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Perching behavior and coloration in temperate and tropical Sarcophagidae (Diptera)

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Abstract: Nearctic Sarcophagidae often perch on lichen-covered logs or tree trunks, on which they are chyptically colored. Costa Rican Sarcophagidae have the same basic color pattern, but rarely land on tree trunks. Nevertheless, *Blaesoxipha plinthopyga* (Wiedemann) takes stations on tree trunks in Costa Rican urban areas. It evidently immigrated from southwestern U.S. deserts, but only to Neotropical urban areas where lizard populations had been reduced. The metallic blues or greens of Neotropical sarcophagids are evolutionary effects of lizard predation. It is suggested that lizards forced sarcophagids from trunks, sometimes to green foliage where they were selected for metallic greens or blues as in Calliphoridae. The tropical abundance of vertebrate carrion feeders may also limit the distribution of *B. plinthopyga*.

Key words: Diptera, Sarcophagidae, synanthropy, cryptic coloration, Lacertilia, sunning, station-taking, evolution.

This paper explains many years observations by means of a series of hypotheses, mainly as they relate to *Blaesoxipha plinthopyga* (Wiedemann) (Diptera, Sarcophagidae) in Costa Rica. This species causes myasis in man (James 1947) and domestic mammals (Laake & Cushing 1930, as *Sarcophaga robusta* Aldrich). Gregor (1972) said it was synanthropic; Lopes (1988) said it occurred mainly in cities in the American tropics.

Normally it breeds in vertebrate carrion (Denno & Cothran 1975, Hardy 1981, pers. obs.). In arid southwestern North Americ it replaces Nearctic carcass-breeding sarcophagids of other areas. Denno & Cothran (1975) reported it from rabbit and rat carcasses in souther n California. The important point, not obvious in the American tropics, is that in southwestern North America it consistently occurs in non-urban settings. Unpublished, non-urban, Nearctic records include Arizona, California, New Mexico, Oklahoma, Texas and Mexico.

Samples were taken in Costa Rica at seven locatities on 20 dates, November to April, but only in the San José urban area. None were seen elsewhere, including urban areas of Guapiles, Golfito, Limón and Puntarenas. The species was common only near the University of Costa Rica campus ("UCR", San Pedro, Montes de Oca, San José), and was seen along railroad tracks at the north edge of the campus on almost every visit during the dry seasons (many more than 20 visits).

Males were discovered perching on UCR tree trunks less than 0.5m above ground, and nine were taken (8:00-9:30 am, 5 Feb. 1988). Several chased small objects flipped past their perches. A few perched on large branches as high as 3 meters, probably because my son and I had disturbed them from lower sites. (Pers. Obs., 8:00 to 9:30 am).

Station-taking in Sarcophagidae: Sarcophagids oftern congregate on mountain tops (Chapman 1954, Dodge & Seago 1954), at

dead animals, mammalian dung, along streams, etc. (many Pers. Obs., 1951-1992). *Blaesoxipha impar* (Aldrich) perched on carcasses (Pers. Obs., Sand Ridge State Forest & St. Joseph, Illinois, 1964), but also on the terminal twings of a white-flowering plum tree (May 1 & 2, 1965, St. Joseph, Illinois), but not on white-flowered *Spiraea* nearby). Nearly all specimens were males (Dodge & Seago 1954, pers. obs.) that persisted for 3-4 hr, rarely for fewer *(Blaesoxipha angustifrons* (Aldrich), 1.5 hr in very early morning) or longer (*Blaesoxipha excisa* (Aldrich), all day, although much more common in the morning) (pers. Obs., 1964-1992).

At Sand Ridge State Forest, Illinois, *Metoposarcophaga pachiproctosa Parker, S. bullata, Sarcophaga libera* Aldrich, aaand a few others perched on tree trunks or fallen logs; in northern Michigan, *Sarcophaga sabroskyi* (Dodge) perched on live, vertical trunks. They did not often occur together, although *S. bullata* and *S. libera* did, although *S. bullata* was more common about carcasses and *S. libera*, on logs.

About 40 species perched on a fire tower, which could not be easily related to natural objects because species populations differ locally. However, a mountain top near Pilot Knob, Missouri, attracted some species found on the Illinois fire tower. The introduced synanthropes, *Sarcophaga argyrostoma* Robineau-Desvoidy. *S. crassipalpis* Macquart and *S. cruentata* Meigen perched on the roof of the tower as well as on the extreme top surface of the moutain peak, as did *Blaesoxipha rudis* (Aldrich) and a sibling species. *Macronycchia aurata* (Coquillett) and *M. confundens* (Townsend) were rare on the mountain, but occurred on fire towers nearer St. Louis, Missouri, and in Arkansas, so the genus must normally assemble at something other than mountain tops.

Males segregate by species, and, unless very different in size, seldom use the same site simultaneously. Some species perched on the roof top of an Illinois fire tower, others at the next level down (about a 2m band), a third level below that, on the inside framework of the tower, on the outside of the framework at tree top height (lower than the third level), in the morning, in the afternoon, to the windward or to the leeward, on the ground at the base of the tower away from the sun's direction, etc. All normally perch in direct sunlight (pers. obs., 14 dates, 60+ hr on the Illinois fire tower more than eight hr, eight additional dates on six other towers in Indiana, Michigan, Missouri and Texas, 1964-1987). Species perching near tower tops tend to rise to the roof when the wind stops, but the wind raraly ceases at that height.

Costa Rican males perched at carcasses or fish head baits *(Peckia, Oxysarcodexia, Sarcodexia and Tricharaea)*, at army ant swarm raids (Formicidae) *(Dexosarcophaga, Nephochaetopteryx, Notochaeta and Oxysarcodexia)*, in sunlit paatches on leaves along clear streams near the ocean (two species of *Sarcodexia*), at dung (Oxysarcodexia, Ravinia and Tricharaea), on bare patches of dirt or sand *(Blaesoxipha and one Peckia)*, at the not very odorous (to us) carapaces of land crabs *(Peckia, Sarcodexia and Tricharaea)*, or at crushed hermit crabs *(Peckia, Sarcodexia and Tricharaea)*.

Laboratory females of S. crassipalpis normally refuse second matings by bending the tips of their abdomens ventrally when 'assaulted' by males. Multiply inseminated females may never have been obtained. Females of about 50 other colonized species similarly refused second matings, although two would not mate at all in laboratory cages (Pers. Obs., Ames, Iowa; Urbana & St. Joseph, Illinois; Lansing & East Lansing, Michigan; and San Ramón de Tres Ríos, Costa Rica).

S. crassipalpis females require a protein meal for egg development, but dried beef blood did not suffice. In nature many sarcophagids seem to obtain protein from carcasses or possibly from dung. The delay between protein feeding and larviposition presumably reflects egg and larval development.

Asilid flies (Pers. Obs., Sand Ridge State Forest fire tower, Illinois) and bembicid wasps (Davis Mountains, Texas) prey on aggregated males. Aggregation results in male concentrations, rendering them vulnerable to predation.

Mating times vary from 5 min, 5s, average for *Metoposarcophaga* sp. near larga (Aldrich), range, 1 min, 40s to 10 min, 20s, n=12, to 2 hr, 13 min, *S. crassipalpis*, range, 1 hr, 30 min to 3 hr, 15 min, n=16. All three spermathecae of the *M. female* copulating for only 1 min, 40s were

filled with sperm, and single copulations regularly filled all three spermathecae in *S. bullata* Parker, which copulates for about as long as *S. crassipalpis*. With mating times of 2 hr, a longevity of 15 days, copulation for 4 hr and a habit of leaving after mating, less than 5% of specimens collected at a site should be females if the sex ratio is 50:50.

Station sites are sites at which males perch and from which they chase presumed females. A station marker is a conspicuous object about which the sites occur. The flies copulate at mating sites.

The following bold face hypotheses explain observations indicated immediately afterwaaards:

Hypothesis 1: sarcophagid males wait for females at specific perch sites. Males predominate at them, but generally do not emerge or find food there. They have no known reason to be on a barren mountain top, for example, except that they chase insects flying by and occasionally capture their females there.

Hypothesis 2: sarcophagid females fly to station sites, are mated, and then leave. Females are scarce at such sites and, judging from laboratory studies of several species, are not normally mated more than once.

Hypothesis 3: markers are long range signals that bring males and females within visual range of each other. Markers are always very conspicuous, such as mountain tops or carcasses. Calyptrates also do not discriminate well visually (Thornhill & Alcock 1983).

Hypothesis 4: the use of different sites about a common marker conserves energy by reducing the number of mistaken pursuits. In lacking a high visual acuity *Ravinia anxia* (Walter) males pursued almost any object between about 4 and 25 mm in size flipped appropriately past their perches (pers. obs., Taum Sauk Mountain, Missouri, and, apart from size, hundreds of observations in North and Central America, 1951-1992).

Hypothesis 5: Tree trunks bases are a normal perch site for *B. plinthopyga*. Males landed there rather tthan at other sites on the UCR campus.

Hypothesis 6: some species have alternate sites. *Blaesoxipha impar* (Aldrich) perched on carcasses and also on a flowering plum tree.

Hypothesis 7: largely male aggregations reflect station-taking behavior, which is normal to sarcophagid mating behvior. Males pursue insects or other passing aerrial objects of propier size and speed. See also introductory paragraphs to this section.

Sunning in Sarcophagidae: In the Rose Lake Conservation AArea some 15 km NE of Lansing, Michigan about 38 species of Sarcophagidae perched on certain logs or newspapers in the morning (personal observations, June-September, 1980-1987). Females were more common than at station sites (on July 27, 1981, 53 males and 21 females were taken). The species were intermixed and the flies generally sttled quietly in creavasses in the bark. On cool days (air temperatures from 8o C. at 8:00 am to 15.5o C. at 10:30) individuals persisted until nearly 11:00 am, EDT, but on warm days (19.5o C. near 8:00 am EDT to 21o C.) the flies disappeared from trunks, logs and newspaper substitutes by 9:30 am, but had become infrequent by 9:00 am (July).

This represents sunning behavior. There was a lesser evening sunning period in Michigan, but not in Costa Rica. Morning sites face east; evening sites, west (each toward the sun).

Sunning sarcophagids were less evident in Costa Rica. A few were seen between 7:00 and 8:00 am near the Golfito city dump (warm, tropical lowland). Nights were evidently below optiumum for egg incubation in sunners. At San Ramón de Tres Ríos (ca 1500 m) morning temperatures ranged from 15.1 to 16.5o C. before 6:30 am in May, but early appearing sarcophagids perched on foliage, as at Golfito, not on three trunks.

Males of two Costa Rican *Sarcodexia* took stations on green leaves overhanging small, clear streams near the sea (Manuel Antonio National Park and Montezuma) only after the 7:00 to 8:00 am sunning period. These *Sarcodexia* occurred on the Pacific coast, but not at Golfito, and sunning was not studied at Manuel Antonio or Montezuma.

Sarcophagids normally deposit larvae rather than eggs. When males were removed from cages of *S. crassipalpis* soon after mating and females had had a protein meal, females became inactive until their larvae had developed, which was first interpreted to mean that sarcophagid females would hide quietly in nature while incubating.

However, egg and larval development depends on temperature. Larvae appeared in as few as five days with continuously lighted electric lamps next to cage fronts, but at about three weeks without lamps (temperatures fell to about 19o C.) More than 30 females from log sites (several dates, Michigan, 1980) had incompletely developed eggs or larvae or none at all, although *Amobia oculata* (Zetterstedt) often had larvae, which may have been somewhat immature.

Hypothesis 8: sunning accelerates egg and laval development by warming females. Feemales never landed in the shade, and moved so as to remain in direct sunlight. Sarcophagids visited sunning sites only in the morning and evening in Michigan (temperatures are normally lower then). The shortening of morning sunning apparently by higer temperatures and of larval development by lighted lamps at cage fronts points to the importance of temperature (Lamps also inhibit diapause by providing a 'long dday-length' as well as higher temperatures).

Hypothesis 9: Sunning is an adaptation for reducing female exposure to predators. Accelerating egg and larval development is apparently more important that the safety of hiding while incubating. Sunning shortens incubation times, so that females wait less before depositing larvae.

Hypothesis 10: females select near optimum temperatures. Females fly to sunning sites, but leave at varying times according to temperature. They also perch in circular bands at fixed distnaces about lighted lamp bulbs in front of cages.

A general explanation for synanthropy: Like *B. plinthopyga* in the American tropics, *Sarcophaga argyrostoma* Robineau-Desvoidy, *S. crassipalpis* Macquart and *S. cruentata* Meigen are urban in North America. *S. carassipalpis* is common in many U.S. cities, usually near rivers. Males take stations on concrete posts or on higer, conspicuous, non-foliage objects along river banks. *S. ruficornis* (Fabricius), a close relative of *S. crassipalpis,* is tropical. It has been transported by commerce to tropical countries where it too appears to be urban (Lopes 1945). *S. argyrostoma, S. cruentata* and *S. ruficornis* have all been introduced into the Hawaiian Islands that have no indigenous sarcophagids (Hardy 1981).

Station-taking and sunning sarcophagids are conspicuous and usually easily collected. But only three *S. crassiplapis* and one *S. cruentata* (among thousands of specimens) were taken in the comparatively undisturbed Rose Lake Conservation Area only 15 km NE of Lansing, Michigan. Both were readily recovered from Lansing. The synanthropes are often not common in collections, because few collecting trips are made to cities.

Hypothesis 11: introduced species are seldom able to find a 'place' in a well-developed exotic fauna. Introduced sarcophagids normally occur in New World urban areas, rarely in less disturbed habitats (Pers. Obs. at Urbana, St. Joseph & Mason Co., Illinois; Ames, Iowa; Lansing, Clinton Co. & Shiawassee Col, Michigan; Woonsocket, Rhode Island, and many other urban and non-urban areas).

Hypothesis 12: Sarcophagids allocate resources differently in different faunal areas. See preceding hypothesis. If different faunas are differently specialized, then the niches will alos be different and an introduced species is unlikely to be precisely preadapted for the niches of a foreign fauna.

Synanthropy in *Blaesoxipha plinthopyga:*

Hypotesis 13: *B. plinthopyga* is synanthropic in the American tropics because it survives only where man has nearly exterminatd lizards, that is, in urban areas. Lizards catch and eat sarcophagids and calliphorids (Pers. obs., North America and Costa Rica), and are abundat in the American tropics except in cities. They rreadily climb tree trunks, but foliage is too weak to suport larger indiviudlas. No lizards were seen in the San José urban area or on the UCR campus.

Hypothesis 14: The apparent absence of *B. plinthopyga* from urban areas away from San José indicates that its occurrence in Costa Rica depends on another factor besides lizard predation. *B. plinthopyga* does not survive well in lowland, humid areas for unknown reasons. The urban areas from which it was not recovered were all lowland areas; the sites near San José are at 1000m or higher.

One important matter can not be ruled out. Gregor (1972) reported that *B. plinthopyga* was

unexpectedly rare (for a synanthrope) in Cuba because he folund only two in 35,500 sspecimens. But *B. plinthopyga* could be expected within reasonable distnaces of source populations, because of reseedings from it. Cuba may have had large but overlooked source populations. This menas that the species may be found anywhere in Costa Rica, but would not persist for long at any distance from the high UCR population.

Hypothesis 15: *B. plinthopyga* persists in peripheral San José areas because of continual reseedings from the higher populations at or near the UCR campus, i.e., the species is truly permanent only at or near the UCR campus, but is continually reseeded to and recovered from nearby areas where it probably breeds and persists for short periods on its own. This would explain higher populations near the UCR campus and lower populations in adjacent areas. This is almost a truism, because conditions will be less favorable on the periphery of the optimum habitat for the species. Species ranges expand and contract. The extent to which sarcophagids move beyond or within territories is not known, however.

Neotropical lizards and sarcophagid coloration: Since flowers became abundant in the Cretaceous, calyptrates could 'choose' to rsemble: 1) bark or dirt, 2) flowers or 3) green leaves. The flies could not mimic all three simultaneously because the patterns are incompatible. Ordinary environments do not provide enough other alternatives, but a few sarcophagids resemble sand backgrounds.

Although Nearctic observations suggest that sarcophagids should perch on Costa Rican tree trunks, they rarely do. Those that do are usually extremely restless and leave quickly. Of 140 Costa Rican species only occasional males of *Peckia hirsuta* (Hall) and those of three undescribed *Sarcodexia* took stations on tree trunks. Males of the *Sarcodexia* took stations on logs embedded in the bare sand of sea beaches, and (one occasion) a few *P. hirsuta* took stations on a tree trunk lying across a sandy path through the woods at Manuel Antonio National Park near Quepos. Most males of the last took stations on the baare sand on paths or around dead *Geocarcinus* or unidentified land crabs (Montezuma, Manuel Antonio National Park, Cahuita National Park). Only three undescribed Sarcodexia consistently perched on logs.

Hypothesis 16: the typical adult sarcophagid color patern is cryptic coloration, especially on lichen-covered tree trunks. Motionless male of *M. pachyproctosa* are virtually invisible on their lichen-covered tree-trunk stations.

The usual pattern conceals sarcophagids less effectively on bare tree bark, dirt or rocks, but, is ineffective on flowers (that many visit for nectar), green leaves (that many visit for Homoptera honeydew, Downes & Dahlem 1987) or stems (visited for extrafloral nectaries). Cryptic coloration is adaptive because sarcophagids lack stings (like Apocrita), armor (like some beetles), chemical defenses (like some beetles or hemipterans), and most cannot bite (like some beetles and hemipterans).

Hypothesis 17: sarcophagids are typically adapted for more arid conditions than Calliphoridae. Sarcophagids lack unusualy lage troracic spiracles common in calliphorids.

The water molecule is about the sme size as the oxygen molecule, so admitting more oxygen automatically results in higher water loss (Hinton 1971; Downes & Dahlem 1987). The smaller average spiracle size of sarcophagids adapts them for arid conditions, but reduces oxygen intake and flight power. Calliphorids inhabit very humid environments and can afford larger spiracles and geater flight power.

Hypothesis 18: sarcophagids are not ordinarily green or blue because they typically inhabit arid environments where green foliage is uncommon. A higher average rainfall is more likely to produce abundant foliage (and a higher humidity), buy sarcophagids were not selected to resemble it because they normally perched on non-green objects, almost the only kind available in arid environments.

Hypothesis 19: Lizards caused the metallic greens or blues of Neotropical sarcophagids. Metallic green and blue sarcophagids occur only in the Neotropical Region, and they rarely perch on tree trunks that are commonly used elsewhere. Lizards presumably excluded most species from trunk perches, so that some chose foliage perches as an alternative.

Leaf green is evidently difficult for insects to imitate, and metallic greens or blues are approximations which are eivdently most effective in shade. Metallic-blue or green

calliphorids, unlike black-and-gray sarcophagids, often perch on shaded foliage.

Hypothesis 20: Neotropical Sarcophaginae must often have perched originally on thee trunks. Most Neotropical Sarcophaginae retain the typical black-and-gray, color patern. Lizards (especially anoles) sometimes forced them to green foliage where they were subject to selection for metallic blues or greens, as in Calliphoridae.

Hypothesis 21: metallic blue and green sarcophagids are recent. Few are as extensively metallic blue or green as calliphorids. Most ar black-and-gray.

Hypothesis 22: the use of tree trunks as station sites is relict behavior. The three *Sarcodexia* could persist on tree-trunk sites because the trunks were out on bare-sand, sea-beaches between low and extremely high tidal lines where lizards are scarce or absent. No other sarcophagids consistently used trunks as stations sites in Costa Rica.

Further comments on sarcophagid coloration: Although sarcophagids are often said to have three to five stripes, most consistently have three or five if illuminated from the rear at about 30o and viewed from above. Five-stripe species may apperar atypical, if otherwise illuminated or viewed. Indigenous Costa Rican Sarcophaginae usually have a bold three-stripe pattern under any illumination or viewpoint, whereas Nearctic species often have five stripes.

The three dark stripes include a median acrostichal stripe and two dorsocentral stirpes just outside the dorsocentral bristle rows. These are common to all striped Sarcophaginae. The extra stripes of the five-stripe apttern are paracostrichal stripes between actrostichal and dorsocentral stripes. Often they are presutural only or continued only briefly past the the transverse suture. If five stripes ar visible, the pattern is five-striped, but five-stripe species sometimes have only three. If the stripes are sperated by dense pollen the specimen usually belongs to the three-stripe group.

Only *Blaesoxipha (Kellymyia) (three species, including B. plinthopyga)* and some *Peckia* of about 140 Costa Rica species, have a five stripe pattern. The five-stripe pattern may occur in some *Peckia* because of the wide range of the species, but more data are needed. However, the five-stripe pattern of *B. plinthopyga* and other sometimes placed in Acanthodotheca, and its rarity in Costa Rica otherwise, is consistent with a comparatively recent immigration from North America.

The Nearctic *Blaesoxipha (Servaisia)*, except for *B. setigera* (Aldrich), which may have originated recently from souther stock, have a five-stripe pattern, although the two Costa Rican representatives do not. This subgenus occurs in both mid Chile and the Old World, so it may be an ancient gropu that has had time to spread widely and adapt locally. However, only nine specimens were available from Costa Rica, and the pollen between the stripes was not dense, so the thoracic color patern is not well-established.

Most derivatives of Neotropical soruces have evidently been in the Nearctic Region long enough to have developed a five-stripe pattern, such as the *Boettcheria* species. However, the few Nearctic *Oxysarcodexia* retain the shree-stripe pattern of their much more numerous Neotropical relatives, suggesting a more recent immigration for that genus.

Vultures and sarcophagids: Vultures may also limit the distibution of *B. plinthopyga* in Costa Rica by removing carrion daily. They are ubiquitous there, but thermals are not large enough to support their soaring until about mid morning, and road kills conspicuous before mid morning virtually disappear by afternoon. For this reason the Nearctic carcass-breeding niche for flies hardly exists in Costa Rica.

In early morngin vultures walk the streets of Limón, and presumably remove much potentianl fly-breeding material, which may explain why *B. plinthopyga* does not survive there. Vultures do not patrol the streets near the UCR campus, and so presumably leave more breeding material there, but vultures also were not observed patroling streets in Golfito, Puntarenas, or Guápiles from which *B. plinthopyga* was not recovered. The observations at Puntarenas may have been too late for vultures there.

However, the matter may not be simple. Vultures were common at the Golfito city dump, and although they were not observed to patrol city streets, they may remove enough breeding material at the dump to prevent the

establishment of permanent breeding populations in the area. Information about what larval food natural sarcophagid populations may requiere for their continuance is not available.

The lizard and vulture hipotheses may both be needed to explain the failure of *B. plinthopyuga* to become established in some areas. Either or both lizards and a vulture-induced scarcity of carrion may prevent *B. plinthopyga* from becoming established in most of Costa Rica. Its presence may requiere that lizards be absent and sufficient larval food be present, and the latter may require that vulture foraging be limited.

The apparent absense of carcasses suitable for fly breeding and their use as station sites by many indigenous Costa Rican sarcophagids may seem contrdictory, but most sarcophagids take stations mainly in the morning (excepting only Ravinia). But morning is precisely the time thermals have not yet become large enough to support vulcute soaring. So carcasses are available for station takers in the morning, but may not last long enough to support fly larvae.

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RESUMEN

Los Sarcophagiade neárticos a menudo se posan en troncos erectos o caídos cubiertos con líquenes, sobre los cuales tienen una coloración críptica. Los sarcofágidos de Costa Rica sin embargo, aunque tienen el mismo patrón de color básico, casi nunca se posan en troncos. Sin embargo, *Blaesoxipha plinthopyga* (Widermann) se posa en troncos en áreas urbanas del país. Evidentemente es un inmigrante de los desiertos ubicados en el suroeste de los Estados Undiso, pero solo ha logrado establecerse en áreas urbanas donde las lagartijas son escasas. Los azules y verdes metálicos de los sarcofágidos neotropicales son aparentemente el resultado evolutivo de la depredación por parte de lagartijas. Se sugiere que las lagartijas han expulsados a los sarcofágidos de los troncos, a veces al follaje verde donde sufrieron selección hacia el color verde o azul, en convergencia con los Calliphoridae. La abundancia de otros organismos que en el trópico se alimentan de carroña puede ser otra causa de la limitada distribución de *B. plinthopyga*.

REFERENCES

Campbell, J. A. 1954. Studies on summit-freeequenting insects in western Montana. Ecology 35: 41-49.

Denno, R. F. & W. R. Cothran. 1976. Niche relationships of a guild of necrophagous flies. Ann. Entomol. Soc. Amer. 68: 741-754.

Dodge, H. R. & J. M. Seago. 1954. Sarcophagidae and other Diptera taken by trap and net on Georgia mountain summits in 1952. Ecology 35: 52-61.

Downes, W. L. Jr. & G. A. Dahlem. 1987. Keys to the evolution of Diptera: role of Homoptera. Environ. Entomol. 16: 847-954.

Ferreira, M. J. de Mello. 1979. Sinantropia de dipteros muscoideos de Curitiba. II. Sarcophagidae. Rev. Brasil. Biol. 39: 773-781.

Gregor, F. 1972. Synanthropy of Sarcophaginae (Diptera) from Cuba. Folia Parasit. 19: 155-163.

Hardy, D. E. 1981. Insects of Hawaii. Vol. 14. Diptera: Cyclorrhapha IV. University of Hawaii, Honolulu. vii + 491 p.

Hinton, H. E. 1971. Enabling mechanisms, p. 71-82. Proc. XVth Internatl. Congr. Entomol., Washington, D. C.

James, M. T. 1947. The flies that cause my iasis in man. Misc. Pub. U. S. Dept. Agric. 631: 1-175.

Laake, E. W. & E. C. Cushing. 1930. Fly trapping on the ranges of the southwest. J. Econ. Entomol. 23: 966-972.

Linhares, A. X. 1981. Synanthropy of Calliphoridae and Sarcophagidae (Diptera) in the city of Campinas, Sao Paulo, Brazil. Rev. Brasil. Ent. 25: 189-215.

Lopes, H. de Souza. 1945. Sobre a presenca, no Rio de Janeiro, de "Parasarcophaga ruficornis" Fabricius, 1794) espécie oriental e a possibilidade de seu transporte por aviao (Diptera, Sarcophagidae). Rev. Brasil. Biol. 5: 401-405.

Lopes, H. de Souza. 1988. Notes on Neotropical Sarcophagidae (Diptera) with descriptions of a new genus and five new species. Rev. Brasil. Biol. 48: 127-137.

Thornhill, R. & J. Alcock, 1983. The evolution of insect mating systems. Harvard University, Cambridge, Mass.