

Seasonal and Spatial Distributions of Adult Screwworms (Diptera: Calliphoridae) in the Panama Canal Area, Republic of Panama

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ABSTRACT The distribution of screwworms, *Cochliomyia hominivorax*, (Coquerel) was studied in a seasonally moist lowland tropical forest in the Republic of Panama using a combination of field collections and satellite imagery. We found that different forest types could be distinguished and mapped using remotely sensed data. To determine the temporal and spatial distribution of flies, we collected flies coming to rotted liver at 82 sites in ten vegetation types (open areas, edge forest, dry scrub forest, forest successional stage 1, forest successional stage 2, forest successional stage 3, forest successional stage 4, forest successional stage 5, mature forests, palm swamp forest, and forest along streams) over three seasons (dry, transitional, wet). Nine of the vegetation types (excluding dry scrub forest) were identified and mapped using SPOT XS and Landsat 5 TM satellite data. Screwworm flies were most abundant during the transition from wet to dry season. Fly numbers were consistently higher in forest habitats, particularly those with trees 20–30 m in height and a fairly open canopy composed of many deciduous species that shed their leaves during the dry season. Screwworm numbers were also high in palm swamp forest, edge forest, and mature growth forest. Traps sampled in open areas had fewer flies and were unrelated to proximity to cattle. Females accounted for 88% of the total fly counts. This study further substantiates the importance of forests in the ecology and behavior of screwworm flies and demonstrates that remotely sensed data can be used to construct the spatial distribution of these flies in a tropical landscape. We discuss implications of this information to the screwworm eradication program.

KEY WORDS *Cochliomyia hominivorax*, screwworm fly, remote sensing, habitat preference

SCREWORM FLY, *Cochliomyia hominivorax* (Coquerel), in its larval stage is a parasite of warm-blooded animals, including domestic cattle and humans, that once ranged from tropical America as far north as Iowa during the warm months of the year (Laake 1950). The Screwworm Eradication Program's mission is to eliminate this parasite by release of mass-produced, sterile adults. Releasing artificially reared, sterilized flies from aircraft into screwworm-infested areas, the USDA-APHIS Binational Screwworm Eradication Programs have eliminated screwworm from North America to the Darien Province of Panama. The elimination of screwworm has benefited the U.S. livestock industry alone by \$500 million a year (Wyss and Galvin 1996). In addition, it has benefited human health significantly. Before the eradication program began in El Salvador and Nicaragua, there were 530 documented cases of human

myiasis from 1990 to 1992, dropping to 143 cases from 1992 to 1995 (LXIII Commissioners' Meeting of the Mexican-American Commission for the Eradication of Screwworm, Mexico City, 13–14 August 2001).

The USDA-ARS Screwworm Research Program supports the USDA-APHIS Screwworm Eradication Program by providing research to improve the implementation of the Eradication Program. One of the principal current goals is to develop efficient methods to monitor native and sterile populations of *C. hominivorax* for verifying the success of the eradication program and detecting outbreaks within the eradicated zone. Standard methods to monitor screwworm populations rely on traps baited with rotting liver (Bishopp 1916, 1937; Laake and Cushing 1930; Lindquist 1938; Parker and Welch 1992), wind-oriented traps with chemical attractants (Jones et al. 1976), and sentinel animals (Thomas and Chen 1990). Tending screwworm traps and sentinel animals in the field is labor-intensive and expensive. To detect low densities of screwworm populations, for example, in the early stages of an outbreak, depends on placing traps or sentinel animals in habitat favored by screwworm. Accurate maps of screwworm habitat would

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lead to greater monitoring efficiency and possibly to earlier control of outbreaks.

The objective of this study was to determine if remote sensing and geographic information systems could improve trap placement and monitoring of adult screwworm flies in the tropics by identifying areas of high fly activity. Studies in the United States and Mexico found screwworm to be most abundant in areas used by livestock (Parish and Cushing 1938, Parman 1945, Brenner 1985). In general, screwworm fly distributions were scattered and seasonally distributed in its northern range. The principal factors affecting screwworm fly distributions and activity in the United States and Mexico was thought to be moisture and temperature (Rahn and Barger 1973, Krafzur et al. 1979). In tropical environments, however, screwworm populations exist year around at higher densities with rainfall (Krafzur et al. 1979, Parker et al. 1993) and habitat (Mangan and Thomas 1989, Parker et al. 1993) the principal factors affecting their distribution and activity. When comparing tropical scrub forest, dry tropical forests, and nonforested areas, the areas of highest screwworm activity are in forests and ecotones (Mangan and Thomas 1989; Parker et al. 1993). These authors, however, made no distinction between the types and varying sizes of forest habitats and other vegetation that create a patchwork on the tropical landscape. Herein we use satellite imagery to map this tropical patchwork and to determine whether habitat, as distinguished by remotely sensed data, can be used to identify where screwworm flies are active. We used fly collection data to establish relationships between screwworm fly activity and the different forest habitats. These forest habitats are most likely where residual screwworm populations persist during eradication and, therefore, are the best locations for detecting and monitoring screwworm flies.

Materials and Methods

Study Area. We conducted this study in the provinces of Panama and Colon, Republic of Panama. Our study area was defined in part by a satellite image from the French satellite SPOT that covers ≈ 30 km on either side of the Panama Canal (Fig. 1). Panama has a warm humid tropical climate with a distinct wet season from May to December and a dry season from January to April. Rainfall varies geographically and yearly from the Pacific to Atlantic coast. In the study area, the average rainfall along the Pacific Coast is 1.9 m in Panama City and 3.2 m in Colon on the Atlantic Coast. The daily temperature fluctuates more than the monthly averages, with average daytime temperatures 30–32°C and average nighttime temperatures 22–23°C. The Holdridge Life-Zone classifies the majority of the natural vegetation in these provinces as tropical moist forest (Holdridge et al. 1971). The forests along the Pacific coast are more deciduous during the dry season; forests along the Atlantic coast are nonseasonal (D'Arcy and Correa 1985). Field sites were located in premontane moist forests along the

Pacific Coast and premontane wet forests in the highlands east of Madden Lake and around Gamboa (Holdridge et al. 1971). The Smithsonian Tropical Research Institute (STRI) in the former canal zone of Panama has supported decades of scientific research on the local vegetation (Croat 1978). This provided reliable data to ground truth the remotely sensed image classification. Eastern Panama is currently the southern limit of screwworm eradication with the still sparsely inhabited and largely intact forest of Darien Province designated as a barrier zone, in which sterile flies are continually released, to prevent reinvasion of screwworm from South America.

Remote-Sensed Image Classification. We acquired SPOT multispectral (XS) data from the SPOT Image Corporation (Reston, VA) for 22 January 1993 and Landsat 5 thematic mapper (TM) data from Space Imaging Inc. (Thornton, CO) for 19 March 1991. These were the most recent satellite-derived remotely sensed imagery available with little cloud cover but, as with most satellite data from the humid tropics, neither image was cloud-free. We geo-referenced both images to the Universal Transverse Mercator projection using nearest neighbor resampling with a root mean square error of <1 pixel. We used isodata unsupervised classification on both images to mask out clouds, cloud shadow, and water. To identify vegetation classes, we used supervised classification: parallelepiped nonparametric decision rule with overlap areas classified using maximum likelihood decision rule (Jensen 1996). We developed training samples for the supervised classification using the software ERDAS Imagine 8.3 (ERDAS 1999) seed pixel method. We chose seed pixels based on spatial coordinates collected from 96 ground vegetation sample locations. We collected at least five vegetation samples for each vegetation class. We collected spatial coordinates using a Magellan ProMark V GPS unit and post processed the data to an accuracy of 2–5 m with a Magellan MBS-1 base station (Magellan, Santa Clara, CA). We visually identified in the images an additional 20 locations in forest of known type but for which we could not obtain the owner's permission to collect ground data. Because of cloud cover, we could not use all ground vegetation samples in both images.

Field Design. We selected 82 sites in the study area that represented seven of the nine different vegetation types including open areas distinguished from the imagery (Fig. 1). The successional stages of the forests are based on forest height, structure, and species composition. The stages generally follow those described by Richards (1952), Budowski (1970), Uhl and Murphy (1981), Gómez-Pompa (1981), and Phillips (1989). We did not sample in the areas classified as city vegetation and mangroves. City vegetation is typically tree cover in yards or small parks within Panama City. We also excluded mangroves for logistical reasons. We collected fly counts in three additional areas we identified in the field. We collected in a patch of dry scrub forest near Madden Lake. This forest is distinct in species composition and structure from the other for-

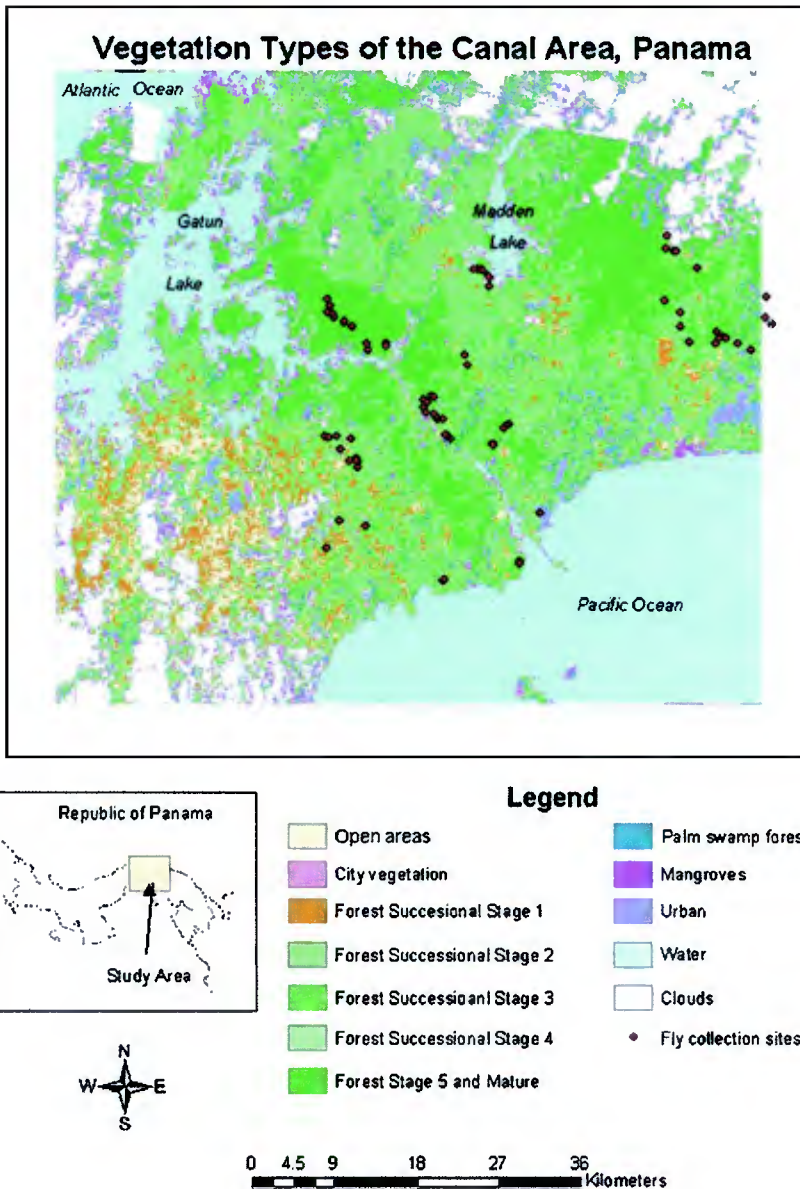


Fig. 1. Vegetation type map of the Panama Canal area, Republic of Panama, based on the interpretation of a SPOT XS and Landsat 5 TM image. The red symbols are the location of trap sites for collecting screwworm field data.

ests in the field but could not be distinguished from secondary forest classes on the imagery. We sampled in an Acacia Plantation and successional forest still with banana plants and fruit trees that were also not distinguished on the imagery. We collected in areas we defined as edge forests and forest along streams based on the importance of these habitats for high fly activity in previous studies from Costa Rica, Mexico, and Texas (Hightower and Alley 1963, Brenner 1985, Mangan and Thomas 1989, Parker et al. 1993). For the study in Costa Rica, edges were defined as the ecotone between croplands and forest and their within-forest category were sites at least 100 m inside the tree line (Parker et al. 1993). They found no significant differ-

ence between the two categories for fly activity. Herein we consider ecotones and forest 100 m from an open area as the same category, edge forest. Our selection of field sites was partly limited to areas we were allowed to access: we could not sample on U.S. military bases and some private land holders did not allow us access to their property. The 82 liver baited trap sites were on both sides of the Panama Canal covering an area of 55 × 40 kilometers (218,000 hectares) (Fig. 1). Field data were collected from 7 November 1995 until 12 September 1996, with an average of five days at each site. We divided the collection period into three seasons of wet, transition, and dry. The study included two wet seasons (7 Nov 1995 to 19 Jan 1996 and 20 May

1996 to 14 Nov 1996), one transition from wet to dry (30 Jan 1996 to 5 Mar 1996) and one dry season (6 Mar 1996 to 3 May 1996). These are the actual dates for fly collections and correspond to the seasons defined by the Panama Canal Authority, which tracks 11 meteorological variables. We only collected four days during the transition from dry to wet season, these data were similar to those from the second wet season and thus combined with them.

Parker and Welch (1992) demonstrated that liver-baited traps were an effective method for gathering data on the behavior and population dynamics of native screwworm flies in tropical habitats. They found liver traps attracted mostly nulliparous and mated females, and few gravid females and males. They had more flies visit liver traps than sentinel animals or swarm-lure-baited wind oriented traps. The procedures and maintenance of the liver-baited trap sites we used followed those established by Parker et al. (1993). Once a trap site was established, we resampled at the same location for an average of 5–6 d. We had three technicians available, so typically we sampled in three different vegetation types on the same day. For 1 mo we had five technicians, which enabled us to sample five different sites on the same day. The number of hours varied at each trap site because some sites were further away or more difficult to reach. Fly activity was recorded at each trap site as the number of flies collected each day. For each fly collected, its sex, time collected, and the ambient temperature were recorded. Also recorded were ambient temperature every 15 min, and number of collecting hours at each field site. Parker et al. (1993) found that seasons affect fly activity so weather conditions such as sunny, cloudy, and raining were noted during the day and whether the activity for other blow fly species was high or low. We collected GPS coordinates for each site using the same methods and equipment used to collect the vegetation training data. In addition to fly activity, we collected vegetation data for each of the 82 sites to verify the accuracy of the SPOT multispectral and Landsat 5 TM classifications.

Statistical Analysis. Because count data, such as counts of flies observed here, are typically believed to follow a Poisson distribution, we used the square-root transformation, which removes the relationship between the mean and variance to satisfy the homogeneity of variance assumption of our mixed model. The square root of the number of flies was then divided by the number of hours a trap was sampled, usually 4 or 5 h a day, to create a rate (on a per hour basis). Our basic explanatory model started with the fixed factors of interest, season, and habitat. We included the random effect of site (within habitat) and time series correlation (modeled as an exponentially decaying function of days apart, similar to a 1-parameter temporal autoregression), because traps were typically monitored over several days within a site. Four kinds of additional environmental variables were available, including the presence of cattle, elevation, site-specific temperature, and the wealth of weather data col-

lected at the Parque Nacional Metropolitano (PNM) by STRI. We did an exploratory analysis to determine which of these additional variables (and possible interactions with the fixed factors) would be most useful for predicting the square root of the fly count. We used the corrected Akaike's information criterion (AIC_c) as a measure of model fit (Burnham and Anderson 1998) and Proc Mixed in SAS (SAS Institute 1999) for model estimation and to produce residual log-likelihoods, from which AIC_c was calculated. Many habitats were not monitored in all four seasons; inference from the model is restricted in these habitats to those seasons for which data were collected.

Results

We used supervised classification techniques to identify vegetation types using a combination of SPOT XS and Landsat 5 satellite data for the Panama Canal area. The resulting classification has 12 categories with nine vegetation classes that include open areas (all pastures, abandoned fields, and agricultural areas), four successional forest types, mature forest, swamp forest, and mangroves (Fig. 1). The clouds class represents areas with cloud cover on both the SPOT and Landsat images. The classification map was used to locate areas for collecting fly activity data. These additional sites were also used to verify the accuracy for the final vegetation map.

We developed a model based on fly activity data collected in the different vegetation types identified on the imagery and environmental parameters for these habitats. In addition to the original variables in the basic model (season, habitat, and site within habitat), we found that field temperature was a useful predictor, as were two of the PNM weather variables, minimum relative humidity, and maximum relative humidity. In general, fly counts did not respond the same way among the different habitats to changes in field temperature and maximum relative humidity (i.e., there were interaction effects). Elevation was not a useful predictor in the model, possibly because any response to elevation is actually a response to habitat type and other environmental variables that co-vary with elevation.

The effect of site within habitat was large, $\approx 19\%$ of the total variance (and more than one third of the variance explained by the model), suggesting that, within a habitat, the location of a trap can have a large effect on fly counts. There was no significant effect of nearby cattle ($F = 0.14$; $df = 2, 66$; $P = 0.8666$) that might explain site-to-site differences.

The effect of season was also large ($F = 6.78$; $df = 3, 125$; $P = 0.0003$) and independent of other predictor variables (Fig. 2). Flies were most abundant during the transition from wet to dry season, with a back-transformed least square mean of 0.1415 flies/trap hour (0.0264 and 0.3479 are back-transformed means ± 2 standard errors, approximately a 95% confidence interval on the mean). Flies were least abundant in the second wet season, with statistics as described above of mean 0.0192, and upper and lower

Seasonal Prediction of Fly Counts for Habitat Type

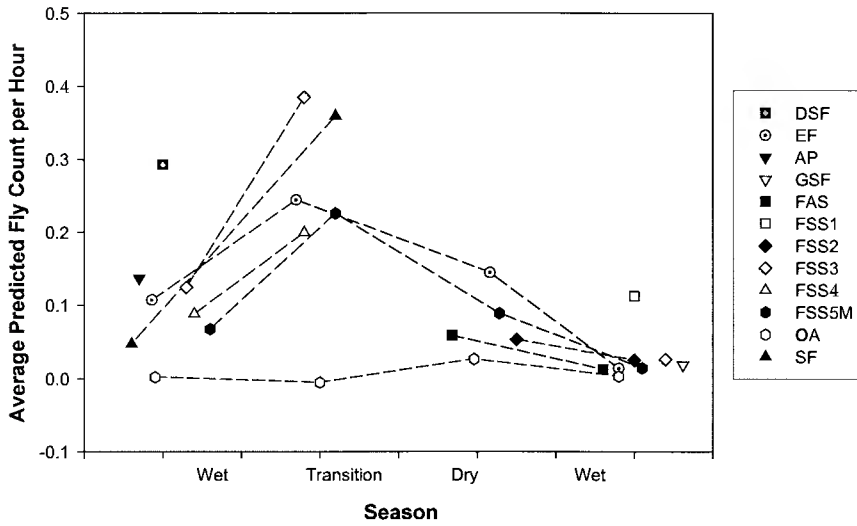


Fig. 2. Graph of average predicted fly counts per hour using the average field temperature, average maximum relative humidity, and average minimum relative humidity for each habitat for the dates we sampled. DSF, dry scrub forest; EF, edge forest; AP, acacia plantation; GSF, garden successional forest; FAS, forest along streams; FSS1, forest successional stage 1; FSS2, forest successional stage 2; FSS3, forest successional forest 3; FSS4, forest successional forest 4; FSS5, forest successional stage 3 and mature forests; OA, open areas; SF, swamp forest.

95% confidence intervals of 0.0000 and 0.1149, respectively. In general, there appeared to be a buildup of flies during the first wet season, which culminated in the wet to dry transition season. Numbers dropped precipitously in the following dry season, the drop continuing into the wet and final season of the study, and then gradually building until the end of the study. The various forested habitats responded similarly to seasonal changes but open areas seemed only marginally affected by season.

Effects of habitats are also strong ($F = 2.57$; $df = 11, 370$; $P = 0.0038$), though their interpretation is muddled by significant interactions with field temperature

and maximum relative humidity, and by not being able to collect samples in all seasons. Predictive expressions for each habitat are given in Table 1. As examples of how habitats differ, forest successional stage 3, sampled in all seasons, had high fly counts, whereas open areas, also widely sampled, tended to have few flies. There was also high fly activity in palm swamp forest, edge forest, and mature growth forests during the transition from wet to dry season. The strongest interaction effects generally occurred for habitats that were only sampled in one season, such as dry scrub forest or acacia plantation, so these effects may not be representative for these habitats. In a model such

Table 1. Expressions giving predicted numbers of screwworm flies for each habitat

Habitat	Predicted number of flies	Seasons
DSF	$(-13.3455 - 0.00277 H_n + 0.1011 H_x + 0.1375 T + S_i)^2$	1
EF	$(0.8297 - 0.00277 H_n - 0.0109 H_x + 0.0232 T + S_i)^2$	1, 2, 3, 4
AP	$(-67.9909 - 0.00277 H_n + 0.6400 H_x + 0.1313 T + S_i)^2$	1
GSF	$(0.4762 - 0.00277 H_n - 0.0306 H_x + 0.1042 T + S_i)^2$	4
FAS	$(0.4879 - 0.00277 H_n - 0.0044 H_x + 0.0108 T + S_i)^2$	3, 4
FSS1	$(16.8134 - 0.00277 H_n - 0.1461 H_x - 0.0454 T + S_i)^2$	4
FSS2	$(-6.1131 - 0.00277 H_n + 0.0489 H_x + 0.0528 T + S_i)^2$	3, 4
FSS3	$(1.7663 - 0.00277 H_n - 0.0180 H_x + 0.0168 T + S_i)^2$	1, 2, 4
FSS4	$(1.0472 - 0.00277 H_n - 0.0055 H_x - 0.0059 T + S_i)^2$	1, 2, 4
FSS5M	$(-1.0406 - 0.00277 H_n - 0.0041 H_x + 0.0695 T + S_i)^2$	1, 2, 3, 4
OA	$(-2.1742 - 0.00277 H_n + 0.0244 H_x + 0.0001 T + S_i)^2$	1, 2, 3, 4
SF	$(9.8207 - 0.00277 H_n - 0.0775 H_x - 0.0682 T + S_i)^2$	1, 2

H_n = minimum relative humidity (measured centrally); H_x = maximum relative humidity (measured centrally); T = field temperature; S_i = season i (where $S_i = (0.16, 0.24, 0.096, 0)$ for $i = (1, 2, 3, 4)$); DSF = dry scrub forest; EF = edge forest; AP = acacia plantation; GSF = garden successional forest; FAS = forest along streams; FSS1 = forest successional stage 1; FSS2 = forest successional stage 2; FSS3 = forest successional forest 3; FSS4 = forest successional forest 4; FSS5 = forest successional stage 5 and mature forests; OA = open areas; SF = swamp forest.

as this one, in which weather variables are correlated, compensating effects of estimated parameters will be seen in the expressions given for predicting fly counts. Even so, it is clear that the effect of the weather variables differs by habitat. For example, there is little effect of temperature on fly counts for open areas, but one exists for dry scrub forest and acacia plantation. In contrast to field temperature and maximum relative humidity, the effect of minimum relative humidity was found to be constant across habitats.

Forests at successional stage three are 20–30 m in height with a fairly open canopy and composed of many deciduous species that shed their leaves during the dry season. There was also high activity in palm swamp forest, edge forest, and mature growth forests during the transitional season. Palm swamp forests were distinguished in the field by the dominance of large palm trees and poorly drained soils. They are common in the alluvial plains in the Panama Canal area. Forests at stage 5 are mature growth forest 30–50 m in height. This stage was based on historical maps of the Panama Canal area and on the experience of biologists from the STRI. Forests at stage four had the highest overall mean during the dry season. Forests at stage 4 are typically more than 30 m in height and composed of longer-lived and slower growing pioneer species with a dense, closed canopy. During the wet season, dry scrub forests had the highest mean. The old growth forest in this vegetation type has a lower canopy of 20–30 m. This small patch of forest was most similar to those in the habitat studies conducted in Belize, Costa Rica, and Mexico (Mangan and Thomas 1989, Parker et al. 1993). We can use information from the model to predict areas most suitable for high screwworm populations in the Panama study area for each season. Figure 3 is a prediction map of high fly activity for the transition from wet to dry season.

Discussion

Other studies of habitat preference of screwworm flies in Mexico, Belize, and Costa Rica were done in dry tropical forests (Brenner 1985, Thomas and Mangan 1989, Parker et al. 1993). This is the first study to examine screwworm habitat preference in a wet lowland tropical forest. The largest area previously studied was 8×6 km. In this study, we sampled from an area of 55×40 km that incorporated the patchwork of forests comprising a lowland tropical landscape. We used liver-baited traps that are feeding stations for adult screwworm flies. These traps are more attractive to the nulliparous females and mated females and some males (Coppedge et al. 1977; Parker and Welch 1991a, 1991b, 1992).

We found a large effect of site within habitat. This demonstrates the sensitivity of these flies to microenvironmental influences, and how carefully a site must be selected for sampling fly abundance. This may be more important for some habitats than others (e.g., open areas may be relatively homogeneous relative to

forested sites). Some factors known to influence trapping success that may differ from site to site (within habitat) are host proximity, wind speed and direction, vegetation density, and plants in flower. The first two are dynamic factors and would vary on a short temporal scale. Host proximity may be difficult to measure in certain habitats and its effect may depend on wind speed and direction. We were not able to detect a host proximity effect in this study. Liver-baited traps have fewer gravid females visits (Guillot et al. 1977a, 1977b; Parker and Welch 199a, 1991b; Parker and Welch 1992), which could explain why we did not find an effect of proximity to cattle. Deonier (1946) used liver-baited traps for a study in Arizona and also found ecological conditions more important to fly abundance than the influence of hosts or ranch management.

The habitat variable serves as a proxy for a number of variables, some of which affect fly abundance. These include host availability and environmental factors, such as relative humidity and vegetation cover. Because the weather data we used, other than field temperature, were collected centrally, in the model microweather differences among habitats could only be captured by the habitat factor or its interactions with the centrally collected weather variables. Because we found significant effects of these variables in our study, we surmise that at least some local weather variables that differ among habitats (e.g., humidity) have a large effect on fly abundance. This study does not provide a complete explanation of the distribution or population size of screwworm flies because we did not sample all habitats for each season.

The expressions given in Table 1 for predicting fly counts for the twelve habitats have widely varying parameter estimates. Although some of this is a result of the inevitable compensatory effects seen when predictor variables are not orthogonal and some may be a result of not sampling certain habitats in some seasons, it also suggests that there are real differences in the way flies respond to changing environmental conditions in different habitats. Figure 2 shows the changes in fly activity over the four seasons. Using the formulas in Table 1, we calculated the average predicted fly count for each habitat. The number of flies are predicted on a square root scale and then squared to get the original scale. We used the averages of field temperature, minimum and maximum humidity for the dates we sampled the fly populations. Prediction expressions differ considerably even when considering only the subset of habitats well represented in all seasons, open areas, forest successional stage 3, edge forest, forest successional stage 5, and mature forest. Some of these differences may reflect actual differences in abundance, some only changes in activity level, but clearly fly trap counts are sensitive to conditions that can, in large part, be related to easily collected environmental data. This should greatly help determine where and when to monitor for screwworm flies.

Areas of High Adult Screwworm Fly Activity During the Transition from Wet to Dry Season Panama Canal Area, Republic of Panama

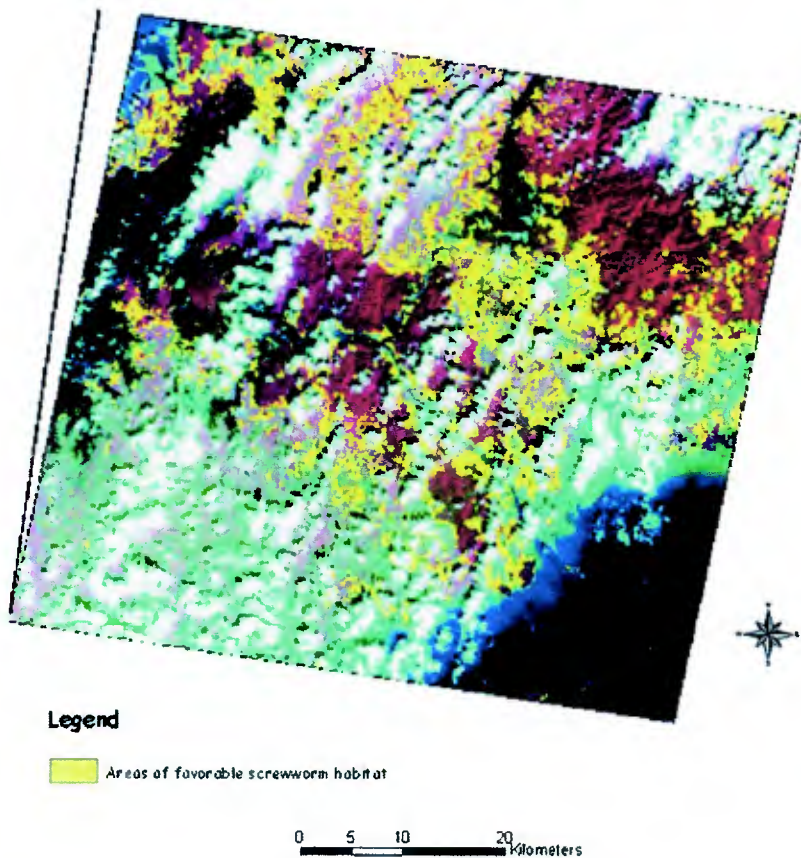


Fig. 3. Color infrared image of Panama Canal area, Republic of Panama from SPOT XS, from January 1993. Healthy vegetation appears dark red in the image. The overlay of yellow represents those areas of predicted high fly activity for the transition from wet to dry season.

Thomas (1993) discussed how screwworm fly behavior changes as it matures so that its place in and response to the environment depends on the age of the fly. He suggested that screwworm has separate locations for nectar feeding, mating, and oviposition. Hightower and Alley (1963) reported that after eclosion the young fly looks for a forest canopy to feed and roost. Thomas (1991) found a similar result in field cages of emerging screwworm flies. Young adult flies were thought to prefer areas with flowering trees because they are dependent on nectar feeding for survival (Mackley and Long 1983). In the Panama Canal area, flowering starts in the dry season with the

overall peak flowering occurring at the onset of the rainy season in April or May (Croat 1978, Angehr et al. 1984). The high flowering period in the forests during the transitional seasons may account for higher fly abundance during this season.

Mating behavior and aggregations of screwworm flies on vegetation was first described by Guillot et al. (1978). Krafzur (1978) and Mackley and Long (1983) also observed male screwworm flies at aggregation sites in Texas. These sites were on nonflowering vegetation in forest habitats. Most aggregations consisted of small numbers of males, from 2 to >8 males (Krafzur 1978). Parker et al. (1993) did not report such aggregations in

Costa Rica and no observations of this nature have been recorded in Panama. This could be because of the difference in the density of tropical vegetation versus the subtropical scrub forests in Texas. Tropical forest canopies are also considerably higher, making these kinds of observations more difficult.

Oviposition sites for screwworms are on the wounds of warm-blooded mammals. Females do not seek out hosts until they are reproductively mature (Hammack et al. 1987, Thomas and Mangan 1989). With mark-release-recapture data, Thomas and Mangan (1989) reported that female screwworm flies prefer forest habitat but they seek out hosts in the nearby pastures with cattle. Forest edges could be a good habitat for collecting flies as they move between openings and back to the forest for feeding, mating, and resting. Thomas (1991) noted that, as the temperature in the field cages rose, the flies would move deeper into the shaded vegetation. The mean daily-recorded temperatures in open areas were higher in all seasons with a maximum recording of 38°C during the dry season.

Although previous studies demonstrate the effect of forest habitats on the behavior and ecology of screwworm flies, this study captures how screwworm flies use a tropical landscape. As in other studies in dry tropical forests, we found that screwworms were more abundant in forest habitats. However, we measured habitat use over the different forest types and seasons to show temporal and spatial shifts in screwworm abundance.

We demonstrated that these forest types could be mapped using remotely sensed data, thus providing a spatial distribution of high fly activity for a given season (Fig. 3). The forests with the highest fly activity were successional forests. We found that SPOT XS data coupled with field training data were needed to distinguish the successional forest stages. Lowland swamp forest and edge forests, also areas of high fly activity, can be accurately distinguished on remotely sensed imagery without using ground training data. These two forest types comprise a larger proportion of the landscape than the stage 3 successional forests (some edge forests would include stage 3 successional forests). Future applications using remotely sensed data to map areas of preferred screwworm habitat could take advantage of the lower cost and availability of Landsat TM data. Such maps have been produced for the Screwworm Eradication Program's mass rearing facility in Tuxtla Gutierrez, Mexico, where traps are used to determine the distribution of released, sterile flies used as part of the Biosecurity measures of the facility. They were also useful to the USDA-APHIS Screwworm Eradication program by providing the optimum localities for trap placement around the production plant and for helping to contain a recent (2003) screwworm outbreak in Chiapas, Mexico. Future application of remote sensing information may enhance the field operations of the USDA-APHIS Screwworm Eradication Program and those of other countries with an interest in controlling the screwworm.

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