

## FIRST-ORDER FIRE EFFECTS ON ANIMALS: REVIEW AND RECOMMENDATIONS

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### ABSTRACT

Models of first-order fire effects are designed to predict tree mortality, soil heating, fuel consumption, and smoke production. Some of these models can be used to predict first-order fire effects on animals (e.g., soil-dwelling organisms as a result of soil heating), but they are also relevant to second-order fire effects on animals, such as habitat change. In this paper, I review a sample of studies of first-order fire effects on animals that use aquatic, subterranean, and terrestrial habitats; use an envirogram as a graphical approach to organize first- and second-order fire effects for a single animal species; recommend how one could obtain better data using Species-Centered Environmental Analysis; and begin to model these effects.

*Keywords:* animals, direct effects, envirogram, fire, first-order fire effects, indirect effects, invertebrates, mortality, vertebrates

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### INTRODUCTION

Whelan *et al.* (2002) identified three levels on which fire affects animals. First, fire can cause injury or death to individuals, or it can motivate individuals to move from or into the burned area. High temperatures, toxic effects of smoke, and oxygen depletion can cause mortality or impairment. Nearby unburned habitat may provide essential resources (food, shelter, water) for some organisms, but a burned site may create ideal habitat for other species to take advantage of post-fire conditions. Second, if enough individuals within a population survive, processes after the fire, such as starvation, predation, or immigration

within the post-fire environment, will determine population viability. Third, the fire regime can modify a species over time to create adaptations to fire. (See Hutto *et al.* [2008] for consideration of adaptations to fire in bird species to infer fire regime.) These three levels roughly correspond to 1) direct or first-order effects that occur over a short time period of days or weeks; 2) second-order or indirect effects, such as vegetation succession, which are influenced by the range of variation in fire characteristics and historical fire interval; and 3) evolutionary effects of fire on animals.

Recently, notable reviews have been made for aquatic ecosystems (Gresswell 1999), reptiles and amphibians (Russell *et al.* 1999), in-

sects in forests (McCullough *et al.* 1998), insects in grassland communities (Warren *et al.* 1987), birds (Saab and Powell 2005), and multiple taxa (Lyon *et al.* 1978, Smith 2000, Kennedy and Fontaine 2009). In these reviews, it is difficult to find studies that describe the full relationship of an animal species to fire—a study that would have theoretical and applied relevance. Here, I summarize a sample of that literature that pertains to first-order fire effects on animals and extend the attempt by Whelan *et al.* (2002) to view the effects of fire on the entire life cycle of a species, while distinguishing short- and long-term effects within a new framework for modeling animal-fire relationships.

### BEHAVIORAL RESPONSES, INJURY, AND MORTALITY

The hazardous effects of fire on animals can be direct and immediate, although some effects, such as shortened lifespan or impaired fitness of wounded individuals following a fire event, may play out over years or decades. Physiological effects of short exposure to fire on animals are poorly known, but some inferences can be made from studies of responses of animals to high ambient temperatures. The highest body temperature that animals can tolerate is about 50°C. Above this temperature, cells undergo denaturation of proteins, enzymes become inactive faster than they can be re-formed, and membrane structure degrades (Schmidt-Nielson 1979). In addition to these heat related factors, oxygen depletion and exposure to toxic compounds following smoke inhalation may be critical factors to animal survival during exposure to fire. The length of time that an organism is exposed to high temperature, anoxia, or smoke is critical; thus, fire detection and avoidance are essential behaviors for survival, especially for less-mobile animals (Whelan 1995).

### Fire Detection, Avoidance, and Attraction

Chemo-reception of smoke, response to heat, visual perception of flames and smoke, and even sounds of fire are some of the means of detection of fire by animals. For example, reed frogs (*Hyperolius nitidulus*) were observed to move away from a fire in western Africa. Based on this observation, aestivating juvenile frogs responded to playbacks of fire sounds in the field by moving to take cover in fire resistant sites (Grafe *et al.* 2002). On the other hand, red bats (*Lasiurus borealis*) hibernating in leaf litter failed to respond to the sounds of fire alone, but did arouse themselves in response to a combination of fire sounds and smoke (Scesny and Robbins 2006). For a species such as the red bat, which may be subjected to multiple fires within a lifetime, there may be strong selection for the ability to detect fires. Bats that flush from day roosts and hibernation sites during fires may be vulnerable in cooler burning weather when arousal from torpor is delayed (Dickinson *et al.* 2009).

For organisms that are highly mobile, avoidance of heat and gases associated with fires by flight or movement on the ground can be relatively easy. For example, sedge wrens (*Cistothorus platensis*) and Henslow's sparrows (*Ammodramus henslowii*) were observed making short flights in the advance of a slow fire in a longleaf pine (*Pinus palustris* Mill.) forest in Florida (McNair 1998). The birds eventually moved into a shrub thicket protected from the fire by wet soil.

Less mobile organisms also avoid fire through a variety of means. Eastern fence lizards (*Sceloporus undulatus*) have been observed burrowing (Bishop and Murrie 2004) and climbing trees (Beane 2006) to avoid fire. Radio-tagged meadow voles (*Microtus pennsylvanicus*) have escaped fire by finding shelter in underground refugia, fleeing to unburned areas, and moving onto the bare ground of a pocket gopher (*Geomys bursarius*) burrow mound (Geluso *et al.* 1986). In a high eleva-

tion oak-pine woodland in Arizona, eight radio-tagged individuals of three species of montane rattlesnakes (*Crotalus lepidus*, *C. molossus*, and *C. willardi obscurus*) retreated to underground shelters in a low intensity ground fire (Smith *et al.* 2001). Cuban parrots (*Amazona leucocephala*) nesting in limestone solution holes in pine forests in the Bahamas had no loss of nests after 20 occupied burrows were burned over by a fire (Stahala 2005). O'Brien *et al.* (2006) measured temperature and CO<sub>2</sub> concentrations during a surface fire within a 1.2 m deep cavity typical of the limestone solution hole used for nesting by the Cuban parrot. Carbon dioxide concentrations rose no more than 3-fold while air temperature rose 0.4°C at the bottom of the burrow. The residence time of the fire was approximately 15 min within 1 m of the cavity entrance. Many additional examples of fire avoidance behavior are provided in Komarek (1969), Bendell (1974), Whelan (1995), and Russell *et al.* (1999).

Fire also attracts some animals in search of food. Birds attracted to fire probably use the smoke column as the visual cue and feed on insects that are carried high into the air (Komarek 1969, Gillon 1971, Gandar 1982, Frost 1984, Braithwaite and Werner 1987). The Australian buprestid beetle (*Merimna atrata*) is attracted to fire because it lays its eggs in trees weakened by fire (Schmitz and Trenner 2003). Thermosensitive neurons found in the abdomen of these beetles may function as infrared receptors enabling their pyrophilous behavior. Similarly, the buprestid beetle *Melanophila accuminata* orients toward various sources of smoke by detecting infrared radiation using organs near the coxal cavities on the mesothorax (Evans 1966). These beetles that oviposit in fire-killed trees may be able to detect a 20 ha forest fire from 1 km to 5 km away, depending on topography. The increase in number of beetles is an immediate response that takes advantage of the abundant food resource provided by trees that have had their in-

sect resistance compromised. Thus, the direct negative effect of fire on trees is a direct positive effect for some beetles. Evans (1971) listed over 30 species of pyrophilous insects.

### Mortality and Injury

For individuals that remain within a fire perimeter, the questions of interest are: Do they actively seek refuge, or do they remain in their pre-fire location? What heat and gas exposures do they experience? Given those exposures, what are their effects relative to injury and death? And, what characteristics of a fire influence the degree of fire exposure? Studies on exposures suggest a wide range of risk, depending on the location of the refuge and its configuration. Clearly, the outcome for fauna exposed to flames is not in question, with the exception, perhaps, of land turtles. One can imagine increasing vulnerabilities to smoke for fauna occupying deep burrows (gopher tortoises, Guelta and Balbach 2005), tree cavities (red-cockaded woodpeckers [*Picoides borealis*] and bats; Guelta and Checkai [1997]; Guelta and Balbach [2005]), shallow burrows (Bahama parrots [*Amazona leucocephala bahamensis*]; O'Brien *et al.* [2006]), and bark flaps (various forest bats; [Anthony Bova, Forest Service, unpublished data]). Missing are studies that model fluid dynamics processes of gases in refugia. Only limited datasets exist at present.

Mortality of animals from fire has been reported in descriptive notes for a large number of taxa (e.g., Erwin and Stasiak 1979; Simons 1989, Esque *et al.* 2003). These studies are of greatest value if they can be used to accumulate data for a species (e.g., sex, cause of death, reproductive condition) in relation to characteristics of a fire for a habitat. Study of marked individuals is a more intensive but productive way to examine fire effects. Means and Campbell (1981) studied a marked population of 68 eastern diamondback rattlesnakes (*Crotalus adamanteus*) over the course of five years of

annual prescribed fires in a 500 ha area in northern Florida. The two individuals killed by fires were both in mid-ecdysis, during which the senses of the snakes were impaired.

In a novel approach, Sandoval (2000) indirectly examined fire effects on a population of wingless, univoltine walking sticks (*Timema cristinae*) in California chaparral. She used regional polymorphic variation (four colors) to infer that the population persisted in an isolated habitat patch as a result of individuals that hatched from *in situ* eggs instead of re-colonization from surrounding populations. These insects appear to be adapted to dry season fire when they are in diapause. Fires applied during spring fires could have devastating effects on larvae and nymphs resting on the foliage.

Losses may be acceptable if the long-term benefits to the habitat increase fitness in individuals within the population that survive or immigrate into the burned area. The biggest concern about mortality caused by fire is the potential loss of an entire population of a rare species. One such example involves the last population of eastern prairie chickens (*Tympanuchus cupido cupido*) in the eastern US. In 1916, a brush fire burned the center of the breeding grounds of the heath hen (estimated population of approximately 2000) on Martha's Vineyard. This was followed by a severe winter during which high numbers of goshawks (*Accipiter gentilis*) preyed on the heath hens and then the population suffered an outbreak of blackhead disease. By 1927, only 13 heath hens were left, and these gradually disappeared (Halladay 1978).

Animals that receive injuries from fire have been noted in many descriptive studies, although little is known about the degree to which fire-related injuries impair fitness or cause premature mortality. In the Florida box turtle (*Terrepenne carolina bauri*), Ernst *et al.* (1995) found fire scars on the carapace in 30% of a sample of 100 museum specimens, but no data were available on the longevity or fitness of the individuals that survived fire with injury.

In a study of koalas (*Phascolarctos cinereus*) after wildfires, injured but rehabilitated individuals survived at equal levels with uninjured individuals (Lunney *et al.* 2004).

## FIRE EFFECTS ON ANIMALS IN DIFFERENT HABITATS

Fires affect faunal behavior and can cause mortality and injury through the direct effects of heat and gases. Fire can also affect individual fitness and population dynamics indirectly within a habitat through changes to vegetation structure and composition, quantity and quality of coarse woody debris, and geophysical alterations, such as erosion. The selective review is organized into aquatic, subterranean, and terrestrial habitats (*sensu* Shaffer and Landenslayer 2006) in order to examine unique first-order fire effects in each of those broad habitat categories that indirectly affect animals. Terrestrial habitat is divided into sections on invertebrates and vertebrates, because of the large body of literature on these taxa.

### *Aquatic*

Aquatic habitats are intimately connected to terrestrial landscapes in fire-maintained ecosystems (Minshall and Brock 1991, Bisson *et al.* 2003). Fire in terrestrial ecosystems plays a role in linked aquatic ecosystems through many dynamic factors (Gresswell 1999, Bisson *et al.* 2003). Mortality and injury of aquatic animals can be caused by fire by raising water temperature to lethal levels, possible toxic effects caused by fire-induced changes in stream pH, and acute levels of toxic chemicals (Gresswell 1999). Longer term fire effects on aquatic animals can result from chronic or pulse erosion, channel re-configuration (Gamradt and Kats 1997), the quality and quantity of coarse woody debris, reduced streamside vegetation, turbidity (Gill and Allan 2008) and stream sedimentation (Bozek and Young 1994, Lyon and O'Connor 2008). These factors have

direct and indirect effects on aquatic organisms (fish and macroinvertebrates) and organisms that have aquatic phases in their life histories, such as emergent insects and amphibians (Dunham *et al.* 2007). Emerging aquatic insects, in turn, are an important source of food for many vertebrates (i.e., bats, birds, amphibians, and fish) and other insects. Modeling first-order effects on trees and shrubs within watersheds (defoliation or mortality) could be used to predict factors critical for aquatic life, such as turbidity, runoff, insolation, and coarse woody debris.

In an example of first- and second-order fire effects, Rinne (1996) found that a fire led to extirpation of several populations of salmonids and reduced populations of macroinvertebrates to zero one year post fire in three headwater streams in Arizona. On the other hand, Mellon *et al.* (2008) reported that emerging macroinvertebrates were significantly higher in streams in burned than in unburned sites in Washington. In a large-scale study of fire in tropical savanna woodlands, fires late in the burn season increased aquatic macroinvertebrate richness (Andersen *et al.* 2005). Beck *et al.* (2005) monitored tributaries of the Big Creek watershed in central Idaho that received varying levels of fire from completely burned to unaffected. Burned sites showed higher insect emergence and bat activity than streams in unburned sites. He hypothesized that increased insolation on streams that were in the burned areas where the canopy was all or partially removed could have increased food for the insects.

Some themes emerge from studies of fire effects on aquatic systems. First, small, isolated populations of non-migratory fish were particularly susceptible to the effects of severe fires (Brown *et al.* 2001, Bisson *et al.* 2003, Burton 2005). This raises the importance of connectedness within aquatic systems that would allow re-colonization. Second, many studies of the effects of fire on aquatic systems lack detailed descriptions of the fire itself (e.g.,

fireline intensity, fuel consumption) that provide the context for understanding general processes for developing models for predicting fire effects on animals. Third, in general, smaller water bodies are more likely to be affected than larger water bodies, flowing water is more affected than standing water bodies, and aquatic habitats next to forests are more affected than those buffered by wetlands.

### *Subterranean*

Fire influences many physical and chemical properties of soil that, in turn, affect the biomass and composition of microbial and soil-dwelling invertebrate communities (Certini 2005). Common factors that influence fire effects on soil organisms include fire frequency, intensity, and season; prevailing weather conditions; soil moisture; and fuel load (Cairney and Bastias 2007). Direct fire effects include loss of vegetation, combustion of the organic horizon, soil heating, loss of nitrogen and carbon to the atmosphere, and deposition of charcoal and ash. Longer term effects include altered moisture and pH, increased erosion, physical effects of charcoal deposition (Boerner 2006; Cairney and Bastias 2007), and the quality and amount of plant tissue below ground (Johnson and Matchett 2001). The First Order Fire Effects Model (FOFEM) can reliably predict soil temperatures at a stand level (Reinhardt *et al.* 2001), but lacks the resolution to predict fire effects in highly variable soils and soil surface conditions (Massman *et al.* 2010).

In long-term experimental studies of the effects of fire, mowing, and fertilization in tall-grass prairie at Konza Prairie Natural Area in eastern Kansas, Callahan *et al.* (2003) determined that exotic earthworms (Aporrectodea) had greatest density and biomass in unburned prairie plots, while native earthworms were most abundant in burned plots. Cicada (*Cicadetta* and *Tibicea*) nymphs were much more numerous in unburned plots than in burned

plots. They concluded that burning and mowing prairie depletes nutrients and results in decreased invertebrate density and biomass. Fire and mowing remove dead plant material from the surface of the soil and make the soil warmer and drier. Also on the Konza prairie study plots, in a nine-year study, Todd (1996) found that obligate herbivorous nematodes increased in plots that were treated with annual prescribed fire.

Coleman and Rieske (2006) found that leaf-litter arthropods decreased by 83% in the first year post fire and in the second year were still only 48% of the levels of invertebrates found in unburned plots in oak-shortleaf pine (*Quercus* sp. L.-*Pinus echinata* Mill.) forest in Kentucky. Fire-induced mortality may play a significant role in leaf-litter arthropod abundance, although these effects may be short-lived. Following the “shock phase” of a fire, the leaf litter is sparse and vegetation cover are reduced, leading to changes in microclimate, including increases in soil and litter temperatures and concomitant decreases in soil and litter moisture.

### *Terrestrial Invertebrates*

Negative effects of fire have been raised as concerns in small populations of rare animals from fish to butterflies. Panzer (2002) examined the compatibility of burning with insect conservation in small isolated prairie fragments. During a seven-year study, he measured post-fire population response in 151 insect species. Of these species, 61 (40%) exhibited a negative response and 39 species (26%) had a positive population response to prescribed fires. The “fire negative” species had a mean population decline of 67%. In 163 negatively affected insect populations of 66 species that were tracked to recovery (at least one post-fire season), population recovery took less than 2 yr (mean = 1.32 yr), and recovered populations were generally larger than populations in unburned habitat (burned to unburned

ratio was 2.39). Panzer (2002) hypothesized that some traits may predispose species to fire susceptibility and “contribute to a predictive understanding of fire susceptibility among grassland insects in general.” He gave the example that fire negative response was more common in prairie remnant species than in widespread species. He concluded that four traits predispose duff-dwelling insects to fire sensitivity: remnant habitat dependence, upland habitat preference, low vagility, and univoltinism. Recommended management practices were to allow unburned refugia—ideally with a suite of microhabitats—in any ecosystem reserve, and burn rotations should allow two years for recovery. Swengel and Swengel (2007) commented that some lepidopteran species highly susceptible to fire were already absent from the preserves in Panzer’s (2002) study, because all of the preserves had a recent history of fire management.

In a five-year study in Florida, Hanula and Wade (2003) compared relative abundance and diversity of ground-dwelling macroarthropods within long-term study plots that were unburned or given 1 yr, 2 yr, or 4 yr winter burn applications. They found the greatest difference in macroarthropod diversity between 1 yr burn plots and unburned plots, but macroarthropods were reduced in all burned plots compared to the unburned plots. Their results indicated that 42 genera were reduced by burning, 32 genera were captured in greater numbers on 1 yr plots, and 11 genera had highest numbers in the intermediate fire interval plots. Twenty-six genera were found in equal numbers on 1 yr and 4 yr burn intervals, but significantly reduced compared to the unburned plots, which suggests that some genera cannot recover within four years post fire. In general, predators were most negatively affected by fire and detritivores were more abundant in fire-maintained sites, but the authors cautioned against making generalizations about fire effects and urged taking a species-specific approach to understanding fire effects on macroarthropods.

Hanula and Wade (2003) recommended that land managers consider excluding fire from parts of the landscape if conservation of arthropod diversity is a priority.

Given that an estimated 90% of terrestrial arthropods spend at least part of their lives in the soil or soil litter (Klein 1988), it would make sense to consider season and intensity of fire to prescribe and apply fire according to the life cycle of target arthropod species. Some species appear to be dependent on fire on the landscapes that they occupy, such as the prairie mole cricket (*Gryllotalpa major*; Howard and Hill [2007]), while others appear to be fire averse (Callahan *et al.* 2003). Retaining refugia for those fire-intolerant species may be an important conservation objective in a fire management plan.

#### Terrestrial Vertebrates

Saab *et al.* (2002) examined stand and landscape conditions selected by birds in burned forests at two spatial scales in southeastern Idaho. The nests of two woodpecker species, the black-backed woodpecker (*Picoides arcticus*) and the Lewis's woodpecker (*Melanerpes lewis*), were found at two ends of a range of habitat conditions. Compared to random sites and other cavity nesting bird species, Lewis's woodpecker nests were found in stands that had relatively low snag density with relatively large diameter snags. The black-backed woodpecker tended to occur in stands with a high density of relatively small diameter snags. Saab *et al.* (2002) related the relative occurrence of these two species to food preferences. Black-backed woodpeckers forage on bark beetles (Scolytidae) and wood-boring beetles (Cerambycidae) that may be abundant following fire. Lewis's woodpeckers are primarily aerial flycatchers during the breeding season that sally from perches in relatively open conditions. First-order fire-effect models that could predict tree mortality according to stand crown closure characteristics

could be used to predict post-fire snag densities that would serve as an index for woodpecker habitat suitability over a 3 yr to 5 yr post-fire period.

Change in food availability is both an indirect effect of fire on animal populations as vegetation composition and structure change over years and a commonly described direct (short-term: days) positive effect on some animals. Birds that feed on conifer seeds, such as Clark's nutcracker (*Nucifraga columbiana*), Cassin's finch (*Carpodacus cassinii*), red crossbill (*Loxia curvirostra*), and pine siskin (*Carduelis pinus*), were more abundant in recently burned forest the first year following catastrophic fire (Hutto 1995). Relative importance of ephemeral sources of food caused by fire on an individual or population level has not been quantified.

The adult beetles attracted to fire and beetle larvae that develop after adults oviposit in freshly killed trees provide an increase in food availability for birds. In a study of bird communities in conifer forests in western Montana and Wyoming following stand replacement fires, Hutto (1995) found that 15 species of birds were more abundant in recently burned areas than in other available land cover types. In particular, the black-backed woodpecker is largely restricted to conifer forests within 1 yr to 5 yr following stand-replacing fire. He hypothesized that black-backed woodpecker populations in unburned forests may not be sustainable without immigration from populations in extensively burned areas. Thus, woodpecker persistence may depend on detection of large-scale fires in forested communities and irruptive movement of individuals into the burned areas at a landscape level.

A recent study of the spotted owl (*Strix occidentalis*) highlighted the problem of conflicting goals in fire management for different species at risk. Buchanan (2009) described a management dilemma between restoration of open-canopy forest that favors some bird species, such as flammulated owl (*Otus flammeo-*

lus), white-headed woodpecker (*Picoides albolarvatus*), and pygmy nuthatch (*Sitta pygmaea*), and providing habitat for spotted owl and the goshawk that favor closed canopy forest. Management inaction could result in catastrophic fires that would eliminate habitat for both groups of species. He called for landscape-level modeling to assess fire effects.

Ager *et al.* (2007) modeled the effects of wildfires on habitat of northern spotted owl (*Strix occidentalis caurina*) in the Five Buttes Interface area composed of 60 867 ha of the Deschutes National Forest and 9378 ha of private land in central Oregon. The owl depends on late-successional forests, and wildfire can reduce the amount of forest in this stage of development. Many managers and researchers agree that fuel reduction through mechanical thinning and prescribed fire may decrease the probability of old-growth habitat loss to wildfire. The interest of these authors was to model owl habitat loss within the Five Buttes Interface area given different levels of fuel-reduction treatments.

Forest inventory databases were used to classify forest stands into 5292 geographic information system polygons (range in size from 3 ha to 1515 ha, mean of 13.3 ha) based on tree diameter, density, species in each stand, as well as biophysical characteristics such as slope, aspect, and elevation. Using the forest vegetation simulator (FVS; Dixon [2003]), six fuel treatment areas (0% to 50% of the forested land) were simulated. The FVS-simulated fuel treatment prescription reduced both surface and ladder fuels by thinning from below and underburning. One thousand wildfires were simulated using randomly located ignitions and burn conditions based on the 2003 Davis fire that burned 8268 ha. Predicted tree mortality followed methods described in First-order Fire Effects Models (FOFEM; Reinhardt and Crookston [2003]).

The average wildfire size among the simulations decreased from 1680 ha to 419 ha between the forest treatments involving 0% to

50% of the landscape. Relatively large treatment effects on wildfire size were observed following small (10% to 20%) simulated fuel reduction treatments. This approach can be used to model strategic location of fuel treatments in order to maximize the effectiveness of management for wildfire mitigation within a complex landscape. It could be applied to evaluate the effects of fire to the habitat of other species of conservation concern.

Roberts *et al.* (2008) developed models that predicted response of small mammals that form part of the prey base of the spotted owl to measures of fire severity, composition of post-fire vegetation, and spatial heterogeneity in areas of burns of different ages in Yosemite National Park, California. Abundance (inferred from capture rate) of deer mice (*Peromyscus maniculatus*) decreased with increasing fire severity, possibly because conifer mortality reduced availability of conifer seeds—an important food source for the mice. Brush mice (*P. boylii*) numbers were best predicted by oak (*Quercus* spp.) cover, and chipmunk (*Neotomias* spp.) numbers were best predicted by a combination of oak cover and an index of patchiness. Increased knowledge of first-order fire effects on the conifers, oaks, shrubs, and herbaceous communities (see Stephan *et al.* [2010]) would improve our ability to predict response to fire of these small mammals.

## SPECIES-CENTERED ENVIRONMENTAL ANALYSIS

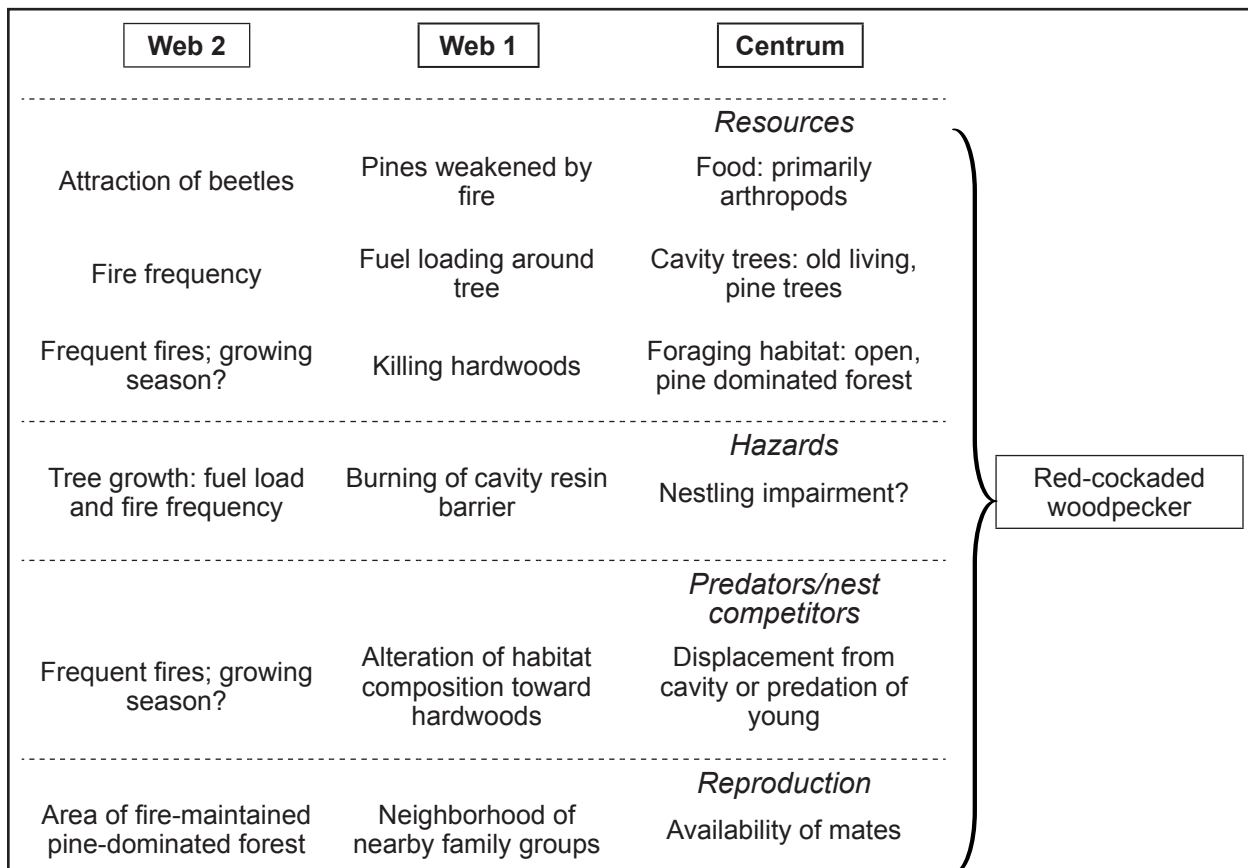
Species-Centered Environmental Analysis (SCEA), developed by James *et al.* (1997), is a systematic approach to developing focused research questions about environmental influences on the fitness of a particular species. The SCEA involves: 1) studying a species and its environment in many places so that comparisons can be made between its status and levels of the environmental factors (if the entire population of interest cannot be measured, random sampling is used); 2) incorporating principles



of experimental design (randomization, replication, control) into a plan for making comparisons that help evaluate, and perhaps eliminate, some alternative explanations; and 3) using modeling to characterize environmental processes affecting population regulation and, if possible, test alternatives experimentally.

James *et al.* (1997) used an envirogram (Andrewartha and Birch 1984) as the first step in SCEA in order to summarize information about environmental factors that would affect numbers of a focal species if their levels were changed, and to organize knowledge and focus attention on questions that need to be addressed. Factors that can directly affect the health and fitness of the study organism—resources, mates, hazards, and predators—are

located in the centrum, immediately adjacent to the organism (Figure 1). Agents that influence the levels or nature of factors in the centrum are located in layers of indirect effects called the “web.” The relationship between the target organism and each of the most distal influences in its environment can be displayed in a linear combination of causal links moving from the centrum to the web. An envirogram is intended to organize the entire life history of an organism and, thus, covers more than just the influence of disturbance; however, fire often affects the life history of the organisms that live in fire-prone environments in multiple places over time.



**Figure 1.** A modification of the envirogram for the red-cockaded woodpecker used by James *et al.* (their Figure 1; 1997). The envirogram of James *et al.* (1997) covers all aspects of the life history of the woodpecker, whereas this envirogram focuses solely on how fire affects a species in both the short term and long term. First-order fire effects models could be used to evaluate the effects of different fires over time.

### A Fire Envirogram

James *et al.* (1997) developed an envirogram to examine environmental influences on the life history of the red-cockaded woodpecker (*Picoides borealis*). Fire entered the envirogram in several places, but their envirogram is comprehensive of the entire life history of the woodpecker. I modified the James *et al.* (1997) envirogram to focus solely on the environmental influences of fire for the red-cockaded woodpecker.

The red-cockaded woodpecker is a useful example to examine how fire affects a species because it lives in a fire-maintained habitat, it is an endangered species whose management is highly important across a large region (upland pine forests throughout the southeastern US), and fire has positive and negative effects on the species. The cavity tree is a critical resource for the red-cockaded woodpecker (Conner *et al.* 2001) because it is used daily for roosting and, seasonally, one cavity tree per family group is used for nesting. The cavity tree is an old, living pine tree, and the woodpecker has the curious habit of pecking and maintaining wounds in the trunk around the cavity to form a resin barrier that deters predators. Cavities take one or more years to complete, and therefore are important to woodpecker fitness.

In the fire envirogram, the first-order effects of fire on red-cockaded woodpeckers are minimal. Fire effects that influence woodpecker fitness over a longer time period include: 1) thinning pine stands by fire to create open habitat structure that is preferred by the woodpecker, 2) killing hardwoods and thereby favoring pine growth and dominance within the upland landscape, 3) killing or reducing the size of woody shrubs and thereby favoring grasses in the groundcover, 4) increasing abundance of beetle larvae in pine trees weakened by fire, and 5) loss of cavity trees. First-order fire effects on vegetation mortality of shrub, pine, and hardwood species, can be modeled

with existing first-order fire effects models. Results of these models can then be used to predict second-order or indirect effects on the fitness of the red-cockaded woodpecker or any other species of interest.

### CONCLUSIONS AND RECOMMENDATIONS

The prevailing wisdom that direct or first-order fire effects on animals (mortality or injury) are less important to a species than indirect effects that influence habitat was not overturned in this review. Fires that would affect a large portion of a population because of temporary immobility of individuals, such as a bat maternity colony, or a fire-susceptible condition, such as ecdysis, are important exceptions to the generalization. Fire behavior in such situations of vulnerability for a species could be modeled, and the results used to inform fire prescriptions in order to minimize lethal fire effects.

A fire envirogram is a useful tool to identify first- and second-order fire effects for a focal species. Fire-caused changes to habitat for animals over time and space are composed of many first-order effects on vegetation. Use of first-order fire effects models to assist with evaluating changes to habitat, as was used in the example of the spotted owl (Ager *et al.* 2007), is likely to be a fruitful incorporation of models into a better understanding of fire effects on animals. A growing challenge will be to accommodate many species—some with conflicting habitat needs—within fire management planning on a landscape scale.

The following recommendations are made to improve study of fire effects on animals.

1. More studies of populations of marked individuals need to be made before, during, and after fires. This will permit better distinction between mortality and emigration and reveal important details about how individuals respond to fire. Studies of marked individuals have elucidated details about how life history

stage and season (Griffiths and Christian 1996) of fire can influence likelihood of mortality from fire.

2. Take quantitative measurements of fire characteristics. Too many studies of fire effects on animal populations fail to report quantitative characteristics of the fires involved in the study. Use of standard descriptors of fire would permit easier comparison among studies and facilitate meta-analysis of multiple studies.

3. To provide targets for modeling, focus needs to be given to chains of causality that start at direct fire effects and end at important habitat effects. Use of devices, such as the fire envirogram presented here, can be used to make causal links between first-order (e.g., tree and shrub mortality) and second-order fire effects such as habitat structure and composition (see Reinhardt and Dickinson 2010). SCEA is an efficient approach to conduct research on such connections.

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## LITERATURE CITED

- Ager, A.A., M.A. Finney, B.K. Kerns, and H. Maffei. 2007. Modeling wildfire risk to northern spotted owl (*Strix occidentalis caurina*) habitat in central Oregon, USA. *Forest Ecology and Management* 246: 45-56. doi: [10.1016/j.foreco.2007.03.070](https://doi.org/10.1016/j.foreco.2007.03.070)
- Andersen, A.N., G.D. Cook, L.K. Corbett, M.M. Douglas, R.W. Eager, J. Russell-Smith, S.A. Setterfield, R.J. Williams, and J.C.Z. Woinarski. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* 30: 155-167. doi: [10.1111/j.1442-9993.2005.01441.x](https://doi.org/10.1111/j.1442-9993.2005.01441.x)
- Andrewartha, H.G., and L.C. Birch. 1984. *The ecological web: more on the distribution and abundance of animals*. University of Chicago Press, Illinois, USA.
- Beane, J.C. 2006. *Sceloporus undulatus hyacinthinus* (northern fence lizard). Fire avoidance behavior. *Herpetological Review* 37: 92.
- Beck, J., R. Wilkinson, and C. Baxter. 2005. Burned streams produce more aquatic insects and consequently higher foraging activity by bats. *Bat Research News* 46: 157.
- Bendell, J.F. 1974. Effect of fire on birds and mammals. Pages 73-138 in: T.T. Kozlowski and C.E. Ahlgren, editors. *Fire and Ecosystems*. Academic Press, New York, New York, USA.
- Bishop, D.C., and T.W. Murrie. 2004. *Sceloporus undulatus* (eastern fence lizard). *Herpetological Review* 35: 397-398.
- Bisson, P.A., B.E. Rieman, C. Luce, P.F. Hessburg, D.C. Lee, J.L. Kershner, G.H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management* 178: 213-229. doi: [10.1016/S0378-1127\(03\)00063-X](https://doi.org/10.1016/S0378-1127(03)00063-X)
- Boerner, R.E.J. 2006. Soil, fire, water, and wind: how the elements conspire in the forest context. Pages 104-122 in: M.B. Dickinson, editor. *Fire in eastern oak forests: delivering science to land managers*. USDA Forest Service General Technical Report NRS-P-1. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Bozek, M.A., and M.K. Young. 1994. Fish mortality resulting from delayed effects of fire in the Greater Yellowstone Ecosystem. *Great Basin Naturalist* 54: 91-95.

- Braithwaite, R.W., and P.A. Werner. 1987. Firebirds of the Top End. *Australian Natural History* 22: 298-302.
- Brown, D.K., A.A. Echelle, D.L. Propst, J.E. Brooks, and W.L. Fisher. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). *Western North American Naturalist* 61: 139-148.
- Buchanan, J.B. 2009. Balancing competing habitat management needs for northern spotted owls and other bird species in dry forest landscapes. Pages 109-117 in: T.D. Rich, C. Arizmendi, D. Demarest, and C. Thompson, editors. *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics*, McAllen, Texas, USA.
- Burton, T.A. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management* 211: 140-149. doi: [10.1016/j.foreco.2005.02.063](https://doi.org/10.1016/j.foreco.2005.02.063)
- Cairney, J.W.G., and B.A. Bastias. 2007. Influences of fire on forest soil fungal communities. *Canadian Journal of Forest Research* 37: 207-215. doi: [10.1139/X06-190](https://doi.org/10.1139/X06-190)
- Callaham, M.A., Jr., J.M. Blair, T.C. Todd, D.J. Kitchen, and M.R. Whiles. 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. *Soil Biology & Biochemistry* 35: 1079-1093. doi: [10.1016/S0038-0717\(03\)00153-6](https://doi.org/10.1016/S0038-0717(03)00153-6)
- Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143: 1-10. doi: [10.1007/s00442-004-1788-8](https://doi.org/10.1007/s00442-004-1788-8)
- Coleman, T.W., and L.K. Rieske. 2006. Arthropod response to prescription burning at the soil-litter interface in oak-pine forests. *Forest Ecology and Management* 233: 52-60. doi: [10.1016/j.foreco.2006.06.001](https://doi.org/10.1016/j.foreco.2006.06.001)
- Conner, R.N., D.C. Rudolf, and J.R. Walters. 2001. *The red-cockaded woodpecker: surviving in a fire-maintained ecosystem*. University of Texas Press, Austin, USA.
- Dickinson, M.B., M.J. Lacki, and D.R. Cox. 2009. Fire and the endangered Indiana bat. Pages 1-154 in: T. Hutchinson, editor. *Proceedings of the fire in eastern oak forests conference*. USDA Forest Service General technical Report GTR-NRS-P-46. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Dixon, G.E. 2003. *Essential FVS: a user's guide to the Forest Vegetation Simulator*. USDA Forest Service, Forest Management Service Center, Fort Collins, Colorado, USA.
- Dunham, J.B., A.E. Rosenberger, C.H. Luce, and B.E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems* 10: 335-346.
- Ernst, C.H., T.P. Boucher, S.W. Sekscienski, and J.C. Wilgenbusch. 1995. Fire ecology of the Florida box turtle, *Terrapene carolina bauri*. *Herpetological Review* 26: 185-187.
- Erwin, W.J., and R.H. Stasiak. 1979. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. *American Midland Naturalist* 101: 247-249. doi: [10.2307/2424922](https://doi.org/10.2307/2424922)
- Esque, T.C., C.R. Schwalbe, L.A. DeFalco, R.B. Duncan, and T.J. Hughes. 2003. Effects of desert wildfires on desert tortoise (*Gopherus agassizii*) and other small vertebrates. *Southwestern Naturalist* 48: 103-111. doi: [10.1894/0038-4909\(2003\)048<0103:EODWOD>2.0.CO;2](https://doi.org/10.1894/0038-4909(2003)048<0103:EODWOD>2.0.CO;2)
- Evans, W.G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae: Coleoptera). *Ecology* 47: 1061-1065. doi: [10.2307/1935658](https://doi.org/10.2307/1935658)
- Evans, W.G. 1971. The attraction of insects to forest fires. *Proceedings of Tall Timbers Conference on Animal Control by Habitat Management* 3: 115-127.

- Frost, P.G.H. 1984. The responses and survival of organisms in fire-prone environments. Pages 273-310 in: P.deV. Booysen and N.M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer-Verlag, New York, New York, USA.
- Gamradt, S.C., and L.B. Kats. 1997. Impact of chaparral wildfire-induced sedimentation on oviposition of stream-breeding California newts (*Taricha torosa*). *Oecologia* 110: 546-549. doi: [10.1007/s004420050193](https://doi.org/10.1007/s004420050193)
- Gandar, M.V. 1982. Description of fire and its effects in the Nysley Nature Reserve: a synthetic report. South African National Scientific Report Series 63: 1-339.
- Geluso, K.N., G.D. Schroder, and T.B. Bragg. 1986. Fire-avoidance of meadow voles (*Microtus pennsylvanicus*). *American Midland Naturalist* 116: 202-205. doi: [10.2307/2425953](https://doi.org/10.2307/2425953)
- Gill, A.M., and G. Allan. 2008. Large fires, fire effects, and the fire regime concept. *International Journal of Wildland Fire* 17: 688-695. doi: [10.1071/WF07145](https://doi.org/10.1071/WF07145)
- Gillon, Y. 1971. The effect of bush fire on the principal pentomid bugs (Hemiptera) of an Ivory Coast savanna. *Tall Timbers Fire Ecology Conference* 11: 419-471.
- Grafe, T.U., S. Dobler, and K.E. Linsenmair. 2002. Frogs flee from the sound of fire. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 999-1003. doi: [10.1098/rspb.2002.1974](https://doi.org/10.1098/rspb.2002.1974)
- Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 128: 193-221. doi: [10.1577/1548-8659\(1999\)128<0193:FAAEIF>2.0.CO;2](https://doi.org/10.1577/1548-8659(1999)128<0193:FAAEIF>2.0.CO;2)
- Griffiths, A.D., and K.A. Christian. 1996. The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology* 21: 386-398. doi: [10.1111/j.1442-9993.1996.tb00625.x](https://doi.org/10.1111/j.1442-9993.1996.tb00625.x)
- Guelta, M., and H.E. Balbach. 2005. Modeling fog oil obscurant smoke penetration into simulated tortoise burrows and bat colony trees. US Army Corps of Engineers ERDC/CERL TR-05-31. Engineering Research and Development Center, Construction Engineering Research Laboratory, Champaign, Illinois, USA.
- Guelta, M., and R. Checkai. 1997. Initial study and results of fog oil smoke penetration into a red-cockaded woodpecker nest cavity. *Bulletin of the Ecological Society of America* 78: 254.
- Halladay, T. 1978. *Vanishing birds*. Sidgwick and Jackson, London, United Kingdom.
- Hanula, J.L., and D.D. Wade. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. *Forest Ecology and Management* 175: 163-184. doi: [10.1016/S0378-1127\(02\)00130-5](https://doi.org/10.1016/S0378-1127(02)00130-5)
- Howard, D.R., and P.S.M. Hill. 2007. The effect of fire on spatial distributions of male mating aggregations in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae) at the Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma: evidence of a fire-dependent species. *Journal of the Kansas Entomological Society* 80: 51-64. doi: [10.2317/0022-8567\(2007\)80\[51:TEOFOS\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[51:TEOFOS]2.0.CO;2)
- Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain conifer forests. *Conservation Biology* 9: 1041-1058. doi: [10.1046/j.1523-1739.1995.9051041.x](https://doi.org/10.1046/j.1523-1739.1995.9051041.x)
- Hutto, R.L., C.J. Conway, V.A. Saab, J.R. Walters. 2008. What constitutes a natural fire regime? Insight from the ecology and distribution of coniferous forest birds in North America. *Fire Ecology* 4(2): 115-132. doi: [10.4996/fireecology.0402115](https://doi.org/10.4996/fireecology.0402115)

- James, F.C., C.A. Hess, and D. Kuftrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. *Ecological Applications* 7: 118-129. doi: [10.1890/1051-0761\(1997\)007\[0118:SCEAIE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0118:SCEAIE]2.0.CO;2)
- Johnson, L.C., and J.R. Matchett. 2001. Fire and grazing regulate belowground processes in tall-grass prairie. *Ecology* 82: 3377-3389. doi: [10.1890/0012-9658\(2001\)082\[3377:FAGRBP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2)
- Kennedy, P.L., and J.B. Fontaine. 2009. Synthesis of knowledge on the effects of fire and fire surrogates on wildlife in US dry forests. Oregon State University, Extension and Experiment Station Communications, Special Report 1096. Corvallis, Oregon, USA.
- Klein, M.G. 1988. Pest management of soil-inhabiting insects with microorganisms. *Agriculture, Ecosystems and Environment* 24: 337-350. doi: [10.1016/0167-8809\(88\)90077-1](https://doi.org/10.1016/0167-8809(88)90077-1)
- Komarek, E.V. 1969. Fire and animal behavior. Tall Timbers Fire Ecology Conference 9: 161-207.
- Lunney, D., S.M. Gresser, P.S. Mahon, and A. Matthews. 2004. Post-fire survival and reproduction of rehabilitated and unburnt koalas. *Biological Conservation* 120: 567-575. doi: [10.1016/j.biocon.2004.03.029](https://doi.org/10.1016/j.biocon.2004.03.029)
- Lyon, J.P., and J.P. O'Connor. 2008. Smoke on the water: can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology* 33: 794-806. doi: [10.1111/j.1442-9993.2008.01851.x](https://doi.org/10.1111/j.1442-9993.2008.01851.x)
- Lyon, J.L., H.S. Crawford, E. Czuhai, R.I. Fredricksen, R.F. Harlow, I.J. Metz, and H.A. Brock. 1978. Effects of fire on fauna: a state-of-the-knowledge review. USDA Forest Service General Technical Report GTR-WO-6. Washington, DC, USA.
- Massman, W.J., J.M. Frank, and S.J. Mooney. 2010. Advancing investigation and physical modeling of first-order fire effects on soils. *Fire Ecology* 6(1): 36-54. doi: [10.4996/fireecology.0601036](https://doi.org/10.4996/fireecology.0601036)
- McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology* 43: 107-127. doi: [10.1146/annurev.ento.43.1.107](https://doi.org/10.1146/annurev.ento.43.1.107)
- McNair, D.B. 1998. Henslow's sparrow and sedge wren response to a dormant-season prescribed burn in a pine savanna. *Florida Field Naturalist* 26: 46-47.
- Means, D.B., H.W. Campbell. 1981. Effects of prescribed burning on amphibians and reptiles. Pages 89-96 in: Proceedings of a symposium: Prescribed fire and wildlife in southern forests. The Belle W. Baruch Forest Science Institute of Clemson University, South Carolina, USA.
- Mellon, C.D., M.S. Wipfli, and J.L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, USA. *Freshwater Biology* 53: 2331-2343.
- Minshall, G.W., and J.T. Brock. 1991. Observed and anticipated effects of forest fire on Yellowstone stream ecosystems. Pages 123-136 in: R.B. Keiter and M.S. Boyce, editors. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press: New Haven, Connecticut, USA.
- O'Brien, J.J., C. Stahala, G.R. Mori, M.A. Callahan, and C.M. Bergh. 2006. Effects of prescribed fire on conditions inside a Cuban parrot (*Amazona leucocephala*) surrogate nesting cavity on Great Abaco, Bahamas. *Wilson Journal of Ornithology* 118: 508-512. doi: [10.1676/05-118.1](https://doi.org/10.1676/05-118.1)
- Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology* 16: 1296-1307. doi: [10.1046/j.1523-1739.2002.01077.x](https://doi.org/10.1046/j.1523-1739.2002.01077.x)

- Reinhardt, E., and N.L. Crookston. 2003. The Fire and Fuels Extension to the Forest Vegetation Simulator. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Reinhardt, E.D., and M.B. Dickinson. 2010. First-order fire effects models for land management: overview and issues. *Fire Ecology* 6(1): 131-142. doi: [10.4996/fireecology.0601131](https://doi.org/10.4996/fireecology.0601131)
- Reinhardt, E.D., R.E. Keene, and J.K. Brown. 2001. Modeling fire effects. *International Journal of Wildland Fire* 10: 373-380. doi: [10.1071/WF01035](https://doi.org/10.1071/WF01035)
- Rinne, J.N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* 16: 653-658. doi: [10.1577/1548-8675\(1996\)016<0653:MBSTEO>2.3.CO;2](https://doi.org/10.1577/1548-8675(1996)016<0653:MBSTEO>2.3.CO;2)
- Roberts, S.L., J.W. van Wagendonk, A.K. Miles, D.A. Kelt, and J.A. Lutz. 2008. Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. *Fire Ecology* 4(2): 83-104. doi: [10.4996/fireecology0402083](https://doi.org/10.4996/fireecology0402083)
- Russell, K.R., D.H. Van Lear, and D.C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin* 27: 374-384.
- Saab, V.A., R. Brannon, J. Dudley, L. Donohoo, D. Vanderzanden, V. Johnson, and H. Lachowski. 2002. Selection of fire-created snags at two spatial scales by cavity-nesting birds. Pages 835-848 in: P.J. Shea, W.F. Laudenslayer, Jr, B. Valentine, and C.P. Weatherspoon, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. USDA Forest Service, General Technical Report PSW-GTR-181. Pacific Southwest Research Station, Albany, California, USA.
- Saab, V., and H. Powell, editors. 2005. Fire and avian ecology in North America. *Studies in Avian Biology* 30: 1-193.
- Sandoval, C. 2000. Persistence of a walking stick population (Phasmatoptera: Timematodea) after a wildfire. *Southwestern Naturalist* 45:123-127. doi: [10.2307/3672452](https://doi.org/10.2307/3672452)
- Scesny, A.A., and L.W. Robbins. 2006. Detection of fire by eastern red bats (*Lasiurus borealis*): arousal from torpor. *Bat Research News* 47: 142.
- Schaffer, K.E., and W.F. Laudenslayer, Jr. 2006. Fire and animal interactions. Pages 118-144 in: N.G. Sugihara, J.W. van Wagendonk, K.E. Schaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, USA.
- Schmidt-Nielson, K. 1979. Animal physiology: adaptation and environment. Cambridge University Press, United Kingdom.
- Schmitz, H., and S. Trenner. 2003. Electrophysiological characterization of the multipolar thermoreceptors in the "fire-beetle" *Merimna atrata* and comparison with the infrared sensilla of *Melanophila acuminata* (both Coleoptera, Buprestidae). *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology* 189: 715-722.
- Simons, L.H. 1989. Vertebrates killed by desert fire. *Southwestern Naturalist* 34: 144-145. doi: [10.2307/3671821](https://doi.org/10.2307/3671821)
- Smith, J.K., editor. 2000. Wildlife fire in ecosystems: effects of fire on fauna. USDA Forest Service General Technical Report RMRS-GTR-42-vol.1. Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Smith, L.J., A.T. Holycross, C.W. Painter, and M.E. Douglas. 2001. Montane rattlesnakes and prescribed fire. *Southwestern Naturalist* 46: 54-61. doi: [10.2307/3672373](https://doi.org/10.2307/3672373)
- Stahala, C. 2005. Demography and conservation of the Bahama parrot on Great Abaco Island. Thesis, North Carolina State University, Raleigh, USA.

- Stephan, K., M. Miller, and D.B. Dickinson. 2010. First-order fire effects on herbs and shrubs: present knowledge and process modeling needs. *Fire Ecology* 6(1): 95-114. doi: [10.4996/fireecology.0601095](https://doi.org/10.4996/fireecology.0601095)
- Swengel, A.B., and S.R. Swengel. 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. *Journal of Insect Conservation* 11: 263-279. doi: [10.1007/s10841-006-9042-9](https://doi.org/10.1007/s10841-006-9042-9)
- Todd, T.C. 1996. Effects of management practices on nematode community structure in tallgrass prairie. *Applied Soil Ecology* 3: 235-246. doi: [10.1016/0929-1393\(95\)00088-7](https://doi.org/10.1016/0929-1393(95)00088-7)
- Warren, S.D., J. Scifries, and P.D. Teel. 1987. Response of grassland arthropods to burning: a review. *Agriculture, Ecosystems and Environment* 19: 105-130. doi: [10.1016/0167-8809\(87\)90012-0](https://doi.org/10.1016/0167-8809(87)90012-0)
- Whelan, R.J. 1995. *The ecology of fire*. Cambridge University Press, United Kingdom.
- Whelan, R.J., L. Rodgerson, C.R. Dickman, and E.F. Sutherland. 2002. Critical life processes of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. Pages 94-124 in: R.A. Bradstock, J.E. Williams, and A.M. Gill, editors. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, United Kingdom.