M-3582

RED IMPORTED FIRE ANTS: IMPACT ON BIODIVERSITY

The imported fire ant is having greater ecological effects than have been documented previously. Both the research reviewed here and the research in progress indicate that the ecological effects of imported fire ants are among the more important negative results of the presence of these ants in North America.

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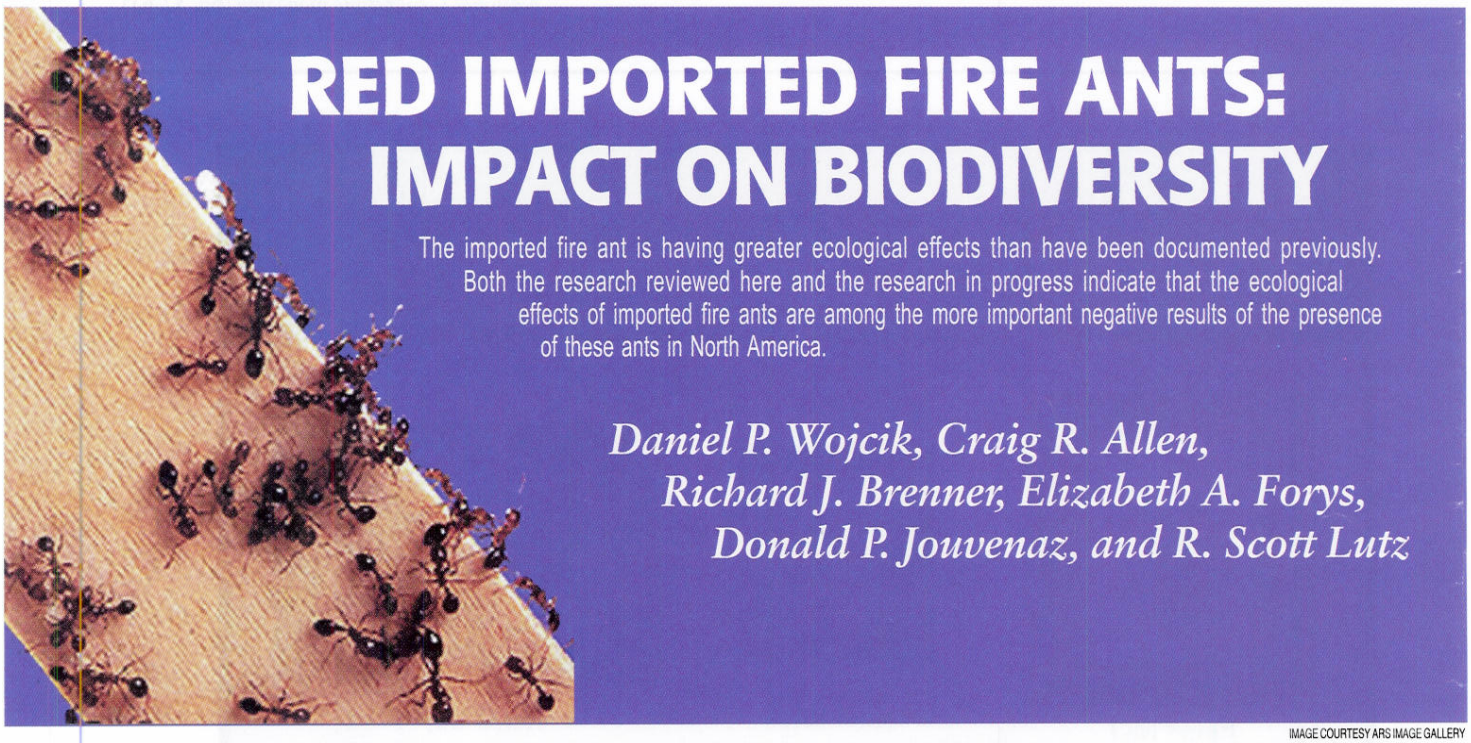

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The red imported fire ant, *Solenopsis invicta* Buren (hereafter referred to as imported fire ant), long considered a regional problem, is receiving renewed attention nationwide, with infestations found in Arizona, Maryland, Nevada, New Mexico, and Virginia (Mitchell 1996). Recently, infestations discovered in several regions of California caused great public concern (Brennan 1999, Schrader 1999). Initially, infestations appeared to be isolated in almond groves in Kern County; presumably these infestations originated from bee hives transported interstate for the purpose of pollinating crops. Separately, ornamental plants arriving in Las Vegas, NV, were infested with fire ants, and records showed that the point of origin was a nursery in Orange County, CA. Further inspections revealed infestations in over 16,000 acres of Orange County. Finally, infestations were identified in some desert irrigated agricultural regions of the Coachella Valley in Riverside County, CA. Subsequently, a toll-free telephone number was established for reporting fire ant mounds in the state of California (800-491-1899).

These infestations are a continuation of a process that began when the imported fire ant was introduced inadvertently into North America in the late 1930s. By 1999, infestations totaled over 121 million hectares (310 million acres) in Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and in Puerto Rico. Although the rate of spread has diminished during the past decade, continued expansion—as has occurred in California—is expected northward along both continental coasts and southward into Mexico and the Caribbean. In fact, in 1998, the USDA's Animal Plant Health Inspection Service (APHIS) added 55 counties in six states to the quarantine area (Arnoldi 1998, Schwalbe 1998). Commercial pesticides are available, but use of traditional toxicants is costly. Most are not registered for large acreage and potentially have adverse collateral impacts, especially when used in recreational areas or environmentally sensitive locations. The federal quarantine that restricts movement of untreated nursery stock into areas not infested by fire ants adds an additional cost for nurserymen and regulatory agencies. Thompson et al. (1995) estimated the economic impact (medical, damage, and pesticide costs) of imported fire ants in the infested southern states to be in excess of $1 billion annually.

In the early 1970s, a polygynous (multiple queen) form of *S. invicta* was detected, and this form has become increasingly more common during the past two decades (Glancey et al. 1987, Porter et al. 1991). Population densities per unit area of this form are two to three times greater than the monogynous form (Macom and Porter 1996), which exacerbates the difficulties and costs to manage this pest and also increases risks to humans and animals.

Although imported fire ants are general predators and scavengers, they are highly aggressive when their nests are disturbed and cause painful stings to humans, pets, domestic animals, and wildlife. Approximately 30% of the people in the infested areas are stung each year; of these, approximately 1% may develop hypersensitivity to the ant's venom and require some type of medical care with costs running into the millions of dollars (Vinson 1997). Today, in the fire ant infested region, more immunotherapy is prescribed for fire ant hypersensitivity than for any other hymenopterous allergy (Freeman 1997).

Vinson (1997) reviewed the introduction and initial expansion of imported fire ants into North America. He discussed many details of their biology, behavior, and impacts but included little discussion of their effects on biodiversity. Therefore, in this article we discuss the impacts of the imported fire ant on biodiversity, an under-emphasized area that currently is receiving more attention.

Impact of Fire Ants on Biodiversity of Invertebrates

Direct Impact on Invertebrates. Imported fire ants feed on a wide variety of invertebrates (Wilson and Oliver 1969, Lofgren 1986, Vinson 1994). They have received some attention as beneficial insects because they are predators of some pest species [e.g., lone star tick, *Amblyomma americanum* (L.) (Burns and Melancon 1977); tobacco budworm, *Heliothis virescens* (F.) (McDaniel and Sterling 1982); sugarcane borer, *Diatraea saccharalis* (F.) (Reagan et al. 1972); boll weevil, *Anthonomus grandis grandis* Boheman (Sterling 1978); and horn fly, *Haematobia irritans* (L.) (Summerlin et al. 1984a)]. Their effects on nonpest species are less well known, but they have been shown to affect some beneficial insects negatively (e.g., the braconid parasitoid *Cardiochiles nigriceps* Viereck [López 1982], dung-inhabiting scarab beetles [Summerlin et al. 1984b], released biocontrol agents and pollinators [Nordlund 1988, Williams et al. 1986], the aphidiid parasitoid *Lysiphlebus testaceipes* Cresson [Vinson and Scarborough 1991], and dung-inhabiting predatory beetles [Hu and Frank 1996]).

The effects of imported fire ants on invertebrate faunas in nonagricultural habitats have been studied in central Texas. Hooper (1976) showed that these ants reduced isopod density but not *Gryllus* cricket density. Porter and Savignano (1990) found that after an invasion by polygyne colonies, some arthropods (isopods, certain mites, tumblebug scarabs) declined significantly, whereas others (ground crickets, a brachypterous cockroach, a symbiotic scarab) increased. Overall, the species richness of non-ant arthropods was 30% lower in infested sites, and numbers of individuals were 75% lower. Ricks and Vinson (1970) demonstrated that imported fire ants preferred some species of arthropods to others but would feed on any insect. The general conclusion was that imported fire ants attacked, killed, and consumed any invertebrate that would not defend itself adequately or escape.

Direct Impact on Other Ant Species. The effects of imported fire ants on other ant species have been demonstrated in several studies, but direct predation on the nests of these other species has been observed only rarely (Hook and Porter 1990). The native fire ants, S. geminata (F.) and S. xyloni McCook, have been displaced as the invading imported species has spread across the southeastern United States (Wilson and Brown 1958, Roe 1973, Porter et al. 1988, Porter 1992, Wojcik 1994). Other species displaced by imported fire ants include Pheidole tepicana Pergande, P. crassicornis tetra Wheeler (Camilo and Philips 1990), Linepithema humile (Mayr) (Glancey et al. 1976), and 18 others (Porter and Savignano 1990).

In contrast, some ant species have survived and even increased in numbers and distribution after imported fire ant invasion, particularly *Dorymyrmex* spp., *Monomorium minimum* (Buckley), and *Forelius pruinosus* (Roger) (Summerlin et al. 1977, Camilo and Philips 1990, Jusino Atresino and Phillips 1994). Wojcik (1994) monitored ant populations with bait traps on transects for 21 years in Gainesville, FL, and found that *S. invicta* gradually increased from 0 to 43.3% of the occurrences (collections per sampling date) (maximum 55.8%) and 63.1% of the specimens (maximum 74.3%) (Fig. 1). Positive correlations in percent occurrences with *S. invicta* populations were shown by three introduced ant species [*Paratrechina longicornis* (Latreille), *Pheidole moerens* Wheeler, and *Tetramorium simillimum* (Smith)], and one native species [*Odontomachus brunneus* (Patton)]. Negative correlations in per-

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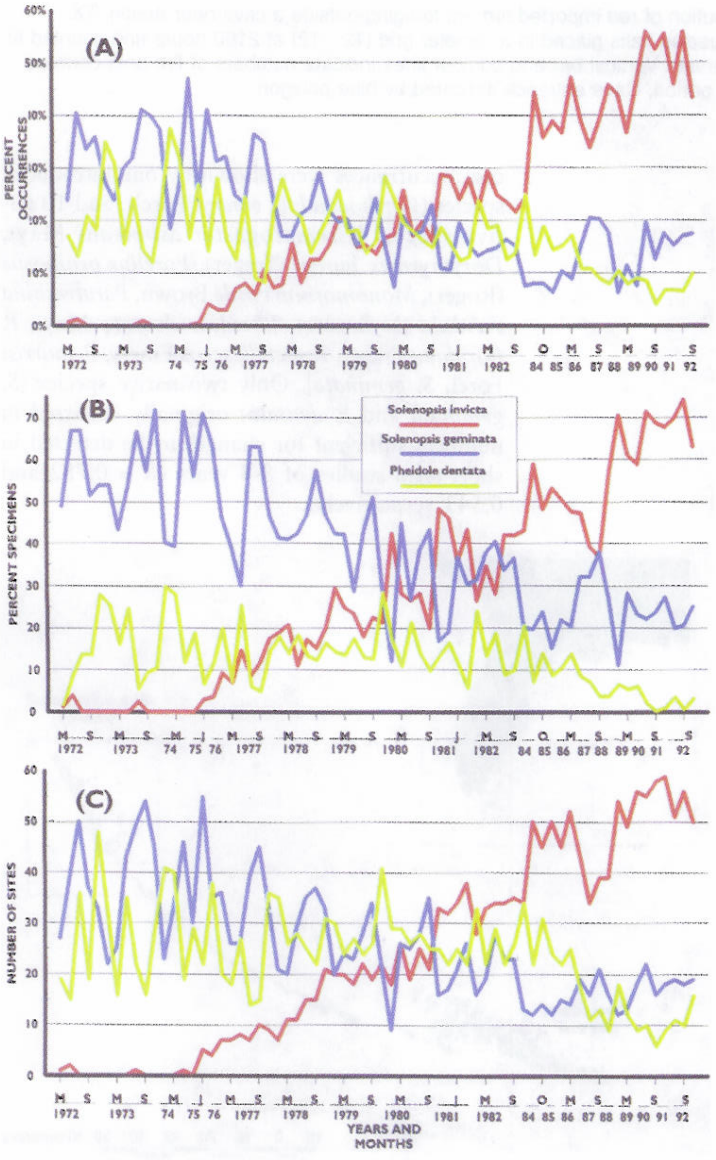

Fig. 1. Percent occurrences (collections per sampling date) (A), percent specimens (B), and number of sites (C) for major species of ants collected on the Gainesville, FL, transect from March 1972 to September 1992. Figure redrawn from Wojcik 1994.

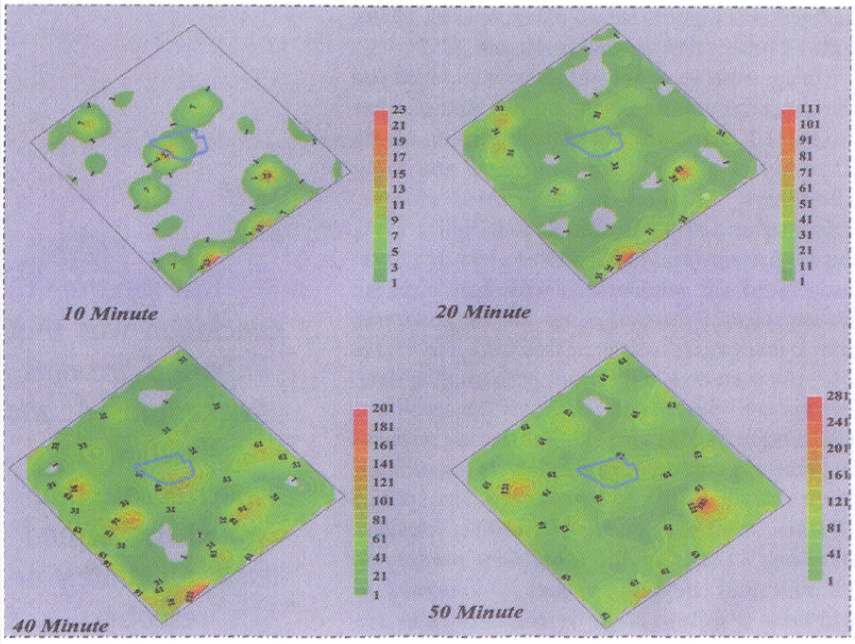

Fig. 2. Distribution of red imported fire ant foraging outside a cave near Austin, TX. Multiple ant species baits placed in a 3-meter grid (12 ´ 12) at 2100 hours and counted at 10-minute intervals. Vertical bar and contour lines indicate numbers of fire ants counted for given time period. Cave entrance indicated by blue polygon.

cent occurrences were shown by one introduced species (*Cardiocondyla emeryi* Forel), and 10 native species [*Crematogaster ashmeadi* Mayr, *Dorymyrmex bureni* (Trager), *Forelius pruinosus* (Roger), *Monomorium viride* Brown, *Paratrechina vividula* (Nylander), *Pheidole dentata* Mayr, *P. floridana* Emery, *P. metallescens* Emery, *P. morrisi* Forel, *S. geminata*]. Only two native species (*S. geminata* and *P. dentata*) originally occurred in numbers sufficient for changes to be detected in short-term studies of 3-4 years (R = 0.782 and 0.543, respectively).

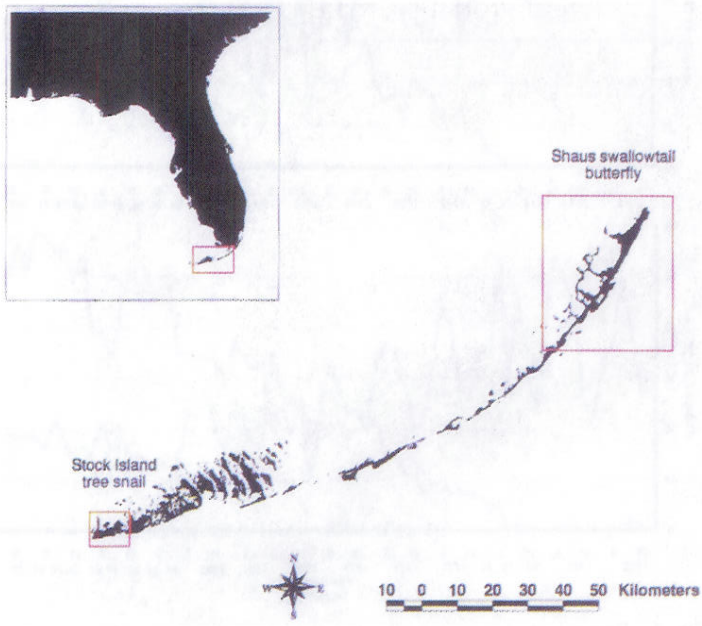

Fig. 3. Location in the Florida Keys of Schaus swallowtail, *Papilio aristodemus ponceanus*, and Stock Island tree snail, *Orthalicus reses reses*, habitat.

Impact on Endangered Cave Invertebrates. Imported fire ants are an important predator of cave invertebrates, including several endangered species (pseudoscorpions, harvestmen, spiders, ground beetles and pselaphid beetles) in Texas (Elliott 1993). Spatially based studies conducted in cooperation with the Department of the Interior, Fish and Wildlife Service (D.P.W. and R.J.B., unpublished data), showed that the ants not only dominate food baits around the caves (Fig. 2) but also foraged deeply into the caves for prey. A special concern was that omnivorous cave invertebrates foraging outside the caves at night could consume pesticide-treated fire ants, which might prove lethal to the endangered species. Fortunately, laboratory studies showed that the active ingredient in Amdro bait (hydramethylnon) did not affect cave crickets forced to feed on Amdro-killed ant cadavers. Temporal separation of foraging activities for target and nontarget organisms allows bait treatment of the areas surrounding the caves during the daylight hours when fire ants are foraging but cave invertebrates are not.

Impact on invertebrates of the Florida Keys. Imported fire ants first were recorded in the Florida Keys in 1976 (Callcott and Collins 1996) but were considered to be restricted to disturbed areas (Deyrup et al. 1988, Porter 1992). However, during a Keys-wide survey in 1996, the ant was collected on 10 of the 14 major keys (Forys et al. 1997) and in every major habitat type including hardwood hammocks, pinelands, salt and freshwater marshes, and disturbed areas (e.g., roadsides, parking lots). Its presence in the tropical hardwood hammocks was of particular concern because several species of rare, endemic invertebrates occur in this habitat. The ant was found up to 40 m into the hammock (Forys et al. 1997) on terrestrial and arboreal bait transects.

The Schaus swallowtail, *Papilio aristodemus ponceanus* Schaus, is a rare butterfly that occurs only in tropical hardwood hammocks in the northernmost Florida Keys and the east coast of southern Florida (Fig. 3); it is listed as endangered at both the state and federal levels (Emmel 1986). Although portions of this habitat are protected for the swallowtail, the butterfly's populations have continued to decline. Adults lay their eggs on a select group of trees, primarily wild lime tree (*Zanthoxylum fagara*), that occur in hardwood hammocks in portions of Monroe and Dade County, Florida (Emmel 1986). The Florida Game and Fresh Water Fish Commission funded our research because of the concern with the vulnerability of the immature stages to fire ant predation.

Using the orangedog, *Papilio cresphontes* Cramer, as a surrogate for the endangered butterfly in experiments, eggs, larvae, and pupae were exposed on an enclosed small wild lime tree accessible to an imported fire ant colony (Forys et al. 1997). The fire ants preyed on all of the swallowtail life stages. In fact, fire ants discovered all stages faster than an alternate meat food source. Field studies are underway to determine the impact on the butterfly by removing *S. invicta* from the habi-

Fig. 4. Stock Island tree snail, *Orthalicus reses reses* (conical shell up to 75 mm length), aestivating on a tree in the Keys. Photograph by Matt Schrock.

tats using toxic baits (E.A.F., C.R.A., and D.P.W., unpublished data).

The Stock Island tree snail, *Orthalicus reses reses* (Say) (Fig.4), is listed by the U.S. Fish and Wildlife Service as threatened and by the State of Florida as endangered (Forys et al. 1996). Historically, it was found in several hardwood hammocks throughout Stock Island and Key West (Fig. 3), although it has been extinct in the wild since 1992 (Forys et al. 1996). Stock Island tree snails spent most of the year aestivating on trees, descending for a few hours during the wet season (May to October) to lay eggs 4-5 cm deep in tree litter (Deisler 1987). Predation by imported fire ants, either when snails are on the trees and ground, was thought to be a major factor in the snail's extinction (Forys et al. 1996).

To assess the vulnerability of Stock Island tree snails to imported fire ants, an experiment was conducted using Florida tree snails, *Liguus fasciatus* (Müller), from north Key Largo as surrogates for the endangered species (Forys et al. 1997). In laboratory experiments, 19 of the 22 tree snails were killed by the fire ants within 3 days, 12 while actively foraging and 7 while aestivating. Field studies are underway to determine the impact on snail populations by removing *S. invicta* from the habitats using toxic baits (E.A.F., C.R.A., and D.P.W., unpublished data).

Impact of Fire Ants on Biodiversity of Vertebrates

Direct Impacts on Vertebrates. Information on the direct impact of imported fire ants on native vertebrates is limited (Allen et al. 1994). However, it is known that these ants prey on altricial (helpless immature) young, pipping young (breaking out of the eggshell), and, rarely, adults. They are attracted to sources of proteins, sugars, lipids, and moisture (Vinson et al. 1967). Feeding on protein sources increases when brood is present in the colony (Sorensen et al. 1983) because high protein foods are needed for larval growth. Fire ant brood production occurs primarily in the warmer months and coincides with the breeding periods of most vertebrates.

Direct Impacts on Mammals. Interactions between imported fire ants and mammals is poorly documented. The death of live-trapped small mammals from fire ant predation has been observed (Masser and Grant 1986, Flickinger 1989), including the altricial young of many species. Hill (1970) quantified the loss of newborn cottontail rabbits, *Sylvilagus floridanus* (Allen), to fire ants in 200 by 200 ft enclosures and observed mortality ranging from 33 to 75%. Allen et al. (1997a) documented increased numbers of white-tailed deer fawns, *Odocoileus virginianus* (Zimmerman), in large plots on which fire ant populations had been reduced. These increases probably were the result of a reduction in direct (e.g., stinging leading to blindness) and indirect (e.g., increased movement leading to increased vulnerability to predators) effects.

Direct Impacts on Reptiles and Amphibians. Oviparous reptiles and amphibians may be vulnerable to fire ant populations, but no experimental evidence exists. Mount (1981) was the first to speculate that fire ants might have a strong impact on a wide diversity of herpetofauna. Kauffeld (1957), D.P.J. (unpublished data), and Bartlett (1997) noted the dramatic decline in the local population of the peninsular intergrade kingsnake (*Lampropeltis getula floridanus* Blanchard × *L. g. getula* L.) on Paynes Prairie State preserve, Alachua County, FL. coinciding with the invasion and rapid population rise of polygynous imported fire ants. Mount et al. (1981) documented the consumption of the eggs of the six-lined race runner, *Cnemidophorus sexlineatus* (L.), by the imported fire ant. This lizard was common on the premises of the Gainesville USDA laboratory before fire ants infested the property (D.P.J., unpublished data). Mortality from the stings of the imported fire ant was observed in adults of the box turtle *Terrapene carolina triunguis* (Agassiz) (Montgomery 1996) (Fig. 5A), an unidentifiable snake (C.R.A., unpublished data) (Fig. 5B), and young of the toad *Bufo houstonensis* (Sanders) (Freed and Neitman 1988). When fire ants are present in nests of the alligator, *Alligator mississippiensis* (Daudin), hatching alligator young are subject of predation (Allen et al. 1997b). Nesting *Pseudemys nelsoni* (Carr) turtles are vulnerable when pipping, with mortality as high as 70% (C.R.A. and D.P.W., unpublished data). There has been considerable concern and debate over the potential impact of fire ants on nesting sea turtles, but, again, no experimental evidence exists. Wilmers et al. (1996) documented an increasing presence of fire ants in sea turtle nests on remote island beaches in the Florida Keys, and Moulis (1996) found a 15% decrease in hatchling release rate for loggerhead sea turtles, *Caretta caretta* (L.), emerging from nests infested with fire ants as compared to uninfested nests. These ob-

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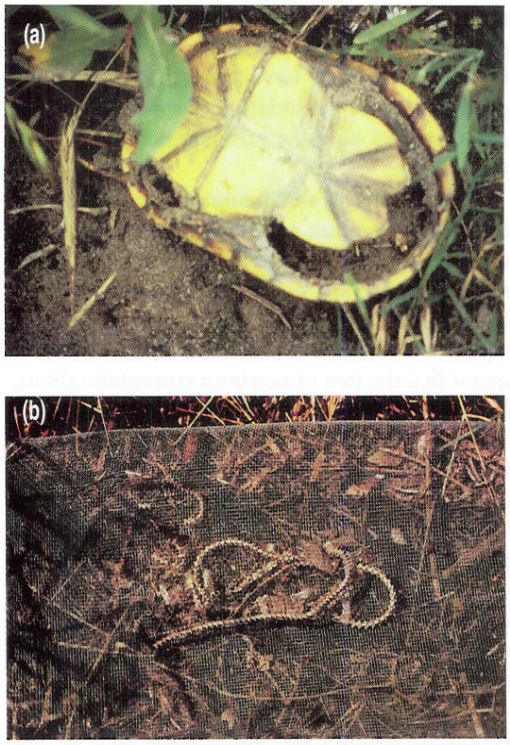

Fig. 5. (A) Remains of box turtle carcass killed and fed upon by red imported fire ants in southeastern Texas. (B) Remains of snake killed and fed upon by red imported fire ants in southeastern Texas. The snake was killed and skeletonized over night in screen trap. Identification was not possible because the skull had been destroyed by the ants. Original photos by C. R. Allen.

servations suggest that potential impacts are considerable, although inherent difficulties with manipulations of large-scale experimental populations in general, and reptile community sampling in particular, make it difficult to assess the impacts of these ants on herpetological communities.

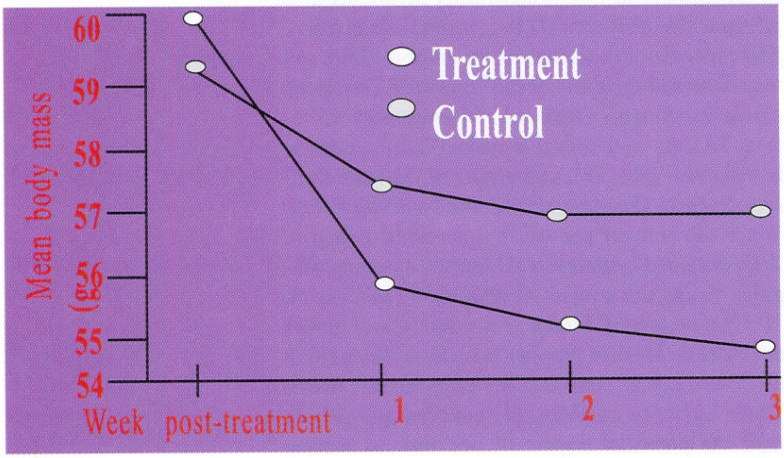

Fig. 6. Effects of red imported fire ant stings on weight gain of hatching American alligators. Fire ants regularly nest in alligator nests and will attack alligator eggs when eggshell cracking occurs during hatching. The ants will enter the eggs and sting and feed upon the unhatched alligators. Alligator eggs ready to pip were placed in artificial nests infested with fire ant colonies. Hatchlings were removed after successfully emerging from the eggs. Hatchling alligators normally lose weight after hatching, before they start feeding. Stung alligators did not gain weight at a rate comparable to unstung check animals, which would put them at a distinct disadvantage in nature. Original figure by C.R.A.; data from Allen et al. 1997b.

Direct Impacts on Birds. Fire ants may be a predator on many species of birds. Recent work suggests that chicks of northern bobwhites, *Colinus virginianus* (L.), are susceptible to fire ants (Allen et al. 1995). The national decline in northern bobwhite numbers has been linked largely to declines in habitat availability and quality. Because fire ants are adapted to disturbed areas (Vinson 1997), the issue of habitat quality decline and invasion by fire ants are inseparable, making their impact additive. Ground nesting species, such as the least tern, *Sterna antillarum* Lesson, are particularly vulnerable to fire ants (Lockley 1995). Negative impacts may be especially severe in colonial breeding species. For example, waterbird nest mortality was as high as 100% on fire ant infested barrier islands (Drees 1994), although mortality varied and was lower for early-nesting birds. Cliff swallows, *Hirundo pyrrhonota* (Vieillott), experienced decreased brood survival in nesting colonies exposed to foraging fire ants (Sikes and Arnold 1986). However, where negative effects on breeding success have been documented, fire ant populations have been reduced to acceptable levels with proper insecticide treatments (Drees 1994, Lockley 1995).

Indirect Impacts on Vertebrates. The indirect effects of imported fire ants on native vertebrates may be more important than direct predation. Allen et al. (1998) found that indirect impacts include reduced survival and weight gain resulting from envenomization, behavioral changes in foraging patterns and habitat use, reduced food availability, community-level changes resulting from trophic cascades, and system-level changes resulting from the impact of these ants on ecological processes.

Reduced survival resulting from fire ant stings has been documented only for northern bobwhite (Giuliano et al. 1996). Fire ant venom is unlike that of most other Hymenoptera, consisting primarily of alkaloids with hemolytic, cytotoxic, and necrotic properties (Fox et al. 1982, deShazo et al. 1990). The loss of digits and appendages by small vertebrates, as well as blinding, may result from fire ant envenomization, and secondary infection is possible.

Reduced weight gain resulting from the stings of imported fire ants has been documented for both northern bobwhite (Giuliano et al. 1996) and American alligators (Fig. 6) (Allen et al. 1997b). Reduced weight gain in juveniles may lower long-term survival and reproduction (Brockelman 1975, Grant 1991).

Behavioral changes, including altered activity (Pedersen et al. 1996) and foraging patterns (Holtcamp et al. 1997), have been documented for small mammals and birds. Changes in foraging and activity patterns likely result from the irritation associated with fire ant stings. Whiting (1994) reported the abandonment of a nesting attempt by the Texas river cooter due to the irritation associated with stings.

Imported fire ant infestations can affect habitat use by vertebrates (Smith et al. 1990, Killion and Grant 1993, Killion et al. 1995, Holtcamp et al. 1997). For example, vertebrates may avoid areas heavily infested with fire ants because of the irrita-

tion associated with fire ant stings, and may experience altered food availability (i.e., insects) resulting from fire ant infestation. Where the optimal habitat of a native species and high fire ant densities occur together, displacement of the vertebrate to suboptimal habitat has a negative population-level impact on the vertebrate species.

Reductions in available food need not result in displacement of vertebrates but may, nonetheless, reduce vertebrate populations. Fire ant impacts on insect species and communities are reasonably well documented (Porter and Savignano 1990, Morris and Steigman 1993), although there is a bias toward determining impacts on species of economic, rather than ecological, importance. In insectivorous vertebrates, reduced food availability due to the presence of imported fire ants may be expected to both increase territory (or home range) and decrease recruitment. In the extreme case of food specialization where the food source is affected negatively by fire ants, population collapses may occur. This is occurring with the Texas horned lizard, *Phrynosoma cornutum* (Harlan), in south and eastern Texas. This lizard feeds primarily on ants of the genus *Pogonomyrmex*, whose populations are reduced by the imported fire ant (Donaldson et al. 1994, Jusino Atresino and Phillips 1994). The lizard largely has been eliminated from the areas infested with fire ants (Price 1990). A thriving introduced disjunct lizard population in Escambia County, FL, declined and disappeared after the imported fire ant became established and fire ant populations increased (D.P.J., unpublished data).

Summary

These studies document the actual and suspected impacts of fire ants on endangered vertebrates and invertebrates and their habitats. Clearly, from an ecological perspective, reducing fire ant populations would help restore the natural biodiversity of animals that existed before the fire ant invasion. The imported fire ant is having greater ecological effects than have been documented previously. Both the research reviewed here and the research in progress indicate that the ecological effects of imported fire ants are among the more important negative results of the presence of these ants in North America.

Acknowledgments

The authors thank D. E. Milne (Center for Medical, Agricultural and Veterinary Entomology, USDA-ARS [CMAVE]) for analyzing the data and preparing Figure 2. The manuscript was improved greatly by the critical reviews of W. A. Banks, T. Fukuda, C. S. Lofgren, R. S. Patterson, and J. Sivinski (all from CMAVE). Research reported in this article was funded, in part, by the Department of Defense, Pollution Prevention Project No. 1053, Strategic Environmental Research and Development Program (SERDP), and under EPA-USDA Interagency Agreement No. DW12937500-01-0; in part, by the Department of Interior, U.S. Fish and Wildlife Service FWS Interagency Agreement No. 1448-00002-95-0749; and, in part, by the Nongame Division of the Florida Game and Fresh Water Fish Commission Project Number: NG95-018. The South Carolina Cooperative Fish and Wildlife Research Unit is supported jointly by a cooperative agreement among the USGS/BRD, the South Carolina Department of Natural Resources, Clemson University, and the Wildlife Management Institute.

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