Novel predator–prey interactions: is resistance futile?

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ABSTRACT

Premise: Prey species may possess inappropriate behavioural, morphological, and/or physiological responses to introduced, novel predators. Thus, introduced predators may exert strong selection on prey species.

Organisms: Black-capped vireo, *Vireo atricapilla*, and the fire ant, *Solenopsis invicta*.

Data: Behavioural response of and time-energy budget for parental vireo defence against nest predation by fire ants.

Field site: Fort Hood, Texas, an 88,500-hectare US military installation.

Results: Fire ants usually attacked vireo nests near midnight as parents slept. All attacked nests – whether with eggs or nestlings – failed. However, adults defended their nests vigorously. Nest defence was prolonged, with a mean duration of 7.7 ± 1.5 hours (25 times longer than that against native snake predators). Compared with brooding or incubation, nest defence is energetically expensive, depleting an estimated 59% of fat stores.

Conclusions: Fire ants are effective nest predators on this low-nesting bird species. The behavioural response of vireos to this novel predator is wholly inappropriate, with no benefits and considerable costs. Besides the energetic costs, defence results in numerous bites and venomous stings. Vireos ought to abandon their nests when first attacked by fire ants.

Keywords: behavioural strategies, invasive species, life histories, predator–prey, *Solenopsis invicta, Vireo atricapilla*.

INTRODUCTION

Whether a species responds appropriately when faced with a novel environmental insult or stress is fundamentally important to evolutionary ecology (Gomulkiewicz and Holt, 1995) and conservation biology (Ashley *et al.*, 2003). Predator–prey interactions provide fertile ground for co-evolution. The escalating evolution of traits of both prey and predator species have been

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dubbed 'rat races' (Rosenzweig, 1973) and 'arms races' (Dawkins and Krebs, 1979). We propose that introductions of novel predator species provide a unique living laboratory for strong selection and likely rapid evolution or extinction of prey species. The fire ant *Solenopsis invicta* (hereafter, fire ant) and the federally endangered black-capped vireo, *Vireo atricapilla*, provide a case study. In this paper, we estimate costs to vireos of fire ant nest predation, and we discuss the likely ecological and evolutionary outcomes of the interaction of this novel predator with its new prey species.

VIREOS AND FIRE ANTS: A CASE STUDY

Black-capped vireos are low-nesting passerines that breed in arid scrub habitats of the central, southern United States and northern Mexico (Grzybowski, 1995). Brood parasitism from the brown-headed cowbird, *Molothrus ater*, and habitat loss reduced their historical range (Grzybowski, 1995; Robinson *et al.*, 1995). Their nests are typically found in oaks, *Quercus* spp., and suspended from a forked branch about a metre off of the ground. Both parents tend the nest from eggs through fledging (Grzybowski, 1995).

Solenopsis invicta, native to South America, successfully invaded the USA, where it has spread throughout the southeastern states (Taber, 2000). It is also found in many other regions around the world (Morrison *et al.*, 2004, 2005). Its current distribution within the US appears to be restricted by extreme heat, aridity, and cold temperatures. Fire ants inject venom to immobilize and kill their prey. They consume both plant and animal tissue, often with pronounced effects on native communities (Wojcik *et al.*, 2001; Holway *et al.*, 2002; Allen *et al.*, 2004). The health effects of fire ant venom include localized skin reactions and whole-body reactions. Localized reactions consist of swollen, sterile pustules or red papules on the skin and necrotic ulcers on the cornea (Drees *et al.*, 1995). The pustules, if broken, can result in serious secondary infection. Whole-body reactions such as anaphylactic shock occur in humans (Deshazo *et al.*, 1990), but have not been reported for domestic or wild animals.

Here we describe the behavioural response and energetic consequences of black-capped vireos to nest predation by fire ants. The impact of this newly introduced predator (since the late 1970s in Bell and Coryell counties, TX) on the life-history trade-offs in adult vireos is unknown. Fire ants impose the well-documented, obvious cost of nest loss (Stake and Cimprich, 2003; Smith *et al.*, 2004). However, adult vireos also mount a vigorous, but apparently ineffectual, defence of their nest against fire ants. The costs of this inappropriate behavioural response by vireos may transcend nest loss. We believe these costs may include:

- reduced breeding season;
- compromised energetic state;
- adverse effects on ability to re-nest and pair bond stability;
- adverse health effects of venom;
- compromised future survival;
- compromised immunocompetence.

Given these costs, vireos should be under strong selection to abandon their nests upon their discovery by fire ants. Although we know of no other study of behavioural responses to nest predation by fire ants in other passerine species, effects similar to those we document and anticipate for black-capped vireos undoubtedly occur in other species whose range

overlaps that of fire ants. We suggest that novel predator–prey interactions such as these must exert strong selective pressure on local prey and offer a unique opportunity to measure rapid contemporary evolution (Stockwell *et al.*, 2003).

METHODS

Study site

Fort Hood is an 88,500-hectare military installation located in Bell and Coryell counties, Texas (30°10′N, 97°45′W; Fig. 1). It has the largest breeding population of black-capped vireos managed by a single authority (Eckrich *et al.*, 1999). Cowbird management has reduced the incidence of brood parasitism at Fort Hood from 90% of nests in 1987 (Hayden *et al.*, 2000) to only 7.9% in 2001, with predation and abandonment accounting for 93% of nest failures (Stake and Cimprich, 2003).
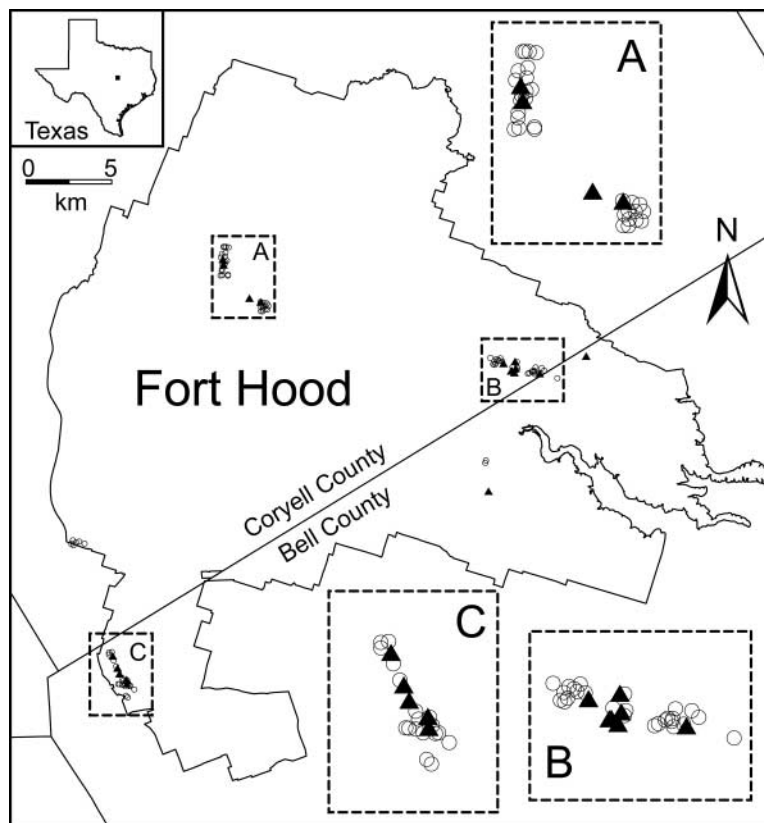
Fig. 1. The distribution of black-capped vireo nests across our study area in Fort Hood, Texas. Black triangles represent vireo nests attacked by fire ants, and open circles represent vireo nests with other outcomes (successful, destroyed by a predator other than fire ants, or abandoned for reasons unrelated to fire ants).

Fire ants as predators on vireo nests

We video-recorded active vireo nests as part of the ongoing monitoring and management of the black-capped vireo at Fort Hood (for details, see Stake and Cimprich, 2003). From 1 April to 31 July in 1998 through 2001, 12 infrared video systems (Fuhrman Diversified, Inc., Seabrook, TX, USA) monitored 142 nests for 1589 exposure days (773 in incubation stage, 816 in nestling stage). The use of infrared allowed us to view diurnal and nocturnal activity. Time-lapse recording at five frames per second documented approximately 24 hours of continuous footage on a 120-min VHS cassette. Of these 142 nests, 134 were monitored to final outcome (success or failure). We focus here on active vireo nests at which we observed visits by fire ants. The use of freeze frame analysis of the video allowed us to simultaneously quantify behaviours of adult birds, nestlings, and ants during fire ant attacks. Nest height, substrate (plant species), and outcome date were recorded for all nests included in the study. Analysis of each tape with observed fire ant activity began 10 min before the initial onset of fire ant activity at the nests. We noted the visibility of the focal nest, sex of vireo adults, clutch size and status (covered by an adult or exposed), nestling number and behaviour, and presence (or absence) of fire ants. We quantified the total time fire ants remained at nests. Duration estimates are minimum measures because taping concluded while fire ants were still active at several of the nests.

Behavioural response and associated energetic cost

We quantified behavioural responses of both nestling and adult vireos to fire ants. We classified nestling behaviour as 'panic' behaviour when nestlings moved erratically from side to side, often opening and closing their mouths and pecking at fire ants. We considered the duration of attacks as the difference between the arrival time and the time the nestlings were motionless and likely dead. We classified behavioural responses of adult vireos as: inactive brooding (sleeping, with head tucked under wing or eyes closed); active brooding (alert while brooding); alert perching (perched on rim of nest or supporting branch, but not engaged in pecking defence); flying (to, from, and around nest); hopping; pecking (at fire ants); and away from the nest (out of view of camera).

We estimated the energetic costs to adult vireos of nest defence during fire ant attacks using results of an analysis by Williams and Nagy (1984). They used doubly-labelled water to measure the daily energy expenditure of savannah sparrows, *Passerculus sandwichensis*. Their direct measures were most consistent with a model developed by Mugaas and King (1981), where each behaviour was given an estimated energy expenditure of some multiple of the basal metabolic rate. We therefore calculated the basal metabolic rate for black-capped vireos using a similar set of allometric equations provided in Aschoff and Pohl (1970). We used the following standard allometric equation for the active phase to calculate activity during nest defence: $M_{\text{Kal}} = 140.9 \times W^{0.704}$, where $M_{\text{Kal}} =$ metabolic rate in $\text{kcal} \cdot \text{day}^{-1}$ and $W =$ mass in grams. We assumed a mass of 9 g for adult vireos (Grzybowski, 1995) to calculate that a vireo during the active phase expends 5.11 $\text{kcal} \cdot \text{day}^{-1}$ or 0.892 $\text{kJ} \cdot \text{h}^{-1}$. Behaviours observed during nest defence were assigned multiples (based on Mugaas and King, 1981) of active basal metabolic rate (ABMR), resulting in the following: brooding, $1 \times \text{ABMR}$, 0.892 $\text{kJ} \cdot \text{h}^{-1}$; alert perching, $1.7 \times \text{ABMR}$, 1.516 $\text{kJ} \cdot \text{h}^{-1}$; pecking, $1.8 \times \text{ABMR}$, 1.606 $\text{kJ} \cdot \text{h}^{-1}$; hopping, $2.0 \times \text{ABMR}$, 1.784 $\text{kJ} \cdot \text{h}^{-1}$; and flying, $11 \times \text{ABMR}$,

$9.812 \text{ kJ} \cdot \text{h}^{-1}$. For vireos outside of the camera's view, we conservatively applied the multiple associated with alert perching.

Fire ant attacks occur at night when adults typically are asleep (Graber, 1961; Stake and Cimprich, 2003). Therefore, we compared the expected energy expenditure of inactive brooding (sleeping) to that observed during nest defence. Mean ambient temperature at the time of fire ant attack was $26 \pm 1°C$, and maximum daytime temperatures reached $34 \pm 1°C$. Ecological energetics have not been investigated in black-capped vireos. Based on work on other small passerines (Weathers and Van Riper, 1982) and hummingbirds (López-Calleja and Bozinovic, 2003), we assumed that these temperatures fall within or close to the thermoneutral zone of the black-capped vireo. Following Walsberg and King (1978), we assumed that the costs of incubation and brooding depend upon microclimatic attenuation and insulatory properties of the nest. Therefore, energy expended by an adult vireo that is brooding young (capable of thermogenesis) within the thermoneutral zone is equal to the basal metabolic rate during the inactive phase. We used the standard allometric equation for passerines during the inactive phase [$M_{Kal} = 114.8 \times W^{0.726}$, where M_{Kal} = metabolic rate in $\text{kcal} \cdot \text{day}^{-1}$ and W = mass in grams (derived by Aschoff and Pohl, 1970)]. For a 9-g vireo, energy expenditure during inactive brooding was calculated at $3.75 \text{ kcal} \cdot \text{day}^{-1}$ or $0.655 \text{ kJ} \cdot \text{h}^{-1}$. Energy expenditure by adult vireos during fire ant activity is presented in terms of both total energy expended and as an hourly rate.

Statistical analyses

We performed all statistical tests using SYSTAT Version 8.0 (Systat Software Inc., Richmond, CA, USA). We used one-way analysis of variance (ANOVA) to test for the effect of nest height on nest fate (abandoned, depredated, successful). We used a chi-square test to evaluate if the species of plant in which a nest was found affected nest fate. We tested the effect of stage of nest cycle (egg, nestling, or previously fledged or failed) on duration of fire ant predation events using a one-way ANOVA. We analysed the relationship between nestling age and time to mortality during fire ant attacks using a one-tailed Spearman rank correlation. We used a Wilcoxon signed rank test to compare the proportion of time: (1) nests were exposed versus incubated; (2) adults were at the nest versus away from the nest; and (3) adults allocated to brooding versus nest defence. We compared the proportions of both time and energy that adult vireos spent on defence behaviours using separate partially hierarchical ANOVA with behaviour and sex nested within individual nests. The mean square of the nested term was used as the error mean square to test the significance of time and energy for each behavioural category. Analyses were conducted on untransformed and rank data. Because both produced comparable results, we report the results for the untransformed data only. We used a one-sample t-test to compare the mean total energetic expenditure and the mean rate of energetic expenditure to that expected during inactive brooding. Average values are given as means $\pm$ standard errors and we considered differences to be statistically significant at an alpha of less than 0.05.

RESULTS

Fire ants as predators on vireo nests

Fire ants caused nest failure at all sampling locations across the study area (Fig. 1). Pooled for all years, nest failures due to fire ants were observed in the breeding season from 6 May to 20 July, while the dates of all other outcomes ranged from 8 April to 28 July (Fig. 2). Fire ant activity ($n = 19$ nests) began at night, typically while the vireos slept. On average, initial fire ant activity at vireo nests began at $23\!:\!50 \pm 0\!:\!38$ h CST. Daily temperatures on days of fire ant attacks averaged $28 \pm 4°$C. Mean air temperature at the time of initial ant activity ($26 \pm 1°$C, range $= 21–39°$C) was significantly lower than the mean daily maximum temperature of $34 \pm 1°$C on those days ($t_{16} = 13.4$, $P < 0.001$). The plant species within which the nest occurred did not affect nest fate (abandoned, depredated, successful) ($\chi^2_{18} = 21.2$, $P = 0.27$, $n = 134$ nests). Most black-capped vireos (52%, $n = 70$ nests) nested in shin oak (*Quercus sinuata* var. *breviloba*). Similarly, 64% of nests ($n = 14$ nests) with fire ant activity were also in shin oak. Plant species did not affect whether fire ants visited the nest ($\chi^2_9 = 8.61$, $P = 0.64$, $n = 134$ nests). Two nests preyed on by fire ants also occurred in each of the following species: Mexican buckeye (*Ungnadia speciosa*), hackberry (*Celtis laevigata*), and Texas ash (*Fraxinus texensis*). One nest was destroyed in Texas redbud (*Cercis canadensis* var. *texensis*) and another in plateau live oak (*Quercus fusiformis*). The mean height of nests preyed on by fire ants was 0.90 ± 0.06 m, ranging from 0.22 to 1.34 m off the ground, and the mean height of all nests in the population was 0.86 ± 0.02 m, ranging from 0.22 to 1.78 m. However, nest fate did not depend on nest height ($F_{7,114} = 0.98$, $P = 0.45$).
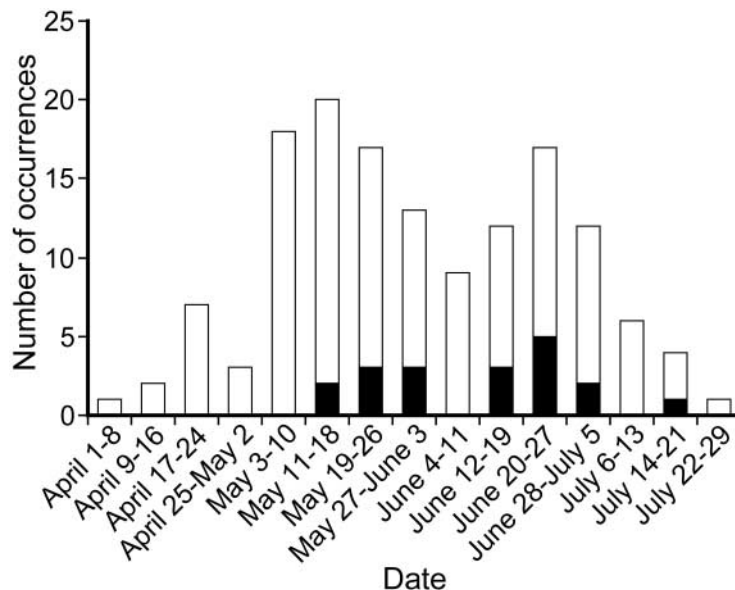
Fig. 2. The number of weekly nest outcomes with failures due to fire ants (black bars) and all other outcomes (successful, destroyed by a predator other than fire ants, or abandoned for reasons unrelated to fire ants; open bars) during the breeding season from 1 April to 29 July (1998 to 2001).

Behavioural response and associated energetic costs

All 15 nests with fire ant activity at the nestling phase of the nest cycle failed. At those nests, fire ants directly killed all nestlings except for one nest that prematurely fledged a single nestling. At that nest, fire ants were present when videotaping began, and two of three 7-day-old nestlings were motionless and likely dead 6 min after taping began. At that time, the third nestling jumped from the nest, its ultimate fate undetermined. At another nest, fire ant predation of nestlings was interrupted by a Texas rat snake that consumed all three nestlings (see Smith *et al.*, 2004).

All observable nestlings ($n = 9$ nests) exhibited panic behaviour before dying. Nestlings at six of these nests exhibited panic behaviour at the start of fire ant activity, and nestlings at the other three nests exhibited delayed panic behaviour 24 min, 30 min, and 1.8 hours following the start of fire ant activity. Time to mortality was highly variable, taking an average of 1.0 ± 0.4 hours and ranging from 6 min to 3.5 hours. For the five nests of known ages, this variation was explained by differences in nestling age (ranging from 1 to 9 days). Time to mortality increased significantly with nestling age ($R_s = 1.00$, $P = 0.02$, $n = 5$ nests).

We did not observe direct predation of eggs by fire ants, but all seven nests with fire ant activity at the egg stage ultimately failed. At four of these nests, eggs remained intact despite fire ant activity, but the nests were ultimately abandoned by adult vireos. At one nest with three eggs, the adult female vireo appeared to puncture two eggs with her bill and eject them from the nest following 9.2 and 9.3 hours of defence against fire ant attack. We were unable to determine whether the adult punctured the eggs in a direct attempt to eject them from the nest or did so inadvertently while pecking to remove fire ants from the nest. She did not remove the third egg, and ultimately abandoned the nest. At another nest, fire ants swarmed over the eggs and continued to do so until hatching. Then, the fire ants attacked the hatchlings until they died 15 min after hatching. At the last nest, fire ants occurred on eggs 3 days before snake predation but were no longer present when eggs were consumed.

Of the six nests that failed due to fire ant activity during the egg phase of the nest cycle, adults incubated four. Two other nests were exposed (no incubating adult present) when fire ant activity began and remained exposed for the duration of taping. During attacks, adult vireos spent a greater proportion of time away from the nest, leaving the clutch exposed 24 ± 6 min, and incubating the nest 12 ± 6 min, but this difference was not statistically significant ($t_5 = 1$, $P = 0.07$).

We observed no direct mortality of adult vireos from fire ants, although adult vireos actively defended their nests during attacks by fire ants. We observed adult vireos ($n = 19$ birds) pecking and removing fire ants from nests during all detectable predation events at the nestling stage. Activities of adults shifted from inactive brooding to active nest defence at all nests following the initiation of fire ant activity. Vireo behaviours during fire ant activity included active brooding, alert perching, pecking, hopping and flying, and did not differ between night and daylight hours at nests. In the presence of fire ants, adults were away from the nest and outside the view of the camera most of the time, a mean of 6.8 ± 1.6 hours (Table 1). The mean observed duration for all fire ant activity at vireo nests ($n = 17$) was 23.3 ± 3.7 hours and ranged from 7.6 to 57.2 hours. Duration of fire ant predation events did not appear to be related to the stage of the nest cycle (egg, nestling, or previously fledged or failed: $F_{2,14} = 1.05$, $P = 0.38$). On average, defence of the nest continued for a minimum of 7.7 ± 1.5 hours (Table 1). However, our results underestimate the length of

Table 1. Time and energy allocated by adult black-capped vireos during fire ant attacks at nine nests by both parents and a tenth nest where only the mother was present (mean ± standard error; range in parentheses)

Behavioural category	Allocation of time (h)		Energetic expenditure (kJ)	
Defence at nest[a]				
Brooding	0.03 ± 0.12	(0–0.54)	0.001 ± 0.25	(0–0.85)
Alert perching	0.17 ± 0.12	(0–1.1)	0.21 ± 0.25	0–1.67)
Pecking	0.47 ± 0.12	(0–4.6)	0.86 ± 0.25	(0–7.38)
Hopping	0.06 ± 0.12	(0–0.46)	0.06 ± 0.25	(0–0.77)
Flying	0.11 ± 0.12	(0–0.66)	1.04 ± 0.25	(0–6.50)
Away from nest[b]	6.79 ± 1.56	(0–21.11)	10.31 ± 2.42	(0–32.00)
Overall response[c]	7.72 ± 1.54	(1.1–21.11)	12.71 ± 2.43	(0.53–32.00)

[a] Defence by adults when they were in the view of the camera; values derived from partially hierarchical analyses of variance with behaviour and sex nested within individual nests defended.
[b] Estimates for adults when they were outside the view of the camera.
[c] Estimates for adults based on the entire duration of fire ant attacks (sum of *a* and *b*).

defence because fire ant attacks occurred mostly at night, and the film crew often interrupted filming when they discovered nest predation in the morning.

During fire ant attacks, adult vireos spent a significantly greater proportion of time away from the nest than they spent at the nest ($n = 19$, $Z = 2.59$, $P = 0.009$). While at the nest, vireos never engaged in inactive brooding and spent a significantly greater proportion of time actively defending the nest (97.3 ± 2.7%) than they spent actively brooding during fire ant attack (2.7 ± 2.7%; $n = 19$, $Z = 4.11$, $P < 0.001$). The proportion of time and energy spent on the defence behaviours differed significantly ($F_{4,9} = 12.08$, $P = 0.001$ and $F_{4,9} = 5.66$, $P = 0.015$, respectively). On average, while adults were at the nest, they allocated 40.1 ± 7.3% of their time to pecking, 29.4 ± 8.4% of their time to flying, 22.5 ± 5.2% of their time to alert perching, 5.3 ± 1.7% of their time to hopping, and 2.7 ± 2.7% of their time to brooding during fire ant attacks. Flying, hopping, and pecking were the most energetically expensive behaviours observed during defence. Adults expended 49.8 ± 8.0% of their energy on flying, 30.4 ± 6.7% of their energy on pecking, 12.9 ± 3.1% of their energy on alert perching, 4.3 ± 1.6% of their energy on hopping, and 2.6 ± 2.6% of their energy on brooding during fire ant attacks. Mean total energy expenditure during nest defence (12.7 ± 2.4 kJ) was significantly (2.6 times) greater than that expected during inactive brooding (5.1 ± 1.0 kJ; $Z = 3.82$, $P < 0.001$). The mean rate of energy expenditure (1.73 ± 0.06 kJ·h^{-1}) during nest defence was also (2.6 times) greater than that expected during inactive brooding (0.655 kJ·h^{-1}; $t_{18} = 17.84$, $P < 0.001$).

DISCUSSION

Fire ants as predators on vireo nests – resistance is futile

At Fort Hood, fire ants, together with snakes, are one of the two leading nest predators of black-capped vireos (Stake and Cimprich, 2003). All nests with observable fire ant activity failed to fledge, regardless of the phase of the nest cycle (egg, nestling). It is possible that we may have missed attacks by fire ants occurring at low densities during our video screening.

However, this is unlikely given that fire ants typically recruit to their prey in large numbers, forming easily detectable swarms (Taber, 2000). Nests at the egg phase generally failed due to abandonment, whereas those at the nestling phase failed due to direct predation by fire ants. Adult vireos attempted, unsuccessfully and at considerable energetic cost, to defend their nests. (A possible exception is a nest where an adult female vireo was first flushed from it by fire ants, but we no longer could detect fire ants at the nest 3 days later when a snake preyed upon it.) Therefore, defence occurs despite the fact that a vireo nest, once located by fire ants, has a high, if not certain, probability of failing. The consequences of this costly, ineffectual, and inappropriate nest defence by vireo parents represent the most intriguing yet uninvestigated aspect of this predator–prey interaction.

Vireo behavioural response – resistance is costly

Vireo parents defending their nests against swarming fire ants expended, by our estimate, 2.6 times more energy than that of a parent simply brooding at night. On average, a 9-g adult metabolized about 12.7 ± 2.4 kJ over a period of 7.7 ± 1.5 hours, expending about 1.73 ± 0.06 $kJ \cdot h^{-1}$. If this energy is fuelled entirely by fat [with a caloric value of 37.7 $kJ \cdot g^{-1}$ (Blem, 1980)], then adults in our study lost 0.34 g (3.7% of their body mass) as opposed to 0.13 g (1.4% of their body mass) expected during inactive brooding. Typical fat reserves during the breeding season have not been determined for black-capped vireos, but they are unlikely to be substantial. For instance, Holmes (1976) reported mean fat reserves of 0.77 ± 0.41 g for the approximately 12-g Philadelphia vireo, *Vireo philadelphicus*. Cooper (2002) reported fat reserves of 0.36 ± 0.09 g for the approximately 11-g mountain chickadee, *Poecile gambeli*, in summer. If the percent body fat of the black-capped vireo is similar to that of the Philadelphia vireo, then black-capped vireos carry less than 0.58 g of fat reserves. Based on these estimates, adult black-capped vireos in our study burned about 59% of their fat fuel stores (at a rate of 7.9% total body fat per hour) in nest defence.

The energy expended during nest defence may have negative consequences. First, although this level of energy expenditure is certainly below the metabolic ceiling for passerines (Dykstra and Karasov, 1993a, 1993b), our estimates of energy expenditure are conservative because we assumed that birds not visible in the video footage spent that time alert perching. However, vireos also were likely to have engaged in costly activities while they were outside the view of the camera. In addition, black-capped vireos vocalize frequently (personal observation), but we did not add any additional expenditure for alarm-calls produced during defence.

The prolonged nest defence against fire ants, therefore, could reduce both the likelihood of re-nesting and the success of re-nesting attempts, thus causing a decline in reproductive success. The length of predation events by fire ants was 25 times longer than those observed by the other major predator of this population, the native Texas rat snake (Stake and Cimprich, 2003; Smith *et al.*, 2004), whose visits averaged only 18 min (Stake *et al.*, 2005). In contrast, fire ant attacks on vireos in our study lasted for almost 8 hours on average. Such prolonged stress can be physiologically costly (Wingfield *et al.*, 1998), compromising the immune system and defence against pathogens later in the breeding season. Even short-term exposure to a predator, however, may have long-term physiological consequences on adult birds. For example, adult house sparrows, *Passer domesticus*, exposed to a predator for one hour showed a significant reduction in immune response, measured by T-cell production,

and a significantly higher rate of blood parasite infections later in that breeding season than control birds (Navarro *et al.*, 2004).

Although the data are sparse, recent studies using radiotelemetry indicate that nest predation causes some females to abandon their territories. Sixty-two percent of dickcissel females, *Spiza americana*, abandoned their territories following nest predation (Walk *et al.*, 2004). Twenty-one percent of eastern meadowlark females, *Sturnella magna*, abandoned their territories following nest predation (Kershner *et al.*, 2004). Given the costly and ineffective nest defence of black-capped vireos against fire ants, abandonment of the territory would not be surprising. Abandonment could have a detrimental effect on annual fecundity and population dynamics, particularly in an endangered species with presumably limited mating opportunities.

Vireos engaged in nest defence against swarming fire ants likely received numerous bites and venemous stings. Fire ant venom consists predominantly of piperidine alkaloids that have a wide range of physiological activities, including mast cell release, and haemolytic, cytolytic, necrotic, antimicrobial, and insecticidal properties and often cause pustules that lead to secondary infection in humans (Goddard, 1996). The effects of these toxic alkaloids and allergens in birds are poorly understood, but various studies have demonstrated compromised growth rates and survivorship in northern bobwhite chicks, *Colinus virginianus*, exposed to fire ants (Allen *et al.*, 1993, 1995; Giuliano *et al.*, 1996; Mueller *et al.*, 1999). Furthermore, suppression of immune response and resistance in birds due to reproductive effort may contribute to heightened adult mortality (Nordling *et al.*, 1998). Finally, if vireos consume fire ants during nest defence, the toxicity of ingested ants (Bennet *et al.*, 1996) could have detrimental effects on adult birds.

The rigours of reproduction combined with the behavioural and physiological responses to fire ants may increase adult mortality of vireos and other bird species newly exposed to fire ants. Reproductive vireos lose not only their immediate investment in the failed nest attempt, but they also engage in energetically costly nest defence and expose themselves to bites and venomous stings.

Fire ant predation as a grist mill of evolution

Attacks by fire ants lead to total nest failure, with no observed exceptions. Nest defence by vireos is costly and inappropriate. So fire ants must be potent forces of selection on black-capped vireos. We envision three likely outcomes of this novel predator–prey interaction. First, if the vireo is incapable of adjusting to the fire ant, the ant may drive its extirpation where the two overlap. Second, humans might perpetually intervene on behalf of the vireo, controlling fire ants and allowing the vireo to exist in their presence. Third, the vireo might evolve better responses (*sensu* Payne *et al.*, 2004) to fire ants. This third outcome could allow birds to avoid fire ants or minimize their negative impacts. Still, the critical question remains: Can evolution occur quickly enough given the small global population size of this species (Gomulkiewicz and Holt, 1995)?

Fire ants preyed upon vireo nests throughout the later months of the breeding season (May to July), but not in April (Fig. 2). If predation from fire ants persists, it may select for earlier nesting and against re-nesting later in the season. A potential constraint on earlier nesting may be increased vulnerability to brood parasitism by the brown-headed cowbird. This likelihood may be minimized at Fort Hood due to active cowbird removal.

Many studies have shown that birds recognize and respond to nest predators and parasites when these threats are sufficiently common (Montgomerie and Weatherhead, 1988; Ghalambor and Martin, 2002; Grim, 2006). Nest predation by native fire ant species has been recorded on bird species other than the black-capped vireo, but it appears to be rare (Holway *et al.*, 2002). It is perhaps thus not surprising that black-capped vireos respond inappropriately to *Solenopsis invicta*. Nest predation by native fire ants may have been sufficiently rare historically that the appropriate predator recognition system never evolved.

An appropriate predator recognition system and behavioural response is demonstrated by the California least tern, *Sterna antillarum browni*, and the southern fire ant, *Solenopsis xyloni* (Hooper-Bui *et al.*, 2004). If the nest of the tern is discovered by southern fire ants in the egg phase, the nest is abandoned for a few hours, after which the fire ants leave the nest and the parents resume care. If attacked during the nestling phase, the least tern permanently abandons its nest. This suggests to us that the fire ants in our study may similarly be exerting strong selection for an appropriate recognition system and behavioural response in black-capped vireos. In this case, vireos should immediately abandon the nest if visited by fire ants and thus avoid the costs associated with nest defence. Several studies of other predator–prey systems suggest such evolutionary responses of prey species to predator species do occur (Reznick and Endler, 1982; Freeman and Byers, 2006; Strauss *et al.*, 2006).

Current thinking holds that nest predation is important in the evolution of nest site selection in birds (Martin, 1988, 1993). One reason black-capped vireos may suffer such a high rate of nest predation by fire ants is their low mean nest height placement. Fire ants are known to forage up to 10 m above ground in vegetation (Taber, 2000). However, fire ants rarely prey on the high (5–7 m) nesting golden-cheeked warbler, *Dendroica chrysoparia*, at Fort Hood (Stake *et al.*, 2004). Perhaps higher nests would reduce fire ant predation and perhaps black-capped vireos will be under strong selection to nest higher than they do now. Few studies have examined nest placement in response to potential nest predation. Dusky warblers, *Phylloscopus fuscatus*, preferred safe nest-sites rather than those offering other advantages (microclimate, proximity to food) when the risk of nest predation was especially high (Forstmeier and Weiss, 2004). The Siberian jay, *Perisoreus infaustus*, chose nest sites offering protection in response to vocalizations of nest predators (Eggers *et al.*, 2006). Evolution of increased nest height placement might be even more likely if it simultaneously reduced predation by snakes.

CONCLUSIONS

Our data are consistent with the hypothesis proposed by Suarez *et al.* (2005) that the impacts of *Solenopsis invicta* on avian nesting success are more severe than those imposed by other species of introduced ants. We found that the costs of fire ant predation to birds exceed nest loss. Adult birds wasted considerable fat reserves in prolonged, fruitless defence and subjected themselves to stress that may have reduced their immune defences. As fire ants continue to expand their range globally, understanding the impact of this novel predator on the future reproductive success of its new prey will be crucial for successful conservation.

More generally, our case study suggests that newly introduced predators can elicit dramatic, but sometimes inappropriate, behavioural responses in their new prey. Moreover, we hypothesize that other newly introduced species likely evoke inappropriate behavioural and physiological responses from their prey. We suspect that novel perturbations of this

sort are particularly potent because new prey species lack co-evolved strategies typically perpetuated by the well-documented 'races' between native predators and their prey.

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