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Boll weevil invasion process in Argentina

Mariano P. Grilli · Marina A. Bruno ·
María L. Pedemonte · Allan T. Showler

Abstract The boll weevil, *Anthonomus grandis grandis* Boheman, is the most destructive cotton pest in the Western Hemisphere. In 1993, the pest was reported in Argentina, and in 1994 boll weevils were captured in cotton fields in Formosa Province on the border between Argentina and Paraguay. The pest has subsequently moved to new areas, and in 2006 it was reported in Argentina's main cotton growing region. This study describes the first stage of the boll weevil invasion into areas of Argentina using a network of pheromone traps from 1997 to 2000 in Pilcomayo and Pilagás departments. A temporal autocorrelation analysis of the numbers of collected boll weevils in seven localities, and a synchrony analysis of 70 rural settlements for the 1997–2000 period, were the approaches we used to characterize boll weevil dispersal and establishment. Total abundances of boll weevils varied but a positive correlation between total number of individuals captured and the number of traps that captured them was detected. While short term temporal autocorrelation was observed, spatial synchrony was not found. The role of alternative hosts in facilitating the advance of boll weevils into Argentina is discussed.

M. P. Grilli (✉) · M. A. Bruno · M. L. Pedemonte
CONICET—Centro de Relevamiento y Evaluación de Recursos
Agrícolas y Naturales, Facultad de Ciencias Agropecuarias,
Universidad Nacional de Córdoba, Av. Valparaiso s/n, CC 509,
5000 Córdoba, Argentina
e-mail: mgrilli@crean.agro.uncor.edu

A. T. Showler
Kika de la Garza Subtropical Agricultural Research Center—
USDA-ARS IFNRRU, 2413 East Highway 83, Weslaco, TX
78596, USA

Introduction

The boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curculionidae), is an invasive pest native to tropical Mexico that has spread into other cotton producing areas in the Americas (Lanteri et al. 2003). This insect is considered to be the most destructive of cotton pests because of its dispersal behavior, high reproductive capacity, multivoltine life cycle and because, in the subtropics, predation, and parasitism provide poor control (Showler and Greenberg 2003; Showler 2007). From relatively low numbers of overwintered adults, this species may develop economically deleterious populations in a single generation (Walker and Niles 1971).

The boll weevil is estimated to have arrived in South America in the middle of the twentieth Century, being first detected during 1949 in Venezuela (Burke et al. 1986). By 1991, when the first boll weevils were detected in Paraguay, local observations showed that the main direction of advance was toward the southwest at a rate of 66 km/year, governed by local winds (Gomez et al. 2000). Johnson et al. (1975) recaptured marked boll weevils at distances ranging from 2 to 66 km from the release point and Guerra (1988) reported that several marked boll weevils were recovered ≈ 320 km from their site of release. Other authors reported that an advance of 80 km/year was typical for this insect (Hunter and Coad 1923) and a dispersal stochastic model, developed by McKibben et al. (1991), shows that maximum dispersal distances can be greater than 100 km for some individuals. But dispersal capability is not enough for an invasive insect to be successful.

Invasion involves three distinct population processes: (1) the arrival, when individuals are transported to new areas outside their native range; (2) establishment, when populations grow to sufficient levels such that the probability of elimination is low; and (3) dispersal, when the insect's range expands into new areas (Dobson and May 1986; Liebhold et al. 1995; Shigesada and Kawasaki 1997). In the instance of boll weevils, all three processes occur.

In the Mesoamerican tropics, boll weevil hosts include cotton, *Gossypium hirsutum* L., *G. barbadense* L., and at least four other genera of malvaceous plants: *Thespesia*, *Cienfuegosia*, *Hampea*, and *Hibiscus* (Cross et al. 1975). In temperate regions, boll weevils usually spend the intercrop period as adults in the stubble and leaf litter or other debris around cotton fields, but in warm subtropical winters, boll weevils are active and feed on alternate food sources, such as citrus endocarps (Showler 2006a, 2007; Showler and Abrigo 2007). When cotton is planted in the spring, overwintered boll weevils arrive in cotton fields before squares become available, attracted by cotton plant volatiles (Tumlinson et al. 1969; White and Rummel 1978). Males that feed from these plants produce aggregation pheromones that attract mainly females, but also other males (Cross and Mitchell 1966). Reproduction mostly begins when the squares (flower buds) are ≈ 3 mm in diameter (Showler 2005; Showler et al. 2005) and eggs are deposited individually in squares at a rate of 7–11 per female per day; this is a mean oviposition rate of 150 eggs per female during 21 days. Injury to squares occurs from both oviposition and feeding (Showler and Cantú 2005, 2008; Showler 2006b).

In Argentina, the boll weevil was first reported in 1993 in the province of Misiones in non-cultivated areas, and in 1994 boll weevils were captured around cotton fields on the border with Paraguay. During that year, boll weevils trapped in previously weevil-free locations revealed expansion into northeastern Formosa Province (Cosenzo et al. 2001). Following those first reports in Argentina, the pest has dispersed to new areas and finally, despite strong action by the Argentinian government to diminish the spread, the pest was reported in Chaco province in 2006, Argentina's principal cotton growing area (Stadler and Buteler 2007). The objective of this study was to describe the first stages of boll weevil invasion into a new area.

Materials and methods

Study area

The study was carried out in Pilcomayo and Pilagás Counties (25°16′3″ S; 58°22′28″ W) of Formosa province in Argentina. The area is mainly subtropical forest where

agriculture is based on smallholders (<3 ha) that rely to a substantial extent on cotton as a cash crop (Cosenzo et al. 2001). These small farmers concentrate around rural settlements that were the original administrative division of the province (Fig. 1) and that now rely on the administrative authority of a nearby town. In each of these rural settlements, there was a coordinator of the National Agriculture and Food Quality Service of Argentina (SENASA) Cotton Boll Weevil Eradication Program managing ∼200 traps (Retzlaff 1998).

Boll weevil data

Adult boll weevils were collected in a network of 8,500 Scout traps (Hercon Environmental U.S.A.), baited with an artificial aggregation pheromone (Mitchell and Hardee 1974), that was replaced every 15 days during the study period. The 8,500 traps covered a total of 164,160 ha, and were grouped in 70 rural settlements within seven localities in each county (Cosenzo et al. 2001).Traps were placed within or adjacent to cotton fields, and each trap was identified by a unique number and checked every 10 days during the 4-year study period. Captured boll weevils were counted monthly for each of the 70 settlements and the seven localities.

Boll weevil eradication program standards

Under the national boll weevil eradication program, the presence of a single boll weevil individual in a trap was considered as a "focal point." If a focal point was detected in a cotton field, a security area of 1,000 m radius was established around it and a detailed inspection of all the cotton fields in this area for boll weevils was performed, insecticide was applied to all cotton fields within the radius, and there was an early season insecticide spray in the same fields during the next season (Retzlaff 1998).

Describing the boll weevil invasion process

One way of describing the properties of an insect invasion time series is by the use of sample autocorrelation coefficients which measure the correlation between observations at different time lags (Chatfield 1980). A useful aid for interpreting autocorrelation coefficients is a correlogram graph in which the autocorrelation coefficient r_k is plotted against the time lag k (Chatfield 1980). Temporal correlograms depicting the correlation between data separated by different time lags were estimated for each of the localities that grouped different rural settlements.

Spatial synchrony was also used to determine coincident change in abundance during a certain time period in geographically separated populations (Buonaccorsi et al. 2001;

Fig. 1 Spatial arrangement of the 70 settlements in the study area, representing the seven localities
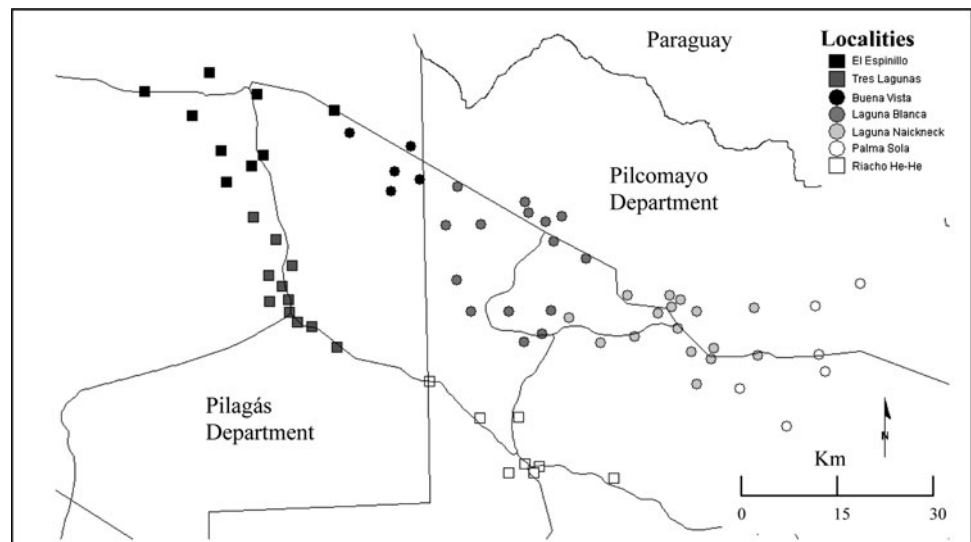
Liebhold et al. 2004). Previous studies of spatial synchrony indicated that synchrony is not homogeneous and populations located nearby tend to be more synchronous than those located farther apart (Ranta et al. 1995; Bjørnstad et al. 1999; Koenig 1999). One method of quantifying spatial synchrony is by plotting the paired correlation coefficients between time series of spatially separated populations against the Euclidean distance separating each pair (Buonaccorsi et al. 2001). We employed the nonparametric covariance function to explore how synchrony varies with increasing distance (Bjørnstad et al. 1999; Bjørnstad and Falck 2001). The nonparametric covariance function is a smoothing spline function fit to the paired cross-correlations as a function of lag distance, producing a direct continuous estimate of spatial covariances. Confidence intervals for the estimated functions were calculated using bootstrap resampling of 1,000 iterations (Bjørnstad et al. 1999; Bjørnstad and Falck 2001; Økland et al. 2005). The analysis was performed using the spatial nonparametric cross-correlation function module within the R statistical package (Hornik 2006). Spatial correlograms, which quantify spatial autocorrelation as a function of lag distance, were calculated using the all of the settlement data.

Results

Numbers of boll weevils captured varied from year to year during the study period, with a maximum of 10,001 individuals captured in 1999, and a minimum of 132 individuals captured in 1997. The correlation between total number of boll weevil captures and the number of focal points in the field was $R^2 = 0.81$ ($P < 0.05$) (Fig. 2). The mean number of individuals captured per focal point was 12, with a range of 2–28.
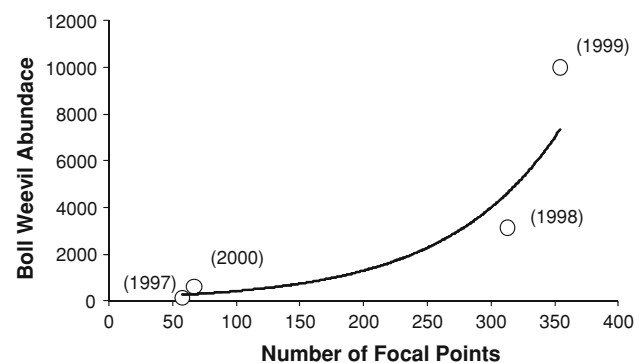

Fig. 2 Relationship between the total numbers of boll weevils captured and the numbers of Foci, $y = 136.73 \times e^{0.0112x}$, $R^2 = 0.88$, $P < 0.05$

Temporal autocorrelation analysis shows a stationary series with a short-term correlation characterized by large values of r_1 followed by two or three coefficients that tend to get smaller. Considering that the lags used for the analysis were in months, this means that autocorrelation was a short-term phenomenon. Values of r_k for longer lags tended to be approximately zero (Fig. 3). While it was not universally evident, correlograms for areas including Palma Sola, Laguna Naick Neck, and El Espinillo showed a seasonal fluctuation during each year.

Spatial synchrony patterns were not found throughout the 4-year study (Fig. 4; Table 1). Mean yearly synchrony ranged between 0.12 in 1997 and 0.31 in 1999, and synchrony was determined to be greatest between nearby populations (local synchrony), and spatial correlation declined with increasing distance (Fig. 4c). There was, however, a discernible contrast in the synchrony of local populations (i.e., synchrony at lag 0) during the different years of this study. Each year, the covariance function stabilized around the mean synchrony with negligible
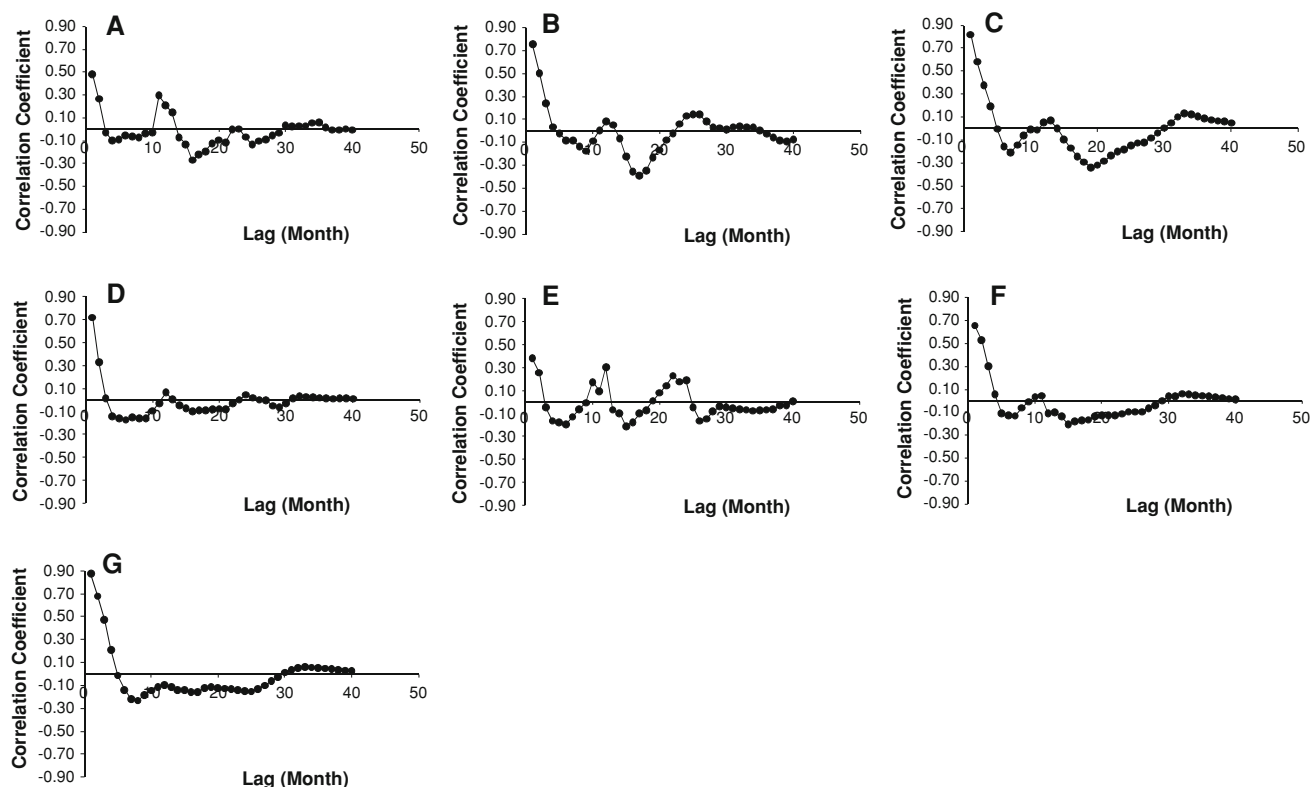
Fig. 3 a–g Temporal autocorrelation for the abundance of boll weevils in each locality during the whole study period. Each locality group had ~10 settlements. **a** El Espinillo, **b** Tres Lagunas, **c** Buena Vista, **d** Laguna Blanca, **e** Laguna Naick-Neck, **f** Palma Sola, **g** Riacho He-He

slope, as the distance between sample sites increased until the maximum lag (80 km) (Fig. 4; Table 1). Greatest local synchrony (0.45 at lag 0) occurred in 1997, and a negative trend during that year was observed with lowest synchrony (0.13) in the maximum lag (80 km) (Fig. 4c; Table 1). When examining the monthly colonization dynamic of boll weevils, no clear pattern emerged regarding incidence and intensity of focal points.

Discussion

A fundamental descriptive feature for invasion dynamics is "invasion speed," which is the rate of range expansion of the invading population caused by population growth (Neubert and Caswell 2000). Invasions of new areas involve the species' arrival, followed by establishment, and spread or expansion into additional available habitat (Hastings 1996; Shigesada and Kawasaki 1997). The period between arrival and establishment of an exotic population depends on the population's growth to a detectable level (Sakai et al. 2001). Reaching a detectable population level is, barring significant immigration, determine by the growth rate of a population originating from a relatively small number of founding individuals (Memmott et al.

2005). Hence, the species range advance rate is related to the rate of dispersal and to the time required to develop a detectable population. Variability in numbers of boll weevils captured during the 4-year study indicated dispersal but not necessarily successive increases in yearly captures.

A SENASA-run boll weevil eradication program was implemented during the study period, involving chemical treatment of cotton fields where boll weevils were detected, destruction of cotton plants during the cotton-free over-winter period, and the deployment of traps (Retzlaff 1998). Although eradication measures might have affected the boll weevil's advance rate, the pest continued to invade previously non-infested areas. The low mean number of individuals (≈ 12) per focal point might have resulted in lack of detection in some places. Low temporal autocorrelation suggested short-term effect and the absence of spatial synchrony. Population synchrony is caused by dispersal among populations, synchronous stochastic effects (known as the "Moran effect") (Moran 1953), and trophic interactions with other species that are either synchronized or mobile (Liebhold et al. 2004). In many instances, populations can operate independently of each other because of density-dependent processes, but interaction between them can result in synchronization (Moran 1953). None of the
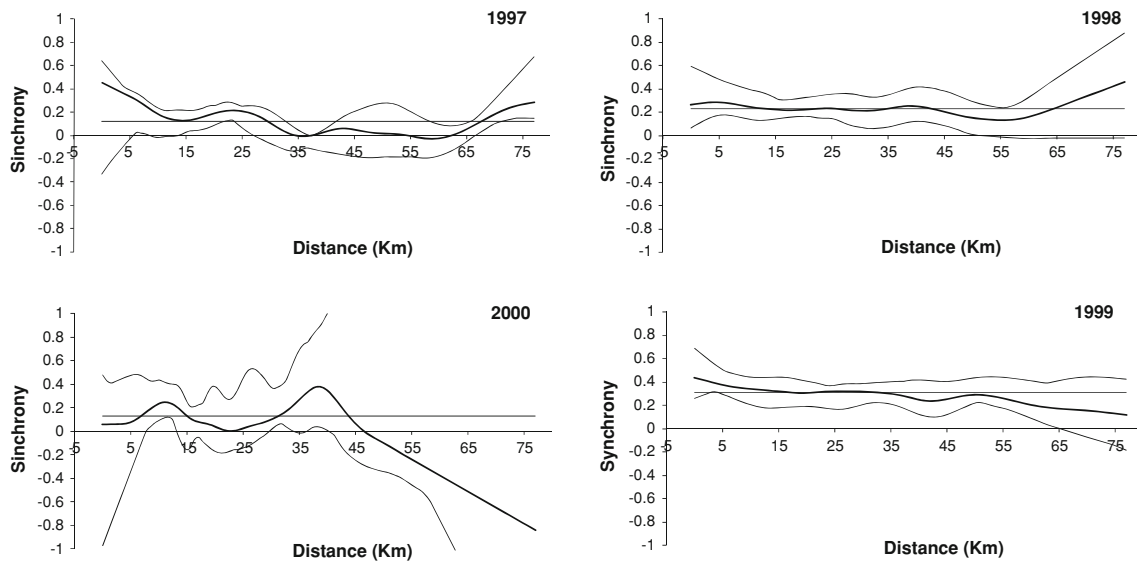
Fig. 4 a–d The spatial covariance functions estimated from the abundance of boll weevils during the study period. The *upper* and *lower lines* represent the 95% bootstrap confidence intervals

Table 1 Spatial synchrony of boll weevils during 4 years of study

Year	Distance (km)					
	0	15	30	45	60	75
1997	0.45 [−0.33 to 0.64]	0.12 [0.03–0.21]	0.09 [0.07–0.2]	0.04 [−0.18 to 0.2]	−0.02 [−016 to 0.09]	0.26 [0.15–0.59]
1998	0.26 [0.06–0.59]	0.22 [0.14–0.30]	0.21 [0.07–0.35]	0.20 [0.08–0.38]	0.16 [−0.02 to 0.32]	0.43 [−0.01 to 0.82]
1999	0.44 [0.26–0.68]	0.32 [0.8–0.44]	0.32 [0.21–0.38]	0.25 [0.12–0.40]	0.20 [0.08–0.40]	0.13 [−013 to 0.43]
2000	0.05 [−0.97 to 0.48]	0.14 [−0.15 to 0.27]	0.10 [0.02–0.36]	0.06 [−0.24 to NA]	−0.37 [−0.74 to NA]	−0.77 [NA–NA]

Values represent correlation coefficients, numbers in brackets represent 95% confidence intervals, spatial synchrony was obtained from the pooled data from all the rural settlements

NA not available data

phenomena known to cause synchronization of population dynamics were evident in our study; hence, we conclude, as indicated by temporal autocorrelation, that the populations did not have time to reach sufficiently high numbers for spatial synchronization to occur. A possible explanation for the absence of synchrony is the effect of regional stochasticity caused by eradication measures, which we assume constituted a catastrophic event for the boll weevil populations (Shaffer 1981; Peltonen et al. 2002) [catastrophic event models involve catastrophe and population mortality rates (Hanson and Tuckwell 1981; Lande 1993)].

Considering that boll weevils move from overwintering habitats to squaring cotton fields over an extended period, rather than at the same time (Rummel and Summy 1997), it is important to consider season-long strategies for reducing substantial overwintered populations encountered in subtropical areas such as northern Argentina and south Texas (Showler 2003, 2006a, b, 2009b). In the subtropics, many boll weevils move from cotton fields after harvest searching for alternative food resources (Showler 2003, 2006b).

Although boll weevils have been collected in tree lines adjacent to cotton fields (Guerra and García 1982), these numbers decline through the winter, suggesting that boll weevils do not derive much nutrition from those plants either as pollen, nectar, or foliage, but overwintering boll weevil populations around citrus orchards remain substantial throughout the winter season (Showler 2006b) because the endocarps of some citrus species can sustain adult boll weevils for the entire overwinter period (Showler and Abrigo 2007). While various pollen grains have been isolated from the digestive tracts of boll weevils collected in the Misiones and Formosa Provinces of Argentina and in Brazil (Lukefahr et al. 1986; Cuadrado 2002), nonmalvaceous pollens have not been shown to sustain boll weevils (Showler 2009b). However, citrus was widely grown in our study area and likely enhanced the invasion process by provisioning a supply of food through the relatively warm cotton-free winters (Showler 2009b). It is important to note that the eradication approach in Argentina does not involve measures to suppress or control boll weevils on alternative

host vegetation, particularly citrus, from which individuals can re-colonize cotton fields (Showler 2006b).

Experiments comparing flight duration between boll weevils captured far from any cultivated cotton field and those trapped at the edge of heavily infested flowering cotton showed that this insect tends to make long-distance flights from cotton fields (Rankin et al. 1994). Based on their dispersal capability, individuals can arrive in cotton plots from distant sources of cotton. Under these terms, it is probable that natural vegetation (with potential sources of nectar) and citrus orchards (Showler 2006a, 2007) play important roles in the ecology and invasion of boll weevils in this part of Argentina (Showler 2009b) by provisioning alternative, energy-rich foods that can sustain flight activity. Alternate food sources explain why adult boll weevils had been collected in Misiones province despite the absence of cotton (Cuadrado 2002; Showler 2009b) because boll weevils likely reproduced in cotton fields, then many dispersed to local citrus orchards and possibly other food sources, including prickly pear cactus, *Opuntia* spp., none of which facilitate egg production (Cross et al. 1975; Bariola 1984; Benedict et al. 1991; Showler and Abrigo 2007). When volunteer cotton or other malvaceous host plants containing the combination of nutrients that is conducive to egg production become available, and when cotton squares are available during the following spring, reproduction resumes (Showler 2008, 2009a, b).

Boll weevils move from cotton fields after harvest when the plants are no longer conducive to egg production because of the age of the bolls (Showler 2004a, b, 2007) which is consistent with the view that the boll weevil is a colonist that moves to new host plant patches when other habitats are overexploited (Showler 2009a, b). A successful colonist must be able to travel efficiently, mature quickly, and produce large numbers of offspring to exploit the new habitat soon after it arrives (Rankin et al. 1994). Once overwintered individuals find a cotton field, populations increase when the squares reach a diameter of 3–5.4 mm. These populations will increase until they are detected and effective control measures are applied.

Although boll weevils exhibit search behavior for host plants, they do not migrate between specific locations in pursuit of food as swarms (Showler 2006a, 2007). Rather, long-range movement is opportunistic, relying on winds or accidental mechanical transfer to spread them to favorable and unfavorable habitats alike (Nathan et al. 2002; Showler 2009a, b). This behavior, and the widespread existence of nectar [sugary fluids, unlike nonmalvaceous pollens, have been identified as food sources that extend boll weevil longevity (Benchoter and Leal 1976; Haynes 1985; Haynes and Smith 1992; Hedin and McCarty 1995; Showler 2009a, b)], explain how boll weevils could be trapped far from cultivated cotton (Johnson et al. 1975; Guerra 1988; Jones et al. 1992; Cuadrado 2002). Such movement from cotton to alternate food sources and back to cotton made the pest appear to occur randomly in space and time in our study because we did not monitor the alternative food resource habitats for boll weevil populations, and observed advances of the pest into new areas was determined, perhaps inaccurately, only by its presence in cotton fields. Considering the pest's relatively high reproductive potential, even a small migrant cohort will inflict economic losses on cotton production as a consequence of population growth within the same season (Rankin et al. 1994; Showler et al. 2005). The recent infestation by boll weevils in the core cotton region of the Chaco Province in Argentina (Stadler and Buteler 2007) reveals a need for improved planning and optimization of control and eradication measures that are consistent with boll weevil ecology in subtropical habitats (Showler 2007, 2009a, b).

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