratios, migratory flights were a significantly higher proportion of *S. vicinus* flights than of *S. acletus* flights (Table 1). W/F ratio for three generations of *S. acletus*, monitored by one to three pairs of stations, averaged 0.14 ($n = 5$, SE = 0.02); the comparable figure for *S. vicinus* was 0.64 (SE = 0.16). In *S. acletus*, W/F ratios for fall and spring flights were similar (0.15 and 0.13), but in *S. vicinus*, ratios for fall flights were significantly lower than for spring flights (0.20 vs. 0.66) (Table 1).

On weekly (Fig. 1) and monthly scales, trends in W/F ratios were inconsistent between years, sites, and replicates.

Males and females sometimes divided their flights differently (Table 2). At both sites, flights of male *S. vicinus* were more often migratory than of females; at site PT, *S. acletus* males exceeded females in the proportion of flights that were migratory, but at site OH, females exceeded males.

Discussion

Migratory and local flights have been empirically recognized in a variety of insects (e.g., butterflies [Williams 1958], milkweed bugs [Dingle 1981] and mosquitoes [Provost 1957]) with important implications to population dynamics and insect control. For example, local flights have no effect on local population density, whereas migratory flights have the potential of depleting or flooding a local population or of stabilizing a population through density-dependent emigration (e.g., aphids [Shaw 1973]; see also Stinner et al. [1983]).

· Recognizing migratory and local flights is occasionally easy (e.g., some butterflies [Williams 1958]). More often it is not. For example, Dingle (1978, 1981) resorted to duration of tethered flights as an index to migration in milkweed bugs, *Oncopeltus fasciatus* (Dallas). Provost (1957, 1960) concluded that the mosquito *Aedes taeniorhynchus* (Wiedemann) was attracted to light and to bait animals during local flights but not during migratory ones. Migratory flights, at their start, could be detected with stationary nets and sticky traps, but the suspected altitude of sustained migration was out of reach of portable, ground-supported traps.

When flying insects can be sampled independent of the habitat in which they are flying, those caught in habitats unsuitable for their continuance (UH) must be migrating, whereas those captured in suitable habitats (SH) may be migrating (i.e., entering or leaving the SH) or flying locally (i.e., staying within the habitat of origin). If all flights of a particular insect species in a limited geographic area are migratory, two nearby sampling stations in that area would likely catch similar numbers, even though one was in SH and the other in UH. If all flights in the area are local, only the SH station should collect specimens. If local and migratory flights occur simultaneously, the quotient obtained by dividing the UH catch by the SH catch should estimate the proportion of flights that are migratory. The accuracy of such an estimate is affected by these four assumptions. (1) All individuals caught in UH are migrating. (2) Density of migrants is the same in UH and SH. (3) Migrants are sampled with equal efficiency in UH and SH. (4) Migrating and locally flying individuals in SH are sampled with equal efficiency. Validity of these assumptions will be discussed relative to the flights of *S. acletus* and *S. vicinus*.

(1) *Scapteriscus* spp. have not been found in woodland soils, nor have males been heard to call from such soils. Thus, individuals flying over woods are flying between habitats (i.e., migrating), unless they are intrahabitat fliers that fail to recognize the limits of their habitat because they use the calls of conspecific males as cues and are misled by the synthetic call. (W stations were located at least 150 m from the nearest field to avoid this problem).

(2) Many factors should influence the density of migrating *Scapteriscus* spp. at any site; consequently, the assumption that density is equal at adjacent UH and SH sites is unlikely to be correct and may bias the estimates of proportion of flights that are migratory. Equality of density seems probable only if migratory flights are in all directions and the major sources are distant from both SH and UH. However, migratory flights are generally downwind (Baker 1978), and SH itself is a likely source of migrants whenever migrants are coming from more distant suitable habitats. In other words, locations of source habitats and wind direction will affect the uniformity of density of migrants.

(3) Even if density of migrants is uniform over SH and UH, migrants may be less likely to land at one station than the other, and different proportions of those
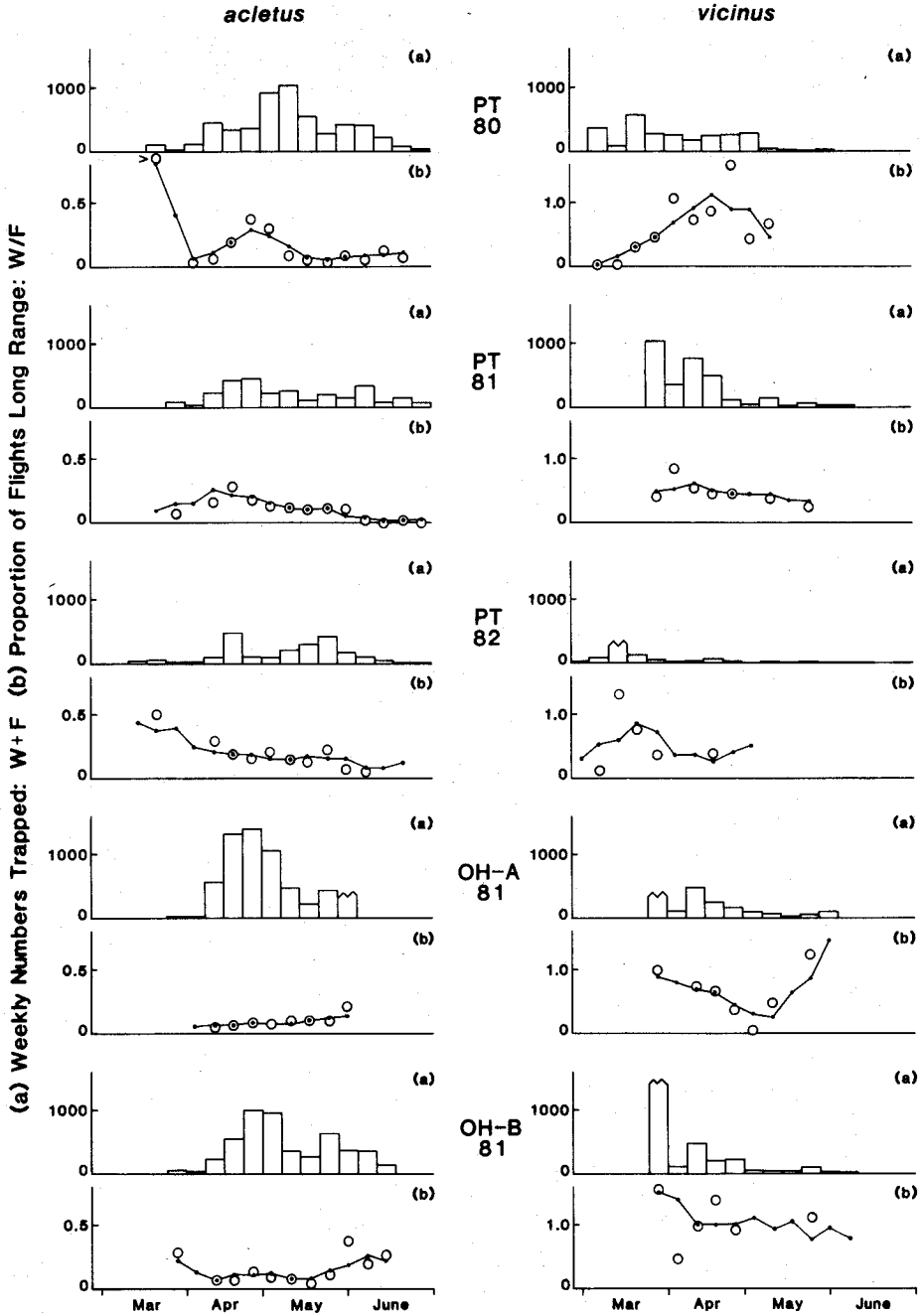
FIG. 1.   Spring flights of *S. acletus* (left) and *S. vicinus* (right) at sites PT and OH, Gainesville, Fla. At site PT, one trapping station was operated in woods (W) and one in a field (F) for 3 years. At site OH, four stations were operated for 1 year, pairs A and B each consisting of one W station and one F station. (a) Weekly numbers trapped (W + F). Bars ending in sawteeth are based on incomplete data and therefore should be longer by an undetermined amount. (b) Estimates of long range flights as a proportion of all flights (W/F). Open circles are estimates based on that week's data when (W + F) ≥ 50. Small closed circles, connected by lines, are 3-week moving estimates of W/F calculated weekly whenever 3-week sample ≥ 50:
$(W_{t-1} + W_t + W_{t+1})/(F_{t-1} + F_t + F_{t+1})$.

landing may be trapped. For example, *Scapteriscus* spp. may have behaviors that cause them to fly higher when over woods or to avoid landing when over woods; in

either case, a smaller proportion of migrants flying near a W station would land as compared with an F station. However, a larger proportion of migrants that do land

Table 1. Proportion of mole crickets that are migratory as estimated by W/F (i.e., numbers caught in woods trapping station divided by numbers caught in corresponding field trapping station); *Scapteriscus* spp. at Gainesville, Fla.

Species, site:generation	Fall flights		Spring flights		Generation total	
	n	W/F	n	W/F	n	W/F
S. acletus						
PT:79-80	907	0.13	4,809	0.16	5,716	0.15
PT:80-81	234	0.10	2,164	0.12	2,398	0.12
PT:81-82	109	0.18	2,250	0.18	2,359	0.18
OH-A:80-81	475	0.16	5,254	0.08	5,729	0.09
OH-B:80-81	763	0.17	3,901	0.13	4,664	0.14
$\bar{x} \pm$ SE ($n = 5$)		0.15 $\pm$ 0.01[a]		0.13 $\pm$ 0.02[a,b]		0.14 $\pm$ 0.02[b]
S. vicinus						
PT:79-80	101	0.31	2,650	0.47	2,751	0.46
PT:80-81	127	0.18	2,630	0.47	2,757	0.45
PT:81-82	22	0.00	750	0.40	772	0.39
OH-A:80-81	63	0.31	1,436	0.66	1,499	0.64
OH-B:80-81	128	0.20	3,239	1.32	3,367	1.24[c]
$\bar{x} \pm$ SE ($n = 5$)		0.20 $\pm$ 0.06[a]		0.66 $\pm$ 0.17[a,b]		0.64 $\pm$ 0.16[b]

[a] Values for fall and spring flights significantly different for *S. vicinus* (ANOVA; $P = 0.01$) but not for *S. acletus* ($P = 0.73$).
[b] Values for *S. acletus* and *S. vicinus* significantly different ($P < 0.001$, ANOVA).
[c] Value for OH-B:80-81 significantly different from all other site:generations of *S. vicinus* (Fisher's protected pairwise comparison of adjusted means; $P < 0.02$).

Table 2. Sex ratios of mole crickets (% male) captured at sound-trapping stations in woods (W) and field (F)

Site; generation or replicate	*S. acletus*		*S. vicinus*	
	W	F	W	F
PT				
79-80	31*[a]	20	16*	11
80-81	19*	13	18*	9
81-82	29*	19	15	12
OH (80-81)				
A	15	25*	12*	6
B	18	21*	15*	10

[a],* Sex ratio significantly higher than for the other station of its pair: chi-square, $P \leq 0.05$.

in response to the W station may be trapped, because they approach the 1.5-m-diameter trapping devices at steeper angles of descent or because those that miss land in UH, making them more likely to fly again and be caught (on the same or subsequent nights).

(4) Migrating individuals flying over SH should be refractory if their flights originated within that habitat. (They would not be migrants if they landed locally.) Migrants (from other habitats and now nonrefractory) may be less likely caught by an F station than a W station because males calling from SH compete with the F trap, whereas no males call from UH. Both these effects lead to underestimates of migrants in SH and hence could account for W/F ratios greater than unity.

Yet another possible biasing factor should be mentioned. The number of local flights in the vicinity of an F trapping station may be influenced by the emitted sound. Crickets hearing loud, long-enduring conspecific calls each evening may be more (or less) prone to fly locally than those in normal acoustical environments.

We conclude that the W/F ratio in mole crickets is better viewed as an index of migration than as an ac-

curate estimator of the proportion of flights that are migratory. The same should apply to other insects studied with this technique—unless their flight behavior is much better known.

The discussion thus far is based on the assumption that the distinction between migratory and trivial flights, made empirically by those studying other insects, can be usefully applied to mole crickets. We believe that it can. The two species we studied are important pests, and our finding inter-habitat flights throughout their flight seasons means that locally applying nonresidual insecticides during such seasons will give no better than transitory control. Furthermore, thoughts of easy local control of mole crickets with sound traps, invoked by the large numbers caught, are quickly squelched by evidence of frequent migratory flights (see also Ngo and Beck [1982]).

A more fundamental consideration relative to our distinguishing migratory and trivial flights is whether mole crickets exhibit a corresponding dichotomy or bimodality in their flight behavior. For instance, do flying mole crickets detect a boundary to their field of origin (e.g., the edge of a woods or lake) and turn back if flying locally but continue if migrating? Or do migrating mole crickets fly higher than locally flying ones, preventing the detection of boundaries (as suspected for *Aedes taeniorhynchus* by Provost [1957, 1960]? Or do mole crickets at takeoff have a wide range of preset refractory periods (to conspecific calls), making those with long periods significantly more likely to find themselves outside the habitat of origin before becoming phonopositive? Any of these (or a combination) could account for our findings, and in none of the three cases would the distinction of behaviors have to be discontinuous or even bimodal.

In the only other study of insect flight that we know to have used a technique similar to ours, Hanski (1980) trapped coprophagous beetles at standardized cow pats placed in an urban field (500 m from the nearest cattle)

and at pats placed in five nearby cattle pastures. He then calculated an index of long distance movement (LDM) by dividing the number caught in the town by the average pasture catch. A critical difference between Hanski's study and ours is that the boundaries of suitable habitat were more difficult for him to define. For example, he concluded that many of the hydrophilid species he captured were not dependent on dung and were not restricted to cattle pastures. For the cattle-dung-dependent species, each of the following spatial units could be considered a "habitat": cow pat, pasture with cattle, or extensive area having scattered pastures. Baker (see pp. 15–17 in Baker [1970]) discussed the difficulty of satisfactorily defining habitat, advancing (and rejecting) two definitions: (1) minimum area within which an animal can obtain what's needed for normal life (e.g., for a dung beetle, a pat, or a pasture), and (2) area within which the animal can move without its destination being beyond its sensory range (e.g., a dung beetle would not be leaving its habitat so long as it could olfactorily detect the next pat upon leaving the last; an area with pastures ≤500 m apart could be one habitat). If a pat is one SH, all dung beetle flight is migratory. If the sensory range of the beetle defines its habitat, none of the flights Hanski studied need be migratory. Only in intermediate cases should Hanski's LDM values estimate the proportion of flights that are interhabitat. In contrast, mole cricket habitats at our study sites seemed easy to define—because fields were embedded in a matrix of woods. Whatever their proximate causes, we were dealing with interhabitat and intrahabitat flights and our W/F ratio was at least an index of migration.

Why *S. vicinus* should have a significantly higher index of migration than *S. acletus* is not clear. The answer is not evident from the food and microhabitat preferences of the two species. *S. vicinus* feeds predominantly on grass, whereas *S. acletus* is largely carnivorous, feeding on insects and other small animals that live in damp soil (Matheny 1981). *S. vicinus* is most abundant in grassy areas, and *S. acletus* is most abundant in bare or denuded areas. We have no evidence that *S. acletus* habitats are less transient or are in larger patches than *S. vicinus* habitats, as suggested by the difference in W/F ratio. A more plausible answer is that *S. vicinus* migrates no more than *S. acletus* but (in spring) flies locally less often, making migratory flights a greater proportion of the total. Concordant with the idea that *S. vicinus* flies locally less often than *S. acletus* are the more restricted spring flight seasons of *S. vicinus* and its greater night-to-night variance in numbers flying (Walker et al. 1983).

In most insects that migrate, females do so more frequently than males (Johnson 1969), in keeping with their ability (once mated) to individually colonize new habitats. Surprisingly, flying males, especially of *S. vicinus*, were often significantly more likely to be migrants than were flying females (Table 2). However, male migrants, as estimated by catches in woods during a generation, never exceeded 29%. In other words, a greater propensity for flying males to migrate was more than counterbalanced by a greater propensity for females to fly. An alternative explanation of the generally higher pro-

portions of males in woods catches is that it is an artifact stemming from differences in landing patterns of males and females. In fields, males are much more likely to land outside the 1.5-m-diameter trapping device than are females (Matheny et al. 1983). When landing in woods, both males and females may come down at a steeper angle to take advantage of the break in the canopy at the trapping station, thereby reducing the difference in the proportion of the sexes that land within 0.75 m of the sound source. A third explanation is that males, having less colonizing potential than females, end their migratory flights sooner, making males migrating from nearby SH more prone to capture than females. Once again, interpreting trapping results is made difficult by our ignorance of details of flight behavior of *S. acletus* and *S. vicinus*.

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