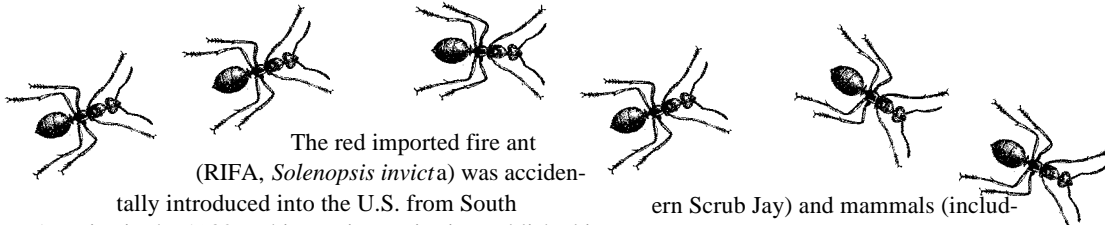


Impact of Red Imported Fire Ants on the Black-capped Vireo, an Endangered Species



The red imported fire ant (RIFA, *Solenopsis invicta*) was accidentally introduced into the U.S. from South

America in the 1930s. This exotic species is established in the southern U.S., from Texas and Oklahoma to Florida and North Carolina, and its range is still expanding. Red imported fire ants are effective predators of many taxa, and they pose a serious threat to both terrestrial and aquatic communities. For example, some studies have shown that RIFA affect arthropod diversity and abundance. This finding, in turn, has led others to suggest that RIFA may negatively affect native bird species indirectly via competition for insect prey. More recently, laboratory studies suggest that RIFA may alter the behavior and decrease the survivorship and body mass of the Northern Bobwhite (*Colinus virginianus*). However, how RIFA affect wild birds is still controversial. Understanding how RIFA impact natural avian populations is essential for effective management. Here, we describe our research on the impact of RIFA on the reproductive ecology of a federally endangered bird species, the Black-capped Vireo (*Vireo atricapillus*).

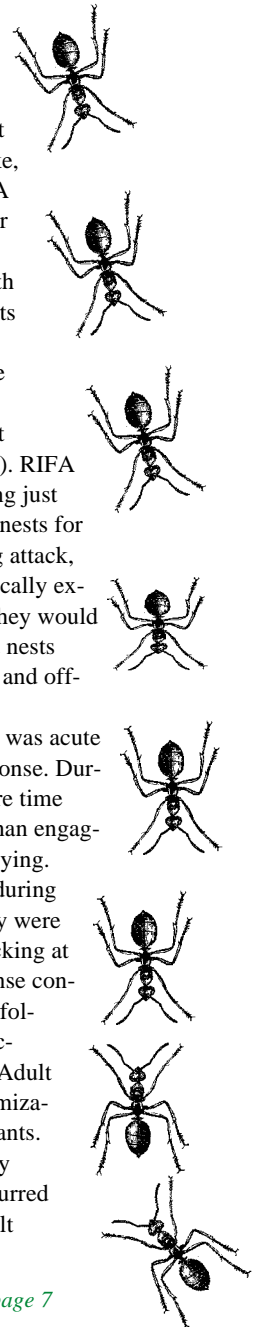
The Black-capped Vireo is a small, largely insectivorous bird that inhabits dense thickets of oak scrub habitat. Although it nests predominantly in oaks, many other plant species are also used. The bird's open cup nest is suspended from a forked branch 0.4–1.3 m above the ground. The species has been extirpated from most of its historic range, and breeding populations in the U.S. are now restricted to Oklahoma and Texas. Brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), which lays its eggs in the nests of other bird species, coupled with habitat loss, caused the endangerment of the vireo. Recently the red imported fire ant has colonized the part of Texas that includes the 88,890-ha army base, Fort Hood, which currently contains the largest breeding population of the Black-capped Vireo. In an investigation of the reproductive ecology of the species, from 1998 to 2001, 139 vireo nests were monitored with infrared video cameras. We analyzed that video footage to determine the influence of predation, particularly that by red imported fire ants, on vireo behavior and nesting success.

Predation accounted for over two-thirds of nest failures in the study. RIFA was the leading predator, accounting for 38% of predation. The Texas rat snake (*Elaphe obsoleta lindheimeri*) was the second leading predator, causing 36% of nest failures. Birds (primarily the West-

ern Scrub Jay) and mammals (including raccoons and ringtails) accounted for the remaining predation. Two nests were visited by a second predator during RIFA activity. In the presence of RIFA, an eastern woodrat (*Neotoma floridana*) nicked one of the eggs but failed to depredate the clutch. A Texas rat snake, however, consumed all three nestlings while RIFA swarmed the nest. RIFA were present for four hours prior to snake predation and 15 minutes before the woodrat approached the nest. In both cases, adult vireos were actively defending nests against the RIFA attack. It is possible that the increased activity during this defense may have alerted secondary predators to the nest.

RIFA activity was independent of vireo nest height and substrate type (tree or shrub species). RIFA attacked vireo nests at night, typically beginning just after midnight. On average, RIFA remained at nests for at least 23 hours after the initial attack. During attack, adult vireos engaged in prolonged and energetically expensive defense against RIFA at a time when they would otherwise be sleeping. Ultimately, all attacked nests were abandoned, causing mortality of the eggs and offspring.

The initial response of adult vireos to RIFA was acute and had the appearance of a flight or fight response. During nest defense, vireos spent significantly more time pecking at and removing RIFA from the nest than engaging in brooding, alert perching, hopping, and flying. Adult vireos expended 2.4 times more energy during nest defense than would be expected while they were sleeping. Vireos expended the most energy pecking at ants and flying to and from the nest. Nest defense continued for hours through the night and into the following morning. No such prolonged defense occurred in the presence of vertebrate predators. Adult vireos likely received bites and stings (envenomization) while defending the nest from swarming ants. Such bites cause painful pustules and secondary infection for humans. Similar costs may be incurred by vireos. Despite their energetic defense, adult vireos never prevented nest failure when RIFA



Continued on page 7

Egg Powdering

continued from page 2

which may have retained the ancestral preening behaviors of females. Observing behaviors of these hard-to-collect tropical insects will be a challenge.

Another challenge is to explain why, if the selection worked to maximize the efficiency of powdering, there are among “powdering” species some with specialized brochosomes and wings but with ordinary legs, some with specialized legs and brochosomes but ordinary wings, some with specialized legs and wings but ordinary brochosomes, and finally some with only specialized brochosomes. One possibility is that modifications to these structures evolved independently and somewhat

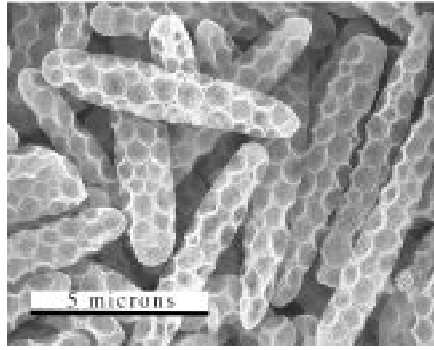


Figure 3. A scanning electron micrograph (SEM) of brochosomes. SEM courtesy of Roman Rakitov, INHS Center for Biodiversity

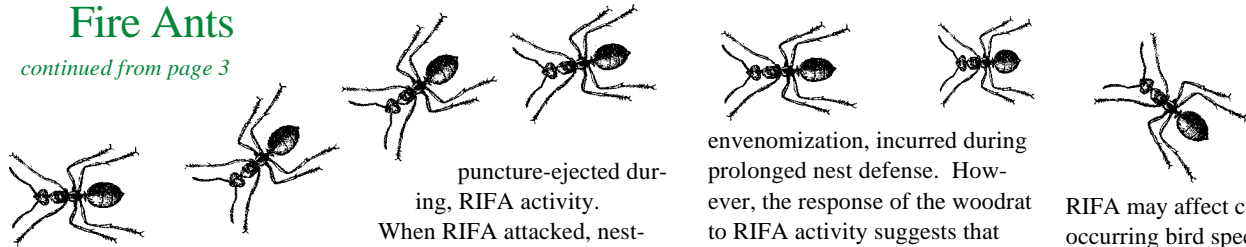
differently in different related lineages. Our results suggest an alternative scenario: multiple secondary losses of individual specializations (such as reversal to the ordinary leg structure) or the powdering behavior as a whole. For example,

within the North American grassland genus *Cuerna*, powdering has been lost independently no less than four times. The species that have lost the behavior can display vestigial elongation of the female leg spines or even vestigial powdering strokes during egg-laying but never produce specialized brochosomes nor place anything onto their wings. If powdering is an ingenious protective strategy, why does it get lost? Recent studies which traced evolution of various traits in different organisms indicate that losses are more common than was previously thought. The puzzling diversity of egg-laying specializations in sharpshooters can be used as a model to study the loss of a biological function in three dimensions: structure, physiology, and behavior.

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Fire Ants

continued from page 3



swarmed nests. All nests with RIFA activity at either the egg (33%) or nestling (67%) stage of the nest cycle failed to fledge vireos. Adult vireos abandoned all nests with RIFA activity and all clutches subsequently failed to hatch, except for one. In this case, the eggs hatched while RIFA were still at the nest and RIFA depredated the hatchlings minutes after hatching. Eggs were incubated significantly less often while RIFA were at a nest than prior to attack. At one nest, an adult vireo grasp-ejected two cracked eggs out of her nest following nine hours of defense. We were unable to determine whether she punctured the eggs to eject them from the nest or did so inadvertently while pecking at ants. Regardless, eggs were in good condition prior to, and

puncture-ejected during, RIFA activity.

When RIFA attacked, nestlings responded by moving erratically in apparent distress within the nest until dead (motionless). The time for nestlings to die increased significantly with nestling age. Time until nestling mortality ranged from eight minutes (one-day-old nestling) to three and a half hours (nine-day-old nestling). At one nest, two of three nestlings were motionless (assumed dead) in response to RIFA, while the third ejected itself out of the nest. Vireos are known to fledge prematurely in response to predators.

These findings suggest that RIFA negatively impact Black-capped Vireos directly, via nest abandonment and mortality of eggs and nestlings. In addition, nest defense by adults leads to an acute and large increase in energy expenditure, coupled with

envenomization, incurred during prolonged nest defense. However, the response of the woodrat to RIFA activity suggests that RIFA may also indirectly benefit Black-capped Vireos. RIFA appeared to deter this small mammalian predator. Other studies indicate that RIFA shift foraging patterns and induce trap mortality of small mammals. Positive indirect effects of RIFA on Black-capped Vireos could arise via reductions in the population size of other predators (e.g., *Rattus* and other vertebrate predators). Positive indirect effects could also arise through changes in a predator's or a competitor's habitat selection and foraging ecology. While it seems unlikely that such positive indirect effects could outweigh the direct negative effects, these positive effects warrant investigation.

Our study found strong negative impacts of RIFA on the Black-capped Vireo. This in turn raises the possibility that

RIFA may affect co-occurring bird species similarly. With the predicted global range expansion of RIFA, management must be employed to deter the spread and future success of this invader.

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