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Red Imported Fire Ant Impacts on Wildlife: A Decade of Research

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ABSTRACT.—The negative impacts of biological invasion are economically and ecologically significant and, while incompletely quantified, they are clearly substantial. Ants (family Formicidae) are an important, although often overlooked, component of many terrestrial ecosystems. Six species of ants are especially striking in their global ability to invade, and their impacts. This paper focuses on the impacts of the most destructive of those species, the red imported fire ant (*Solenopsis invicta*), and focuses on impacts on native vertebrates. Red imported fire ants often become the dominant ant species in infested areas outside of their native range due to their aggressive foraging behavior, high reproductive capability and lack of predators and/or other strong competitors. The evidence suggests that mammals, birds and herpetofauna are vulnerable to negative impacts from fire ants, and some species are more likely to experience negative population-level impacts than other species. Assessing the ecological impacts of fire ants on wild animal populations is logistically difficult, and very few studies have combined replicated experimental manipulation with adequate spatial (>10 ha) and temporal (>1 y) scale. Thus, most studies have been observational, opportunistic, small-scale or 'natural' experiments. However, significant research, including an increase in experimental and mechanistic investigations, has occurred during the past decade, and this has led to information that can lead to better management of potentially affected species.

INTRODUCTION

Biological invasions are a growing threat to human enterprise and ecological systems. The rate of introductions continues to increase, and many countries are developing organized plans to strengthen bio-security in the face of these threats. The negative impacts of biological invasion are economically and ecologically significant and, while they remain incompletely quantified, they are clearly substantial. For example, Pimentel *et al.* (2001) estimated that the economic costs of non-indigenous species for the United States, the United Kingdom, Australia, South Africa, India and Brazil exceeded US$314 billion per y. Ecological and environmental costs are considerably more difficult to quantify, but include the extinction of indigenous biota, disruption of community structure and changes in ecological processes, with concomitant losses of ecosystem services and capital.

Ants (family Formicidae) are an important, although often overlooked, component of many terrestrial ecosystems. They often comprise a large percentage of the animal biomass

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in some ecosystems (Holldobler and Wilson, 1990) and may be functionally irreplaceable. They provide valuable ecosystem services such as nutrient turnover, energy flow and seed dispersal (Handel *et al.*, 1981). The taxon includes ecologically important predators, scavengers, herbivores, detritovores and granivores. Ants often participate in complex interactions with other species, and there are a surprising array of tightly co-evolved mutualisms between plants and ants. The Formicidae include a relatively large number of introduced or invasive species (>150 species; McGlynn, 1999). Six species of ants are especially striking in their global ability to invade, and their impacts: *Anoplolepis gracilipes* (crazy ant), *Linepithema humile* (Argentine ant), *Pheidole megacephala* (big-headed ant), *Solenopsis invicta* (red imported fire ant), *Solenopsis geminata* (tropical fire ant) and *Wasmannia auropunctata* (little fire ant) (Holway *et al.*, 2002). This paper focuses on the impacts of the most destructive of those species, the red imported fire ant, and focuses on impacts on native vertebrates.

Red imported fire ants (hereafter 'fire ants') were introduced through the port of Mobile, Alabama, in the 1930s (Buren, 1972; Buren *et al.*, 1974). Fire ants are native to South America where their abundance is restricted by competition with other ant species (Buren *et al.*, 1974) and the presence of co-evolved predators (Porter *et al.*, 1997) and enemies (Jouvenaz, 1983). They often become the dominant ant species in infested areas outside of their native range due to their aggressive foraging behavior, high reproductive capability and lack of predators and competitors. In South America, fire ants are predominantly monogynous, meaning that each colony contains only one fertile queen (Jouvenaz *et al.*, 1989; Ross *et al.*, 1996). Density of monogyne fire ants averages about 100 mounds/ha. In the United States, two forms of red imported fire ants exist, monogynous and polygynous (Greenberg *et al.*, 1985; Porter *et al.*, 1991). Density of polygyne fire ants is usually three times or more than that of the single queen form (Macom and Porter, 1996). Polygyne colonies in the United States usually average around 500 mounds/ha (Vinson and Sorenson, 1986; Macom and Porter, 1996) and densities as high as 1400 mounds/ha (Greenberg *et al.*, 1985; Porter *et al.*, 1991) have been recorded. Porter *et al.* (1992) reported densities in the U.S. to be 35 times higher than densities in South America, and attributed this disparity to the high frequency of polygyne colonies on sites in North America. In Queensland, Australia, colony densities as high as 5000 mounds/ha have been recorded in limited areas (C. Vanderwoude, Fire Ant Control Center, Department of Primary Industries, Queensland, Australia, pers. comm.). The high densities associated with polygyne infestations greatly increase the probability of interaction with, and negative impacts on, native species. However, single queen infestations may have similar, though less obvious, impacts.

Allen *et al.* (1994) reviewed the impacts of fire ants on native wildlife. That paper covered 13 peer-reviewed papers (also included, due to the limited information available, were agency reports and non-reviewed proceedings) published during the approximately 60-y period beginning with the introduction of the red imported fire ant in the early 1930s. Since then, 47 research papers have been published, greatly expanding knowledge of fire ant impacts on wildlife. In contrast with earlier papers, these more recent papers are more likely to be experimental and investigate mechanisms of impact (Fig. 1). During the past 10 y fire ants have continued to spread at an alarming rate. They have now been documented as present on many Caribbean Islands (Davis *et al.*, 2001), have made the inevitable jump to the West Coast of the United States and successfully invaded Australia in 2001 (Moloney and Vanderwoude, 2002). In the continental United States they have increased their range to more than 132 million ha infested within the United States Department of Agriculture (USDA) quarantine area. This includes 13 states (AL, AR, CA, FL, GA, LA, MS, NC, NM, OK, SC, TN, TX) and Puerto Rico. Fire ants have been detected in other states (AZ, NV), but

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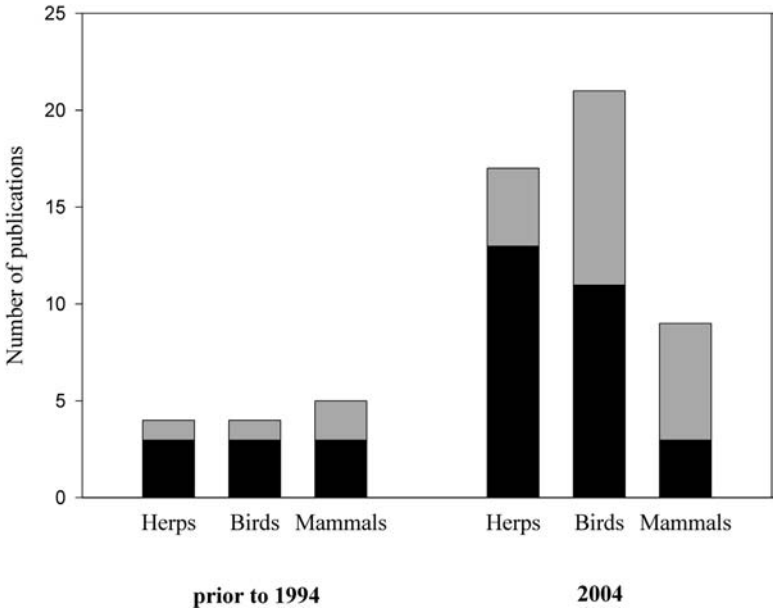

FIG. 1.—Peer-reviewed publications concerning fire ant impacts on native wild vertebrates, separated by taxonomic group. 1994 refers to papers published from the time of fire ant introduction into the United States from approximately 1932 until 1992, reviewed in Allen *et al.* (1994). 2004 refers to papers published between 1993–2003. Black indicates non-experimental publications and gray indicates experimental publications

those were not quarantined in 2003 (A. Callcott, USDA-APHIS, Gulfport MS, pers. comm.). This paper reviews those papers focusing on the impact of red imported fire ants on wildlife published in the past 10 y (and a couple missed in the original review) and synthesizes the state of our knowledge regarding those impacts as of 2004.

IMPACTS ON REPTILES AND AMPHIBIANS

The global decline of amphibians and reptiles has been linked to six causal factors: habitat loss and degradation, environmental pollution, disease, global climate change, unsustainable use and introduced invasive species (Gibbons *et al.*, 2000). While many scientists agree that habitat loss is the largest single factor contributing to these declines, the impacts of introduced invasive species may also be substantial.

There are a variety of life history traits that may make both reptiles and amphibians particularly susceptible to fire ants, including egg-laying and the disturbance associated with this activity (Allen *et al.*, 1994), and delayed hatchling emergence. Much experimental and observational data has accumulated since Landers *et al.* (1980) first reported red imported fire ants preying upon hatchling gopher tortoises. Their observation of ten hatchlings that were "destroyed" by fire ants is typical of earlier publications. Predation occurred when hatchlings hatched from the egg, but had not yet emerged on the soil surface, and before hatchlings could completely emerge from the egg.

While there is some documentation of direct impacts of fire ants on herpetofauna, either by observation or experimentation, indirect impacts may be harder to assess. Indirect

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impacts may include reduced survival and weight gain, behavioral changes, changes in foraging patterns and habitat use and reduced food availability. The first experimental evidence of indirect impacts of fire ants on herpetofauna focused on neonatal American alligators (*Alligator mississippiensis*). Allen *et al.* (1997b) tested the hypothesis that envenomization by fire ants has an impact on hatchling alligator survival and body mass. Hatchlings that emerged from nesting material containing red imported fire ants exhibited significantly less weight gain than those from the reference group in the controlled laboratory environment. Alligator nests that contain fire ants may also receive less maintenance by female alligators resulting in reduced nest success. That hypothesis was investigated by Reagan *et al.* (2000) in southwestern Louisiana. They documented that both female attendance and nest success were lower for alligator nests with fire ants present, supporting the findings of Allen *et al.* (1997b).

The potential effects of fire ants on turtle species also includes both direct and indirect impacts. Whiting (1994) documented indirect impacts to an adult *Pseudomys texana*, which abandoned a nesting attempt after being irritated by fire ant stings. Conners (1998a) found six hatchling *Chelydra serpentina* that had either emerged from the nest or were just below the surface that appeared to have been preyed on by fire ants. While there are few reports of predation on adult turtles, five adult three-toed box turtles (*Terrapene carolina triunguis*) were killed by fire ants in Texas (Montgomery, 1996). Box turtles (adults and juveniles) may be particularly susceptible to fire ant predation due to their defensive reaction to close the plastron and become immobile. Even a tightly closed box turtle shell has some gaps large enough for fire ants to penetrate and the turtle's immobility allows more fire ants to swarm over it. Fire ant predation on hatchling and juvenile gopher tortoises (*Gopherus polyphemus*) has been recently documented (Epperson and Heise, 2003).

Both Allen *et al.* (2001a) and Buhlmann and Coffmann (2001) provided experimental evidence of fire ant impacts on turtles. Allen *et al.* (2001a) assessed the impacts of fire ants on Florida red-bellied turtle hatchlings, *Pseudomys nelsoni*. This species is similar to sea turtles in that hatchlings do not emerge from the nest until most or all of the clutch has hatched, which may make them particularly susceptible to fire ants. Of all eggs hatched, 100% of those from control groups survived, while only 29% of those in the fire ant infested enclosures survived. Hatchlings were most susceptible to fire ant predation while still in the egg after pipping. While fire ants were not able to breach an intact eggshell, they entered the egg as soon as a hole was pipped. Similar results were observed in work with slider turtles. Buhlmann and Coffmann (2001) assessed the effects of fire ants on a species with delayed emergence, *Trachemys scripta*, in South Carolina. They found that the closer the nest was to a fire ant mound, the greater the percentage of eggs and hatchlings killed by *Solenopsis invicta*. Only 55% of fertile eggs in fire ant infested areas hatched resulting in surviving turtles vs. 100% survival in the control areas. Fire ants established underground foraging tunnels to the nest and were "monitoring" the eggs for signs of hatching. While fire ants were unable to breach fully turgid, intact eggs, as soon as the eggs were pipped they entered the nest and attacked hatchlings. Survival of overwintering turtle hatchlings in a nest frequented by fire ants is unlikely. Delayed emergence decreases hatchling mortality by providing a sanctuary from predators and harsh environmental conditions (Gibbons and Nelson, 1978). Fire ants may negate the value of the nest cavity as a sanctuary by establishing foraging tunnels into the cavity following egg laying.

Investigation into the potential impacts of fire ants on sea turtles has received more attention than most other reptile species. Allen *et al.* (2001a) sampled fire ants on sea turtle nesting beaches in Florida and found them present on 13 of 18 of the specific sampling sites. Work with Loggerhead turtles (*Caretta caretta*) in Georgia (Moulis, 1997) and Florida

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(Wilmers *et al.*, 1996; Parris *et al.*, 2002) as well as Green turtles (*Chelonia mydas*) in Florida (Wilmers *et al.*, 1996) documented the increasing presence of fire ants in sea turtle nests. In Georgia a small percentage (<11%) of turtle nests were infested with fire ants (Moulis, 1997), but the impacts on infested nests were considerable. The average hatchling release rate (defined as the number of hatchlings entering the water per number of eggs × 100) was significantly lower (15%) in nests infested with fire ants. Ants entered the nests just prior to hatchling emergence and it was assumed that as hatchlings pipped they were attacked by fire ants. Parris *et al.* (2002) documented fire ants stinging and consuming loggerhead hatchlings that had recently pipped. They also found skeletonized hatchlings that were consumed before they emerged from the nest. Hatchlings also sustained injuries including blinding and wounds on flippers and heads due to stinging that may have influenced survival (Parris *et al.*, 2002).

Little has been published concerning the impacts of fire ants on amphibian populations (Freed and Neitman, 1988), but amphibians appear to be a highly vulnerable taxon. Observations of the endangered Houston toad, *Bufo houstonensis*, in Texas documented fire ant predation on newly-metamorphosed toadlets (Freed and Neitman, 1988, not included in Allen *et al.*, 1994). Toadlets were attacked by fire ants as they emerged on the shore or on surface vegetation while older toadlets (~1 wk old) were observed evading fire ants.

Impacts on snakes and lizards have received more attention than amphibians (Conners, 1998b; Donaldson *et al.*, 1994; Tuberville *et al.*, 2000). The red imported fire ant has been implicated in the decline of the Texas horned lizard (*Phrynosoma cornutum*) (Donaldson *et al.*, 1994), the southern hognose snake (*Heterodon simus*) (Tuberville *et al.*, 2000) and the peninsular intergrade kingsnake (*Lampropeltis getula floridanus*) (Wojcik *et al.*, 2001). For each species, the decline coincided with the invasion of red imported fire ants, but experimental evidence is lacking. The current and future status of Texas horned lizards was evaluated using museum specimens, historical records, surveys and resident interviews (Donaldson *et al.*, 1994). This particular species is a dietary specialist that feeds predominately on harvester ants of the genus *Pogonomyrmex* and was historically found throughout the state of Texas. Reasons suggested for its decline include direct and indirect impacts from the invasion of red imported fire ants. Fire ants may decrease the availability of prey (*i.e.,* harvester ants) as well as attack and prey upon incubating eggs and hibernating individuals. Webb and Henke (2003) documented two defensive strategies utilized by the Texas horned lizard (*Phrynosoma cornutum*) when confronted with fire ants. The two strategies appear to be dependent upon the number of fire ants present. In the first strategy, horned lizards ate fire ants ("consumption strategy") when there were ≤12 fire ants present. In the second strategy, horned lizards ran away ("flee-and-bury") when >20 fire ants attacked. Both strategies appear to frustrate attacks by fire ants on Texas horned lizards (Webb and Henke, 2003). The southern hognose snake is a highly fossorial, egg-laying species that may also be vulnerable to the impacts of fire ants. Tuberville *et al.* (2000) found that the decline and extirpation of this snake from many parts of its range is concurrent with the range expansion of fire ants and suggests future research into the potential impacts on eggs and fossorial adults. Conners (1998b) suggested that fire ants were most likely responsible for the failure of more than half of a clutch of rough green snake (*Opheodrys aestivus*) eggs found collapsed after ants built a mound over their nest.

IMPACTS ON BIRDS

Direct and indirect impacts from fire ants have been documented on birds (Allen *et al.*, 1994), and most attention has focused on the northern bobwhite. Allen *et al.* (1994)

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reviewed the literature pertaining to fire ant impacts on birds, finding 20 sources published between 1933 and 1993. However, of those, only five were peer-reviewed articles (Allen *et al.*, 1994) and only one was experimental (a "before and after" natural experiment) (Sikes and Arnold, 1986). Since 1994, there has been a dramatic increase in the number of peer-reviewed papers (n = 21), and many of those studies provided experimental evidence for the impact of fire ants upon birds.

Northern bobwhite (*Colinus virginianus*) has been the subject of much of the research on the impacts of fire ants on birds. Brennan (1993) suggested that the relationship between northern bobwhite decline and fire ants was a "red herring" because there was not enough evidence to conclude that there was any real connection between the decline and fire ant abundance. Allen *et al.* (1993, 1995) refuted those claims and highlighted the need for additional manipulative research. In response to this debate, and continued northern bobwhite decline, several other studies have also been conducted on fire ants and bobwhites over the past 10 y. Allen *et al.* (1995) evaluated abundance trends from 1966–1992 for bobwhites in Texas. They found that in counties where fire ants were not yet present, bobwhite abundance was stable over this period. However, in counties where fire ants were present, bobwhite abundance was declining precipitously and the number of years a county had been infested with fire ants explained 75% of the variation (decline) in northern bobwhite abundance. Allen *et al.* (1995) also experimentally reduced fire ant abundance on ten 202 ha study areas, and by the second year of monitoring, bobwhite density was twice as high on treated areas. Additionally, Allen *et al.* (2000) evaluated bobwhite abundance before and after fire ant invasion in the southeastern United States and reported that bobwhites declined in response to fire ant invasion in the southeastern U.S. as a region, and in South Carolina and Florida, but not in Georgia. Several researchers have investigated the mechanisms for impact by fire ants on northern bobwhites. Giuliano *et al.* (1996) demonstrated that bobwhite chicks stung by fire ants exhibited reduced survival rates, and surviving chicks had reduced body mass. Bobwhite chicks exposed to 50 fire ants for 60 s and 200 fire ants for 15 s had significantly reduced survival rates, and these exposures corresponded to a range of only 6 to 22 fire ants attacking an individual chick (Giuliano *et al.*, 1996). At the higher levels of exposure (200 fire ants for 60 s), chicks exhibited reduced weight gain (Giuliano *et al.*, 1996).

Pedersen *et al.* (1996) examined the response of pen-raised bobwhite chicks to the presence of fire ants. They compared chick behavior in control areas and areas where fire ants were suppressed. Fire ants altered daily activities of bobwhite chicks; bobwhite chicks in control areas spent less time sleeping, with more time walking and responding to fire ants, than chicks in plots where fire ants were suppressed. Mueller *et al.* (1999) compared hatching success and survival of bobwhite chicks for 2 y, under natural and suppressed fire ant conditions. They reported that bobwhite chick survival increased in areas where fire ants were suppressed. In particular, the proportion of chicks surviving to 21 d was higher for nests treated for fire ants than untreated nests. Mueller *et al.* (1999) also reported that the probability of chick survival decreased as the amount of fire ant activity increased in a nest. In another recent study, in 1997 and 1998, researchers compared hatching success from treated and untreated bobwhite nests (Dabbert *et al.*, 2002). Only 2% of chicks were killed while hatching from nests untreated for fire ants, but survival of chicks to 21 d from treated nests (60%) was far greater than chicks from untreated nests (22%) (Dabbert *et al.*, 2002). Thirty-eight percent of bobwhite chick mortality was attributed to fire ant stings (Dabbert *et al.*, 2002).

Limited research has focused upon the interaction between fire ants and loggerhead shrikes (*Lanius ludovicianus*). Lymn and Temple (1991; not included in Allen *et al.*, 1994)

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suggested that loggerhead shrike numbers were lower in habitats after fire ant invasion in counties bordering the Gulf of Mexico. They speculated that the reason for this decline was due to competition with fire ants for food, primarily invertebrates (Lymn and Temple, 1991). However, Yosef and Lohrer (1995) did not observe fire ants attacking or killing eggs, nestlings, fledglings or adult shrikes in central Florida. Their study compared fire ant colony densities to shrike territory size, number of nesting attempts per season, total number of eggs laid per pair, number of young fledged per pair, prey capture rates of adult shrikes and percent of total time spent in flight either changing perches or in pursuit of prey. They concluded that varying fire ant mound densities had no effect on any of the variables analyzed and, thus, fire ants did not influence the reproductive success of loggerhead shrikes (Yosef and Lohrer, 1995). However, their comparisons of fire ant density and shrike breeding parameters had low statistical power (mean = 0.11), which made the possibility of detecting fire ant impacts on shrike behavior unlikely. Additionally, the (1995) reported density of up to 13 fire ant mounds/m^2 exceeds any published reports of fire ant density by many orders of magnitude. In contrast, Allen *et al.* (2001b) reported greater invertebrate abundance and diversity and loggerhead shrike abundance on sites treated to reduce fire ant populations as compared with sites untreated for fire ants. The latter authors suggested that the mechanism of impact on shrikes was through a reduction of native invertebrates that served as food for shrikes; shrike abundance was negatively correlated with invertebrate abundance as assessed by light traps. The authors also included an observation of shrike-cached food consumed by fire ants prior to the return of the bird that cached the insect (Allen *et al.*, 2001b).

In a comparison between two sites (one island and half of another island) treated with fenoxycarb for fire ants and sites (one island and the other half of the treatment island) untreated for fire ants on spoil islands used as nesting colonies by waterbirds (*Casmerodius albus*; *Ardea herodis*; *Phalacrorox olivaceus*; *Egretta thula*; *Hydranassa tricolor*; *Ajaia ajaja*; *Larus atricilla*; *Gelochelidon nilotica*; *Sterna forsteri*), fire ants had little effect on mortality of young birds before the end of May (Drees, 1994). However, during June and July of both y of the study, fire ants reduced waterbird production by 92% on the untreated sites (Drees, 1994). The lack of early-season mortality was likely influenced by temperature because fire ants are less active in cooler temperatures. As well, fire ant protein needs increase when they have brood in their colonies, which occurs late in the spring and throughout the summer months.

Fire ants have also been documented to cause mortality of least tern (*Sterna antillarum*) chicks (Lockley, 1995; Krogh and Schweitzer, 1999). Lockley (1995) conducted an experiment between least tern nesting sites on a continuous beach in Mississippi. He compared one site treated for fire ants with fenoxycarb and one site untreated for fire ants. Least tern chicks suffered 33% mortality on the site untreated for fire ants and 6.3% mortality on sites treated for fire ants (Lockley, 1995). Krogh and Schweitzer (1999) observed fire ants biting chicks and also found chicks partially consumed by fire ants, but were unable to determine if fire ants killed the chicks.

Several other species of birds are known to suffer from impacts by fire ants. Kopachena *et al.* (2000) documented 25% mortality for barn swallow (*Hirundo rustica*) chicks at one site in Texas. Interestingly, they also noted that there was no mortality of barn swallows at another site in their study with three times the density of fire ant mounds (Kopachena *et al.*, 2000). Further, the researchers reported that data pre- and post-invasion by fire ants suggested no long-term effects on barn swallow populations (Kopachena *et al.*, 2000). Dickinson (1995) observed two instances of fire ants preying on the newly hatched young of crested caracaras (*Caracara plancus*) in Texas. Dickinson and Arnold (1996)

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documented the occurrence of seven crested caracara nests in Texas. Of the nests (n = 5) laid between January and March, 72.6% were successful, while overall nest success was 45.7% (Dickinson and Arnold, 1996). Dickinson and Arnold (1996) reported that predation by fire ants on caracara nestlings resulted in reduced nesting success for nestlings hatching in June. Fire ants have been implicated as a cause for the decline of common ground doves (*Columbina passerina*) in South Carolina (Cely and Glover, 2000). Fire ants were observed in Florida preying on a hatchling black rail (*Laterallus jamaicensis*) as it emerged from its egg (Legare and Eddleman, 2001). Legare and Eddleman (2001) noted that fire ant mounds were constructed under 16% (three nests) of the black rail nests in their study area. Twedt *et al.* (2001) implicated fire ants as predators of forest birds in Mississippi including, but not limited to, blue-gray gnatcatchers (*Polioptila caerulea*), eastern towhees (*Pipilo erythrophthalamus*), indigo buntings (*Passerina cyanea*), northern cardinals (*Cardinalis cardinalis*) and yellow-billed cuckoos (*Coccyzus americanus*). While their study did not address specific predators of forest birds, they reported that fire ants were present in managed cottonwood stands, but absent from bottomland hardwood stands (Twedt *et al.*, 2001). Fire ants were implicated in 58% of predation events and 11% of nest failures in managed cottonwoods, which created a significant difference in predation rates between managed cottonwood and bottomland hardwood stands. Stake and Cimprich (2003) monitored black-capped vireo (*Vireo atricapillus*) nests by video surveillance for 3 y in Texas. They reported that fire ants predominantly visited vireo nests at night (92% of visits) and were responsible for 31% (n = 15) of nest depredations on black-capped vireo nests at Fort Hood, Texas.

IMPACTS ON MAMMALS

Prior to the 1960s, all reports of fire ant impacts on mammals were anecdotal. In the late 1960s and early 1970s, two reports were published, one documenting negative impacts on cottontail rabbits (Hill, 1970) and one suggesting no impacts on muskrats (Newsom *et al.*, 1976). In the 1980s, researchers began concerted efforts to assess fire ant impacts on mammals, especially small mammals, following reports of significant losses of live-trapped mice to fire ants in Texas (Masser and Grant, 1986; Flickinger, 1989).

Killion *et al.* (1995) removed fire ants (by directly treating each mound) from a 1.43 ha plot of brush prairie in coastal Texas and monitored small mammals in grids on either side of a barrier fence through the middle of the treated area. Season and fire ant density were both significant predictors of northern pygmy mouse (*Baiomys taylori*) captures. Additionally, recruitment time of fire ants to *Baiomys* burrows was slower than recruitment to random points and the number of new *Baiomys* captures was higher on sites with lower fire ant densities. Killion and Grant (1993) also documented a significant negative association between pygmy mice captures and fire ant mound densities when analyzed at a 100 m^2 spatial resolution, but not when analyzed at 400 or 900 m^2, but found no association between pygmy mice and ant foraging activity at any spatial scale. Ferris *et al.* (1998) investigated the impact fire ant abundance on small mammal captures at broad spatial scales. They established 15 sampling stations along 83 km, capturing a gradient of fire ant mound densities. Total captures of small mammals were negatively related to fire ant mound density. Based on data published in theses or dissertations, they suggested that hispid cotton rats (*Sigmodon hispidus*) may be relatively "immune" to fire ant impacts, in contrast to other native small mammals. However, Pedersen *et al.* (2003) documented that *S. hispidus* altered habitat use in the summer in the presence of fire ants, but not in the winter, and that *B. taylori* exhibited no change in habitat use with fire ants present regardless of season. Wilkins and Broussard (2000) noted that 80% of their small mammal

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traps in grassland habitat in central Texas were 'infested' with fire ants. In all habitats in two study sites, small mammal species richness was lower than expected and previously documented and trap success was lower than for similar habitats elsewhere. Fire ants, along with overabundance of deer and other disturbance were suggested as potential causes.

Two studies have investigated the influence of fire ants on small mammal foraging behavior. Lechner and Ribble (1996) combined laboratory and field studies to assess behavioral interactions between fire ants and three small mammal species. In the laboratory, the authors conducted studies in a Y-shaped maze, where crushed fire ants were present in the end of one of the maze arms. They found that *Baiomys taylori* avoided the arm of the maze with fire ants present, whereas *Sigmodon hispidus* and *Peromyscus leucopus* were indifferent to the presence of crushed fire ants. *Peromyscus* used in the maze experiments were released after trials, trailed to their escape refuges or burrows and the distance to the nearest fire ant mound was measured. Distance of mounds from *Peromyscus* refuges and from random points did not differ. Additional field-work compared densities of fire ants to small mammal captures in a trapping grid of 6,150 m transects with paired traps. On this large grid, there was no significant relationship between fire ant mound density and small mammal abundance, but there was a hint of a slight positive association, suggesting, the authors believe, that fire ants and small mammals were responding to the same favorable habitat conditions. A second field component used smaller 6 by 6 small mammal trapping grids. Here too there were low capture rates. There was no relationship between captures and fire ant density at a 100 m^2 scale, but at the 400 m^2 scale there was a negative correlation between fire ants and *Baiomys*, and at a 900 m^2 scale all species were negatively associated with fire ants.

Holtcamp *et al.* (1997) documented behavioral tradeoffs in *Peromyscus* when foraging in the presence of fire ants. With fire ants present, mice tended to spend more time in, visit more often and harvest more seeds from rich patches. In the absence of fire ants, those variables (# visits, proportion seeds removed, time) did not differ between rich and poor patches. With fire ants present, mice left a given patch at lower final seed densities, thus attaining a higher within patch 'harvest' rate indicating that mouse foraging was more efficient in the presence of fire ants. Also, with fire ants present, mice spent more time handling seeds out of patches, as fire ants were confined to patch areas (about three times more often mice moved from the patch to consume a seed with fire ants present when compared without). But, despite spending more time handling seeds, that is moving out of patches to consume seeds, there was no difference in net yield with fire ants present because mice concentrated efforts in rich patches. This suggested that in the wild there may be a significant cost to foraging in the presence of fire ants.

There was only one experimental investigation of impacts on mammals, other than rodents, in the past decade. In the coastal plain of Texas, in areas of predominantly polygyne fire ants with densities of about 200 mounds/ha, Allen *et al.* (1997a) established five pairs of 202 ha study sites. One member of each pair was randomly selected and treated to reduce fire ant populations via aerial treatments with hydramethylnon (Amdro®). Pre-treatment and post-treatment fire ant and deer fawn recruitment (fawns/doe) were monitored. Fire ant populations were reduced following treatments and fawn recruitment was higher on treated areas as compared to untreated areas following treatment (about 2 times higher on treated areas). Additionally, fawn recruitment was negatively associated with June indices of fire ant abundance. One y after treatments stopped, fire ant populations were again similar on treated and untreated sites and fawn recruitment did not significantly differ (Allen, unpubl.). The authors suggested mechanisms for the documented impact,

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blinding and debilitating injury of fawns due to their behavioral reaction to danger of 'freezing' and increased coyote predation caused by increased fawn movements in reaction to the irritation of stings. Mueller *et al.* (2001) provided observations in support of the latter "increased movement" hypothesis. Mueller *et al.* (2001) observed a fawn with apparent irritation to the hindquarters running across a pasture in Texas during the middle of the day. Capture of the fawn revealed fire ants on its hindquarters. The authors suggested the fawn was running due to fire ant irritation and was vulnerable to predation because of movement during the day and animation of the doe associated with irritation of the hindquarters (*e.g.,* scratching).

SYNTHESIS

The evidence suggests that some vertebrates are more likely to experience negative population-level impacts from fire ants than others. The hatching/birthing period is particularly hazardous for most species. Egg-laying species are probably more vulnerable than live-bearing species, ground-nesting species more vulnerable than canopy nesting species and altricial young more vulnerable than precocial young. Species that breed and live in open habitats are more vulnerable than species living in closed canopied habitats, which tend to have much lower fire ant densities. The timing of hatching/birthing may also be a factor in effects. Species that are born when fire ants are most active and when fire ants have brood and, thus, increased protein needs, are most vulnerable. Adult vertebrates may be vulnerable as well, though predation is rarely the mechanism. Fossorial species are more likely to be affected than terrestrial species. Adults, however, may be displaced by irritation resulting from stings and food availability may be decreased, especially for insectivores. Behavior also affects the vulnerability of a species to impacts. Inappropriate defensive behaviors such as freezing when danger is sensed (*e.g.,* deer fawns) clearly can affect the outcome of contact between wildlife and fire ants. Reptile species whose young stay in underground nests until all the young have hatched prior to emergence are vulnerable, as are those that overwinter in their nests.

The increased level of research has led to information that can lead to better management of potentially affected species. However, the expense required for large scale fire ant treatments, along with the potential non-target impacts of substances available to reduce fire ant populations and the rapid recovery of fire ant populations even where successfully suppressed, make fire ant population reductions to benefit wildlife practical only under limited circumstances. Where a potentially impacted species has a very limited range (*e.g.,* Lower Keys marsh rabbit, *Sylvilagus palustris hefneri*, Big Pine Key ringneck snake, *Diadophis punctatus acricus*; Forys *et al.*, 2002) or where breeding aggregations occur (*e.g.,* least tern *Sterna antillarum*; Lockley, 1995) fire ants may be controlled relatively effectively and cheaply with a variety of baits (Williams *et al.*, 2001). Bait application techniques that incorporate methods of precision targeting can reduce the potential of affecting any non-target species, including native ant species, to near zero.

Despite a large increase in the volume of research over the past decade, knowledge gaps remain. Little research has been conducted on the impacts of fire ants on mammals other than small mammals in Texas. Similarly, only one observational study focused on fire ant impacts on amphibians. We suspect that amphibians are an especially vulnerable taxon, and research of population-level impacts of fire ants on vulnerable amphibian species should be initiated. As well, little is known of long-term impacts. Assessing the ecological impacts of fire ants on wild animal populations is logistically difficult, and very few studies have combined replicated experimental manipulation with adequate spatial (>10 ha) and temporal (>1 y) scales (Table 1). Thus, most studies have been observational, opportunistic,

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TABLE 1.—Summary of research published 1993–2003 on fire ant–wildlife interactions. Wildlife species studies are listed alphabetically for reptiles and amphibians, birds and mammals

Species	Impact	Study type	Extent	Duration	Citation
Alligator mississippiensis	hatchling survival/ weight gain	experimental	<1 ha	<1 y	Allen *et al.* 1997b
Alligator mississippiensis	nest success/ female attendance	natural experiment	>10 ha	>1 y	Reagan *et al.* 2000
Bufo houstonensis	juvenile predation	observational	<1 ha	<1 y	Freed and Neitman 1988[1]
Caretta caretta	hatchling predation	observational	>10 ha	>1 y	Moulis 1997
Caretta caretta	hatchling predation	observational	>10 ha	>1 y	Parris *et al.* 2002
Caretta caretta	hatchling predation	observational	>10 ha	>1 y	Wilmers *et al.* 1996
Caretta caretta	co-occurrence	observational	>10 ha	>1 y	Allen *et al.* 2001a
Chelonia mydas	hatchling predation	observational	>10 ha	>1 y	Wilmers *et al.* 1996
Chelonia mydas	co-occurrence	observational	>10 ha	>1 y	Allen *et al.* 2001a
Chelydra serpentina	hatchling predation	observational	<1 ha	<1 y	Conners 1998a
Gopherus polyphemus	juvenile survival	observational	>10 ha	>1 y	Epperson and Heise 2003
Heterodon simus	abundance/ distribution	observational	>10 ha	>1 y	Tuberville *et al.* 2000
Lampropeltis getula	abundance	observational	>10 ha	>1 y	Wojcik *et al.* 2001
Opheodrya aestivus	egg predation	observational	<1 ha	<1 y	Conners 1998b
Phrynosoma cornutum	abundance/ distribution	observational	>10 ha	>1 y	Donaldson *et al.* 1994
Phrynosoma cornutum	defense strategy	observational	>10 ha	>1 y	Webb and Henke 2003
Psuedemys nelsoni	hatchling survival/ weight gain	experimental	<1 ha	<1 y	Allen *et al.* 2001a
Pseudomys texana	nesting interference	observational	<1 ha	<1 y	Whiting 1994
Terrapene carolina	adult predation	observational	>10 ha	>1 y	Montgomery 1996
Trachemys scripta	hatchling survival	experimental	<1 ha	<1 y	Buhlmann and Coffman 2001
Caracara plancus	survival	observational	>10 ha	<1 y	Dickinson 1995
Caracara plancus	survival	observational	>10 ha	<1 y	Dickinson 1996
Colinus virginianus	abundance	anecdotal	>10 ha	>1 y	Allen *et al.* 1993
Colinus virginianus	abundance	anecdotal	>10 ha	>1 y	Brennan 1993
Colinus virginianus	abundance	experimental/ natural experiment	>10 ha	>1 y	Allen *et al.* 1995
Colinus virginianus	survival/behavior	experimental	laboratory	<1 y	Giuliano *et al.* 1996
Colinus virginianus	foraging behavior	experimental	<10 ha	<1 y	Pedersen *et al.* 1996
Colinus virginianus	survival	experimental	>10 ha	>1 y	Mueller *et al.* 1999
Colinus virginianus	survival	experimental	<10 ha	>1 y	Dabbert *et al.* 2002
Colinus virginianus	abundance	natural experiment	>10 ha	>1 y	Allen *et al.* 2000
Columbina passerina	survival	anecdotal	>10 ha	>1 y	Cely and Glover 2000
Hirundo rustica	survival	observational	<10 ha	<1 y	Kopachena *et al.* 2000
Lanius ludovicianus	abundance	natural experiment	>10 ha	>1 y	Lymn and Temple 1991[1]
Lanius ludovicianus	abundance	experimental	>10 ha	>1 y	Allen *et al.* 2001b

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TABLE 1.—Continued

Species	Impact	Study type	Extent	Duration	Citation
Lanius ludovicianus	abundance/ behavior	observational	>10 ha	>1 y	Yosef and Lohrer 1995
Laterallus jamaicensis	survival	observational	>10 ha	>1 y	Legare and Eddleman 2001
Sterna antillarum	survival	experimental	<10 ha	>1 y	Lockley 1995
Sterna antillarum	survival	observational	<10 ha	>1 y	Krogh and Schweitzer 1999
Forest birds	survival	observational	>10 ha	>1 y	Twedt *et al.* 2001
Vireo atricapillus	nestling predation	observational	>10 ha	>1 y	Stake and Cimprich 2003
waterbirds	abundance/ behavior	experimental	<10 ha	>1 y	Drees 1994
Baiomys taylori	capture rate/ abundance	experimental	<10 ha	<1 y	Killion *et al.* 1995
Baiomys taylori	capture rate	natural experiment	<10 ha	<1 y	Killion and Grant 1993
Odocoileus virginianus	recruitment	experimental	>10 ha	>1 y	Allen *et al.* 1997a
Odocoileus virginianus	movement	observational	<1 ha	<1 y	Mueller *et al.* 2001
Peromyscus maniculatus	foraging behavior	experimental	laboratory	<1 y	Holtcamp *et al.* 1997
Sigmodon hispidus-other	capture rate	natural experiment	>10 ha	<1 y[2]	Ferris *et al.* 1998
Sigmodon hispidus/	foraging behavior	experimental	10 ha and	<1 y	Lechner and Ribble 1996
Baiomys taylori/ Peromyscus leucopus	foraging behavior	experimental	laboratory		
Sigmodon hispidus/ Baiomys taylori	habitat use	experimental	>10 ha	>1 y	Pedersen *et al.* 2003
Small mammals	capture rate	observational	>10 ha	<1 y[2]	Wilkins and Broussard 2000

[1] Not included in Allen *et al.* (1994)
[2] Sampling in this study lasted for 13 mo

small-scale or 'natural' experiments. They lack the statistical power to detect more subtle impacts (modest effect sizes), but these relatively small—but incremental—impacts may be very substantial. Our knowledge has significantly increased, but we still know relatively little concerning the complex impacts fire ants may have on native wildlife and ecosystems.

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