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Invasive Dynamics of Africanized Honeybees in North America

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There have been many *a posteriori* ecological interpretations of newly introduced species in Europe and elsewhere, yet few studies have rigorously tested predictions about the dynamics of such invasions [1]. In this study, we examine the range expansion of an exotic insect, the Africanized honeybee in North America, and demonstrate how one can predict the dynamics of its spread using recent past events. African honeybees were introduced into Brazil in 1956 for the purpose of improving honey production among managed colonies in that country [2]. The subsequent range expansion of African-derived or "Africanized" honeybees has been intercontinental in scope, ranging from Uruguay and northern Argentina [3, 4] to southern Texas [5]. While the bees appear to have reached their southernmost distributional limits, to the north they continue to expand their distribution in Mexico and the United States. Climatic factors are expected to limit the northern distribution of these insects to southern or central United States [4, 6–8]. Initial northward movement of Africanized honeybees through subtropical South American latitudes was relatively slow (80 km/year in 1957 – 1963) [7]. However, as the bees reached more tropical latitudes in northern South America, their rate of invasion increased (258 km/year in 1963 – 1976) [7]. Subsequently, range expansion from Panama to southern Mexico reached an average speed of 360 km/year [9]. Long-distance movement associated with range expansion is thought to result from reproductive and absconding swarm processes (natural range expansion) rather than human-assisted dispersal [7]. The rapid spread is partly due to accelerated colony growth and frequent issuing of reproductive swarms [10].

The arrival of Africanized honeybees at various locations in Mexico was established from swarms captured in bait hives consisting of 25-l cardboard boxes covered with plastic bags. Bait hives contained mixtures of citral, citronella, and geraniol to increase their attractiveness to passing swarms. These substances are analogs to Nasanov pheromone produced by worker honeybees [11]. Swarm captures were recorded by SARH workers (Mexican Agricultural Ministry) and by members of the joint program between USDA-APHIS and SARH. Bait hives were hung from trees 3 m above the ground and were placed along roadways in clusters of two to three every 300 to 500 m. Bait hives were monitored twice a month or more often. Higher densities of traps were used near the cities of Tapachula (Chiapas, Mexico), Puerto Escondido (Oaxaca, Mexico), and Veracruz (Veracruz, Mexico). In most instances, bait hives were in place at least 2 months before the arrival of large numbers of swarms. Alcohol samples from swarms were processed through morphological identification procedures at state laboratories and also at two central laboratories in Jalapa (Veracruz, Mexico) and Puerto Escondido (Oaxaca, Mexico). Forewing and femur measurements were taken at state laboratories followed by discriminant function analysis of 25 morphological characters at the two central laboratories [12]. Northward movement of Africanized honeybees proceeded most rapidly along the Pacific coastal area and in the lowlands adjacent to the Gulf of Mexico (Fig. 1). Movement into the interior of Mexico was limited initially by the Sierra Madre mountains. Distance (km) and time (months) between sequential pairs of detection sites were measured to determine the transit time and rate of expansion for each step. The analysis focused on incremental movement between detection sites rather than cumulative movement of the advancing front. Since rates of range expansion were not normally distributed, analysis of variance tests for range expansion are given using log-transformed data. Statistical distributions that describe the transit time required to move over fixed distances were derived from random walk models [13]. Two distributions for modeling transit times are the inverse Gaussian distribution and the gamma distribution. The gamma distribution was chosen for its mathematical tractability and wealth of possible curve shapes.

The average speed of Africanized honeybee range expansion through Mexico from October 1986 to October 1990 was 32.15 km/month (ranging from 6.5 to 173 km/month). The overall distribution of expansion rates was highly skewed with most values being less than 80 km/month (> 75% of all intervals, $n_{total} = 33$). Small seasonal variation was observed in the rate of range expansion. Expansion rates were slightly faster in sample intervals ending in July–August (averaging 48.7 km/month) while slower rates were found in periods ending in March–April and September–October (19.7 and 27.8 km/month, respectively). These differences were not statistically significant ($F = 1.35$, $df = 5, 27$, $P = 0.28$). Rates of range expansion were not significantly different between coasts ($t = 0.1948$, $P > 0.50$, $n_A = 12$, $n_P = 21$) with Atlantic and Pacific swarm routes averaging 32.8 and 31.7 km/month. A gamma distribution was fitted to detection site data from October 1986 through October 1989. The fitted distribution was then used to predict time of first capture for detection sites from November 1989 to October 1990 (Table 1). The model predicted a mean arrival time of Africanized honeybees at the Mexico – United States border near Brownsville, Texas to be June 1990 with a 95% prediction interval of December 1989 to

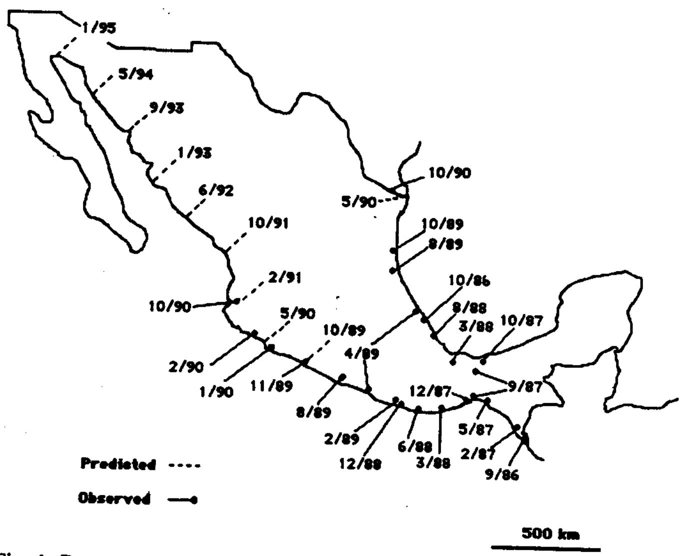

Fig. 1. Range expansion of Africanized honeybees in Mexico. *Points with solid lines* indicate month and year of first detection. *Dashed lines* indicate month and year of movement predicted by range expansion model

Table 1. Predicted and observed transit times of Africanized honeybees in Mexico and USA. For each interval i, d_i is the distance from the last assumed observation in the baseline period; T_i is the time interval required to reach locality from last assumed observation in baseline period; $\hat{T}_i$ is the predicted time required to reach locality; $(\hat{L}_i, \hat{U}_i)$ are 95% prediction boundaries for predicted time. Location of last assumed observation on the Pacific coast was La Unión, Guerrero; location of last assumed observation on the Atlantic coast was Soto la Marina, Tamaulipas

i	Locality	d_i [km]	T_i [months]	$\hat{T}_i$ [months]	$(\hat{L}_i, \hat{U}_i)$ [months]
1	L. Cardenas, Michoacán	40	2	1.26	(0, 5.54)
2	Michoacán/Colima border	258	4	8.09	(2.29, 17.47)
3	Manzanillo, Colima	320	5	10.02	(3.34, 20.30)
4	50 km S Nayarit/Jalisco border	482	8	15.09	(6.44, 27.40)
5	Tomatlan, Jalisco	514	9	16.11	(7.10, 28.75)
6	Puerto Vallarta, Jalisco	556	13	17.43	(7.97, 30.50)
7	Hidalgo, Texas	257	12	8.05	(2.27, 17.41)
8	Nogales, Arizona	1856	not known	58.16	(39.14, 80.55)

March 1991. A previous estimate for the arrival at the Mexico – US border had been August 1990 with a 95 % prediction boundary of November 1989 to November 1991 [13]. Africanized honeybees were first detected in the United States near Hidalgo, Texas on October 15, 1990 [5]. A second major point of entry into the United States is expected near Nogales, Arizona. The model predicts a mean arrival time of Africanized honeybees at the Mexico – US border near Nogales, Arizona to be July 1994 with a 95 % prediction interval of December 1992 to May 1996. Previous studies have projected their arrival in Nogales, Arizona as early as 1990 to 1991 [8].

Biological invasions are now occurring globally at unprecedented levels owing to increased human movement and activity between the continents. By applying testable models to exotic species as they proceed with invasion, we can begin to understand the dynamics of the invasive process. First detection of Africanized honeybees in the United States occurred in southern Texas in 1990 only 4 months after predicted. The success of our prediction for arrival at the second US entry point (near Nogales, Arizona) remains to be seen. Confidence boundaries about the predicted arrival time in southern Arizona were large. Such error is partly an outcome of extrapolating the forecast over a long distance, in this case, approximately 1850 km. Additional error in range expansion forecasts probably arises from sampling error in detecting the true arrival times of first swarms. Capture success of bait traps is likely to be dependent on the number of available alternative nest sites. First detection sites reflecting the arrival of initial swarms would be most accurate in those locations where alternative nest sites are limiting. In addition, attractiveness of traps used for the survey would clearly affect the time of detection of range expansion [14]. Other factors contributing to variability in the rate of range expansion may include changes in vegetation, rainfall, and temperature. Seasonal patterns in swarming and absconding cycles could be tied to flowering phenologies of important honeybee resource plants [15]. Such factors will probably have increasing effects on the rate of expansion as the bees approach their northern climatic limits.

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